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# TEMPERATURE RELATIONS AND PHENOLOGY OF THE NORTHEAST GREENLAND FLOWERING PLANTS

BY

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WITH 28 FIGURES IN THE TEXT AND 15 PLATES

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# PREFACE

The present work is the result of botanical field investigations made during a number of years in Northeast Greenland (c. 70° N. lat.—c. 78° N. lat.), chiefly on the Danish Three-Year Expedition to East Greenland 1931—34. After this expedition had come to an end, my investigations were continued during a stay in the same regions in 1934—35 and on a summer expedition in 1937.

The botanical investigations of the Three-Year Expedition were chiefly planned with a view to the solution of plant-geographical and plant-sociological objects. It was only in the course of the working years that the outlines of this work gradually began to take shape on the background of the regularity in the distribution of the vegetation viewed in relation to local climatic conditions. On account of the short duration of the summer and its low temperatures the local climate, dependent on the variation in the melting time of the snow and the exposure of the terrain, will be of relatively greater importance for the distribution of the plants in the Arctic than in the temperate regions. Thus it became evident during the work in the field that the productivity of the soil measured by the development of the vegetation depends to no small extent on what may be accomplished within the short space of time in which the temperature affords a chance for the life functions to manifest themselves. The recognition of this fact will naturally determine the scope and aim of the present investigation. The aim has been to enlarge our knowledge of the seasonable life manifestations of the plants in relation to the local thermic conditions prevalent in the habitat proper, with a view to forming an opinion on the plant-geographical conditions of the area in question.

Nearly ten years have elapsed since the start of the Three-Year Expedition. In the course of these years I have been so fortunate as to spend six summers and two winters in Northeast Greenland.—To be confronted with a vegetation so entirely different from that of one's own country, means not only that one gains a knowledge of that vegetation, but even more one learns that nothing can be taken for granted. One's

eyes are opened to botanical problems which extend beyond the boundaries of country and climate, problems relating to the existence of plant-life in any place on the face of the globe.

To myself—and no doubt to many others—the working years under the standard of the Three-Year Expedition were happy years, the influence of which extends beyond the completion of the volumes of the "Meddelelser om Grønland" appearing under the heading "Treaars-expeditionen til Christian den X's Land". I here wish to express my deep gratitude for the past years to the man on whose initiative the expedition was started, who was responsible for its planning and preparation, and to whom the honour of its altogether successful accomplishment is due, the leader of the expedition, Dr. LAUGE KOCH. Dr. KOCH's many years' experience of arctic scientific exploration in connection with his will and power to utilise it for the benefit of the members of the expedition removed a legion of difficulties. Everything was new to us, but nothing was unknown.

During the botanical investigations in the field as well as during the working up of part of the material I have been so fortunate as to cooperate with my colleagues, Dr. ph. P. GELTING and cand. polit. G. SEIDENFADEN, both men of an exceptionally wide outlook, and whose stimulating influence, though of widely different nature, deserves much appreciation. From GELTING's angle of view the Greenland landscape becomes living and plastic, while SEIDENFADEN always finds a way out of all difficulties and knows how to do away with the gap between theory and practice.

The fact that the botanical studies could be made in touch with the parallel geological and zoological investigations of the expedition has also been of importance in the shaping of that general picture of the nature of the country which is an indispensable basis for biological research in the field. For good companionship—more especially during the wintering—I am indebted to my comrades at the station. The radio operator Mr. A. DE LEMOS was kind enough to attend to the meteorological apparatus during my absence from the Ella Ø station in the summer months of 1932; he continued the temperature registrations and other meteorological observations during the succeeding years, which contributed greatly to render useful the observations made during the first year.

During the work at home after the end of the journeys, also, I have received help of various kinds from several persons.

To the Chief gardener of the Botanical Garden of the University Mr. A. LANGE I am indebted for placing the garden at my disposal for cultivation of the arctic plants brought home.

The State meteorologist Mr. HELGE PETERSEN has kindly given me valuable expert assistance in regard to meteorological questions, for which I tender him my best thanks.

Special thanks are due to my chief, Keeper of the Botanical Museum Dr. phil. O. HAGERUP, for the good working conditions afforded me at the Museum during the working up of the material and the preparation of the manuscript and for valuable help of different kinds. Thus all the pen-drawings were kindly executed by Dr. HAGERUP. I likewise thank Professor Ph. D. KNUD JESSEN for the stimulating interest he has constantly taken in the present work.

The manuscript has been translated from the Danish by Miss E. GLEERUP. The blocks have been executed by Messrs. MIDDELBOE, Copenhagen. I am greatly indebted to them for the commendable care with which their work has been done.

Copenhagen, March 1940. *Thorvald Sørensen.*

# I. INTRODUCTION

In an investigation of living individuals it is difficult to avoid a more human outlook, allowing the feelings more play. This is true in general, and it is especially true when, coming from more southern, kindlier, latitudes, where one has grown up in company with the plants and has to a certain extent become accustomed to share their fates, one is confronted with the rigorous high-arctic conditions.—East Greenland, as it emerges from the ice on the first approach to its bleak shores, conveys the immediate impression that here all plant-life has stopped. —However, the often dearly bought results of explorations of the north coast of the continents made by various expeditions have taught us that the arctic vegetation knows no other limit than the usual one. As long as there is soil, there will be vegetation, too.

While in more southern tracts the competition of the plants for a place in the sun takes place quite openly before our eyes, but manifests itself as luxuriance, in the Arctic it chiefly takes place in secret. It escapes immediate observation, but gives us merely the impression of paucity. The beeches of the Danish forest, placed at intervals like pillars in a hall under the leafy canopy, convey an impression of luxuriance. The Arctic Willow, spreading its small assemblages of knotted branches at intervals of metres across the surface of the ground, whose relief is hardly interrupted by the erect catkins of a finger's length, has a poor effect. Nevertheless the beech-wood and the miserable growth of willows, which hardly even deserves the name of a heath, to say nothing of a scrub, represent the climax formation each of its own geographical area. And, *mirabile dictu*, even the number of species of such types of vegetation comes within the same order of magnitude. Thus on closer inspection— of the individual concrete plant community—the impression of paucity is changed. We are still far from the boundary posts which mark the final limit of plant-life.

Extremes have always held a special attraction for human nature. But with an instinctive conception of heat as the life-giving factor and cold as its antagonist, the perplexing multitude of forms of the Tropics

will seem a matter of course even in its boundlessness, while each solitary flowering *Saxifraga* cushion, each nodding poppy, lured from the bud by the midnight sun of the North after an endless Polar night, seems a glaring self-contradiction. The arctic landscape presents the most glaring contrasts between a poor vegetation and an overwhelming luxuriance of flowers, between a suppression bordering on extinction of all living things on the one hand, and the mobilisation of all vital forces on the other. We seek an explanation, but are merely left wondering. However, we must be allowed to assume that this staccato display of life in the vegetation is its natural—and spontaneous—reaction to the extreme temperature conditions of the climate.

Every climate sets its special mark on the vegetation, which manifests itself in morphological and physiological characteristics whose sum total is usually termed adaptation. A study of the vegetation within the extreme climates is all the more alluring since the trend of the adaptation must here be assumed to be especially one-sided. The Arctic affords a marked example of an extreme climate, characterised by a very long and very cold winter and a very short summer, whose temperatures rise only a few degrees above zero. Popularly expressed, the arctic climate is inimical to plant-life.

LUNDEGÅRDH (1925, p. 378) regards the arctic plants as "Kampfformen (Oligophyten)", which are defined (l. c. p. 376) as "Formen, die ganz unzweifelhaft während scharfer und anhaltender Selektion entstanden sind, und deren Habitus und Funktionen als Kampfmittel gegen dominierende ökologische Faktoren aufgefasst werden müssen."— The weak point of this concept is that it has too wide a range, in so far as there hardly remains any space for its alternative, the mesophytes, "deren geographische Verbreitung im Optimumsgebiet sämtlicher Faktoren fällt."

The arctic flora is characterised by its small number of species, the vegetation being one-layered, and measured by the scale of the temperate regions it presents only one phenological aspect. Whether these properties of the vegetation should be regarded as evidence that the flora is essentially composed of "Kampfformen" and the vegetation is oligophytic, deserves closer consideration. The number of species must be viewed in the light of the fact that the gradation of habitats, chiefly in regard to the moisture factor, is less differentiated than in the temperate zone, because the surface water and the ground water become identical as a consequence of the constantly frozen subsoil. Roughly, only one type of vegetation is represented which manifests itself sociologically in the fact that certain common species are present within all associations with the exception of the actual hydrophyte communities. In considering the number of species as a possible sign

of oligophytism, we must therefore compare it with the number of species in a well-delimited temperate vegetation type, for instance a single aspect of the Danish mesophyte communities (IVERSEN 1936). The ground vegetation of the Danish forests will immediately suggest itself; with a certain approximation it must be said to be one-layered and to have only one aspect, viz. that of the spring. A comparison between the arctic and the temperate flora, from the point of view suggested, will not prove so very unfavourable to the arctic one, quite the reverse.

Thus it is not the number of species which directly contributes to give the arctic vegetation its special character. But it is the small size of the plants, their stunted growth, their compact stature, in short, their habitus, which immediately conveys the idea of tough endurance, of a struggle for life, of "Kampfformen".

Such a general, regional, occurrence of low growth is common to the arctic and the alpine regions. The question whether the nanism associated with these areas is of a constitutional or of a modificatory nature, has often been the subject of discussion. However, a reply can only be obtained by cultivation experiments. The alpine vegetation, in particular, has been subjected to experimental investigations in this respect. Transplantation of lowland plants to the mountains (e. g. BONNIER 1884, 1888, 1890, 1895, KERNER 1891) has shown that such plants often by modification assume the characters of alpine plants to a certain extent, not only in habitual-morphological, but also in anatomical and physiological respects. This has given rise to the view that such characters produced by modification in lowland plants are hereditarily fixed in the alpine forms. Transplantation of alpine species in the opposite direction (cf. e. g. NÄGELI 1884, LASNIEWSKY 1896), however, does not indicate any universal validity of this assumption. Experiments carried out in recent times (TURESSON 1922, 1925, CLAUSEN et al. 1932, 1938, 1939) fully show how complicated conditions are as regards the nature of the adaptation and how untenable is the generalisation of some few isolated experimental results. We must be content to affirm here that the morphological and anatomical "alpine" characters in the plants of high mountains are to a great extent such as are subject to the possibility of modification in lowland plants.

From early times till the present day the question as to whether a direct comparison between alpine and arctic regions, both in regard to climate and to vegetation, is justifiable, has been the subject of discussion (GRISEBACH 1872, KERNER 1869, CHRIST 1879, BONNIER 1894, RÜBEL 1912, SENN 1922, DU RIEZ 1924). The similarity of the species content at any rate seems to justify a direct correlation of the two areas. Thus no less than 65 species, i.e. more than one-third of the phanerogams of Northeast Greenland, are found in the Central Alps

(cf. JEROSCH 1903, KULCZYNSKI 1924), and in Greenland these species are not associated with certain ecologically defined localities, but are fairly equally distributed over the different plant associations.

One of the features common to the alpine and the arctic vegetation, which has often been pointed out, is the rich representation of cushion plants. While the abundance of cushion plants in the alpine (SCHRÖTER 1908) and more especially in the Antarctic (e. g. MEIGEN 1894) vegetation seems indisputable, the records of the frequency of this growth-form in the Arctic (e. g. KJELLMAN 1883, GELTING 1934) seem to some extent to be due to a divergent conception of the term, which is all the more understandable since the cushion form is not an absolute, but a relative concept. "It is merely a question of degree in reduction of internodes and closeness of growth", says COCKAYNE (1912, p. 20), discussing ecology and evolution (cf. also RAUNKIÆR 1907).

Of the species enumerated in the synopsis of the cushion plants of our globe in HAURI & SCHRÖTER (1914) only few are arctic, and only five out of about 180 species growing in Northeast Greenland fall within the concept of cushion plants as defined by these authors; however, five other species are listed as facultative cushion plants.

As regards the markedly Antarctic cushion plants which "an Härte wenig hinter einem Stein zurückstehen" (MEIGEN 1894, p. 460) MEIGEN has advanced the supposition that the cushion form is to be considered an inhibition phenomenon. Actually the Antarctic cushion plants, for instance the *Azorella* type (DIELS 1896), have only little in common with the arctic ones, and perhaps they are most likely, as assumed by DIELS (l. c.), remnants from an earlier earth period, and in a general sense are not to be regarded as adaptation or inhibition forms at all, for they show more agreement with the cushion forms of the South-American paramos than with those of the lowland vegetation occurring nearer to it. The case is quite different in the arctic forms, which all agree more or less with those of the adjoining temperate regions. Any "established" cushion form has hardly developed, and its variation in relation to the habitat shows it to be the dwarf bush or rosette perennial in a more or less modified shape. A closer study of the arctic "cushion plants" of the literature thus seems to show that we are not here concerned with plants of an actual, solid, cushioned growth, but with plants of a low, more or less stunted growth. Such forms may result from many-headed rosette hemicryptophytes whose mesocorms have come to protrude above the surface of the soil with advanced age (e.g. *Potentilla* species), or from chamaephytes which by reduction of the length of the years' shoots and the internodes have obtained a stunted and densely compressed growth-form (e.g. *Dryas*, *Cerastium*). That the plant individuals in question frequently represent forms due to environ-

mental factors, appears from the fact that only a comparatively small number of individuals within these species have assumed an actual cushion shape, and that notably those individuals which grow in the most exposed places exhibit the compressed cushion-shaped stature.—Precisely on account of the habitat, the "bare" ground without a continuous cover of vegetation, they have probably especially struck the eye of the traveller.

Of course I do not mean to say that the small size generally characterising the arctic plants is only produced by modification, "nutrition forms" (NÄGELI 1884, KERNER 1869. Cf. also STREITZ 1924, p. 44). The arctic flora is to a great extent composed of forms differing specifically from those of the temperate regions. But the systematical characters are as a rule such as are of no importance for the ecology of the species (HILDEBRAND 1907). "Die Sache wird doch dadurch kompliziert, dass von vornherein wenig Wahrscheinlichkeit dafür besteht, dass in freier Natur eine Einheitlichkeit der "Formung" vorliege. Vielmehr müssen wir wohl im Bereich der meisten Faktoren mit der Ausbildung modifikativer neben genotypischen Reaktionstypen rechnen" (MONTFORT 1936, p. 2). In the first instance the type of growth, as well as all the other outer and inner characters of the species, is probably genetically conditioned. Thus in many cases it seems to bear a relation to the chromosomatic polyploidy of the species (STÄHLIN 1929, HAGERUP 1932, FLOVIK 1938). On the other hand, it should be pointed out here that the widespread, no doubt hereditarily conditioned nanism in the Arctic may be further accentuated through modifications due to the direct influence of the extreme climate and soil conditions.

From early times the small size of the arctic plants has been regarded as an adaptation to the "unfavourable" plant climate. "Hierauf beruht die Möglichkeit, den jährlichen Kreislauf des Wachstums auf das kürzeste Zeitmass einzuschränken", says GRISEBACH (1872, p. 33).—RESVOLL regards the small size of the plants as an expression of a "widely extended economy" (1917, p. 97), and GELTING (1934, p. 324) establishes that "the annual production of organic tissue is reduced to a minimum, a phenomenon which is of increasing importance towards the north".

The idea of the thorough economy has something plausible about it, though it is of a purely anthropomorphic nature.—Far more concise and logically unimpeachable is OSTENFELD's (1923, p. 256) assumption as to the economy of the arctic plants in relation to their small dimensions: ". . . here in the arctic regions where the vegetation's consumption of the salts of the soil is comparatively scanty, the annual production of organic matter being so inconsiderable, sufficient food resources will undoubtedly be present everywhere so that the chemical conditions of the soil can scarcely be unfavourable for the develop-

ment of vegetation."—Whether or not this assumption is justifiable, his view is that the arctic plants are so small and consume so little that there is hardly any limit to their modesty as regards the necessaries of life, as is the case in the majority of more southern species. This view actually touches upon a very essential characteristic of the arctic vegetation, though it must be said to be merely an expression of one aspect of the truth, carried to an extreme; for it does not concern the question as to the direct causal-mechanical cause of the dwarf growth phenomenon as such (cf. HOLTERMANN 1907).

In more southerly regions nanism is of a more local occurrence and is chiefly observed in localities with soil extremely poor in nutritive substances or in moisture. Examples of such localities are afforded by bogs and limestone mountains exposed to the sun. In such localities the vegetation is to some extent made up of nanistic starved forms (KRAUS 1906, MONTFORT 1918, SCHANDERL 1930. Cf. also METSÄVAINIO 1931). However, the dwarfish growth in the Arctic may possibly in part be due to other modifying causes than lack of nutrition and moisture, viz. to the perpetual light of summer and the cold of the soil, agencies which, as has been shown by experiments, may have similar morphological effects (KRAŠAN 1882, VÖCHTING 1898, LIDFORSS 1903, 1908, SENN 1922). The supposition that in the Arctic we have to do with a general mass occurrence of nanistic starved forms, becomes increasingly probable if we consider the relatively profuse growth displayed by the vegetation in manured localities, as for instance near fox pits and around deserted hunter's cottages. The starved forms have their special chances in the Arctic on account of the inconsiderable thickness and density of the cover of vegetation. In the luxuriant, dense, and tall vegetation of the temperate regions the low-growing starved forms are at the outset doomed to death; there the starved forms become essentially shade forms. In arctic regions the contrary is the case, for here even the lowest plants are not exposed to lack of light (cf. also CHOUARD 1937).

If in the temperate regions we pass from the more luxuriant and damper plant communities to the meagre and dry ones, the competition for light will decrease, and at the same time the question as to the access to moisture and accordingly to mineral nutritive substances becomes burning: the zone of the struggle is displaced vertically from the above-ground parts of the plants to the subterranean parts. A corresponding displacement takes place generally, from temperate to arctic regions. The cardinal plane of competition intersects the surface of the ground in some biochore or other. While in the more southerly, more luxuriant, vegetation light is the critical minimum factor for the starved forms, the access to mineral substances in the soil becomes the critical factor for the arctic starved forms. In agreement with this

we find a comparatively immense root system in the arctic plants as compared with the above-ground parts. A vigorous development of the root in relation to the above-ground parts has been demonstrated by experiments to result from want of nutrition (cultivation in dilute nutritive solutions) or from insufficient access to intake of water (e. g. MÖLLER 1883, PETHYBRIDGE 1899, GERNECK 1912, HARRIS 1914, TURNER 1922, AALTONEN 1923). In addition to the relation between root and top, certain common features in arctic plants exhibit parallelism with experimentally produced starved forms, for instance scanty development of mechanic tissue in stem and leaves (RIPPEL 1919), a character also appearing in lowland plants transplanted to alpine regions (LAZNIEWSKY 1896). Finally, xerophilous features in the structure of the leaves are found in arctic and alpine plants (WAGNER 1892, BØRGESEN 1895, Structure and Biology of Arctic Flowering Plants 1909—20. Cf. also SENN 1922). Of these a small cell size and a large number of stomata, found chiefly on the upper surfaces of the leaves, may be pointed out (cf. KOKINA 1926, SALISBURY 1927, TUMANOV 1927, STUBER 1938). Such structural features, too, have been produced by cultivation in dilute nutritive solutions (PETHYBRIDGE 1899). "These structural changes, which may be termed "xeromorphic", tend to facilitate the water supply and simultaneously to increase the gaseous exchanges. By virtue of this, xeromorphic plants are distinguished not by a lower but by a higher rate of such processes as transpiration and assimilation" (MAXIMOV 1929a, p. 372). In accordance with their xeromorphic structure comparatively high intensities have been ascertained in arctic plants both for transpiration (STOCKER 1931, cf. also PISEK & CARTELLIERI 1933) and assimilation (MÜLLER 1928, KOSTUTSCHEV et al. 1930).

It is probably still doubtful whether the xerophilous features in the structure of the arctic plants are actually induced by lack of moisture. At any rate STOCKER (1931), on the basis of transpiration investigations on arctic plants near Abisko, arrived at the result that the intake of water is often insufficient owing to the low temperature of the soil, even in cases when the water content of the soil leaves nothing to be desired.

On account of the inconsiderable bio-chemical processes taking place in the soil in the Arctic the question as to the supply of nitrogen becomes burning.—Experimental investigations (MÜLLER-THURGAU 1897, MÜLLER 1932) have shown that want of nitrogen gives rise to a vigorous development of the root system and a relatively slight development of leaves. Precisely these characters are a conspicuous common feature of most arctic plants. The assumption as to a causal connection between these morphological peculiarities and a general lack of nitrogen in the Arctic is therefore natural (cf. p. 254 et seq.).

In connection with our reference to the nanistic character in arctic plants it should merely be mentioned that GAUCHERY (1899) in dwarfish individuals of temperate species (France) has demonstrated morphological and anatomical peculiarities which are in direct contrast with the characters pointed out above, common to temperate starved forms and normal arctic plants. For GAUCHERY's dwarf forms were distinguished by a substantial reduction of the root system and the water-conducting tissue. This disagreement is no doubt due to these plants of dwarfish stature being shade forms which during their development have become outmatched in the struggle for light in the dense growths. They cannot, therefore, be compared to starved individuals cultivated in dilute nutritive solutions or to the arctic dwarfs.

For the differentiation of species the character of the minimum factor most likely plays an essential part. In a closed cover of vegetation a certain standard height during each aspect might be of essential importance for the plants owing to the competition for light. The case is different in the open vegetation types, where the competition is removed to the root zone (cf. AALTONEN 1923).—However, closed, though one-layered, types of vegetation are not lacking in arctic regions. Even here the light factor must be assumed to be reduced to a relative minimum for the lowest growing forms. The "poorer" the vegetation, the more subordinate will be the above-ground dimensional development of the species composing it. In the open vegetation each individual is apt to engage in the struggle for life, if otherwise its constitution is of such a kind that it is capable of adapting itself to the physical factors of the place. Here the minimum factor is the mineral nutrition, and the development of the root system, therefore, is one of the features within the morphology of the arctic plants which manifests itself in a special degree as a direct adaptation.

In this connection it seems to me of the greatest interest to establish that precisely the species and groups of species which in Northeast Greenland beyond comparison present the greatest abundance of forms —so many, indeed, that systematists have hitherto had to give up entirely as regards a rational systematisation of the confusion of forms —namely *Draba*, *Potentilla*, and *Melandryum*, are principally associated with the open ground without a dense vegetation.

The arctic climate is universally characterised by low temperatures. The vegetation of arctic regions is a distinct proof that a low temperature in itself is not generally to be regarded as inimical to plants.—One of the most essential characteristics of the arctic plants is their resistance to cold (LUNDEGÅRDH 1925, p. 382). However, no external morphological features capable of protecting the living tissue against the cold is known to us (SCHIMPER 1898). It has already been demonstrated, by KJELLMAN

(1883) for the arctic plants and by SCHRÖTER (1908) for the alpine ones, that the winter buds are in no remarkable degree equipped with bud scales, rather the opposite. Later RAUNKIÆR (1911) demonstrated statistically a relative chamaephyte maximum for the arctic flora; that is to say, owing to their position in relation to the surface of the ground the winter buds are even as a rule less protected in the Arctic than in the temperate regions.

"Worin eigentlich die Verschiedenheiten der Organisation bestehen, dass bei gewissen Pflanzen der Saft zu Eis erstarren kann, bei andere nicht, ohne das Leben zu gefährden, ist bis jetzt ein physiologisches Räthsel", says GRISEBACH (1872, p. 32). It is true that the numerous experiments which have been made since then in order to further elucidate the problem have given us a certain insight into the cellular conditions of plant tissues resistant to cold as compared with more sensitive tissues. However, in the last instance the results gained contribute little towards the solution of the frost resistance problem as expressed by GRISEBACH.

Actually the question of resistance to frost is practically of less importance than might perhaps be expected at the outset when we are concerned with high-arctic plants. A general unlimited power of tolerating such low temperatures as on the whole occur in the most extreme climates, is such a universal characteristic of these plants that the question—on considering the high-arctic vegetation by itself without any side-glances at the south—no longer obtrudes itself as a problem at all. At any rate it is no specially arctic problem. On the contrary. A well-founded judgment of an ecological factor is only possible in cases in which it can be demonstrated that the factor is of decisive importance for the thriving of the plant or its existence altogether. Not the low temperature as such, but much more the indirect effect of its duration seems to be of decisive importance for the ecology of the high-arctic vegetation (RESVOLL 1909, 1917, GELTING 1934). Even though the risk of dying from cold does not seem to threaten the vegetation within the area dealt with here, the physiological and morphological peculiarities of plants which—according to the knowledge of our time—are correlatively associated with resistance to cold, will be briefly mentioned.

Physiology has shown that the injurious effects of the cold is connected with formation of ice in the tissues, no matter whether the injurious effect is due to a purely mechanical injury of the cells, as a consequence of the pressure from the growing ice crystals, or to a too intense (irreversible) dehydration of the cytoplasm (a summary of the various theories is given by MAXIMOV 1929b). Recent investigations (WALTER 1929, MAXIMOV 1929b) speak mostly in favour of the latter assumption. Thus measures of a physical or chemical nature which prevent the formation of ice or keep it within reasonable bounds, stimulate the

resistance to cold (KESSLER 1935, KESSLER & RUHLAND 1938).—Whether formation of ice actually takes place in the tissues of arctic plants exposed to the extremely low winter temperatures, is doubtful. Experiments have shown that even very low temperatures are at times required in order to produce a formation of ice, thus for instance in *Pyrola rotundifolia* a temperature of 31.6° C. below zero, according to LEWIS & TUTTLE (1920). Similarly GATES (1914) states that at a temperature of 29° C. below zero the evergreen leaves of *Chamaedaphne* had not yet become frozen. WIEGAND (1906) has studied the formation of ice in the buds of a number of American trees at low winter temperatures. At temperatures up to 26.5° C. below zero ice crystals had only formed in species whose buds showed a water content of 37—49 per cent. and whose tissue was comparatively large-celled, while species, in whose buds the water content was 22—31 per cent. and whose tissue was relatively small-celled, constantly remained without any formation of ice (cf. also ARRHENIUS & SÖDERBERG 1917). Thus there seems to be a distinct correlation between water content and cell size on the one hand and resistance to frost on the other hand. SIERP's investigation "Über die Beziehungen zwischen Individuengrösse, Organgrösse und Zellengrösse mit besonderer Berücksichtigung des erblichen Zwergwuchses" (1914) shows a more or less pronounced correlation between the size of the individual and the cell size. There is therefore reason to assume that the arctic plants are to a certain extent protected by their dwarfish growth against the injurious effects of the very low temperatures, their small-celled tissue poor in water preventing or moderating the destructive intracellular ice formation.

MÜLLER-THURGAU (1880, 1886) and other investigators after him (e. g. MIYAKE 1902, LIDFORSS 1907) have demonstrated that the plants procure for themselves protection against the frost by a winter mobilisation of their spare nutrition for the formation of molar-active substances (various kinds of sugar), which give the cell-sap a greater concentration with a corresponding depression of the freezing-point, or, according to the view held by modern investigators, for the formation of highly absorption-active hydrophilous colloids which counteract the dehydrating influence of the formation of ice crystals on the plasma (MAXIMOV 1929b). Whether arctic plants have recourse to such protective measures, is so far unknown, but it seems probable, all the more so since the rapid development of these plants in the spring implies the presence of comparatively large reserves of matter.

Finally it should be pointed out that the resistance to high degrees of cold depends on the resting state of the plant (e. g. STRAUSBOUGH 1921, WINKLER 1913, KESSLER 1935, KESSLER & RUHLAND 1938). Exposed as they are to continuous frost throughout the winter, plants in

high-arctic regions must be assumed to rest absolutely from the setting-in of the frost in the autumn till the thaw of spring, whether this resting stage is of an autonomous or an aitionomous nature (cf. PFEFFER 1904).

The great temperature fluctuations during the growth period must then seem to us to be far more critical than the winter frost itself. At the beginning of the growth period nocturnal temperature falls to far below zero are the rule, and even at midsummer frost is by no means a rare thing. Morphological (mechanical) measures for protection of the young buds and leaves, for instance the dense pubescence so frequently found, is no doubt of a certain value in this respect (cf. GRÜSS 1892, HEDLUND 1912).—GRÜSS, who has subjected unfolding buds to special morphological and physiological investigations, has shown that "Ein junges, aus theilungsfähigen Zellen bestehendes Gewebe ist gegen Temperaturschwankungen um so wiederstandsfähiger, je mehr es mit Interzellulargänge durchsetzt ist, und je reicher das Plasma an öligfettigen Bestandtheilen ist" (l. c. p. 662). A loose leaf structure and a great intercellular volume seem to be characteristic of the leaf structure of the arctic plants (WAGNER 1892, BONNIER 1894, BØRGESEN 1895), and thus may perhaps be regarded as a character furthering the power of resistance of the plants to the great nocturnal falls of temperature. Strangely enough there seems to be a contrast in this respect between the Arctic and the alpine nival zone, whose species generally have a relatively compact leaf structure and an insignificant intercellular volume (BONNIER 1894, LOHR 1919). As regards the content of matter of the growing shoots and leaves during the leafing of arctic plants we are greatly in want of information. GELTING (1937, p. 153) has demonstrated a comparatively high fat content in the wintering shoots of certain chamaephytes (e. g. *Saxifraga oppositifolia*, *Cassiope tetragona*, *Dryas*), furthermore an increasing sugar content in the young, half-expanded winter-green leaves of *Dryas* at the end of the winter; and he assumes that the latter is due to a temporary accumulation of assimilata, the passage to the still frozen subterranean parts being prevented. Altogether, at low temperatures the equilibrium between starch and sugar is shifted towards the sugar side (HENRICI 1920, JOST 1923). If only for this reason, we may count upon a relatively high content of sugar in the arctic plants in the winter and earliest spring, when the vital functions begin to stir in the above-ground shoots even before the upper layers of the soil have attained a positive temperature. And all the more so since a large number of the arctic species have reserves of matter stored in their above-ground organs.

At times, however, oil and fat seem to replace starch to a certain extent, even in the vegetation period (TUTTLE 1921). The ericoid dwarf shrubs, in particular, seem to be distinguished by an exceptionally

high content of fat (cf. TUTTLE, l. c., and GELTING 1937, Tables 24 and 25).

Thus, even though in arctic plants certain facts can be demonstrated, all of which, however, require to be closely tested, and which have some connection with the quite physical foundation for the insensitivity of the arctic vegetation to low temperatures, it can hardly be disputed that the actual, deeper-lying, cause of the resistance to cold is more probably in the last instance to be found in the specific plasmatic constitution of the plants (KJELLMAN 1883, KIHLMAN 1890, MEZ 1905, ÅKERMAN 1927, MEYER 1932). And thus "it seems probable... that attempts to resolve the problem by gross physiological measurements are doomed to be unsuccessful" (MEYER l. c. p. 317).

As stated above, the low temperatures, whether in the resting or the vegetation period, seem hardly to produce directly injurious effects on the arctic plants. However, this fact only touches the negative side of the interaction of temperature conditions and plant life in the Arctic. The positive aspect, which is at least just as essential, regards the building up of living tissue, the production of matter, which depends on a suitable equilibrium between the assimilation of carbon dioxide and the respiration.

Investigations on the assimilation of arctic plants have been made by MÜLLER (1928) on Disko, 69° N. lat. He arrived at the result that low temperatures are favourable at low light intensities, since the respiration will then be kept at such a low level that there may even be a slight assimilation surplus in the light, though only faintly luminous, Polar nights. "Man könnte somit sagen, dass die Blätter der untersuchten Pflanzen [*Salix glauca* and *Chamaenerium latifolium*] zwar Sonnenblätter sind und während des Tages wie Sonnenblätter arbeiten, aber während der kühlen Nacht sich wie Schattenblätter verhalten." (l. c. p. 36). But the author immediately adds: "Man kann dies aber nicht als eine spezielle Anpassung der arktischen Pflanzen betrachten; man würde für subarktische Pflanzen wahrscheinlich ganz ähnliche Verhältnisse finden."

MÜLLER has shown, however, that at a temperature of 20° C. the sun-leaves of the arctic experimental plants work with considerably less economy than for instance the sun-leaves of Danish plants (cf. BOYSEN-JENSEN 1918). That is to say, the daily assimilation surplus is inconsiderable. This viewed in connection with the fact that the arctic plant species have their extreme outposts ("relicts") to the south, in localities with especially low night temperatures (e.g. bogs), induces MÜLLER to draw the following interesting conclusion: "Die arktische Pflanzen haben also eine südliche Grenze da, wo die Nächte lang, warm und dunkel sind." (l. c. p. 32).

That the arctic plants show a comparatively small increase of substance at a temperature of 20° C. does not mean, however, that they work uneconomically in nature. According to the investigations of KOSTUTSCHEV and his collaborators (1930) on the assimilation of plants in their natural habitats on the Murman Coast by the Arctic Ocean, the arctic plants exhibit high daily assimilation results, sometimes even higher than ever observed in more southerly tracts (e. g. Peterhof), likewise under natural conditions of growth. In contrast to the plants of more southerly regions, the arctic plants assimilate without interruption as long as the light intensity is sufficient (MÜLLER 1928, KOSTUTSCHEV 1930), a phenomenon closely connected with that of the gaseous exchange of the leaf; for the stomata do not close (cf. also STOCKER 1931). This in connection with the low temperatures at which the plants normally occur thus favours a high production of substance, while even an increasing intensity of assimilation at higher temperatures than the normal temperature of the plants is unable to eliminate the effect of an even more rapidly increasing intensity of respiration.— This does not apply especially to the arctic plants; quite similar conditions were, for instance, found by HENRICI (1919, 1920) for the Swiss alpine and lowland plants and by JOHANNSEN (1926) in Swedish fern species, though here the inconsiderable production at higher temperatures is due to a closing of the stomata. Altogether we may thus conclude with JOHANNSEN (l. c. p. 20) that "der Assimilationsapparat der Pflanzen der normalen Temperatur der Standorte angepasst ist". Experiments carried out by HENRICI (1920) and HARDER (1924) show that this adaptation is open to modifications, that is to say that the same plant may to a certain extent appear as a heat or cold plant according to the conditions of the habitat. However, in culture plants indigenous to different geographical latitudes but cultivated under the same temperatures LUNDEGÅRD (1924, 1927), and after him for instance BELJAKOFF (1930), found different temperature optima for assimilation, species of the most northerly provenience showing the lowest temperature optima. "Es scheint also eine gewisse Beziehung zwischen Lage der Optimas und pflanzengeographischer Verbreitung zu bestehen" (LUNDEGÅRDH 1927, p. 294). According to the available investigations on the dependence of assimilation and production of matter on the temperature conditions, and more especially KOSTUTSCHEV's determinations of assimilation in natural habitats, we may conclude that as regards the production of matter the arctic plants are adapted to the arctic temperature climate. That nevertheless the mass of the arctic vegetation is so insignificant per areal unit, according to the calculations by MÜLLER (1928) 5.5 t dry weight per ha for a Greenland willow scrub as against 63.7 t for a Danish beech wood (25 years

old), MÜLLER (l. c. p. 37) regards as a consequence of the short vegetation period and the low temperature.

Altogether, observation of the vegetation throughout the year within the area to be dealt with here will hardly supply any visible proof of a directly injurious effect of the cold as such. On the contrary, the absolutely low winter temperatures and the relatively low night temperatures in the summer are probably favourable for the plants, for by reducing the intensity of respiration they stimulate the economy of the plant (LUNDEGÅRDH 1925, MÜLLER 1928, JOHANNSEN 1926).

The arctic summer is short. The plants have to grow, flower, and produce fruits in the course of a summer whose positive temperatures only extend over 2—3 months. Even though this development is normally ended within the allotted time, the catastrophic effect of the capriciousness of the climate is much more conspicuous in arctic regions than in our latitudes. It is true that in our country an unfavourable period, especially in the spring, causes a noticeable retardation of the development of the vegetation, but a delay of a fortnight, or even a month, may be made up for in the course of the long summer. In the Arctic the case is different. There a corresponding unfavourable spring means not only a retardation of the advent of summer, but a material reduction of the duration of the whole growth period. Even though the plants are on the whole adapted to an extremely short summer, in such unfavourable years the insufficiency of this adaptation will be obvious. The species occurring near their northern limit will be overtaken by the winter when still in flower. In such cases we may thus witness the destructive work of the winter not prepared for, the tragedy which so strongly impressed KJELLMAN, who depicted it to us in his unsurpassed description of "polarväxternes lif": "Ett arktiskt landskap vid vinterns inbrott liknar närmast en trakt söder ut, hvilken härjats af en häftig frostnatt, innan ännu hösten var att vänta. Många växter hafva lagts i dvala, medan de ännu voro stadda i full utveckling. De stå der med förfrusna lifskraftiga blad, med svällande blomknoppar i blomställningarna, med halföppna blomknoppar, utslagna blommor, halfmogna eller nästan mogna frukter. Hvilan har ej inträdt efter förberedelse. Under det de voro som bäst verksamma, förlamades de af den stelnande kölden. De göra intryck att hafva jägtat för att nå ett mål, oroligt arbetat in i sista stund." (KJELLMAN 1883, p. 497.) (An arctic landscape at the advent of winter most nearly resembles a region farther south ravaged by a night's severe frost before the autumn was expected to set in. Many plants have sunk into torpor while still in full development. They are standing there with frozen, vigorous leaves, with swelling buds in the inflorescences, with half-open flower-

buds, expanded flowers, half-ripe or nearly ripe fruits. The rest did not set in after preparation. While still active, they were paralised by the congealing cold. They convey the impression of having aimed at reaching a goal, of having worked anxiously till their last hour.) In Northeast Greenland, however, such a general destructive effect on the vegetation at the beginning of the winter is an exception. Normally the frost, snow-covering, and darkness of the winter come as a natural rest at the end of a working day. The autumnal colouring of the vegetation in the last sunny days of summer affords sufficient evidence of this. Only in the small hollows and in deep mountain ravines, precisely in those places in which the short duration of the summer is further accentuated by the late melting of the snow, has the vegetation retained its green colour. Here—and normally only here—do we find evidence of the insufficiency of the adaptation, and yet chiefly for such species only as are here outside their normal ecological range, while the actual snow-patch plants, which are less conspicuous owing to their small size, have already completed the growth of summer in a harmonious way. However, even these will at last be at a loss in the neighbourhood of the perennating snow-fans, where they will hardly every year reach the daylight from the eternal darkness beneath the congealed snow-masses.

Entirely in accordance with the short space of time within which the life functions of the plants have any chance of working is the rapid development of the vegetation in the spring. The flowery pride of the arctic spring has from early times greatly impressed Arctic travellers.— The phenomenon, as already pointed out by Lecoq (1854) and later by Hult (1881), is not only due to internal causes, owing to specific physiological properties of the species, but also to external causes associated with the sudden rise of temperature at the transition between winter and summer in the Arctic, or, as expressed by Hult (l. c. p. 20): "la débâcle s'avance vers le Nord plus lentement que la chaleur de l'été". However, owing to the unequal distribution of the snow-covering in arctic regions according to the configuration of the landscape there are considerable local differences in the date of the melting of the snow. Thus immediately on appearing, the snow-patch vegetation will awake to the most intense insolation of midsummer. This is an essential cause of the development observable in the arctic snow-patch vegetation, which as regards rapidity is unparalleled within the phanerogamic vegetation of the globe. The pre-floration period, the time interval from the plant is thawed out of the snow till its incipient flowering, gives a clear idea of the rate of development. Concrete data for the pre-floration time of a number of species are available from Scandinavia, Greenland, and the Alps (Cleve 1901, Resvoll 1917, Fries 1925, Rompel 1928, Gelting 1934, Söyrinki 1938).

Thus the more or less locally conditioned sudden rise in temperature contributes to a further accentuation of the rapid development of the vegetation, which appears quite unmistakably as an adaptation to the extremely short space of time within which arctic plants must necessarily pass and complete their annual life. At the outset it must be regarded as probable that the very possibility of such an extreme shortening of the productive season, without the individual itself or the survival of the race suffering from it, is due to special developmental-morphological and physiological peculiarities in the plants. Whether special external conditions essentially influence the rate of development, is hardly quite clear so far. The supposition that the continuous light throughout the period of growth is of importance has frequently enough been advanced in this connection. In the exact investigations on assimilation and production of matter in arctic plants in recent times it has acquired a more actual foundation.

Thus even though the sudden rise of temperature in the spring on the one hand and the uninterrupted arctic summer day on the other hand may each in its own way contribute to the concentrated display of life of the arctic vegetation, the inherent passiveness of the living tissue in the differentiation of organs sets a limit to the rate of development. The natural limitation of the rate of development in connection with the short duration of the summer would be bound to impede the seasonal completion of generative reproduction to such an extent that the race became extinct, if the formation of the reproductive organs were not prepared long beforehand.—"Je mehr wir in das Leben der mehrjährigen Pflanzen Einsicht gewinnen, desto entschiedener stellt sich heraus, dass wir es mit analogen Zuständen zu thun haben, wie mit dem Puppenzustande im Thierreiche. Nach langem Winterschlafe ein Sonnenblick— und der Schmetterling, in der ganzen Fülle seiner complicirten Organisation, steht plötzlich vollkommen erwachsen, fix und fertig vor uns: er hat die Entwickelungszeit des Zustandes seiner Kindheit schon im vergangenen Jahre, vor und während seiner Vermummung übersprungen. Beinahe eben so verhält es sich mit den Knospen der mehrjährigen Pflanzen, zumal derjenigen des Hochnordens. Stark vorgebildet liegen, von den Knospenhüllen verdeckt, die Blätter und Blüthen des beginnenden Jahres seit dem verflossenen Sommer zum Aufbrechen bereit." (MIDDENDORFF 1864, p. 660). Precisely this circumstance that the development of the organs takes place in stages, enables the arctic vegetation to keep pace with the quickly passing summer even in the development of the reproductive organs. "En somme, la végétation..... offre, comme la nôtre [that of France], un maximum qui a lieu dans le même temps, mais elle emploie un intervalle plus court pour atteindre ce maximum, un intervalle un peu plus long pour s'en éloigner, et, en

résumé, les époques sont parcourues plus rapidement que sous notre latitude." (LECOQ 1854, p. 167).

As a consequence of the short duration of the vegetation period the arctic species differ only slightly in their time of flowering, the only phenological phenomenon of which we are fairly well informed. As pointed out by HULT (1881, p. 38), it is insufficient for a successful study of the periodical phenomena to know only the time of their final stages, which are prepared through a series of morphological differentiations. In addition we must direct our attention towards their "apparition".—In a greater degree than is the case in more southerly regions, the floral development of the plants in the Arctic is discontinuous, interrupted at some stage or other by the hibernal resting period, which lasts for more than half a year. The time of the initial stages of development of the organs is therefore of just as great an interest as the final stages for an estimate of that reaction of the plants to the prevalent climatic factors which is revealed in the participation of the individual species in the immediately observable aspect of the vegetation.

Like, for instance, RAUNKIÆR'S life form spectrum, the succession of aspects is a summary expression of the plant climate and is accordingly a geographical concept (cf. GAMS 1918). Just as the biological spectrum is of a purely abstract nature—the different, logically antagonistic, life forms all of them contribute to the common spectrum—so also is the aspect of the vegetation: At a given time each individual species attains the same result in its own way. The lines of development of the species intersect each other at the point phenologically fixed. Where geography has attained its object, the problems of botany turn up. To fix the time of the periodical life manifestations of the plants in relation to the periodical variation of the climate must be one of the most elementary conditions for a closer understanding of the relations between the plant and its environment, in the widest sense of this word.

Attention has early enough been called to the importance of more exact phenological observations for a better understanding of the area and occurrence of the plant species as determined by the climate, in short, of their ecology, even before ecology as such had been introduced into the botanical world of concepts, and even less so as an independent botanical branch of knowledge. Thus already HERMANN HOFFMANN (1857, pp. 461—462) wrote as follows "Wir werden . . . genötigt sein, . . . Entwickelungs-Beobachtungen über die einzelnen wichtigeren Vegetations-Stufen der Pflanzen anzustellen, wir werden sie von ihrer Keimung bis zu ihrer Laubentwickelung, endlich bis zur Blüthe und Fruchtreife Schritt für Schritt in allen wesentlichen Veränderungen verfolgen müssen, um dann endlich die Frage zu stellen: welche klimatischen Bedürfnisse hat eine bestimmte Pflanze für eine bestimmte Stufe

ihres Lebens, welches ist also der nothwendige unentbehrliche und constante Witterungs-Coëfficient für ihr Keimen, ihre Samenreife, zuletzt für ihr ganzes Leben, ihre Existenz."

Since the above quotation appeared, nearly one hundred years have elapsed. Only three years ago one of the most prominent field botanists of our time said: "Die vielseitigen phänologischen Wahrnehmungen bilden eine unumgängliche Ergänzung der modernen physiologisch-ökologischen und anatomischen Untersuchungen, die zurzeit überall im Gange sind, um den Haushalt der Pflanzen in der Natur klarzulegen. Ohne gebührende Beachtung der wichtigsten periodischen Erscheinungen im Leben der Pflanze kann keine wirkliche Lebensgeschichte einer Pflanzenart geschrieben werden." (LINKOLA 1936, p. 84).

The object of the following pages has been to contribute, in however fragmentary a way, to the elucidation of the periodical life phenomena of the vegetation within a delimited geographical area whose climatic character is entirely dominated by the temperature factor.

# II. THE AREA OF INVESTIGATION

The coast of East Greenland, which extends from c. 60° N. lat. in the south to c. 82° N. lat. in the north, may naturally be divided into two sections with Scoresby Sund, situated in about 70° N. lat., as the line of demarcation; south of this sound the coast-line extends in a southwesterly direction, north of it it runs due north. Northeast Greenland proper comprises the coast-stretches northward from Scoresby Sund. Geographically the land is well delimited, confined as it is between the inland ice to the west and the drift-ice masses of the Greenland Sea to the east. To the north the coast-land has its natural limitation where the broad Nioghalvfjerds Gl. (79 Fjord) issues from the inland ice and extends right into the sea. To the south Northeast Greenland is bounded by the fjord complex of Scoresby Sund, for south of this the inland ice, stretching across the high mountains, approaches the shore and leaves only a narrow and inaccessible coastal zone free of ice.— Northeast Greenland may be characterised as the area of the large fjord complexes. The ice-free land attains its greatest width to the south, in the Scoresby Sund complex, where the ramifications of the fjord extend up to about 300 km inland. North of this area, in the Franz Joseph Fjord area, the coast-land is up to about 200 km wide, while in the northernmost fjord complex, Skærfjord and its ramifications, it is hardly more than about 75 km.

Northeast Greenland is a wild and inaccessible mountain land. By deep valleys and fjords, extending both in a west-east and a south-north direction, the country is divided into islands and mountain plateaus. The fjords form the only routes of communication; travelling on them with dog-sledges is possible from the end of October to midsummer. For navigation with boats the fjords are only accessible from the middle of July, or often from a much later date, until October.

All the year round the coast of Northeast Greenland is blocked by drift-ice masses carried southward from the Polar Basin by the cold East Greenland current. Only in a couple of summer months does the ice scatter so much that the coasts are accessible to ships, and then

as a rule only with difficulty. The summer is always drawing to a close at the time when it is possible for ships to penetrate through the drift-ice. The first fleeting impression of the country is limited to a picture of mountains in sunlight. There is something merciless about the sharp outlines, something like a set smile. The land seems barren to the eye, the vegetation fails to cover the rocks. But it gains on closer acquaintance. Its high-arctic vegetation is concealed in ravines and valleys, which are coloured by a closed vegetation. The picture of bare rocks is converted into a landscape, perhaps not precisely smiling, not with a prolific luxuriance of emerald-green meadows, but with yellowish-grey grass steppes, brown heaths, dark moors, and with grazing herds of musk-oxen. This is Northeast Greenland in its late summer aspect.

A profusion of flowering plants on the gravelly hillocks and in each rock fissure, leaping hares, rushing cascades of thaw-water on the rock ledges, and the configuration of the landscape accentuated by garlands of flowering *Cassiope* heather—this is Northeast Greenland in the spring. But between the autumn landscape and that of the spring there is an eternity of cold and darkness.

Northeast Greenland forms a well-delimited whole, not least in a plant-geographical respect. In the present work, however, the Scoresby Sund area proper had to be left out of consideration as lying outside the actual working field of the Three-Year Expedition. The more exact delimitation of the area of investigation has been made in accordance with the district division given by SEIDENFADEN & SØRENSEN (1937, p. 144 et seq.), and comprises districts 5, 6, and 7, that is to say, the tracts of land situated between 71°10′ and 79°30′ N. lat.—In recent years this area has been subjected to such comprehensive botanical investigations that our knowledge of the flora in its broad features must be regarded as satisfactory (SEIDENFADEN 1930, 1931, MENZIES 1932, VAAGE 1932, SØRENSEN 1933, GELTING 1934, SEIDENFADEN & SØRENSEN 1937).

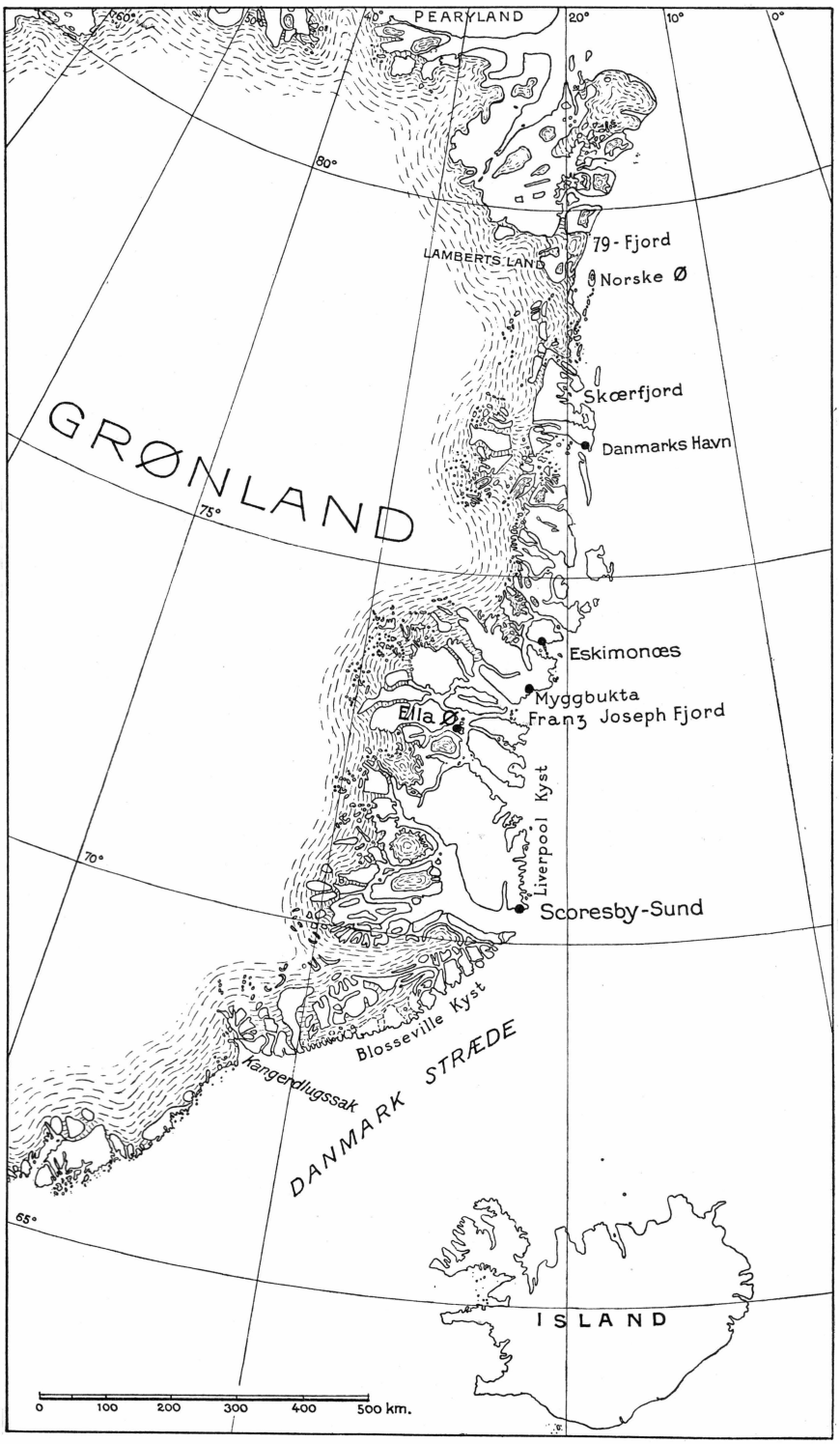



Fig. 1. Map of Northeast Greenland.

# III. THE TEMPERATURE CONDITIONS OF NORTHEAST GREENLAND

## Brief survey of the climate of Northeast Greenland.

The meteorological data for Northeast Greenland are rather incomplete. The outer limits of the area may with a certain approximation be said to be Scoresby Sund, in c. 70° N. lat., and Danmarks Havn, in c. 77° N. lat. Scoresby Sund has midnight sun for about two months, Danmarks Havn for about two and a half months.

Meteorological observations are available from Scoresby Sund from 1926 and subsequent years, while only the observations made by the Danmark Expedition 1906—08 are at hand from Danmarks Havn. From the Norwegian meteorological station Myggbukta, in c. 73°30′ N. lat., observations are available from 1922 (Birkeland & Schou 1932). Temperature and precipitation for the three stations are given here (Table 1) after Helge Petersen (1938).

The temperature records for the three stations show but small differences. It is especially noticeable that the July temperature is almost the same, while the winter temperature is remarkably lower northward. All stations have roughly three months with positive mean temperatures, Scoresby Sund, however, somewhat more and Danmarks Havn somewhat less than three months. The advent of winter is somewhat delayed in the south, while the progress of spring in the north takes place at a very rapid rate and shows comparatively small differences in time along the stretch Scoresby Sund—Danmarks Havn.

The precipitation is inconsiderable, decreasing markedly northward, especially the summer precipitation. The latter, however, is compensated in some degree along the outer coast by frequent fogs. The exceedingly scanty precipitation at Myggbukta does not seem to be a valid expression of the precipitation in the central parts of the area, but must probably be ascribed to purely local conditions prevailing at this station (Petersen 1938).

The climate as a whole is markedly continental. The continentality increases towards the north, though on a scale which is extremely small

Table 1. Monthly mean temperatures and monthly mean precipitation for Scoresby Sund, Myggbukta, and Danmarks Havn.

| | Temperature | | | Precipitation | | |
|---|---|---|---|---|---|---|
| | Scoresby Sund | Mygg-bukta | Dan-marks Havn | Scoresby Sund | Mygg-bukta | Dan-marks Havn |
| | C° | C° | C° | mm | mm | mm |
| Jan. | — 17.4 | — 20.3 | — 21.9 | 45 | 5 | 31 |
| Febr. | — 18.7 | — 21.4 | — 27.4 | 43 | 11 | 18 |
| March | — 16.8 | — 20.9 | — 22.4 | 14 | 5 | 18 |
| April | — 12.4 | — 16.4 | — 19.5 | 38 | 4 | 3 |
| May | — 4.4 | — 7.0 | — 7.3 | 7 | 1 | 4 |
| June | 1.8 | 0.4 | 1.1 | 25 | 6 | 5 |
| July | 4.5 | 3.7 | 4.4 | 14 | 12 | 1 |
| Aug. | 3.3 | 3.0 | 2.2 | 11 | 11 | 8 |
| Sept. | — 0.2 | — 2.5 | — 4.0 | 27 | 1 | 7 |
| Oct. | — 7.0 | — 9.7 | — 14.4 | 28 | 5 | 6 |
| Nov. | — 12.7 | — 15.6 | — 20.4 | 26 | 11 | 26 |
| Dec. | — 15.5 | — 18.9 | — 20.9 | 39 | 6 | 19 |
| Year... | — 8.0 | — 10.5 | — 12.6 | 317 | 78 | 146 |

as compared with the change of the climate towards continentality that makes itself felt in the up to 200 km broad foreland from the outer coast to the edge of the inland ice.

## Insolation and temperature climate.

The temperature-climate is principally determined by the radiant energy which the earth receives from the sun. The solar constant, $J$, the (suppositive) quantity of energy received at the boundary of the atmosphere by an area of 1 sq. cm at right angles to the direction of radiation in one minute, has been calculated to be c. 2 g. cals. Only a part of this quantity, determined by the distance traversed by the sun-rays through the atmosphere and the permeability of the latter, and by the position of the surface of the earth in relation to the direction of the sun-rays, will be of benefit to the surface of the earth. The oblique direction of incidence of the sun's rays in relation to the horizontal plane contributes to a reduction of the actual amount of heat received in the Polar countries as compared with more southerly regions. The permeability of the atmosphere to the radiation of the sun is given as the coefficient of transmission, $p$, which is reckoned $= 1$ for the theoretical case that the radiation suffers no loss in intensity during its passage through the atmosphere; for all realisable cases as fractions of 1. The

average value of $p$ for the whole earth is stated to be about 0.6 (MILANKOVITCH 1930, p. A. 66), for high mountain climates it rises to 0.8—0.9.

In Fig. 2 the solstitial irradiation (energy received per sq. cm on June 22nd) for different latitudes is shown after MILANKOVITCH (l. c. Fig. 11, p. 165). From this it will appear that the influence of the geographical latitude makes itself felt in such a way that the higher latitudes are at a relatively greater disadvantage with decreasing $p$. $p$ decreases rapidly with the increasing content of vapour in the atmosphere. As a

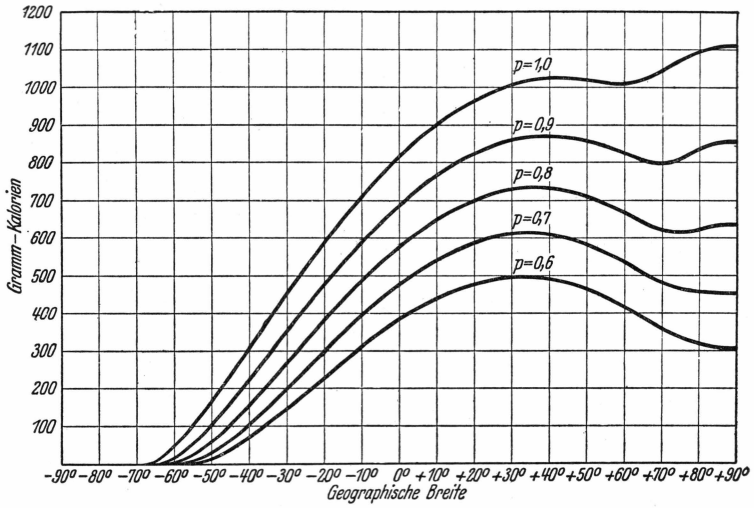



Fig. 2. The solstitial irradiation (22nd June) in different latitudes and at different transmission coefficients, $p$ (after MILANKOVITCH 1930).

consequence the intensity of irradiation in arctic regions is influenced in a higher degree by the moisture of the atmosphere than in more southerly regions, a fact which contributes to emphasise the difference in the temperature climate between continental and oceanic climates in the Arctic. This will be especially obvious on considering Fig. 3 (after MILANKOVITCH l. c. Fig. 12 p. 165), which shows the variation in the semiannual irradiation intakes in different latitudes with varying $p$. The low position of the sun of course plays a greater role for the whole year (or the summer half-year alone) than for the longest day (cf. Fig. 2). It will be evident from the above that owing to its continental climate and great atmospheric aridity Northeast Greenland as a whole is relatively well off in spite of its northerly position. Moreover we have here one of the reasons why the formation of fog along the outer coast causes a much greater depression of the summer temperature in relation to the inland than might be expected, compared with a corresponding gradation in the cloud-covering in more southerly regions.

It is of the greatest importance to maintain that the direct radiation of the sun is thus relatively more intense in Northeast Greenland than is usually the case in our country. The degree of exposure therefore is of special importance for the local temperature conditions.

Some theoretical considerations on the insolation and exposure-climate of Northeast Greenland will first be given. Owing to the northern

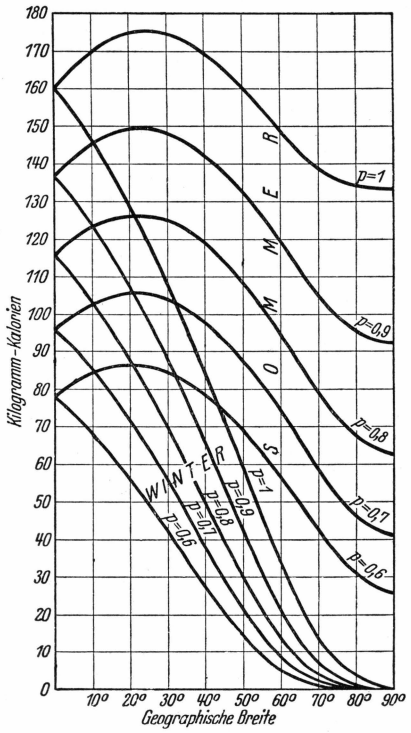



Fig. 3. Semiannual intake of irradiation at different latitudes and different transmission coefficients, $p$ (after MILANKOVITCH 1930).

position of the country there will only be a normal distribution of day and night for short periods about the vernal and the autumnal equinox. The more northerly the latitude, the more will the radiation intake be concentrated about midsummer. The radiation quantity (g. cals. per sq. cm per 24 hours[1]) for various geographical latitudes is given below after MILANKOVITCH (1930, p. A 62—A 63):

Coefficient of transmission $p = 0.8$

| | 21 March | 6 May | 22 June | 8 August | 23 September |
|---|---|---|---|---|---|
| 90° ..... | | 360 | 634 | 357 | |
| 70° ..... | 132 | 447 | 624 | 442 | 130 |
| 50° ..... | 367 | 609 | 707 | 603 | 361 |
| 30° ..... | 556 | 689 | 728 | 682 | 548 |

[1]) The diffuse sky radiation included.

Although the amount of energy received about midsummer is relatively great for the northern regions, it does not attain the same numerical height as for the temperate regions. As the absorption during the short summer must not only compensate the simultaneous terrestrial radiation, which is very considerable owing to the dry air, but also the immense loss by radiation which takes place continually during the dark winter, the temporary great absorption of heat is not capable of raising the temperature of the air very much above zero.

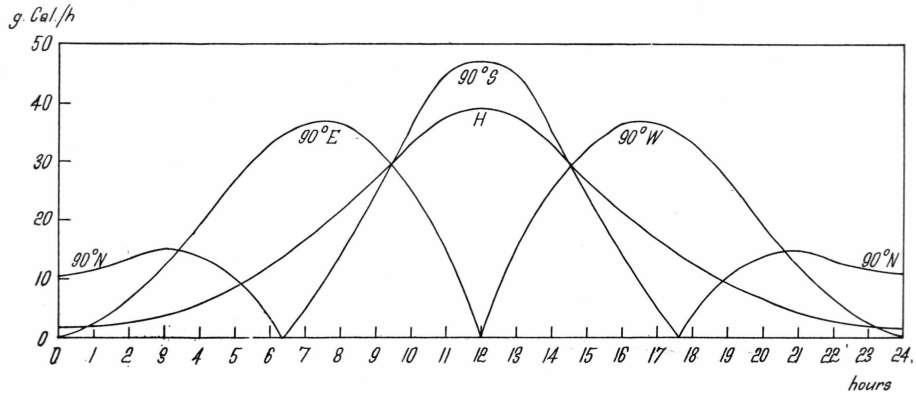



Fig. 4. The twenty-four hour distribution of the solstitial irradiation (22nd June) in 74°N. lat. (g cal per h per cm²) for horizontal ground, north- and south-facing and east- and west-facing walls. Transmission coefficient $p = 0.8$.

Similarly to the insolation, the vegetation period of the plants is concentrated around the summer solstice. It is limited to that part of the summer which has midnight sun, or an even shorter period. We shall therefore here content ourselves with considering more closely the intake of solar energy on June 22nd, which will thus with a certain approximation reflect conditions during an essential part of the vegetation period of the plants. Fig. 4 is a graphic representation of the diurnal course of the irradiation value for a horizontal plane, a north-facing and a south-facing wall, a west-facing and an east-facing wall in 74° N. lat. (the approximate latitude of Eskimonæs) on June 22nd, computed according to the formula given by SCHUBERT (1929, p. 57). The coefficient of transmission has been roughly estimated to be 0.8, which is hardly too much for a clear sky considering the sparse moisture of the air. Correction for the distance travelled by the rays through the atmosphere has been inserted after a table in HANN (1908, p. 103).

The curves show great differences in the duration and intensity of irradiation according to the orientation of the plane irradiated. Similarly the insolation for different angles of inclination can be computed. Representing especially different types of insolation, the insolation curves for

30° northern exposure and 40° southern exposure are shown in Fig. 5. While in the first case the intensity of irradiation is fairly equal throughout the day and night, in the latter case it shows an overwhelming maximum about noon. The insolation curves for 30° easterly and 40° westerly exposure have been inserted for comparison.

Fig. 6 shows graphically the insolation on June 22nd at different exposures and angles of inclination, computed by summation of the

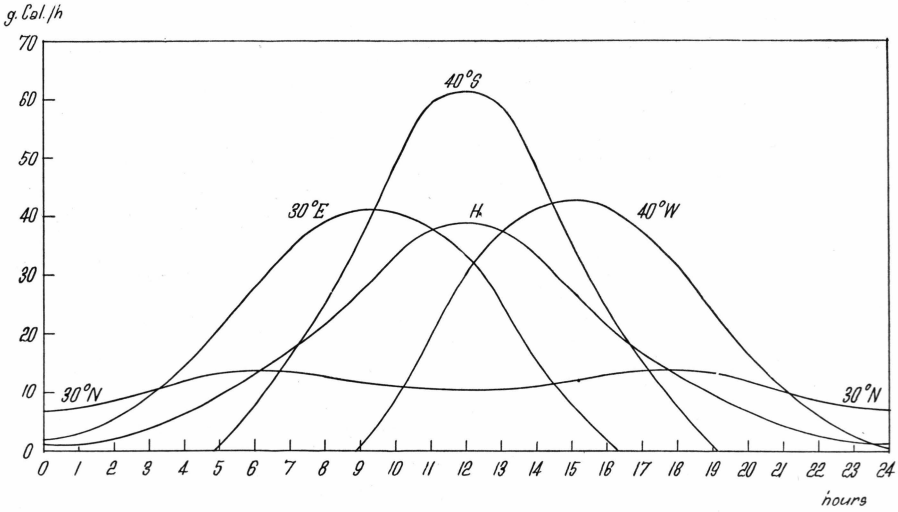



Fig. 5. The twenty-four hour distribution of the solstitial irradiation (22nd June) in 74° N. lat. (g cal per h per cm²) for slopes with a southern exposure of 40°, a northern exposure of 30°, an eastern exposure of 30°, and a western exposure of 40° compared with that of a horizontal plane. Transmission coefficient $p = 0.8$.

hour values of the day and night (cf. the curves in Fig. 4)[1]). It will be seen that only slopes with a southern exposure and with an angle of inclination of up to c. 70° receive greater amounts of heat than the horizontal plane. The most favoured are slopes with an inclination of about 40°, which receive an amount of heat of about 20 per cent. more than the horizontal plane. At an exposure of 70° to the south and up to the vertical wall (angle of inclination 90°) the supply of heat is less than for the horizontal plane. Exposure to the east (or west) and north gives less income of heat than the horizontal position of the plane. At easterly and westerly exposures the insolation decreases slowly at small degrees of inclination, more rapidly with increasing inclination; at northerly

[1]) The lack of agreement between the irradiation values computed and those stated on p. 31 after MILANKOVITCH (for the horizontal plane c. 390 g cal/cm² per twenty-four hours as against c. 630 according to MILANKOVITCH) is due to the fact that in my computations no regard has been taken to the diffuse sky radiation, but only to the direct radiation of the sun (for this cf. PETERSEN 1926, p. 152).

exposures, however, fairly rapidly at low inclinations, but more slowly at angles of inclination exceeding c. 40°, that is to say, after the degree of inclination at which the south sun is no longer capable of exerting its influence by noon has been attained. Slopes with a northern exposure and a high degree of inclination are in an especially un-

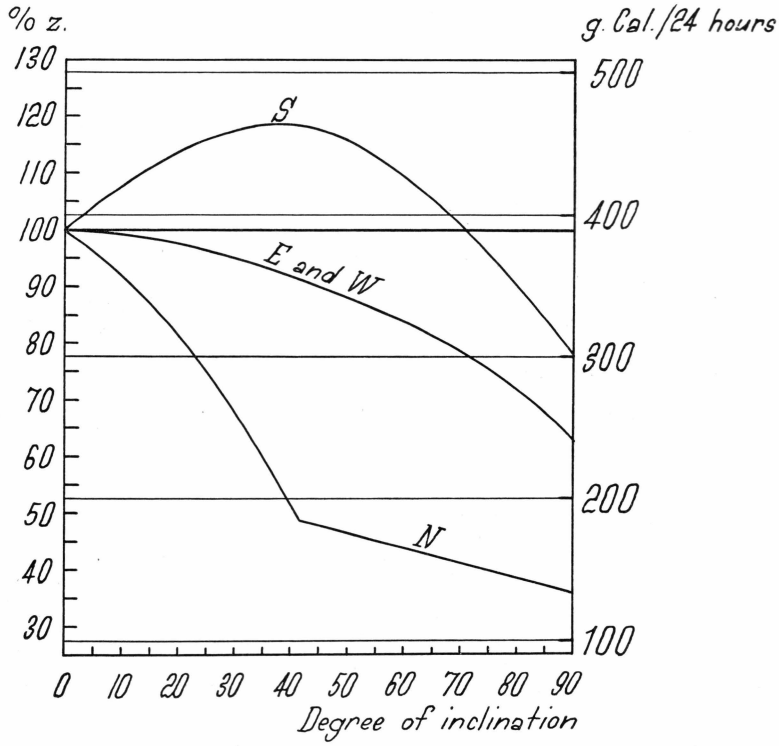



Fig. 6. The twenty-four hour value of the solstitial irradiation (22nd June) in 74° N. lat. at varying exposures and angles of inclination. Transmission coefficient $p = 0.8$. $z$: the irradiation intake of the horizontal plane.

favourable position; they receive less than half the amount of energy received by the horizontal plane.

The quantity of heat received is of course no expression of the thermic climate in general, similarly as the heat intake of the individual areal unit indicates nothing definite about the thermic conditions of the corresponding elementary space, its temperature. A far-reaching levelling of the temperature takes place by radiation and conduction and by air and water currents. In addition to these levelling agencies generally active in all regions, in the Arctic we further find two which highly influence the elementary climate, viz. the soil-ice and the snow-covering. As the whole water content of the layer of soil at the disposal of the roots of the plants must be thawed anew every spring, the rise of temperature

is retarded in spring and summer, especially in the wet localities. The snow masses accumulated in the course of the winter act in the same direction and in an even more differentiated degree. Owing to its unequal distribution according to the configuration of the surface of the ground, the snow-covering becomes the predominant factor in the differentiation of the local elementary climates, this factor in a preponderating degree determining the duration of the yearly season within which the soil is not icebound. Even on slopes with a southern exposure and intense insolation a heavy snow-covering causes a very great retardation, in fact relatively the greatest; for the direct influence of the insolation will not make itself felt until the snow-covering has been reduced to an inconsiderable thickness owing to the more or less complete reflection from the snow. The great local pollution of the accumulated snow, however, furthers the melting of the snow in no small degree, more especially in places with intense insolation.

Thus the effect of the direct insolation is modified in various ways. However, what makes an estimate of the direct insolation and its local distribution of such great interest, is that the surface of the ground, that is to say the uppermost layers of the soil, is the only conductor of heat communication to the air as well as to the deeper-lying layers of the soil. Thus the surface of the soil is exposed to a temporary comparatively strong heating during the direct insolation.

Scattered registrations of the temperatures of the soil surface in different parts of the globe have revealed astonishingly high insolation temperatures as compared with the air temperatures of the place (e. g. Filzer 1936, Krogerus 1937, Leick & Propp 1931—32, Schade 1912, 1934. Reference is further made to the synoptic works of Drude 1918, 1932, and Geiger 1927, 1930).

A methodical difficulty in making such observations is found in the limitation of the observation spot. By employing the recent, refined, methods (e. g. Huber 1937) which aim at limiting the third dimension to the least possible, highly surprising temperature fluctuations as a consequence of direct insolation have been demonstrated. However, the absolute, extreme temperature values for an approximated theoretical, mathematical soil surface should not be overestimated as an ecological factor, more especially if we are concerned with the phanerogamic vegetation, even if it is low and one-layered. The plantal organism itself with its life functions is not limited to a two-dimensional plane, but has a certain vertical extension, similarly as the very presence of a vegetation prevents the establishment of the most extreme surface temperatures. In practice no exact limit, upper or lower, for the vertical extension of the plant body can, of course, be given, and likewise the temperatures to which the various organs of a plant are exposed at the same moment

must be very unequal, more especially in the Arctic; for in the eternally frozen subsoil a great fall in temperature must always be expected as we pass from the crown of the rootstock to the deepest-striking roots. Thus the registration of the actual temperature conditions in the habitat of the plants can never claim to be absolutely exact, even though the observations themselves are precise enough. Similarly such observations will always be exposed to criticism owing to the difficulty in defining what is to be observed.

## Ordinary meteorological observations.

After these preliminary remarks on insolation climate and elementary climate, I proceed to detail a series of actual temperature observations made on Ella Ø (c. 72°50′ N. lat.) in 1931—32, and at Eskimonæs, Clavering Ø, (c. 74°10′ N. lat.) in 1934—35.

It must at once be admitted that observations which merely extend over two isolated years, are of limited general validity. The temperature conditions in Northeast Greenland, as well as in Greenland as a whole (PETERSEN 1938), are often rather variable in the various years and may exhibit great deviations from the normal. In order to form a correct estimate of observations for an isolated year it is of essential importance to be informed as to whether the year in question is normal to the area, or to what extent it deviates from the normal. Before proceeding to a closer consideration of the results of the elementary climatic observations an attempt will be made here to answer the question: Were the years 1931—32 and 1934—35, and more especially the summers of 1932 and 1935, warm or cold in relation to the temperature conditions prevalent at the stations in question?—Here the difficulty arises that no meteorological data are available for the two stations. In order to meet this defect I have carried out the usual meteorological service during the two years, on Ella Ø in 1931—32 and on Eskimonæs in 1934—35, by means of the usual apparatus for temperature observations. The observations on Ella Ø were continued during the two succeeding years by the radio operator A. DE LEMOS, which fact of course highly increased the value of the observations for this station.

Ella Ø 1931—34. The monthly mean temperatures (here computed on the basis of the mean value of the daily maximum and minimum) for the observations September 1931—June 1934 are given in Table 2 together with the corresponding ones for Myggbukta according to "Jahrbuch des Norwegischen Meteorologischen Instituts 1933—36" (Oslo 1934—37) (November and December 1931 are lacking for Myggbukta).

The graphic representation in Fig. 7 shows a very clear agreement between the annual course of the temperature for the two stations.

Table 2. Monthly mean temperatures for Ella Ø (E), and Myggbukta (M), 1931—34, and the difference between the two mean temperatures.

| | 1931 | | | 1932 | | | 1933 | | | 1934 | | | Mean Diff. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | E | Diff. E—M | M | E | Diff. E—M | M | E | Diff. E—M | M | E | Diff. E—M | |
| Jan. . . | .. | .. | .. | —19.0 | —19.2 | — 0.2 | —12.7 | —15.9 | — 3.2 | —21.0 | —23.7 | — 2.7 | — 2.1 |
| Febr. . | .. | .. | .. | —14.2 | —12.6 | 1.6 | —18.3 | —18.6 | — 0.3 | —24.3 | —25.0 | — 0.7 | 0.2 |
| March | .. | .. | .. | —15.8 | —14.2 | 1.6 | —17.1 | —17.5 | — 0.4 | —15.5 | —17.2 | — 1.7 | — 0.2 |
| Apr. . . | .. | .. | .. | —17.3 | —17.9 | — 0.6 | —18.3 | —19.2 | — 0.9 | —13.0 | —11.4 | 1.6 | 0.1 |
| May . . | .. | .. | .. | — 2.7 | — 0.8 | 1.9 | — 6.4 | —10.5 | — 4.1 | — 6.3 | — 4.2 | 2.2 | 0.0 |
| June . | .. | .. | .. | 3.4 | 6.2 | 2.8 | 1.9 | 3.9 | 2.0 | 2.8 | 5.8 | 3.0 | 2.6 |
| July . . | .. | .. | .. | 5.6 | 9.6 | 4.0 | 5.9 | 10.2 | 4.3 | 3.6 | .. | .. | 4.2 |
| Aug . . | .. | .. | .. | 2.6 | 8.4 | 5.8 | 3.4 | 9.0 | 5.6 | 2.8 | .. | .. | 5.7 |
| Sept. . | .. | 0.6 | .. | — 1.1 | (4.0) | 5.1 | — 0.4 | 3.5 | 3.9 | 2.2 | .. | .. | 4.5 |
| Oct. . . | — 12.2 | — 9.8 | 2.4 | —12.3 | — 7.9 | 4.4 | —10.3 | — 7.0 | 3.3 | — 6.7 | .. | .. | 3.4 |
| Nov. . | .. | — 11.1 | .. | —17.1 | —18.3 | — 1.2 | —12.3 | —11.1 | 1.2 | —15.2 | .. | .. | 0.0 |
| Dec. . . | .. | — 22.4 | .. | —16.6 | —17.2 | — 0.8 | —12.4 | —12.9 | — 0.5 | —18.0 | .. | .. | — 0.7 |

Very conspicuous are the much higher summer temperatures and the generally slightly lower winter temperatures for Ella Ø than for Myggbukta, affording unmistakable evidence of the increasing continentality of the climate from the outer coast towards the inner fjords.

An approximate expression of the monthly mean deviation of the Ella Ø temperatures from those of Myggbukta was obtained as shown in Fig. 8, the individual deviations (cf. Table 2) being marked in the positive and negative directions from the 0°-axis. It must be assumed that the deviation actually represents a continuous function of the season; it has been attempted to illustrate this by a wavy curve drawn arbitrarily after the points marked. The approximate monthly deviation of the Ella Ø temperatures from those of Myggbukta then amounts to:

| Jan. | Febr. | March | April | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| —1.5 | —1.5 | —0.8 | +0.1 | +1.4 | +2.8 | +4.2 | +4.8 | +4.3 | +2.6 | +0.2 | —1.0 |

Starting from the mean temperature of Myggbukta, calculated for the period 1922—32 (H. Petersen 1938), an approximate value for the mean temperature of Ella Ø may be obtained by an addition of the corresponding Ella Ø deviations to the monthly means for Myggbukta. Table 3 gives the monthly mean temperatures for Ella Ø computed in this way and those actually registered in 1932. From these it will appear that the summer of 1932 was comparatively warm, and that the spring set in exceptionally early. This is in good agreement with the statements

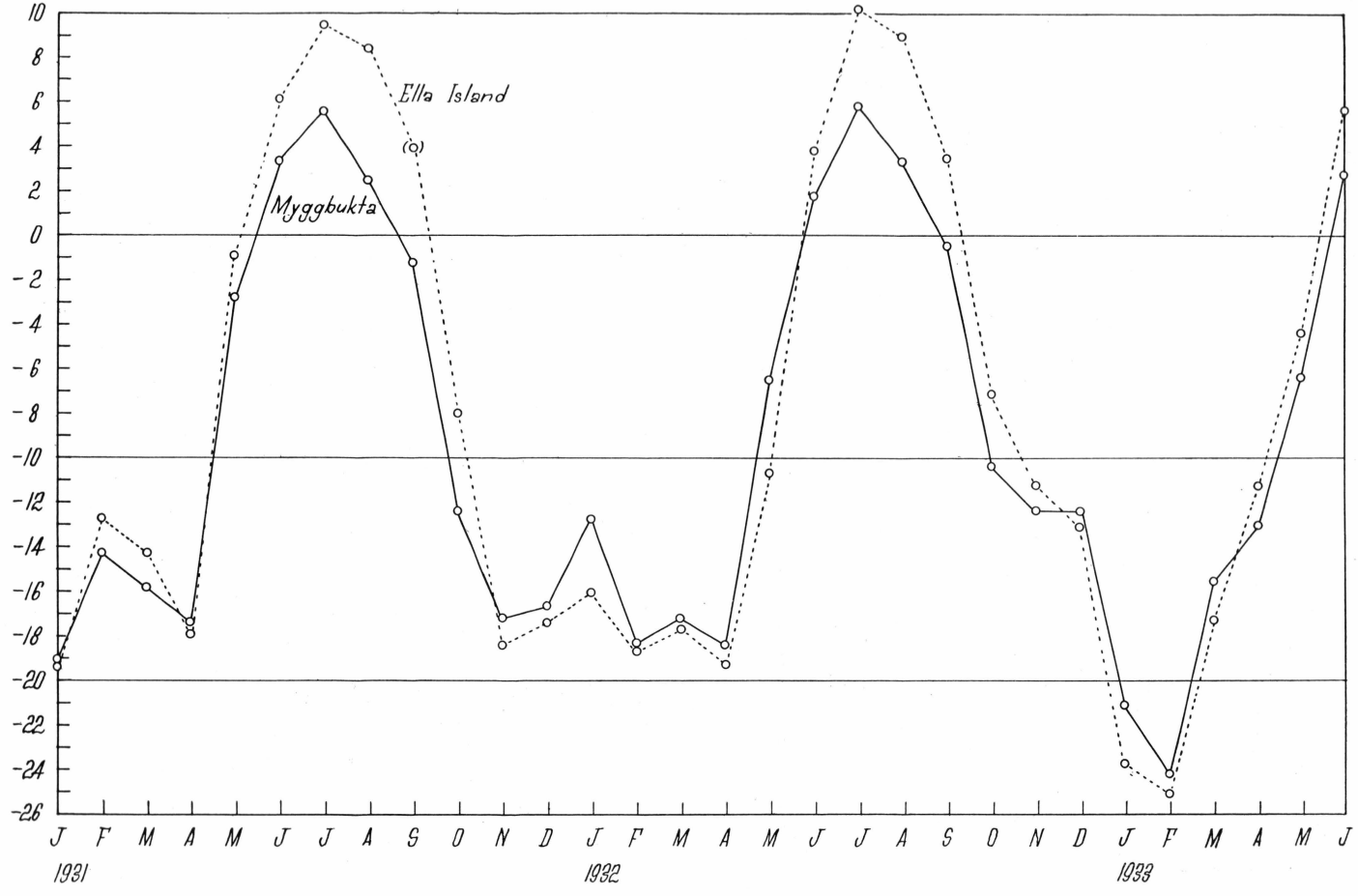



Fig. 7. Graphic representation of the monthly mean temperatures for Myggbukta and Ella Ø 1931—1933.

Table 3. Monthly mean temperatures for Ella Ø, computed (cf. the text) and observed in 1932.

| | Jan. | Febr. | March | April | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean computed (1922—32) ..... | — 21.8 | — 22.9 | — 21.7 | — 16.3 | — 5.6 | 3.2 | 7.9 | 7.8 | 1.8 | — 7.1 | — 15.4 | — 19.9 |
| Mean observed 1932 | — 19.2 | — 12.6 | — 14.2 | — 17.9 | — 0.8 | 6.2 | 9.6 | 8.4 | (4.0) | — 7.9 | — 18.3 | — 17.2 |

of local trappers, who, having lived in the area for several years, have acquired a practical knowledge of the climatic conditions.

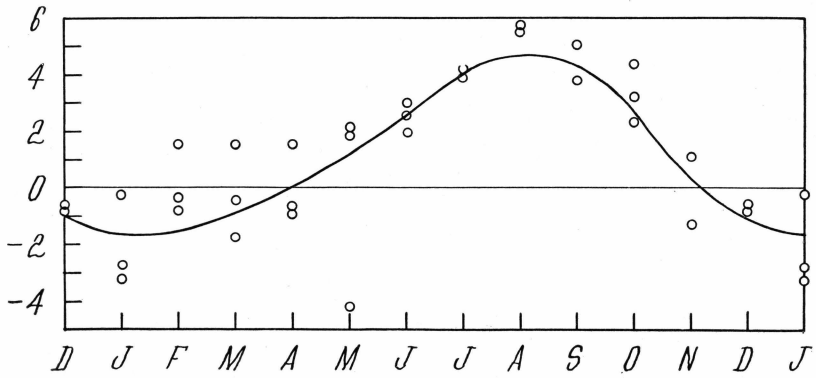



Fig. 8. Graphic representation of the approximate difference between the monthly mean temperatures of Ella Ø and Myggbukta (Ella Ø temperature less Myggbukta temperature). The points indicate the individual monthly temperature differences for 1931—1934 (cf. Table 2).

Eskimonæs 1934—35. From this station observations are only at hand from the year 1934—35. The monthly mean temperatures for this year were as follows (mean temperature for twenty-four hours here computed according to the formula $M = \frac{2(8\,h + 14\,h) + 5(21\,h)}{9}$ (cf. PETERSEN 1938)[1])

| | Sept. | Oct. | Nov. | Dec. | | | | |
|---|---|---|---|---|---|---|---|---|
| 1934 ... | 1.9 | —8.4 | —15.2 | —16.3 | | | | |
| | Jan. | Febr. | March | April | May | June | July | Aug. |
| 1935 ... | —18.8 | —19.5 | —17.2 | —17.2 | —7.5 | —0.9 | 1.8 | (2.3) |

Fig. 9 shows the mean temperatures of Myggbukta (1922—32) and temperatures for Myggbukta and Eskimonæs for 1934—35. The situation of Eskimonæs in relation to the outer coast is almost like that

[1]) The maximum thermometer was lost in the course of the winter, for which reason maximum temperatures are lacking for this series of observations.

of Myggbukta, so no great difference between the two stations is to be expected. A comparison of the Eskimonæs curve for 1934—35 with that of Myggbukta for the same period shows a slightly higher winter temperature and a remarkably lower summer temperature for Eskimo-

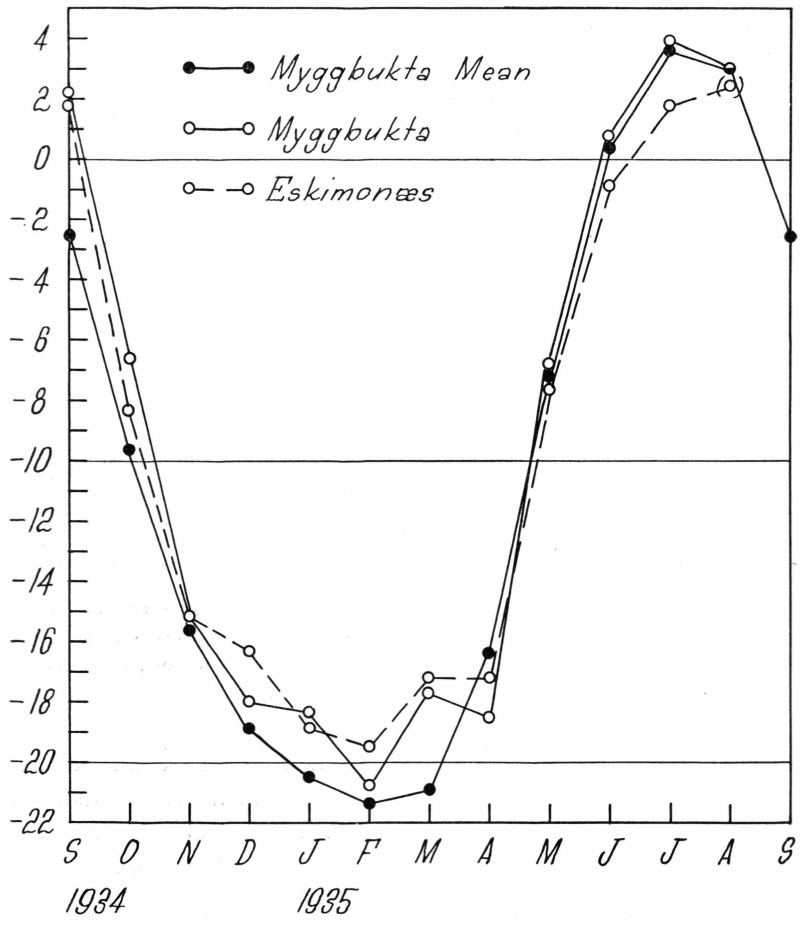



Fig. 9. Graphic representation of the monthly mean temperatures of Myggbukta 1922—32, Myggbukta 1934—35, and Eskimonæs 1934—35.

næs. This points to a more oceanic climate for Eskimonæs.—A comparison of the two Myggbukta curves shows that in the autumn of 1934 the winter cold came unusually late. For the summer of 1935 the two curves cover each other to a surprising extent.

As regards Eskimonæs we must then conclude that the autumn of 1934 was extraordinarily mild and the summer of 1935 must be regarded as normal.

It should be mentioned, however, that the local trappers regarded 1935 as a cold summer. This divergence between the rough estimate and the purely meteorological one may perhaps be explained by the circumstance that the normal temperature of Myggbukta is computed for 1922—32, while the experience of the trappers is chiefly derived from more recent years. Various circumstances, for instance the favourable navigation conditions in 1932—34, indicate that all these years have been comparatively favourable, while 1935, again, most likely corresponded to the twenties.

For a comparison between the microclimatic observations on Ella Ø in 1932 and at Eskimonæs in 1935 (see below), it should expressly be pointed out, according to the above, that the difference in temperature-climate normally characterising the two stations is here further accentuated by the fact that the observations on the summer-warm Ella Ø were made in a warm summer, while the observations at the relatively summer-cold Eskimonæs are derived from a normal or perhaps a cold summer.

The air temperatures measured at the two stations in the two years do indeed give the impression of two entirely different climates. Ella Ø has four months with positive mean temperatures, the warmest month having a mean temperature of up to 10°, while Eskimonæs has only three months with positive temperatures, and in the warmest month (July) the mean temperature rises only a couple of degrees above zero.

Table 4 gives observations on clouds, fog, and precipitation for the

Table 4. Observations on cloud-covering, fog, and precipitation for Ella Ø 1931—32 and Eskimonæs 1934—35, computed in percentages of all the observations made three times in the course of twenty-four hours, viz. at 8, 14, and 21 o'clock.

| | | Sept. | Oct. | Nov. | Dec. | Jan. | Febr. | March | April | May | June | July | Aug. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Clear | Ella Ø 1931—32 | 59 | 49 | 36 | 66 | 47 | 43 | 42 | 58 | 68 | 50 | 61 | 52 |
| | Esk.næs 1934—35 | 26 | 33 | 30 | 69 | 32 | 49 | 53 | 83 | 45 | 47 | 31 | 38 |
| Cloudy or haze | Ella Ø 1931—32 | 31 | 41 | 26 | 20 | 16 | 35 | 22 | 37 | 18 | 32 | 29 | 17 |
| | Esk.næs 1934—35 | 21 | 42 | 33 | 20 | 36 | 20 | 26 | 9 | 30 | 25 | 35 | 22 |
| Sky overcast | Ella Ø 1931—32 | 10 | 10 | 38 | 14 | 37 | 22 | 36 | 15 | 14 | 18 | 10 | 31 |
| | Esk.næs 1934—35 | 53 | 25 | 37 | 11 | 32 | 31 | 21 | 8 | 25 | 28 | 34 | 40 |
| Precipitation | Ella Ø 1931—32 | 5 | 2 | 16 | 6 | 9 | 5 | 13 | 12 | 6 | 0 | 6 | 9 |
| | Esk.næs 1934—35 | 21 | 10 | 12 | 3 | 11 | 14 | 10 | 2 | 2 | 2 | 5 | 17 |
| Fog | Ella Ø 1931—32 | 0 | 0 | 0 | 0 | 7 | 0 | 2 | 2 | 1 | 0 | 0 | 4 |
| | Esk.næs 1934—35 | 2 | 0 | 2 | 0 | 5 | 12 | 9 | 3 | 5 | 28 | 18 | 5 |

two stations in the years in question, computed in percentages of all the observations made three times in every twenty-four hours. It appears immediately from the table that the low summer temperature for Eskimonæs in 1935 bears a distinct relation to a heavy cloud-covering and abundant formations of fog.

## Elementary temperature observations.

Ella Ø 1931—32. The following series of observations were taken:

Soil surface temperature (thermograph), level ground: October 1st—December 30th, 1931. February 3rd—March 24th, 1932. Grassy south-facing slope, angle of inclination c. 20°: March 26th—August 23rd, 1932.

Soil surface temperature (thermometer), level ground: February 24th—March 28th, 1932, April 18th—May 30th, 1932.

Soil surface temperature beneath 50 cm snow (thermometer), February 12th—May 20th, 1932.

Soil surface temperature beneath 100 cm snow (thermometer), February 12th—May 20th, 1932.

Soil temperature, depth 20 cm, level ground (thermometer) Oct. 1st—December 31st, 1931.

Soil temperature, depth 50 cm, level ground (thermometer) Oct. 1st—December 31st, 1931.

Graphs of these results are shown on Plate 12.

As to the arrangement of the observations and the working up of the numerical material for the preparations of the curves (Pl. 12) the following should be noted:

Soil surface temperature measured with a thermograph. The heat-percipient brass bulb (diameter c. 2 cm) was covered with two layers of grey filter-paper, and was placed with half the diameter below and the other half above the surface of the ground, more or less covered with withered plant remains. The covering with filter-paper was to ensure a colour and degree of moisture for the heat-percipient element similar to that of the surface of the ground and of tufts of plants. Graphic representation: mean temperature per twenty-four hours, computed as an average of every second of the twenty-four hour values of the day and night.

Soil surface temperature measured with a thermometer. A mercury thermometer was employed, secured in a frame, the heating element being just covered by the soil. Thus the observation gives the tem-

perature at a depth of c. 2 cm. Reading three times a day. Graphic representation: Daily mean computed according to the formula

$$M = \frac{2(8h + 14h) + 5(21h)}{9}.$$

The temperature of the soil at depths of 20 and 50 cm. Measured by means of special thermometers constructed for the purpose in wooden cases placed in tubes of German silver, which were dug down in the late summer. Reading three times daily. The temperature showed only a slight fluctuation in twenty-four hours. For convenience the 21-reading is therefore used in the graph.

The soil surface temperature below the snow was measured by the same thermometers placed in the snow in holes made in the snow-drifts by means of a stick of the same diameter as the wooden case. In order to avoid circulation of the air a closely-fitting case was placed at the surface of the snow. Here, too, the 21-reading was used for the preparation of the curve.

On plate 12 the daily mean of the air temperature has also been inserted, and along with the curves the thickness of the snow in the thermograph observation spots is indicated.

As the most important results the following should be pointed out (cf. the curves, Plate 12, and Tables 38, 39, and 40 (p. 292 et seq.).

The soil surface temperatures of level ground, autumn and winter 1931—32. As long as the soil is not covered with snow, the surface shows a lower mean temperature than the air. The mean difference for October is c. 3°. For some few days, especially on days with a clear sky and a sudden fall of the air temperature, the difference may exceed 6°. At the same time the surface of the soil shows comparatively large daily oscillations. The mean of the daily amplitude for October for the air temperature was 4.7°, for the soil surface temperature 7.1°. After the snow-fall at the beginning of November conditions at the surface of the soil changed their character. The newly fallen loose snow has a strongly isolating effect. The great fall of the air temperature at the beginning of December is felt but slightly at the surface of the soil below the snow-covering: mean temperature for December for the air —22.4°, at the surface of the soil —14.0°, i.e. a mean difference of 8.4° in favour of the soil surface. The daily oscillations below the snow-covering are inconsiderable; for December the mean is 1.2°, while the daily mean amplitude for the air temperature amounts to 8.6°. The observations for February and March show a less isolating effect of the snow-covering, which is due partly to the thinner snow-covering and partly to the more densely packed snow. For the

two months the means of air and soil surface temperatures show very close agreement, while the daily amplitude is much smaller for the soil surface. The very high value of the amplitude for the air temperature for February (cf. Tab. 39, p. 293) is connected with the occurrence of foehn winds in this month. The greatest diurnal oscillation in the air temperature for the whole year was measured on February 24th, viz. 26.6°. On the same day the soil surface temperature below a snow-covering of c. 20 cm showed an amplitude of 11.6°.

The thermometer registrations of the soil surface temperature on level snow-free ground (24th February—28th March) show that the effect of the insolation becomes more and more marked in the course of March. However, as a rule the soil surface temperature does not rise very much above the air temperature.

Soil surface temperature in the spring and summer of 1932. On largely snow-free slopes with a southern exposure of 20° the soil surface temperature averages 5—7° above the air temperature in spring and summer (incl. April—August). The difference attains its maximum in June and July. However, this maximum is but little pronounced as compared with the preceding and succeeding months, May and August (see Table 38, p. 292). It is of interest to note that the daily mean for the soil surface with a southern exposure passes the 0-line about three weeks before the air temperature. While the daily amplitude of the air temperature is highest for April, which must be regarded as normal (cf. WEGENER 1911, p. 320), and declines towards midsummer, the amplitude for the soil surface rises immensely in the months at the height of summer (cf. Tab. 39, p. 293). In the spring the thaw-water has a levelling effect on the temperature oscillations of the soil surface, while later in the summer the dry soil surface is exposed to great temperature oscillations. The greatest daily fluctuation was observed on August 1st, viz. no less than 46° (maximum of soil surface temperature 49°), while in the same twenty-four hours the air temperature shows an amplitude of only 7.5°, maximum 15.5°. It will appear from Table 40 (p. 293 et seq.) that the great diurnal fluctuations of the soil surface are not only due to the immense rise of temperature in the day, but also, though to a less extent, to the fact that the night temperature falls below the air temperature.

The temperature curve for a horizontal soil surface (18th April—30th May) is situated somewhere between the air temperature curve and the curve for the soil surface with a southern exposure of 20°. The irregular course of the curve as compared with the curve for a southern exposure at the end of May is due to the rapid desiccation of the upper soil layers of the level observation locality, because this locality, unlike that with the southern exposure, had no influx of thaw-water.

The temperature readings at the soil surface below 50 and 100 cm snow (12th February—20th May) show the isolating effect of the snow. While the fluctuations of the air temperature are still marked below a snow-covering of 50 cm, the smooth course of the 100 cm curve shows an almost constant temperature. As a rule the temperature is some degrees higher beneath a snow-covering of 100 cm than beneath 50 cm. Immediately on the rise of the air temperature about May 1st the temperature decline takes the opposite course, from above downwards. On May 8th the thickness of the snow had decreased by 5 cm and on May 17th by 10 cm. Already at this date the temperature at the soil surface below the snow had increased to 0°, where it remained constant, till the final melting of the snow, that is to say, on May 27th at the 50 cm observation place and on June 2nd at the 100 cm observation place. Thus the melting of the snow had taken place at a rapidly increasing rate during the last stages, that is to say, after the time when the mean temperature of the air rose above 0°. At the observation spot the soil surface sloped quite inconsiderably towards the southeast.

The readings of the soil temperature at depths of 20 and 50 cm (1st October—31st December) show only little of interest except that the frost in the soil spreads rapidly downwards. Even a few days after the mean temperature of the air had fallen below zero, the uppermost 20 cm of the soil were frozen, and after only a fortnight the frost had reached a depth of 50 cm. From this point both the curves descend gradually, to ascend again with the increasing snow-covering.

Eskimonæs 1934—35. The following series of observations were taken:

Soil surface temperature (thermograph) September 1st, 1934—August 14th, 1935.

Soil temperature at 60 and 100 cm depth (thermometer) 9th October 1934—14th August 1935.

The observations were made on a grassy tongue of solifluction soil with a slight southern exposure (inclination 8°), moving down across a solid gravelly substratum. The frontal height of the tongue was about 1 m, which indicates the maximal depth of thawing in the observation spot. Arrangement of the instruments precisely as stated for the corresponding observations on Ella Ø. The soil thermometers were placed beside the thermograph. The tube fittings were put in place about the 1st of September.

With the domed configuration in relation to the surroundings, which usually characterises the solifluction soil tongues, and its unsheltered position towards the fjord, the observation spot must be said to be exposed to the wind, and only for very short periods was it snow-

covered during the winter. The soil thermometers were read once a day, in the winter months by noon, in the summer in the evening.

Graph showing the results of the observations, Pl. 13. Soil surface temperature: daily mean computed as mean value of the hour values every two hours. Soil temperature: direct representation of the values read every day. The inserted air temperature curve shows the daily mean on the basis of three readings computed according to the usual formula (cf. p. 39). Along with the temperature curves the thickness of the snow at the observation spot is indicated as in Pl. 12.

On the results of these observations the following remarks may be made referring to Pl. 13 and Tables 38, 39, and 41 (p. 292 et seq.): The month of September was unusually rainy with only few sunny days, which possibly accounts for the small difference between the soil surface and the air temperature. The difference between the two mean values for September is only 0.2°, and it is chiefly only in the first half of the month that the soil surface exhibits temperatures noticeably higher than those of the air. In October, when the insolation is already entirely without importance, the soil surface temperature still remains somewhat higher than the air temperature, which fact must be due to conduction of heat from below. The snow-covering, which, however, attains a thickness of only 10 cm, likewise favours the temperature of the soil surface. Terrestrial radiation takes place during the actual winter months, so that the temperature of the soil surface falls slightly below that of the air, unless a snow-covering—as in January —exerts its isolating influence.

Not until April will the effect of the insolation be noticeable in the curves. From now on the difference between the temperatures of the soil surface and the air will constantly increase, culminating in June, to decrease again slightly in July and more markedly in August. It will appear from the curves that the mean temperature of the soil surface passes the 0-line about one month before the mean temperature of the air.

It will be evident from the curves for the soil temperatures that at the time when the mean temperature of the air falls definitely below zero, the whole thawed layer of soil has been cooled to the 0-point. However, not till after about three weeks has the frost penetrated to a depth of 60 cm, and after the lapse of further 2—3 weeks to a depth of 100 cm, which practically means to the constantly frozen layer. Throughout the winter the two soil temperature curves have an approximately parallel course with small deviations caused by intermittent strong fluctuations of the air temperature. About the middle of April the 60 cm curve begins to ascend as a consequence of the heating by insolation of the uppermost layers of the soil. As early as about April 20th

the temperature decline changes, taking the opposite direction, which state continues till the autumnal frost. The intersections of the 60 cm curve and the air temperature curve with the 0-line occur at about the same time, which is a very eloquent proof of the significance of insolation for the temperature conditions of the upper layers of the soil. The 100 cm curve rises but slowly in the course of the summer. About the middle of August the soil has not yet thawed to a depth of 1 m.

### Comparison between the Ella Ø and the Eskimonæs series.

A comparison of the courses of the air and soil surface temperature curves in the two observation series shows a fairly good agreement. In the spring and summer months the correspondence in the difference between the soil surface and air temperature is even greater than might be expected at the outset, if the unequal exposure of the two observation spots (that of Ella Ø about 20° as against 8° of Eskimonæs) is taken into consideration (cf. Table 38, p. 292). The cause may be that the climate of Ella Ø is of a more independent character (GEIGER 1929) than that of Eskimonæs. The Ella Ø station lies isolated from the cold air masses of the Polar Sea by a broad belt of land with high mountains. The cold easterly winds blowing at the coast do not reach it. Eskimonæs, however, is entirely unsheltered, and cold air masses are constantly carried to it by the prevalent easterly winds of the summer. While the air temperature depends to a great extent directly on the temperature of the inflowing air masses, the temperature of the soil surface is more directly influenced by the insolation.

An essential difference, however, is shown by the two soil surface observation series as regards daily amplitude in the summer months (cf. Table 39, p. 293). The amplitude values for Ella Ø amount to almost twice the Eskimonæs values. The causes of this are no doubt diverse, in the first place the angle of inclination, in the second place the degree of moisture of the soil (slower desiccation of the soil in the Eskimonæs observation place), and finally the difference in wind conditions. While calm weather is almost normal to Ella Ø, the wind, though mostly light, blows almost constantly at Eskimonæs. It is a well-known experience that the very pronounced temperature extremes for the soil surface only occur in calm weather.

# IV. SUCCESSION OF ASPECTS AND PHENOLOGICAL SEASONS

## Phenological seasons.

Owing to the short duration of the Northeast Greenland summer, the phenological seasons follow each other in rapid succession. One of the immediately conspicuous characteristics of the phenology of these high-arctic regions is that in spite of the winter cold persisting till far into the light season the seasonal development of the vegetation so to speak almost keeps pace with the almanac, precisely as in the temperate regions (cf. EKSTAM 1897).

The spring stages progress so rapidly that there is hardly any basis for establishing so fine a phenological gradation as proposed for instance by IHNE (1895) and DRUDE (1896) (cf. also GAMS 1918) for Central Europe. In certain respects the classification suggested by POUND & CLEMENTS (1898) and HARVEY (1908) for the American prairies are formally more applicable to conditions in Northeast Greenland. Thus HARVEY erects the following succession of aspects for the prairies of South Dakota: prevernal, vernal, æstival, serotinal, autumnal, and a postfloral aspect. A similar gradation in the succession of aspects is demonstrable for Northeast Greenland, perhaps with the omission, however, of the postfloral aspect. A general postfloral aspect preceding the setting-in of the permanent frost hardly exists, except perhaps in very warm summers.

The Northeast Greenland aspects may be characterised as follows:

1) Prevernal aspect (pre-spring) from the beginning to the end of May. The snow melts on level ground where its thickness has not exceeded c. 20 cm, and on favourably exposed slopes where the snow-covering is loose, up to c. 40 cm. On the southwardly exposed slopes, snow-free in the winter or thawing early in the spring, the soil thaws down to appreciable depths in the daytime. The limit between prevernal and vernal aspects is naturally marked by the flowering of the earliest species, and for the central parts of the area investigated, by the breaking up of the rivers (cf. p. 63).

2) Vernal aspect (spring) from the end of May to the end of June. This aspect is characterised by the leafing of the summer-green dwarf bushes (*Betula*, *Vaccinium*, *Arctostaphylos*, *Dryas*) and the flowering of the spring plants. The most conspicuous is the purple-coloured *Saxifraga oppositifolia*, in addition white *Drabae* and *Melandrya*, and yellow *Potentillae*.—During the vernal aspect the melting of the snow proceeds rapidly. The *Cassiope* heath becomes snow-free about the middle of the month, and the transition to the æstival aspect is naturally marked by the disappearance of the snow-covering from the level land as a whole. Only the actual snow-patches have not yet thawed from their winter dormance.

3) Æstival aspect (height of summer) from the end of June to July 15th—20th. This aspect is principally characterised by the flowering of the *Cassiope* heather, which is sharply delimited as to time. *Dryas*, whose flowering is much more prolonged, flowers at the same time. Altogether this season is the flowering time par excellence. —The moderate snow-patch vegetation will be thawed out of the snow, and desiccation begins to exert its influence on the dry hill-tops. The aspect ends with the withering of the flowers of the *Cassiope* heather.

4) Serotinal aspect (the late summer), the latter half of July and the beginning of August. This is especially the flowering period of the *Gramineae*. In addition a number of southern species flower, which on damp south-facing slopes form the northernmost outposts of the herb slope vegetation proper. The pygmae flora of the snow-patches now expands its not very resplendent flowers, the river deltas are coloured red by flowering *Chamaenerium*, and the bogs look white with the woolly heads of *Eriophorum*, the birch "scrubs" and the luxuriant *Cassiope* heaths are ornamented with the delicate *Pyrola*-flowers, while the blue-bell in patches lends to the slopes, now turning yellowish, a new and more intense brilliance of colour.

5) Autumnal aspect (autumn), the latter half of August and the beginning of September. This aspect is characterised by the vivid autumnal colouring of the foliage of the dwarf-bushes, passing from yellow in *Salix*, a flaming carmine in *Arctostaphylos* to the brown of the dwarf birch and the deep purple of *Vaccinium*. Occasional flowers, which have no possibility of developing mature fruits, still linger in the late-melting snow-patches. Retarded *Melandrya* and *Papaver* hang their too heavy nodding heads on long etiolated scapes in shady ravines and from rock fissures on the north-facing rock-walls, now left for ever even by the cold rays of the midnight sun. The white crystals of the frost rime grow larger day by day, following sharp lines in the landscape, marking the shadows of the mountains, which increase in length

in geometrical progression according as the midday sun sinks. On the shady side life congeals in its winter torpor, while on the sunny side the autumnal splendour of colours lends a soothing touch to the cessation of the life functions. The last phase of the short summer has irrevocably run its course to the bitter end. It is winter again, in the middle of September. Not till eight or nine months have elapsed, will the race begin again at the same precipitate speed in the sunlight of an eternal day.

## Phenological observations from Eskimonæs and its surroundings 1935.

For the information of the reader the relations of the individual species to the phenological seasons outlined above are shown in Table 5, which gives a schematic representation of the flowering of a number of species based on observations made on Clavering Ø in the summer of 1935. A total of 138 species are tabulated, that is to say, the species accessible to observation in the given place. At the time of the breaking up of the rivers (June 3rd) four flowering species were met with, viz. *Saxifraga oppositifolia*, *Salix arctica*, *Potentilla nivea*, and *P. emarginata*. By mid-spring—June 14th, the approximate date for the complete thawing of the *Cassiope* heath—27 species had commenced flowering, i.e. about 20 per cent. (of the 138 species). At the beginning of the summer—June 28th—the number of the flowering species had increased to 72 or about 52 per cent. As yet no species could be said to be definitely out of flower. At the end of the summer—July 20th—89 species, or about 64 per cent., were in flower, while 15 species or 11 per cent. had not yet been observed in flower. Species which were now for the most part out of flower amounted to 34 or about 25 per cent. It should be noted that the list of species now out of flower does not precisely comprise the earliest flowering species, in flower on June 14th. Certain early-flowering species with a wide ecological range continue their flowering in other localities which become snow-free later, throughout the summer. Typical examples of such species are *Salix arctica*, *Cerastium alpinum*, *Minuartia rubella*, and *Potentilla emarginata*. Other later-flowering species stop flowering astonishingly early in accordance with their narrow range of occurrence. Such species are for instance *Betula nana*, *Rhododendron lapponicum*, *Pedicularis flammea*. According to the table, 79 species or about 57 per cent. are in flower on August 1st, that is to say, about two weeks after the end of the summer aspect. If we compare this figure with the percentage of flowering species on June 14th (i.e. about two weeks prior to the beginning of the summer aspect), viz. about 20 per cent., it shows a remarkable obliqueness in the distribution around the summer season. However, no objection can be raised on this account against assigning the summer aspect to the

Table 5. Flowering times for the flora of Eskimonæs and its surroundings 1935.

---- occasionally in flower; **xxxx** frequently in flower; **XXXX** generally in flower.

| Month | June | | | | | | July | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | 1—5 | 6—10 | 11—15 | 16—20 | 21—25 | 26—30 | 1—5 | 6—10 | 11—15 | 16—20 | 21—25 | 26—30 | 31 |
| *Alopecurus alpinus* | | | | | | | | --- | -xxx | XXXX | XXXX | XXXX | X |
| *Antennaria alpina* | | | | | | | | | | --x | xXXX | XXXX | X |
| *Arctagrostis latifolia* | | | | | | | | | --- | -xxx | XXXX | XXXX | X |
| *Arctostaphylos alpina* | | -- | --xx | xXXX | XXXX | XXxx | -- | | | | | | |
| *Arenaria ciliata* | | | | | | -- | --xx | xXXX | XXXX | XXxx | -- | | |
| *Armeria vulgaris* | | | | | | | | --- | xxxX | XXXX | XXXX | Xxxx | x |
| *Arnica alpina* | | | | --- | --xx | xxxX | XXXX | XXXX | Xxxx | --- | | | |
| *Betula nana* | | | | ---x | xXXX | XXXx | x--- | | | | | | |
| *Braya humilis* | | | | - | ---x | xxXX | XXXX | XXXX | XXXX | XXXX | XXXX | XXXX | X |
| *Braya linearis* | | | | - | ---x | xxXX | XXXX | XXXx | xx-- | | | | |
| *Braya purpurascens* | | | | -- | ---- | -xxx | xxXX | XXXX | XXXX | XXxx | xx-- | --- | |
| *Calamagrostis arundinacea* | | | | | | | | | -- | --xx | xXXX | XXXX | X |
| *Campanula rotundifolia* | | | | | | | | | | ---- | -xxx | xxXX | X |
| — *uniflora* | | | | | -- | ---x | xxxx | XXXX | XXXX | XXXX | XXXx | xxxx | x |
| *Cardamine bellidifolia* | | | | | -- | ---- | -xxx | xxxX | XXXX | XXXX | XXXX | XXXX | X |
| *Carex alpina* | | | | | | | | --- | -xxx | xxXX | XXXX | XXXX | X |
| — *atrofusca* | | | | | | | -- | ---x | xxXX | XXXX | XXxx | x-- | |
| — *capillaris* | | | --- | --xx | xXXX | XXXx | x-- | | | | | | |
| — *incurva* | | | | | | --- | ---x | xxxx | XXXX | XXXX | XXXX | xxxx | x |
| — *Lachenalii* | | | | | | | | --- | -xxx | xxXX | XXXX | XXXX | X |
| — *misandra* | | | | --- | ---x | xxxx | xXXX | XXXX | XXXX | XXXX | XXXx | xx-- | - |
| — *nardina* | | -- | -xxx | XXXX | XXXX | XXxx | xx- | | | | | | |
| — *parallela* | | | | | | | -- | ---x | xxxx | XXXX | XXXX | XXXX | X |
| — *pedata* | | | ---x | xxXX | XXXX | Xxx- | | | | | | | |
| — *rariflora* | | | | | | | ---- | -xxx | xXXX | XXXX | XXXX | XXXX | X |
| — *rigida* | | | | | ---- | --xx | xxxx | xXXX | XXXX | XXXX | XXXX | XXXX | X |
| — *rupestris* | | -- | ---- | -xxx | xxxX | XXXX | XXXX | XXXX | XXXX | Xxxx | --- | | |
| — *saxatilis* | | | | | | | ---- | --xx | xxxx | xXXX | XXXX | XXXX | X |
| — *scirpoidea* | | | | | - | ---- | xxxx | xXXX | XXXX | XXXX | XXxx | x--- | |
| — *subspathacea* | | | | | | | --- | xxxX | XXXX | XXXX | XXXX | XXXX | X |
| — *supina* | | | --- | --xx | XXXX | XXxx | xx-- | | | | | | |
| — *ursina* | | | | | | | | ---x | xxXX | XXXX | XXXX | Xxxx | x |
| *Cassiope tetragona* | | | | | --- | xxxX | XXXX | XXXX | xxx- | -- | | | |
| *Cerastium alpinum* | | - | ---- | --xx | xxxX | XXXX | XXXX | XXXX | XXXX | XXXX | xxxx | xx-- | - |
| *Chamaenerium latifolium* | | | | | | | | | - | --xx | xxXX | XXXX | X |
| *Chrysosplenium tetrandrum* | | - | -xxX | XXXX | Xxx- | ---- | ---- | - | | | | | |
| *Cochlearia officinalis* | | | | | | | -- | --xx | xXXX | XXXX | XXXX | XXXX | X |
| *Draba alpina* | | | | | | - | ---- | --xx | xXXX | XXXX | XXXX | xxxx | x |
| — *Bellii* | | | | - | --xx | xXXX | XXXX | XXXX | XXXX | XXxx | x--- | - | |
| — *cinerea* | | -xxX | XXXX | XXXX | XXXX | XXXX | XXXX | Xxxx | xx-- | ---- | ---- | - | |
| — *crassifolia* | | | | | | ---- | xxxX | XXXX | XXXX | XXXX | xxx- | ---- | - |
| — *daurica* | | --- | -xxx | xXXX | XXXX | XXXX | XXXX | XXXX | XXxx | xx-- | - | | |
| — *fladnizensis* | | --- | -xxx | XXXX | XXXX | XXXX | xxx- | --- | | | | | |
| — *lactea* | | | | --- | -xxx | XXXX | XXXX | XXXX | XXXX | XXXX | XXXX | XXXX | X |
| — *micropetala* | | | | -- | ---- | --xx | xxxX | XXXX | XXXX | XXXX | XXXX | XXXX | X |

Table 5 (continued).

| Month | June | | | | | | July | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | 1—5 | 6—10 | 11—15 | 16—20 | 21—25 | 26—30 | 1—5 | 6—10 | 11—15 | 16—20 | 21—25 | 26—30 | 31 |
| *Draba nivalis* | | | - | -xxX | XXXX | XXXX | XXXX | XXXx | xx-- | -- | | | |
| — *subcapitata* | | | --- | xxxX | XXXX | XXXX | XXXX | XXXX | XXXX | Xxxx | ---- | --- | |
| *Dryas octopetala* | | | - | ---- | --xx | xxXX | XXXX | XXXX | XXXx | xx-- | -- | | |
| *Dupontia Fisheri* | | | | | | | | | | | | - | - |
| *Elyna Bellardi* | | | -- | -xxx | XXXX | XXXX | xx-- | | | | | | |
| *Empetrum nigrum* | | | --x | xxXX | XXXX | xx-- | | | | | | | |
| *Erigeron compositus* | | | | | | | --- | xxxX | XXXX | XXxx | xx-- | - | |
| — *unalaschkensis* | | | | | | | | ---- | xxxX | XXXX | XXXX | XXXX | X |
| — *uniflorus* | | | | | | | - | -xxX | XXXX | XXXX | XXxx | x-- | |
| *Eriophorum callitrix* | | | -- | xxXX | XXXX | XXXX | xx-- | | | | | | |
| — *polystachyum* | | | -- | --xx | xXXX | XXXX | XXXX | XXXX | XXxx | xxx- | ---- | | |
| — *Scheuchzeri* | | | | - | --xx | xXXX | XXXX | XXXx | xxxx | x--- | --- | | |
| *Euphrasia latifolia* | | | | | | | -- | xxXX | XXXX | XXXX | xx-- | | |
| *Eutrema Edwardsii* | | | --- | -xxx | XXXX | XXXX | Xxx- | - | | | | | |
| *Festuca brachyphylla* | | | | | | | | | | | --- | -xxx | X |
| — *rubra* | | | | | | | | | | | | --- | - |
| — *vivipara* | | | | | | | | | | | | +++ | + |
| *Hierochloe alpina* | | | | ---x | xXXX | XXXX | XXXx | x-- | | | | | |
| *Hippuris vulgaris*[1]) | | | | | | | | | | | | | |
| *Juncus arcticus*[1]) | | | | | | | | | | | | | |
| — *biglumis* | | | | | | --- | --xx | xxXX | XXXX | XXXX | XXXX | XXXX | X |
| — *castaneus* | | | | | | | | | | -- | ---x | xxXX | X |
| — *triglumis* | | | | | | | | | | | ---x | xxXX | X |
| *Kobresia bipartita* | | | | | | | | ---x | xxXX | XXXX | XXXx | x-- | |
| *Koenigia islandica* | | | | | | -- | ---x | xXXX | XXXX | XXXX | XXXX | Xxxx | x |
| *Lesquerella arctica* | | | -- | ---x | xXXX | XXXX | XXXX | XXXX | xx-- | - | | | |
| *Luzula confusa* | | | | - | ---- | ---- | xxxX | XXXX | XXXX | XXXX | XXXX | XXXX | X |
| — *nivalis* | | | | | --- | --xx | xxXX | XXXX | XXXX | XXXX | XXXx | xxxx | x |
| — *spicata* | | | | | | -- | --xx | xXXX | XXXX | Xxx- | | | |
| *Matricaria inodora* | | | | | | | | | | | | - | - |
| *Melandryum affine* | | | - | ---- | ---x | xxXX | XXXX | XXXX | XXXx | xx-- | | | |
| — *apetalum* | | | | | | - | ---- | --xx | xxxx | xXXX | XXXX | XXXX | X |
| — *triflorum* | | | | | ---- | -xxx | xxXX | XXXX | XXXX | Xxx- | | | |
| *Minuartia biflora* | | | | | | ---- | xxxX | XXXX | XXXX | XXXX | XXXX | XXxx | x |
| — *rubella* | | | --x | xxxx | ---- | -xxx | xXXX | XXXX | XXXX | XXXX | XXXx | xxxx | x |
| — *stricta* | | | | | | - | --xx | XXXX | XXXX | Xxx- | | | |
| *Oxyria digyna* | | | --- | ---- | ---- | ---- | --xx | xxXX | XXXX | XXXX | XXXX | XXXX | X |
| *Papaver radicatum* | | | | - | ---- | -xxx | XXXX | XXXX | XXXX | XXxx | xxx- | ---- | - |
| *Pedicularis flammea* | | | | | --- | --xx | xxXX | XXXX | Xxx- | - | | | |
| — *hirsuta* | | | | | ---- | xxxX | XXXX | XXXX | XXXX | XXXX | XXxx | xxxx | x |
| — *lapponica* | | | | | | | | - | --xx | XXXX | XXXX | Xxx- | |
| *Phippsia algida* | | - | ---- | ---- | ---- | --xx | xxxX | XXXX | XXXX | XXXX | XXXX | XXXX | X |
| *Poa abbreviata* | | | | | | - | -xxX | XXXX | XXXX | XXxx | x-- | | |
| — *alpigena colpodea* | | | | | | | | ++ | +++ | +++ | +++ | +++ | + |
| — *alpina* | | | | | | | | | | | --- | xxxX | X |
| — *arctica* | | | | | | | | | | ---x | xxXX | XXXX | X |
| — *glauca* | | | | | | | | -- | ---- | -xxx | XXXX | XXXX | X |

[1]) Not in flower on August 1st.

Table 5 (continued).

| Month | June | | | | | | July | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | 1—5 | 6—10 | 11—15 | 16—20 | 21—25 | 26—30 | 1—5 | 6—10 | 11—15 | 16—20 | 21—25 | 26—30 | 31 |
| *Poa Hartzii* | | | | | | | | | ---x | xxXX | XXXX | XXXX | X |
| — *pratensis* | | | | | | | | | | | | --x | x |
| *Polygonum viviparum* | | | | | | | --- | ---- | --xx | xxxX | XXXX | XXXX | X |
| *Potentilla Crantzii* | | | | | | | | --- | --xx | xxXX | XXXX | XXXX | X |
| — *emarginata* | -- | ---- | ---x | xxXX | XXXX | XXXX | XXXX | XXXX | XXXX | xxxx | xxxx | xxxx | x |
| — *nivea* | --- | --xx | xxxX | XXXX | XXXX | XXXX | XXXX | XXXX | XXxx | xxxx | --- | | |
| — *rubella* | | | | | - | ---- | xxxX | XXXX | XXXX | XXXX | XXxx | x--- | - |
| — *rubricaulis* | | --- | xxxX | XXXX | XXXX | XXXX | XXXX | XXXX | XXxx | x--- | | | |
| *Puccinellia angustata* | | | | | | | | | - | --xx | xxXX | XXXX | X |
| — *phryganodes* | | | | | | | | | | | -xx | XXXX | X |
| — *Vahliana* | | | | | | | | | | -- | -xxX | XXXX | X |
| *Pyrola rotundifolia* | | | | | | | | | | -- | ---x | xxXX | X |
| *Ranunculus affinis* | | | ---- | -xxx | XXXX | XXXX | XXXX | XXxx | xx-- | - | | | |
| — *glacialis* | | | | | -- | -xxx | XXXX | XXXX | XXxx | xx-- | ---- | | |
| — *hyperboreus* | | | | | | | | | --- | xxxX | XXXX | XXXX | X |
| — *nivalis* | | -- | ---- | -xxx | XXXX | XXXX | XXXX | XXXx | x-- | | | | |
| — *pygmaeus* | | | | | --- | ---- | --xx | xxXX | XXXX | XXXX | XXXX | XXxx | x |
| — *sulphureus* | | | | --- | --xx | xXXX | XXXX | XXXX | XXXX | XXXX | XXxx | x--- | |
| — *trichophyllus*[1] | | | | | | | | | | | | | |
| *Rhododendron lapponicum* | | | | -- | xxXX | XXXX | Xxx- | - | | | | | |
| *Rumex acetosella* | | | | | | | | | | | -- | --xx | x |
| *Sagina intermedia* | | | | | | | | | -- | ---x | xxXX | XXXX | X |
| *Salix arctica* | --- | ---- | xxxx | xxxx | XXXX | XXXX | XXXX | XXXX | XXXX | XXXX | XXXX | XXXX | X |
| — *herbacea* | | | | - | --xx | xxXX | XXXX | XXXX | XXXX | xxx- | - | | |
| *Saxifraga aizoides* | | | | | | | | | | --- | ---x | xxXX | X |
| — *caespitosa* | | | | | | -- | -xxx | XXXX | XXXX | XXXX | XXXX | XXxx | x |
| — *cernua* | | | | | | - | ---- | xxxX | XXXX | XXXX | XXXX | XXxx | x |
| — *flagellaris* | | | | | | | | | | - | --xx | xxXX | X |
| — *hieraciifolia* | | | | | | | | | | -- | -xxx | XXXX | X |
| — *Hirculus* | | | | | | | | | | --- | --xx | xxXX | X |
| — *Nathorsti* | | | | -- | ---x | xxXX | XXXX | XXXX | XXXX | XXXX | XXXX | XXXX | X |
| — *nivalis* | | | | --- | --xx | xxXX | XXXX | XXXX | XXXX | XXXX | xxx- | -- | |
| — *nivalis tenuis* | | | | | | | | ---- | -xxx | xxXX | XXXX | XXXX | X |
| — *oppositifolia* | ---- | -xxx | XXXX | XXXX | XXXX | XXXX | xxx- | ---- | ---- | ---- | ---- | ---- | - |
| — *rivularis* | | | | | | - | ---- | xxxX | XXXX | XXXX | XXXX | xxxx | x |
| — *stellaris comosa* | | | | | | | | | | | | - | - |
| *Sedum roseum* | | - | -xxX | XXXX | XXXX | Xxx- | | | | | | | |
| *Silene acaulis* | | | | | | -- | --xx | xxXX | XXXX | XXXX | XXXX | XXxx | x |
| *Stellaria humifusa* | | | | | | | -- | xxXX | XXXX | XXXX | XXXX | XXXX | X |
| — *longipes* | | | | | | | --- | -xxx | xxXX | XXXX | XXXX | XXXX | X |
| *Taraxacum arcticum* | | | | | -- | --xx | xxXX | XXXX | XXXX | XXXX | xxx- | ---- | - |
| — *phymatocarpum* | | | | | -- | --xX | XXXX | XXXX | XXXX | Xxxx | --- | | |
| *Thalictrum alpinum* | | | | | | | | | | | | --- | x |
| *Tofieldia coccinea* | | | | | | | | --- | xxxX | XXXX | XXXX | XXxx | x |
| — *palustris* | | | | | | | | | - | ---- | xxxx | xXXX | X |
| *Trisetum spicatum* | | | | | | | | | | ---x | xxXX | XXXX | X |
| *Vaccinium uliginosum* | | | | - | --xx | XXXX | XXXX | XXXX | XXXx | xx-- | -- | | |

[1]) Not in flower on August 1st.

first half of July, as done above. It is true that the late summer aspect exhibits a relatively varying abundance of flowers, but it is less conspicuous in the landscape than that of the summer aspect, which has been established precisely under the impression of the mass effect of the wealth of flowers borne by the physiognomically dominant vegetation types.

The phenological character of the plants which is especially considered here is the flowering. Not because it is in itself the most important, but because it is the most easily observable; and in fact, in these regions it was the only one which could be determined for the species of the area to such an extent and with such reliability that it could be employed as a general basis for comparison.

The question as to whether the arctic flora should be regarded as a spring flora on the basis of the flowering times (for previous literature, cf. SÖYRINKI 1938, p. 105 et seq.), is of little interest in this connection. The result of one's judgment will depend on the flora of the area which instinctively, more or less unconsciously, is taken as the standard, rather than on the succession of aspects of the arctic vegetation itself. An additional difficulty, so aptly expressed by SÖYRINKI (l. c. p. 95), is that "die Ungleichmässigkeit des Fjeldgeländes . . . lässt eine mannigfaltige Buntheit im Nahbild der Jahreszeiten aufkommen".—If, as proposed by CLEVE (1901), we regard the prefloration period as decisive for our judgment, and unite species with a more strictly defined short prefloration period under the concept spring plants, it will give rise to still more confusion, for in that case the spring plants will to a great extent be characteristic of the snow-patch vegetation (cf. also RESVOLL 1917). We then arrive at the paradoxical result that the spring plants of the Arctic generally flower late in the summer.

## The participation of the chief ecosystems in the general succession of aspects.

It cannot be too strongly emphasised that the phenological seasons outlined above are based on the seasonal developmental stages of the vegetation within an area regarded as a unity. Thus the phenological seasons are an expression of the course of development of the whole vegetation present, as a function of the climate regarded as a geographical factor. The succession of aspects directly indicates to what extent the area is arctic in a plant-climatic respect, even without any exact climatic observations at all (cf. GAMS 1918, p. 367).

As suggested in the characterisation of the phenological seasons, the individual vegetation types of the area participate in a very unequal degree in the consecutive aspects, or reversely, the vegetation types are to a great extent delimited phenologically.

In a previous paper (SEIDENFADEN & SØRENSEN, 1937, p. 109 et seq.) I have attempted to divide the vegetation types of the northernmost area into ecosystems (TANSLEY 1935). In Table 1 (l. c. p. 110):

"Survey of the main ecosystems and vegetation types of NE. Greenland 74°30′—79° N. lat." eighteen ecosystems are enumerated, numbered I—XVIII. With certain deviations in the content of species (l. c. p. 134 et seq.) this division into types also applies to the more southern parts of the area of Northeast Greenland treated here. To the eighteen types should here be added four, three of which, comprising species absent from the northern area, are listed in the table without any number, while the fourth does not include species which are lacking north of 74°30′ N. lat. In the south this last-named type, which might be designated "Moist seasonally soliflucting Fields" (Veg. type Willow Heath, Willow Snow-patch), to a great extent replaces the type so conspicuous in the northern areas, "Constantly wet (and active) Polygon Fields". In this connection it may further be mentioned that a number of the "moist to wet" ecosystems enumerated for the northern areas are subject in the south to desiccation in the course of the summer, so that they should perhaps be referred to the "moderately moist" group.

Thus without proceeding to a detailed division, we obtain twenty-two ecosystems for the area. They are listed in Table 6 marked A—V (the numbering applied in the 1937-paper is added in parentheses). At the same time an attempt has been made to give a tabular view of the participation of the individual ecosystems in the aspects of the country, illustrated by their flowering intensity. Further the approximate date for the melting of the snow-covering is indicated. According to the melting times the ecosystems are arranged in a 4-graded scale, denoted I—IV, according to the duration of the snow-covering. The dates given for flowering and melting of the snow are based on observations and notes made during five summers. In regard to time the table will in the main apply to the climatic transitional zone between fjord and coastal areas, in fact the only zone in which all ecosystems are represented.

It will be seen that the spring flowers are produced by the dry, early snow-free ecosystems, those of the summer by these and by the moderately moist and the relatively early snow-free, moist ecosystems, those of the late summer chiefly by the moist and wet ecosystems. The flowers of the autumn are mostly restricted to the latest-thawing and wet ecosystems.—It will further be seen from the table that strictly speaking each ecosystem, (or more concisely, each individual ecotope (Sørensen 1936)) has only one aspect in so far as flowering alone is taken into consideration. Even though all the species within the same ecosystem do not flower absolutely at the same time, the flowering of all the species continues without interruption, the time limits overlapping, and is concluded at such a rapid rate that no phenological line of demarcation can be drawn. However, the ecosystems in which

Table 6. Survey of the most important ecosystems of Northeast Greenland, with flowering intensity at different

| Ecosystem. — Vegetation Type. | Approximate time for melting of snow or ice | Thawing type |
|---|---|---|
| A. (I) Dry Barren Ground.—Desert | 10.—30. May or no snow covering | I |
| B. (II) Dry Loess Fields and Terraces.—Steppe | 10.—15. May or no snow covering | I |
| C. (III) Dry Disintegrating Summits and Crests | no snow covering | I |
| D. (IV) Dry Bird Places | no snow covering | I |
| E. (V) Dry Sunny Slopes.—Meagre Xerophilous Herb Slopes | 10.—30. May | I |
| F. (VI) Dry Clayey Flats and Raised Beaches | 10. May—10. June or no snow covering | I |
| G. (VII) Moderately moist sheltered Precipices and Rock Ledges.—"Copses" | 20.—30. May | I |
| H. Moderately moist sheltered Sunny Slopes.—Mesophilous Herb Slope | 1.—15. June | II |
| I. (VIII) Moderately moist Fronts of Solifluction Tongues and Terraces.—Grass Brinks | 10.—30. May | I |
| J. (IX) Moderately moist well drained Fields (Fossil Polygon Fields).—Ericaceous Heaths | 10.—15. June | II |
| K. Moderately moist, seasonally overflowed Ground.—Alluvial Meadows | 1.—10. June | II |
| L. Moist seasonally soliflucting Fields.—Willow Heaths | 15.—30. June | III |
| M. (X) Moist to wet sheltered Sunny Slopes and Patches.—Meagre Hygrophilous Herb Mats | 10.—30. June | III |
| N. (XIII) Wet Body of Solifluction Tongues and Sliding Slopes.—Grass Meadows | 15. May—15. June | II |
| O. (XI) Wet Snow-Patches and (active) Polygon Fields.—Snow-Patch Vegetation | 1.—30. July | IV |

indication of the approximate time for the melting of the snow and of their times during the summer months.

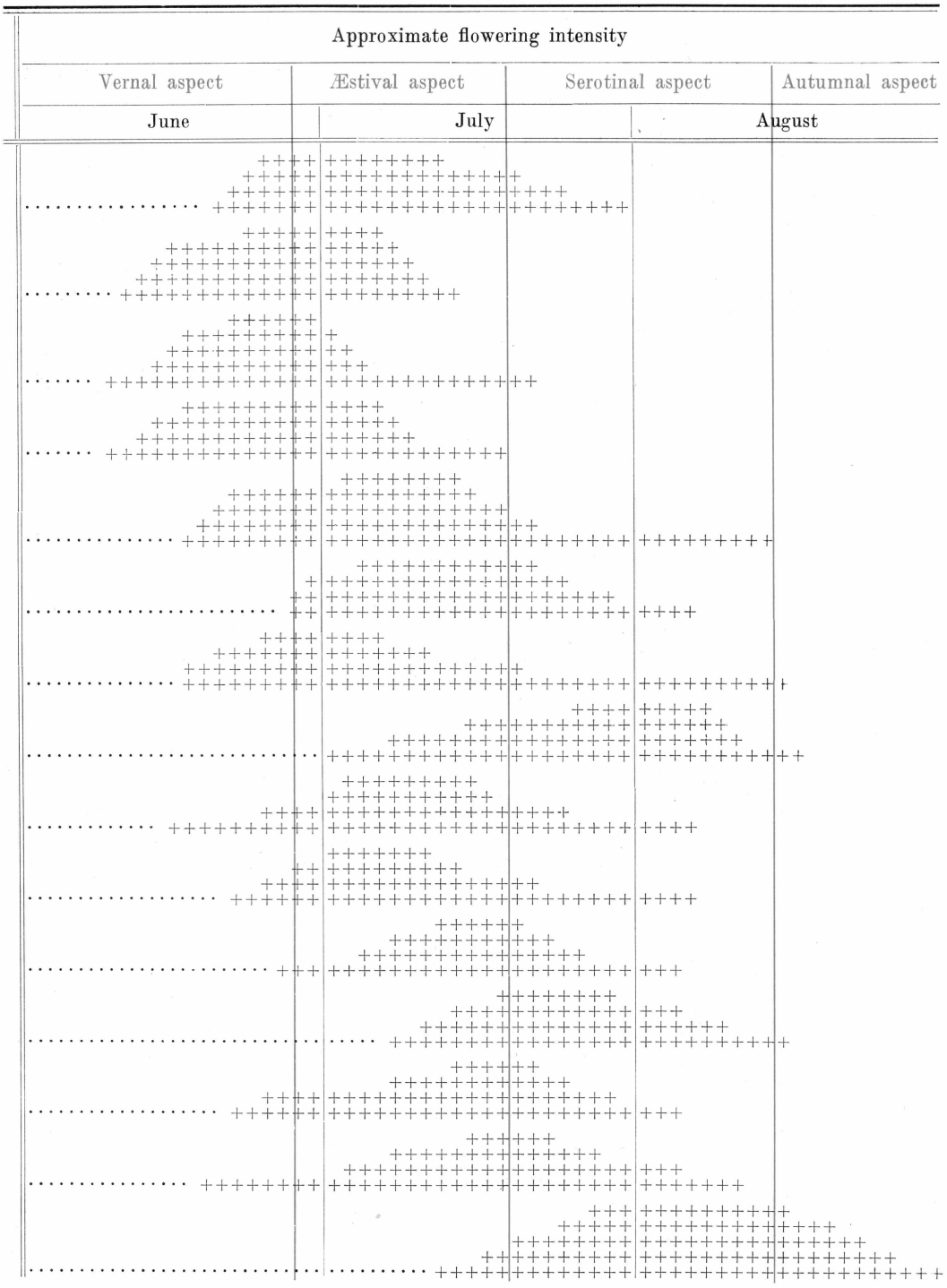


Table 6.

| Ecosystem. — Vegetation Type. | Approximate time for melting of snow or ice | Thawing type |
|---|---|---|
| P. (XII) Wet constantly irrigated Fields. "Denuded Bogs" .... | 15. May—30. June (or no snow covering) | II-III |
| Q. Wet stagnant Sliding Slopes. Knolly Bogs..... | 1.—15. June | II |
| R. (XIV) Wet Solifluction Clay. Morasses ..... | 1.—30. June | II-III |
| S. (XV) Water-soaked Ground. Swamps..... | 15.—30. June | III |
| T. (XVI) Fresh Alluvial Flats (River Deltas).—Alluvial Pioneer Vegetation..... | 1.—30. June | II-III |
| U. (XVII) Pools and Tarns.—Fresh Water Vegetation..... | 20.—30. June | III |
| V. (XVIII) Sea-shore Lagoons.—Salt Marshes..... | 10.—30. June | II-III |

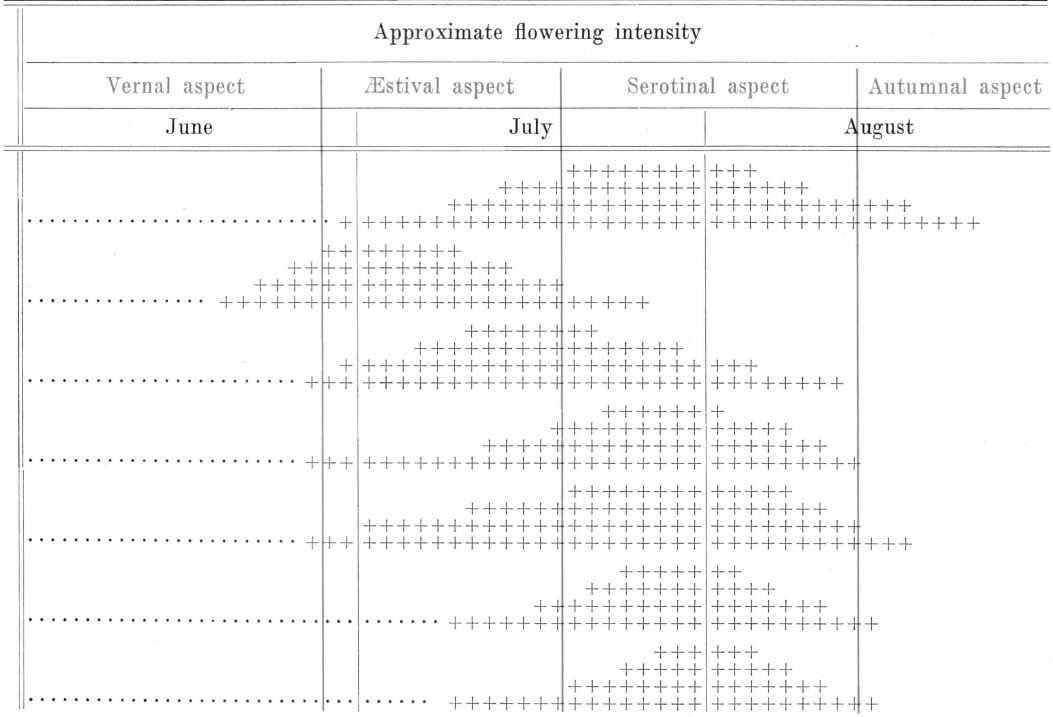
the species *Campanula rotundifolia* and *Pyrola grandiflora* are included, viz. E and G respectively, to a certain degree form exceptions to this rule. These ecosystems are characterised by an early melting of the snow, and the majority of their species by early flowering, completed at the time when the two above-mentioned species reach the flowering stage. An especially long flowering period is exhibited by T, the river deltas, with a pioneer vegetation without equilibrium, constantly recruited from the greater part of the other ecosystems.

## Annual fluctuations in the progress of the phenological seasons.

To illustrate how far the phenological seasons are confined within dates, a comparison will be made between the summer of 1932, with a very early melting of the snow and a high summer temperature, and that of 1935 with normal thawing and possibly a summer temperature slightly below the normal.

For 1932 GELTING (1934, p. 311) states the date for the breaking of the rivers near Eskimonæs to be c. May 13th. In 1935 the rivers did not break till June 3rd. Thus the difference in time between the setting in of the thaw in the two years amounts to about 21 days. *Saxifraga*

(continued).




*oppositifolia*, which is usually the first flowering species within the area, is recorded by GELTING (l. c. p. 128) to be "in flower: May 23rd (possibly a few days earlier)". In 1935 the first open flowers were observed on June 1st. As compared with 1932 *Saxifraga oppositifolia* was thus 10—12 days retarded in 1935. The difference in the time when *Saxifraga* flowered in the two years was accordingly only half the difference in time between the breaking of the rivers. Compared with the course of the air temperature the obliquity is even more remarkable. As registrations of the air temperature from Eskimonæs 1932 are lacking, observations made at Ella Ø in that year will be used as a basis for comparison.

| | Breaking of the rivers | Mean temperature of 24 hours intersects the 0-line | *Saxifraga oppositifolia* in flower |
|---|---|---|---|
| Ella Ø 1932 | 18th May | c. 24th May | 21st May |
| Eskimonæs 1932 | c. 13th May | ? | 20th—23rd May |
| Eskimonæs 1935 | 3rd June | c. 20th June | 1st June |

From these figures it appears with all desirable plainness that the beginning of spring as a phenological season follows the calendar with

a certain persistency in spite of the failing rise of the temperature. Whether this rule is valid for the other species also, determining the succession of aspects as a whole during the warm season, can be decided with a certain approximation by comparison of the flowering of the whole flora in the two extreme years.

As a basis for comparison I have here used the incipient flowering of about 50 species of common occurrence around the station of Eskimonæs. The flowering dates for 1932 have been taken from GELTING's Table 9 (1934, pp. 312 et seq.), for 1935 from my own notes.

All species flowered later in 1935 than in 1932. The difference in time of flowering was for nearly all species between six and eighteen days, the average being 12—13 days. There was no remarkable general tendency to special deviations for early flowering species on the one hand or late-flowering species on the other hand, though late-flowering species showed a somewhat greater average retardation than the early-flowering ones. Of the systematic groups the *Gramineae* showed a tendency to specially late flowering in 1935. However, *Poa pratensis* alone falls entirely outside the limits of all the other species, showing a difference between the flowering times of the two years of no less than 38 days (it was omitted in the computation of the average). For this species as well as for the other *Gramineae* the retardation seems especially to affect the period from the appearance of the panicle above the sheath to the anthesis[1]). Arctic *Gramineae* seem not rarely to be entirely arrested in development at this stage (cf. GRÖNTVED 1936)

Thus it will appear from this comparison that as a whole the sequence of aspects within the area has shifted in an "unfavourable" direction, viz. by the same time interval (c. 12 days) as was indicated for the flowering of *Saxifraga oppositifolia*. With the temperature conditions of the two succeeding summers in mind it may be concluded with a fair degree of certainty that the phenological difference in time between "favourable" and "unfavourable" summers hardly exceeds about two weeks.

It deserves mention, however, that the biological consequences of a cold summer are of far greater importance than the aforementioned two weeks would seem to suggest. According to my observations, the ripening of the fruits, or the chances of their ripening, were noticeably poorer for a number of species in 1935 than in 1932. This is not surprising if we take into consideration that for the species normally flowering late it is not so much the fact that the summer is shortened by a week or two which is decisive, but the circumstance that the ripening

[1]) According to verbal information from Dr. GELTING, his "flowering dates" for *Gramineae* indicate the true anthesis, not the mere appearance of the flowerhead above the sheath.

of the fruits is shifted to a date when the insolation is decreasing so much that the limit for the minimum of ripening is thereby easily passed.

### Succession of aspects in relation to the distance from the open sea.

The climatic difference between fjord and coast areas repeatedly pointed out also makes itself felt phenologically. As a consequence of the configuration of the south coast of Clavering Ø in connection with the position of the mountain masses the climatic belts lie especially close together around Eskimonæs. Eskimonæs itself lies at the transition between the fjord and the coast climate belt (cf. GELTING 1934). Granatdalen, situated only 11 km farther westward, has a typical fjord climate. A direct phenological comparison of the two climatic belts was therefore possible at any time, or, rather, it was inevitable. The retardation of the coast-land as compared with the fjord area is slight in the spring, but increases noticeably in the course of the summer. By midsummer the difference between Eskimonæs and Granatdalen amounts to c. 6—7 days. In the late summer and the autumn the difference increases and is further accentuated physiognomically by the late-flowering snow-patch vegetation of the fjord areas being areally negligible as compared with that of the coast-land. The phenological Tables 5 and 6 have chiefly reference to the transitional zone. Thus for the fjord areas the summer aspect is advanced so as to comprise the time interval from c. 22nd June to c. 12th July. The succeeding aspects advance in corresponding degree or still more, whereas the aspects of the outer coast-lands are delayed as compared with Eskimonæs.

Thus the fjord areas are favoured climatically not only by the definitely higher summer temperatures, but also by the fact that the early aspects of the vegetation (spring and summer) are shortened in favour of the later aspects (late summer and autumn); this may be of importance for the development of the fruits in southern "heat-demanding" species, which, as is well known, extend farther northward in the fjord areas than in the coast-lands (cf. e. g. BÖCHER 1933a, GELTING 1934).

The thaw of spring sets in at about the same time throughout the whole land area between the sea ice and the inland ice. The duration of the vegetation period proper, that is to say, the time interval from the setting in of the thaw to the first permanent frost of autumn, agrees more closely for the two climate belts than their contemporaneous aspects would seem to suggest. The phenological autumn of the coast-land, however, is further shortened somewhat by the earlier occurrence of the winter frost here than in the fjord areas.

The result of these facts is, then, that the higharctic summer of the most continental climate areas despite its short duration shows a complete harmony in regard to the sequence of aspects, while the less markedly continental and the oceanic areas show a certain obliquity in the sequence of aspects, an extension, not in harmony with the duration of the growth period, of the spring and summer aspects at the expense of the autumnal aspects.

Already CHRIST (1879, p. 262) called attention to the unfavourable autumn of the arctic climates (the knowledge at that time of arctic climate and vegetation was chiefly limited to coast regions with a relatively oceanic climate as compared with the alpine one). However, the question as to a possible general difference in the progress of the phenological seasons in the Arctic and in the Alps still remains partially open. GAMS (1918, p. 364) arrives at the "anfänglich überraschenden Ergebnis, dass in der alpinen Stufe Frühling und Herbst sich berühren, dass es also gar keinen "Alpensommer" gibt." This suggests, despite all, a harmonious sequence of aspects, and the conditions do not seem to be equal to those of the Northeast Greenland coastal areas, but possibly to those of the continental fjord areas. Whether GAMS would sanction an actual "polar summer" for these continental areas, must be left an open question.

### Succession of aspects in relation to geographical latitude.

The area treated here as a whole has a north-south extension of nearly seven degrees of latitude, viz. from c. 70° to c. 77° N. lat. The question now arises with what degree of approximation the phenological data given above as chiefly valid for the medial latitudes apply to the more northerly and more southerly regions.

In the spring the sun takes about four days to travel through one degree of latitude. Provided that the phenological spring advances northward at the same rate as for instance with a certain approximation is the case for the temperate Europe (LECOQ 1854, p. 159, WALTER 1927, p. 121), a difference of about 28 days might be expected for the seven degrees of latitude (the stretch from Scoresby Sund to Danmarks Havn). The meteorological observations at Scoresby Sund (c. 70° N. lat.), Myggbukta (c. $73^1/_2$° N. lat.), and Danmarks Havn (c. $76^3/_4$° N. lat.) show, however, that the daily mean temperature passes the 0-line almost simultaneously at the three stations, normally about June 5—10th. The comparatively rapid rise of the temperature northward may possibly be explained by the rapid increase in the length of the day with increasing latitude. To illustrate the advance of the botanical spring in Northeast Greenland some few phenological data from Scoresby

Sund 1892 (according to HARTZ 1895) and from Danmarks Havn 1907 and 1908 (according to LUNDAGER 1912) will be given below, compared with my own observations at Eskimonæs on Clavering Ø in 1935.

| | Character of spring temperature | Mean temp. of 24 hours passes 0-line (indicated by period of about 8 days) | Breaking of rivers | *Saxifraga oppositifolia* in flower |
|---|---|---|---|---|
| Danmarks Havn 1907 | »mean« | c. 3rd-10th June | 20th June | 4th June |
| Danmarks Havn 1908 | »mean« | c. 8th-16th June | 18th June | 7th June |
| Clavering Ø 1935 | inconsiderably below mean | c. 11th-18th June[1] | 3rd June | 1th June |
| Scoresby Sund 1892 | do. | c. 6th-13th June | 15th May | 23rd May |
| Difference Scoresby Sund — Danmarks Havn | | | c. 35 days | c. 14 days |

Even though these figures are few, and only directly comparable with some reservation, they seem to me to be of great interest for an estimate of the phenological differences between the south and the north.

The spring aspect, determined by the flowering of *Saxifraga oppositifolia*, is shifted about two weeks on passing from Scoresby Sund to Danmarks Havn. The earliest flowering *Saxifragae* are always to be found in localities free of snow in the winter. Thus the two weeks' retardation northward applies in the first instance to snow-free localities. It is remarkable that the rivers in the south break a considerable time before, to the north a considerable time after, the flowering of *Saxifraga*. The late breaking of the rivers to the north shows distinctly how much slower the snow melts there. This implies in the first instance that the vegetation types of the summer aspect move to localities with a more moderate winter snow-covering; they are restricted to a narrower interval in the snow-covering scale and so decrease in area. Secondly it means that much larger areas become occupied by vegetation types whose seasonal culmination falls in the late aspects. Proceeding northward we actually encounter a retardation of the later aspects corresponding to the west-easterly one just mentioned from the fjord areas to the coast-land. The permanently wet ecosystems influenced by the delayed and slow melting of the snow increase considerably in area northward at the expense of the seasonal-dry ecosystems so characteristic of the southern fjord-land. In other words, to the north the vegetation as a whole has a relatively oceanic character similar to that of the southern coast-land, although the climate as such does not grow more oceanic with increasing geographical latitude.

[1]) Likewise for Myggbukta.

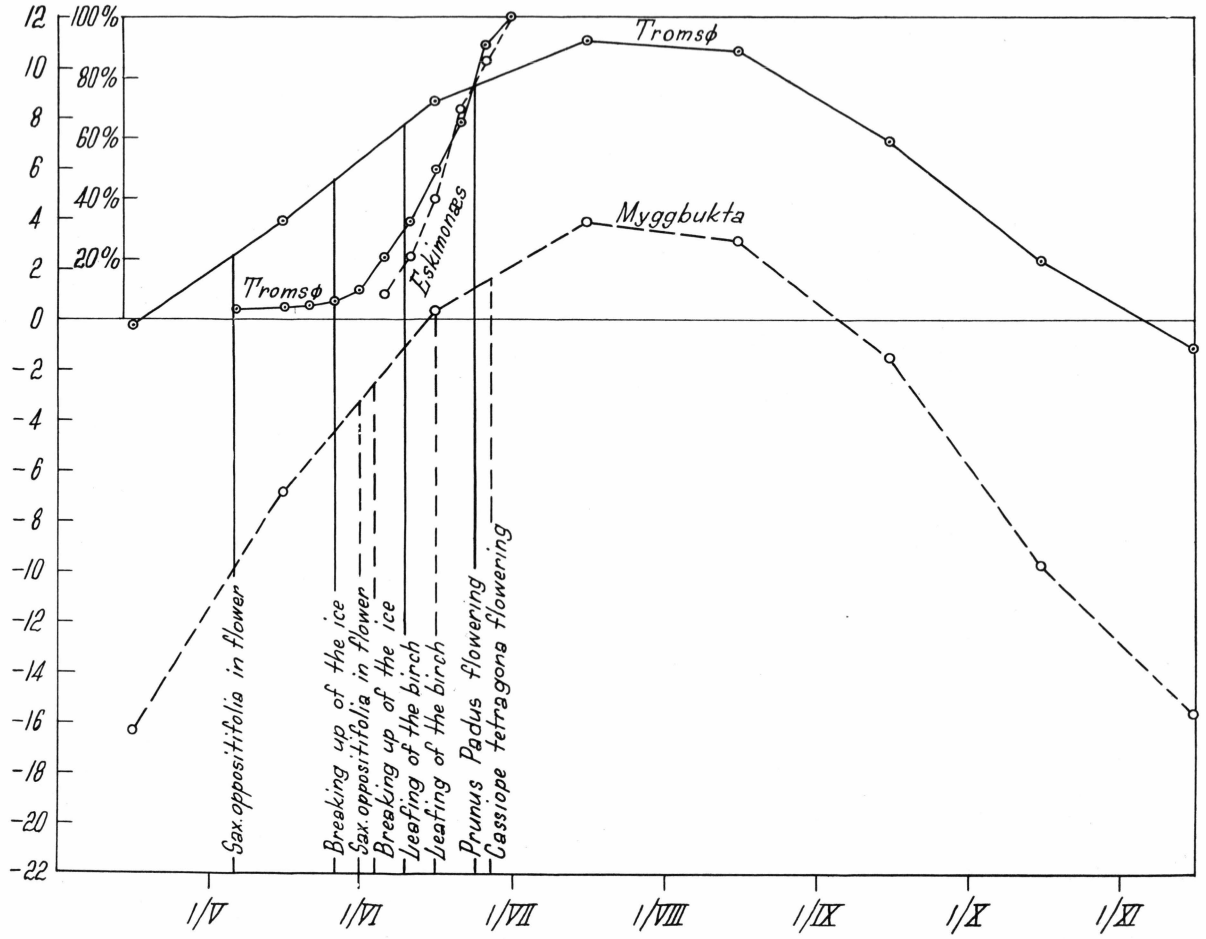



Fig. 10. Comparative representation of some phenological cardinal points for northern Norway and Northeast Greenland. Temperature curves (monthly means) for April-November for Tromsø and Myggbukta. The vertical lines indicate for the two areas: First flowering of *Saxifraga oppositifolia*, breaking of the ice of the rivers, leafing of the birch (*Betula odorata* and *Betula nana* respectively), and flowering of *Prunus Padus* at Tromsø and of *Cassiope tetragona* on Clavering Ø; the curves show the sequence of the first flowering of the spring plants within the two areas (ordinate: percentage of all the species flowering before the end of June, in flower at the date indicated by the abscissa. See further the text on p. 66).

## Succession of aspects in relation to climate-character. A comparison of the progress of spring in Northern Norway and in Northeast Greenland.

The retardation demonstrated for the later phenological seasons in the coast-land coinciding with the increasing oceanity of the climate might invite a closer consideration of the phenology of a typical oceanic-arctic area. Such an area is found in northernmost Norway, whose phenology has been treated with extraordinary care and in great detail by HOLMBOE (1912). The investigation comprises the county of Tromsø, which extends from c. 66° N. lat. to the north coast of Norway in about 71° N. lat. The chief phenological lines of demarcation of the spring have been accurately established on the basis of notes made during many years by local observers, partially supported by answers received to inquiry forms, and not least on the basis of the author's own observations. Of important phenological dates in HOLMBOE'S work only such will be pointed out here as are of interest for a comparison with the conditions prevailing in Northeast Greenland, viz.: the first flowering of the two earliest spring plants, *Saxifraga oppositifolia* and *Tussilago Farfara*, about May 1—5th, the breaking of the rivers about May 25th, the leafing of the birch wood about June 9th, and the flowering of the bird cherry (*Prunus Padus*), which is regarded by the author as evidence of the beginning of summer, on c. June 20—24th. A comparative illustration of the advance of spring in northern Norway and in Northeast Greenland is attempted in Fig. 10. As a measure for the course of temperature within the two areas the monthly means for Tromsø (c. 69°40′ N. lat.) and for Myggbukta (c. 73°30′ N. lat.) are here shown in a graph. In addition the most important phenological data for the county of Tromsø (after HOLMBOE l. c.) and for Clavering Ø 1935 are given. As the data for Clavering Ø are derived from a single year only, they are of course less reliable; general validity may, however, to some extent be ascribed to them, for as regards the course of the temperature, the spring and early summer of 1935 were almost like those of a normal year (cf. p. 40).

It will be seen that at Tromsø the flowering of *Saxifraga oppositifolia* sets in long before the breaking of the rivers, precisely as at Danmarks Havn—not, as on Clavering Ø, almost simultaneously with, or, as in Scoresby Sund, even later than the breaking of the rivers. On Clavering Ø the flowering of *Saxifraga oppositifolia* sets in nearly one month later than at Tromsø, while the time for the breaking of the rivers and the leafing of the birches (for Norway *Betula odorata*, for Greenland *Betula nana*) differs by less than one week. The flowering of the bird cherry in northern Norway and that of the *Cassiope* heather

in Northeast Greenland occur at about the same time. Thus if we regard these two phenomena as indicators of the beginning of the summer for the two areas respectively, it means that the summer begins simultaneously in the two places.

HOLMBOE (l. c.) gives a list of the first flowering of the spring plants in 1910 and 1911. The observations extended to the beginning of July. A total of 160 species are stated to be in flower before the end of June. For Clavering Ø the number of species in flower within the same calendar-period is 78 (see Table 5, p. 51). The time sequence for the flowering of the spring plants for the two areas is shown graphically in Fig. 10 according to a method previously employed by GELTING (1934, pp. 315 et seq.). The flowering times are divided into 5-day groups. For the flowering curves (Fig. 10) the 5-day period is the unit of the abscissa, while the ordinate indicates the percentage of the spring-flowering species (i. e. the species flowering before the end of June) which had commenced flowering at the time indicated by the abscissa.—Apart from the comparatively few, very early flowering species the sequence of flowering for northern Norway is to an astonishing degree the same as that found in Northeast Greenland. The great increase of the flowering begins about June 1st in both areas in spite of a difference in air temperature for the two places of about seven degrees.

A direct comparison of the phenological data for the two countries in their relation to the course of the temperature is rendered materially difficult by the excessive difference in the thickness of the snow-covering. According to HOLMBOE (l. c.) a snow-covering of about 2 m seems to be normal to the flat land at the end of the winter. For comparison I may mention here the result of some observations on the thickness of the snow-covering made on Ella Ø in April, 1932. The observations were made along a number of arbitrarily drawn lines in the much broken terrain around the wintering station, a sample being taken for every 20 m along the lines. The average thickness of the snow for all the samples (c. 1600) including the snow-free ones amounted to c. 28 cm. It should be pointed out that the snow was almost everywhere fairly hard, blown together by the winter storms, which had also swept all projecting hills and rocks in the terrain free of snow. The commonest thickness of the snow-covering on level ground was 20—40 cm, no less than 34 per cent. of all observations lying within this interval. Only 1 per cent. showed a thickness of the snow of 1.5—2.0 m, and in no place did the thickness of the snow-covering exceed 2 m[1]). On Clavering Ø and altogether in the coast-land the snow-covering, however, seems normally to be noticeably thicker. The abrupt bend in the flowering

[1]) The observations were made by running a stick down to the frozen surface of the ground.

curve for the Tromsø region at the beginning of June is no doubt connected with the melting of the snow on level ground. HOLMBOE states that normally the snow melts in the course of May. In Northeast Greenland it melts at the end of May and in the first 2—3 weeks of June. Thus the final melting of the snow on level ground must be stated to take place about two weeks later on Clavering Ø than in Tromsø, whereas the great rise in the spring flowering on Clavering Ø (here following immediately upon the flowering of the first species) is only about five days retarded as compared with the county of Tromsø. Thus the Northeast Greenland spring runs more rapidly through its phases than the Norwegian spring.

With the first flowering of *Saxifraga oppositifolia* as a basis we may with a certain right speak of a longer duration of the spring itself in northern Norway than in Northeast Greenland. However, the summer aspect has not been subject to a retardation similar to that demonstrated for the coast-land of Northeast Greenland as compared with the fjord-land. The phenological difference between the two areas as regards the early aspects must then most correctly be said to manifest itself in a prolonged "first spring" for the oceanic climate area of Norway, while compared with that area such a "first spring" is practically lacking in the continental climate area of Northeast Greenland.

### Phenology as an aid in plant sociological research.

The phenodiagrams (Table 6, pp. 56—59) generally show a great similarity. Their one-peakedness illustrates the rapid flowering and shedding of the flowers within each vegetation type. The phenological difference between the various ecosystems is accordingly not to be found in the type of the course of development, but rather in the calendar date for the active sector in the yearly life cycle. For each individual ecosystem it may with some right be claimed that summer is lacking; for the relative spring-flowering is immediately succeeded by the final autumn aspect. That the growth period, defined as that part of the year in which the soil is, on the whole, thawed, can be divided into phenological seasons for the whole area dealt with on the basis of the flowering of the species, is due solely to the ecosystematic differentiation of the country.

As to the content of species the ecosystems overlap one another, a great number of the species being represented in different ecosystems in spite of the difference in the time of flowering of the latter. The ecosystems are therefore generally more constant in a phenological respect than the species which form the main constituents of their vegetations. (The differential species—provided any such are found—which naturally

show a relative ecological and accordingly phenological constancy, are often, if not always, less dominant quantitatively).

The most important differentiating factor in a phenological respect is the snow-covering, that is to say, not its thickness, but the time when it melts, which, unlike its thickness, is in the main constant within each ecosystem. The time interval between melting and flowering is likewise fairly constant for each ecosystem, the general rule being that the later the snow melts, the sooner will the flowering set in. Exceptions to this rule may, however, occur (cf. CLEVE 1901).

Since, as stated above, the individual species are frequently not limited to a certain ecosystem, but distributed over a number of ecosystems, the fixing of a certain prefloration period for each species will to a certain extent be illusory. For the same species the prefloration time will as a rule be the shorter the later the melting of the snow takes place, since the rise of the temperature will be the more rapid. The prefloration time will often be more constant for the ecosystems than for the individual species.

It will be evident from the above that a natural delimitation of the ecosystems of the area must necessarily pay due regard to the phenological data—even though it may be done unwittingly. All the more so since the small number of species and the disproportionately high percentage of ubiquists is contrary to a natural division of the vegetation according to the content of species. Accordingly the immediate impression of a "phenotypic" kaleidoscopic multiplicity (elementary associations) parallel with a "genetic" uniformity (content of species) to the trivial will easily run the danger of stiffening in the not very well-defined "fell-field" of WARMING.

# V. DEVELOPMENTAL MORPHOLOGY AND MICROPHENOLOGY

## Problems and historical remarks.

From early times the flowering of the plants has been the chief object of observation within phenology, for as a developmental stage it is more easily accessible to direct observation than any other stage. Apart from this, flowering as an object of phenological observation has the advantage that it marks a cardinal point in the life cycle of the plant, in so far as it is the incipient stage of the termination of a series of phenomena—morphological and physiological stages—connected link by link with the consistency of the doctrine of causality. The preceding links of this chain become less and less distinct, to be lost at last in the unknown. It becomes more and more difficult to fix the time even of the phases of the morphological development the further we pass from the end. If we turn back the hand of the ingenious clockwork of the ontogenesis, we shall see whole shoots and generations of shoots fit into each other like Chinese boxes, until the finely differentiated organs vanish into simple embryonic primordia, which, in turn, even to the aided eye, are merged in the indeterminable, meristematic cell-mass of the growing point. Here the links of the chain become immaterial in nature, physiological states (cf. KLEBS 1918), by which the limit of the morphophenological observation is reached.

Investigations on the chronological sequence in the development of the organ-primordia were termed microphenological by SAMUELSSON (1913). The development of the floral organs is of special interest in this respect, as the primordia of these organs, in contrast to the purely vegetative ones, are expressions of an altered physiological state, resulting in a discontinuity of the vegetative development. Notably the early-flowering plants of spring induced earlier investigators to speculate on, and sometimes even to investigate, the formation of flower buds, for instance SPRING (1842, cited by FRITSCH 1857), FRIES (1842), LECOQ (1854), HOFFMANN (1857, 1865), KERNER (1869), GÖPPERT (1871), and KRAŠAN (1873).

The floral development and wintering, especially of trees and shrubs, a great many of which flower in the spring, have been subjected to study. The first exact investigations in this respect seem to be those made by ASKENASY on the floral development of the cherry-tree (1877). Later ALBERT's systematical researches on the floral development of a number of European trees and shrubs appeared (1894). In addition scattered investigations from American quarters are at hand from about the same period, thus CHAMBERLAIN (1897, 1898), COULTER & CHAMBERLAIN (1903), WIEGAND (1906), MOORE & BEHNEY (1908), MOORE (1909). CHAMBERLAIN (1898, p. 127) arrives at the result that "it seems probable that all plants of a given species in a given locality pass the winter in about the same stage of development"; and he continues (l. c. p. 128): "I should be inclined to think that the stage at which a sporangium rests for the winter is determined largely by its power to withstand unfavourable conditions."—More detailed microphenological investigations were later made by LAGERBERG (1909) on *Adoxa*, by SAMUELSSON (1913) on *Bicornes*, and by DAHLGREN (1914, 1915) on *Primula officinalis* and other species. DAHLGREN (1915, p. 2) in contrast to CHAMBERLAIN comes to the following result: "Die Entwicklungsstufen einer Spezies, welche man beim Eintritt der Winterruhe an einem Ort beobachtet, sind ..... nicht immer ohne weiteres mit denen zu vergleichen, welche man an anderen Orten bei derselben Spezies erhalten hat." And further: "Mehrere Pflanzen überwintern ohne Zweifel nicht auf einen so ganz bestimmten Stadium, sondern setzen ihre Entwicklung fort, wenn die Erde nur ungefroren bleibt."

As regards the wintering of the floral organs of arctic plants, the more scattered observations of the early travellers may be mentioned, thus those of MIDDENDORFF (1864), KJELLMAN (1883), KIHLMAN (1890), and WARMING (1886a, b). Of more special investigations those of RESVOLL on *Ranunculaceae* (1900), *Salices* (1909), and on the Scandinavian snow-patch plants (1917) should especially be noted, further those of HAGLUND (1905) on arctic dwarf bushes, those of HELGI JÓNSSON (1895) on some Icelandic species, and those of RÜBEL (1908) on *Loiseleuria procumbens*.

Interest in the microphenology of plants seems to have languished during the last few decades, until recently it was revived indirectly through other branches of research, e. g. through cytology, the object of which is to fix the time of the reduction division in the anthers (cf. e. g. HAGERUP 1928, BÖCHER 1932), and through photo-periodicity-research, which attempts to determine the precise date of the first floral primordial stages (e. g. PURVIS & GREGORY 1937).

The flowering of the plant and the succeeding fructification may be said to be the goal towards which the whole vegetative development

of the plant is directed, in so far as the survival of the race through all future time is the aim of all living things. The formation of the reproductive organs must therefore be viewed in relation to the whole floral shoot and in the last instance in relation to the whole vegetative development of the plant during the invigoration periods and the phenological data associated with this development. While the final stages of the development of the shoot or the individual are accessible to immediate observation, it is as a rule far more difficult to fix the time for the initial stages. It must be assumed that the initial and final stages are regularly dependent on each other as regards periodicity, but our knowledge of this is still rather deficient. The biological basis for the diversity of the shoot structure is doubtless to some extent to be found in conditions determining the time of the initial vegetative and floral stages. Scandinavian investigators, in particular, have supplied important contributions to biological morphology, beginning with Areschough (1857, 1877, 1896) and Nilsson (1885) and continuing under the stimulating guidance of Kjellman and Warming: Brundin (1898), Cleve (1898, 1901), Johansson (1899), Lindmark (1902), Haglund (1905), Resvoll (1900, 1909, 1917), Sylvén (1906), and others. —Various systematical groups of the arctic, more especially the Greenland, plants have been thoroughly treated in the "Structure and Biology of Arctic Flowering Plants", started on the initiative of Warming, to which a generation of Danish botanists has contributed: Galløe (1910), Hagerup (1915), Heide (1912), Jessen (1911, 1913), Mathiesen (1916, 1921), Mentz (1909), Olsen (1914), Petersen (1908), Porsild (1920a), Seidelin (1910), Warming (1908a, 1909, 1920). As the greatest result of biologic-morphological research we find about the turn of the century Raunkiær's erection of his life-forms (1907), prepared through the gigantic work "De danske Blomsterplanters Naturhistorie I" (1895—99). In a way Raunkiær's life-form system marks the termination of the biologic-morphological school of research, at the same time as it became the vital nerve in much ecologic-sociological research.

The phenological line of research is of an early date and had eminent devotees as for instance Lecoq (1854) and Hoffmann (1857, 1865) about the middle of the last century, but gradually it passed into idle speculative discussions on theoretical threshold values, sums, and quotients of temperatures (e. g. Linsser 1867, v. Oettingen 1879, Staub 1882, Hoffmann 1886, 1887). The climax of this line of research was reached by Hult (1881), who erected his "loi des quotients constants de temperature", which says that a plant species is in equal degree adapted to the temperature-climate to which it has become accustomed throughout its area of distribution—provided it is found there! Since then phenology has to some extent lost its character of an in-

dependent discipline, but has held its own as a not unessential aid in descriptive and ecological plant geography (cf. e. g. DRUDE 1896, POUND & CLEMENTS 1898, HARVEY 1908, GAMS 1918, WALTER 1927, GELTING 1934), a line of research towards which already SCHWENDENER'S paper "Über die periodischen Erscheinungen in der Natur" (1856) pointed. On the other hand, phenology has further served as a basis for theoretical speculations on the descent of the plant species (e. g. HÖCK 1910, SCHARFETTER 1922).

At present phenology seems to be on the verge of a renaissance, whose prophet is LINKOLA, who pleads in favour of the application of phenology in autecological research (1936). The phenology of earlier times was of a comprehensive character, in so far as it was not the individual observations, but only the total of many observations from different times and places which conveyed the result for the establishment of the phenological seasons within the various climatic areas. In contrast to this, modern ecological phenology is of an intensive character, each single observation being in itself a result illustrating the reaction of the plant species to the meteorologically determined climatic conditions "auf kleinsten Raum" (KRAUS 1911).

Among the most essential, and the only directly observable expressions of the reaction of the plant to the environmental factors alternating rhythmically with the seasons are its alterations in form, whose sum total determines the whole construction of the plant individual. Thus it is obvious that the recent phenological method of research is actually a further development of the biologic-morphological method, only with an enhanced demand for a fixing of the time when the vital manifestations of the plant are expressed through the alteration in form associated with its organic development. The idea has in fact been anticipated in RAUNKIÆR'S life-forms, the manifestations of these being assigned to the "unfavourable" season, that is to say, to the season in which the external life functions are arrested or reduced to a minimum. —It should be pointed out here that THORE C. E. FRIES (1913) in his investigations on the arctic-alpine vegetation of Torne Lappmark attached great importance to phenological observations. The subsequently commenced, largely planned investigation on the ecology and phenology of the vegetation of the Abisko region (1925) unfortunately came to an abrupt end owing to the too early death of the eminent investigator. In most recent times, besides LINKOLA (e. g. 1922, 1935) and his collaborators (e. g. SÖYRINKI 1938—39), Russian enquirers (e. g. LAPSCHINA 1928, SEMENOVA 1939) especially have produced works of a phenologic-morphological nature.

## Survey of the developmental and biological morphology of the flowering plants of Northeast Greenland.

An investigation of the phenology of a whole flora in accordance with the principles outlined above is a difficult and time-consuming undertaking, and naturally I did not by far succeed in following the plants of Northeast Greenland from the cradle to the grave. Certain very important phenological characteristics could not be ascertained, thus a more precise fixing for the individual species of the time when they begin to grow in the spring and stop growth in the autumn, and the same applies to the time of fructification. Apart from rougher phenological data stated in the preceding chapter, the present work had to be limited to an investigation of the developmental morphology of the vegetative and floral wintering organs made on the preserved material brought home, supplemented by summer material in a herbarium state. The winter material was chiefly collected in the autumn, when the frost set in in September, to a less extent in the early spring. As regards a number of species it was impossible to collect later than the middle of August. A comparison of August and September material for a number of species has shown that the winter stage of development, at any rate as regards the morphological differentiation, was reached as early as the middle of August. Supplemental investigations on the power of survival of green plant-parts after wintering were made in the field when the snow melted in the spring. The collections were made in the years 1931—35 in various places within the area here treated, so that the observations on all common species are based on the examination of many different samples. For certain southern species, only known from a single find or from quite few summer finds within the area proper, winter material from the Scoresby Sund area has been examined, in which area I was able to make collections at the end of August, 1937. Only as regards two species, *Saxifraga tricuspidata* and *Gentiana detonsa* (in part), has material from West Greenland been used for the investigation; it was placed at my disposal from the collections of the Botanical Museum of Copenhagen.

In the following pages the results of these investigations will be recorded. Only the most necessary morphological results concerning the structure of the shoots have been included, in so far as they were judged to be of interest for an elucidation of the dynamics of the morphology, which was the object of the investigation. In addition to the sequence of the development of the shoot and its duration as also the yearly growth, measured by the number of leaves, attention has especially been concentrated on an investigation of the wintering state of the shoot apices and more especially on the degree of development of the

floral organs during the wintering. The added information about the beginning of the reduction division in relation to the outer morphological degree of development is the result of preliminary investigations made at the Eskimonæs station in 1934—35 preparatory to the collecting of material for a cytological examination. In the microscopic examination of the anthers, to estimate the degree of development of their contents, aceto-carmine coloration was used.

The investigation does not deal in the first instance with the morphology of the species in an ordinary sense, but with their developmental morphology. A treatment of the literature on the morphology of the particular species is accordingly beyond the scope of the present paper. However, the "Structure and Biology of Arctic Flowering Plants" (Medd. o. Grønl. vol. 36—37, cf. list of lit.) touches the problems investigated here in so many respects that this work as well as other works on the same subjects cannot be left unnoticed as purely morphological literature. The ensuing treatment of the individual species, however, is based exclusively on the investigation of the plants of Northeast Greenland, as I considered it of importance in view of the direct comparison that the material for examination should as far as possible be derived from the same limited climatic area.

The investigation comprises all the flowering plants recorded from Northeast Greenland. The nomenclature employed is in accordance with the "List of the Vascular Plants found in East Greenland" in: SEIDENFADEN & SØRENSEN 1937 (pp. 170—180). The same applies to the definition of species; however, the two varieties of *Festuca brachyphylla*, mentioned in the author's publication of 1933 (p. 138) under the names *F. ovina var. brevifolia* and *var. supina*, as also *Saxifraga nivalis var. tenuis*, are treated separately in the present investigation, because each of these varieties differs from the corresponding main species in regard to developmental morphology or leaf production. Furthermore it should be noted that *Dryas integrifolia* has been omitted in view of the poor delimitation of this species from *D. octopetala* in Northeast Greenland, and the lack of typical material for examination. The present investigation, in accordance with Table 7, comprises a total of 184 species and varieties.

The plant families represented in Northeast Greenland are treated separately below. As regards the most important results of the investigation of the individual species the reader is referred to Table 7, pp. 164—179.

The wintering floral stages of a number of species are shown in photographic reproductions in Pls. 1—11.

## *Monocotyledones.*

### *Cyperaceae.*

Lit.: Cf. RAUNKIÆR 1895—99, RESVOLL 1917.

The family comprises 29 species, twenty-four of which belong to the genus *Carex*. It includes hemicryptophytes and geophytes, the species being almost equally distributed over the two life-forms. The sympodial stem axes have either short joints, so that the growth becomes tufted, or they are more or less elongated, forming subterranean rhizomes. The shoot construction is fairly regular in most *Carex* species, likewise in *Kobresia* and *Elyna*. The *Eriophorum* species have a more irregular shoot sequence, especially as regards the placing of the principal buds. In the *Eriophorum* species the rhizomes are differentiated morphologically into a thin rhizomatic part (which in *E. callitrix* is very short) and a more or less tuberously thickened part, which bears the rosette leaves. The tuber, as usual in rhizomes and leaf primordia, is filled with starch during the wintering.

Innovation shoots are initiated either intravaginally or extravaginally (cf. HACKEL 1882). The intravaginal shoots have a large two-keeled, very durable prefolium, while other scale leaves are lacking. The extravaginal shoots have a small prefolium; the proximal part of the shoot carries a varying number of scale leaves in addition to the prefolium. Only one of the two shoot types is represented in each species. In *Carex supina*, however, which has extravaginal rhizomatic propagation shoots, the final short-jointed floral shoot generations are initiated intravaginally.

Shoot dimorphism is found in a number of species, a more or less pronounced differentiation being found in "long shoots" with unlimited possibilities of rejuvenescence, and "short shoots" entirely without or with a limited possibility of rejuvenescence. Floral "short shoots" without rejuvenescence and with a time of development a year shorter than that of the "long shoots" occur facultatively in *Carex alpina* and *C. pedata*, more regularly in *C. nardina*. Especially remarkable is the occurrence of floral short shoots in *C. scirpoidea*. Here the short shoots are anticipated; the first recognisable primordia are, however, probably most frequently formed in the primordial leaf axils the year before the expansion. After the expansion of the subtending leaves the bud primordia rapidly develop into large scaly buds containing primordia of three foliage leaves and an inflorescence. Fairly often the mother shoot also forms an inflorescence primordium, but in most cases the shoot apex is destroyed so that only the inclosed leaf primordia, but not the inflorescence, are expanded the following year. In moderately vigorous plants two coordinate leaf rosettes with culms are often seen in the

flowering year. These are either two "short shoots" with the sterile mother rosette in the middle or one short shoot and the flowering mother axis. In weaker shoots floral short shoots are lacking, and in such cases the mother axis will often flower.

In *Elyna Bellardi* unbranched short shoots (two per shoot generation) are constantly formed, but these take the same time, or even one year longer, to develop than the mother axis.

Floral short shoots, which again produce similar short shoots, are normally found in *C. subspathacea* and (less regularly) in *C. aquatilis stans*. After 2—3 shoot generations the power of survival decreases, and the whole sympode dies. This shoot type is most pronounced in *C. supina*, where the short-shoot chain is much branched and continues through 4—5 generations, so that closely packed, tufted shoot bundles of limited life duration are formed.

Another form of shoot dimorphism is found in *C. misandra* and *Kobresia bipartita*, in which purely vegetative leaf rosettes without rejuvenescence are normally formed. In *C. misandra* they become 4—6 years old with up to 20 leaves. They often function a couple of years after the flowering and withering of the mother shoot. In *Kobresia* they are short-lived, have only 2—6 leaves, and die simultaneously with the mother shoot. In this species there is actually shoot trimorphism, the vegetative leaf rosettes being formed as side shoots on flowering short shoots lateral to the main axis. (For the sake of completeness it should be mentioned here that I do not regard the irregular alternation between long rhizomes and almost erect shoots which either die or form new rhizomes, as can often be observed in *C. incurva*, *rigida*, *rupestris*, and *Eriophorum Scheuchzeri*, from the point of view of shoot dimorphism as described above).

The development of the shoot as a rule takes 3—7 years (including the years of initiation and flowering) or sometimes more, especially in species with rhizomes. In species with intravaginal rejuvenescence, *Carex capillaris*, C. *misandra*, *C. nardina*, *Elyna Bellardi*, and *Kobresia bipartita*, the innovation buds are formed in the axils of the green leaves and unfold the following year. In *C. misandra* the innovation shoots are often more or less anticipated, especially in vigorous shoots, so that the first wintering of the shoots may take place at all stages of development, from small bud-primordia to rosettes with some few leaves. In species with extravaginal rejuvenescence the innovation buds occur in the axils of scale leaves or foliage leaves, pass the first winter as buds, and in the succeeding year the shoot develops either into an actual rhizome or (in the tufted species) to a long bud surrounded by scale leaves. The rhizome stage, usually lasting one year, may exceptionally last two years in *Carex sparsiflora* and *Eriophorum Scheuchzeri*, and it

is rather frequently so in *Carex rupestris*. In *Carex supina* the rhizome stage always extends over two, sometimes three years. Anticipation of the buds in the axils of foliage leaves occurs frequently in *C. alpina* and *C. pedata*. The floral short shoots in *C. scirpoidea* are always anticipated (cf. above). Anticipation of rhizomatic shoots from the axils of scale leaves occurs normally in *C. microglochin* and *C. parallela* as also in *C. subspathacea*. However, in these species the bud primordia are formed the year before in the axils of scale leaves which are themselves still in the bud stage.

The course of development is generally more or less fixed for each species, so that each shoot generation normally takes a certain number of years from its formation as an innovation bud to its flowering. Only few species have the power to increase the vegetative invigoration stage over a greater number of growth periods than the usual one. Even in species in which such an increase is possible for physiological reasons, the shoots will finally weaken and die vegetatively if flowering has not taken place within a period of up to about 10 years. Species with an arbitrary increase of the vegetative growth periods before the flowering are: *Carex incurva*, *C. misandra*, *C. rupestris*, *C. sparsiflora*. The property mentioned is evidently associated with a certain physiological independence in the individual shoots, manifesting itself in the fact that the flowering of the shoots does not necessarily take place in the order indicated by the primary sequence of development. Thus an older shoot sometimes flowers later than a younger shoot within the same shoot chain. *Carex capillaris*, *Eriophorum callitrix*, and *E. polystachyum* likewise show a power of increasing the vegetative growth periods, but here the flowering sequence is always regular.

In the other species a prolongation of the vegetative stage either does not take place, that is to say, weaker vegetative shoots die after the same number of years within which the fertile shoots attain flowering; or the shoot continues for one or two years more in a vegetative, mostly weakened state with a reduced yearly leaf production, and subsequently dies.

In most species the rejuvenescence of shoots as a rule takes place from the lower leaf axils, that is to say, independently of the flowering of the shoot; though, of course, with the limitation that the flowering shoots as the more vigorous ones are more rapidly and more extensively rejuvenated than the non-flowering weaker shoots. The innovation buds of the latter are often retarded one or sometimes several years; if so, the buds do not open at the usual time, but only after resting one or several years.

However, some few species rejuvenate from the upper leaf axils, that is to say, the lower buds do not develop and the rejuvenescence

of the shoot is associated solely with the buds formed near the shoot apex, which do not develop till the flowering year of the mother shoot. This mode of rejuvenescence occurs with great constancy in *Carex capillaris*. *Eriophorum callitrix* and as a rule also *C. alpina* and *C. microglochin* behave in a similar way. "Apical" rejuvenescence involves in the first place that no more than two (green) shoot generations are found at the same time. In the second place it has the very important biological consequence that if a shoot has not within a reasonable term of years gathered sufficient strength for the formation of flower buds, will it die from senile decay without having developed innovation buds at all. During my work in the field I often observed old unbranched decayed or dead rosettes of *C. capillaris*. It is likewise evidently closely connected with the aforementioned mode of rejuvenescence that purely vegetative populations of the above-mentioned species are never found, while such are very frequent among species with "basal" rejuvenation as for instance *Eriophorum polystachyum*, *Carex rigida*, and *Carex Lachenalii*.

The number of years with a development of foliage leaves per shoot generation, provided anticipation does not take place, is normally one year less than the lifetime of the shoot generation in species with intravaginal rejuvenescence and two years less for most species with an extravaginal rejuvenescence. The yearly number of leaves formed during the vegetative development of the shoot ranges from 2 to 5, and is surprisingly constant for each species; 3 and 4 are the numbers most frequently found. Deviations from the number of leaves characteristic of the species are infrequent. *Carex pedata* seems to be least constant, its yearly leaf production varying between 3, 4, and 5.

The last, flowering, year's-shoot always develops a smaller number of leaves than the purely vegetative ones. There is a close correlation between the number of leaves in the flowering year and the degree of development of the inflorescence in the wintering stage. The more advanced the floral development, the smaller the number of leaves. In the *Eriophorum* species, which are the only *Cyperaceae* of the area having stem leaves, the lamina of the latter even develop the year before the flowering, and no green leaves develop in the flowering year. In all other species one or a few leaves develop simultaneously with the culm.

A distinct seasonal periodicity in the leaf size has only been observed in a few species, most pronounced in *Carex rariflora*. The periodicity in the leaf size occurs as a result of one or two leaves, which are only half-developed when the winter sets in, being arrested in growth the succeeding year. In a great number of the species—and this seems especially to be true of species growing on dry soil—the growth of

such half-developed leaves is continued intercalarily at the base of the leaf after wintering. This is especially conspicuous in *Carex nardina* and *Elyna Bellardi*. The yearly addition of three leaves in *Carex nardina* always consists of the lower half of a leaf whose upper half has functioned the preceding year + two whole leaves + the upper half of the last leaf visible, whose lower part will not develop till the succeeding year. Similarly, in *Elyna Bellardi* $^1/_2 + 1 + {}^1/_2 = 2$ leaves are constantly developed every growth period. In *Carex capitata* three leaves often develop simultaneously, although the mean annual production hardly exceeds two leaves.

Winter-green leaves (or parts of leaves) functioning two growth periods are only found in *Carex capitata* and *C. sparsiflora* (in the latter, however, the leaves often wither owing to drought at the end of the first summer) and in *C. misandra*, in which as a rule only the proximal half of the leaves hibernate in a green state and function at least during the first part of the succeeding growth season.

In most species the vegetative development exhibits a more or less strict periodicity, so that the vegetative innovation shoots hibernate at relatively fixed stages characteristic of each species. However, some species are irregular to some extent. This applies especially to *C. misandra* and *C. pedata* (frequent anticipation) as also to *C. incurva*. Further to *C. alpina* and the *Eriophorum* species, especially to *E. callitrix*. *Carex capitata* is entirely aperiodical.

The floral development in the wintering stage is generally well advanced. In the majority the anthers are distinctly developed as such, the ovary is well-developed, with papillary stigmas and a distinct primordium of the nucellus. In the *Carex* species at this stage of development the utricle surrounds the ovary. A particularly advanced development of the inflorescence during hibernation is exhibited by the *Eriophorum* species. In *E. callitrix* and *E. polystachyum* the inflorescence hibernates at the surface of the ground or is distinctly above-ground, only surrounded by the sheaths of the stem-leaves. In *E. Scheuchzeri*, however, the floral hibernating buds are subterranean; but the development of the flowers themselves in the *Eriophorum* species is not more advanced than in many *Carex* species (cf. Pl. 2, Figs. 22—24).

A less advanced degree of floral development than that of the majority is shown by *Carex alpina* (Pl. 1, Figs. 1—3), *C. aquatilis stans* (Pl. 1, Fig. 5), *C. atrofusca* (Pl. 1, Figs. 6—7), *C. incurva*, *C. rigida* (Pl. 2, Figs. 4—6), *C. saxatilis* (Pl. 2, Fig. 9), *C. subspathacea* (Pl. 2, Figs. 15—16); in these species the utricle does not surround the ovary, or only incompletely so; its stigmas are only suggested. In some species, for instance *C. alpina* and *C. atrofusca*, the stalk of the female flower is distinctly seen to be of a compound nature (cf. e. g. Pl. 1, Figs. 3

and 7). In *Kobresia bipartita* (Pl. 2, Figs. 25—26) the floral parts are hardly noticeably differentiated. A special position is held by *Carex supina*, whose primordial cone of growth is just recognisably "floral" as an articulated process still without any actual floral structures (Pl. 2, Fig. 17).

The stage of development at which the floral buds hibernate is fairly constant in each species. A certain correlation between the degree of constancy in the vegetative and the floral hibernation stages, however, often seems to occur. Thus especially varying floral stages of development may be observed in *Carex incurva*, which is irregular in regard to vegetative hibernation stages also. In the *Eriophorum* species, however, the floral hibernation stage is relatively constant, in spite of the frequent vegetative irregularity. *Carex capitata* occupies a position apart, being evidently quite aperiodical, which is often manifested by the frequent occurrence of destroyed floral axes, the hibernation having evidently been unsuccessful, if the development of the buds has passed a certain stage. Similarly, retarded flowering culms often occur in the late summer.

As regards the time interval between the formation of the primordia of the organs and their final development, it is a general rule that all primordia of leaves as well as of flower buds, are initiated one year before their unfolding, that is to say that the number of leaf primordia is equivalent to the yearly leaf production of the shoot. Sometimes the floral character of the cone of growth may be ascertained even during the second hibernation before the flowering, thus normally in *Carex aquatilis stans* and *C. atrofusca* and sometimes in *C. nardina* (Pl. 1, Fig. 19). In accordance with this the number of leaf primordia mostly exceeds the number of leaves produced annually by two. Only in *Carex supina* the number of leaf primordia is less than the annual production of leaves, that is to say, the additional growth of the year is only partially initiated during the preceding growth period. A special position is occupied by *Carex saxatilis*, whose leaves, innovation buds, and inflorescence axis are initiated two years before their development. In this species the number of leaf primordia is twice that of the yearly production, and the inflorescence axis (as well as the vegetative parts of the plant) hibernate twice as primordia before the final development, the first time as a long, distinctly articulated and papillary cone of growth (cf. Pl. 2, Fig. 10), the second time as a distinct spike, though still at a comparatively low stage of development. It is altogether surprising that no positive correlation at all is found between the duration of the primordial stage and the degree of development of the inflorescence primordium during the last hibernation before the flowering. If anything, the correlation is negative. *C. saxatilis* shows a less advanced degree of development in this respect than the majority of species with a one-

year primordial stage. *C. aquatilis stans* and *C. atrofusca*, with a relatively prolonged primordial stage, are likewise among those which are least developed during the last hibernation.

A two-year development of the much advanced inflorescences of the *Eriophorum* species might perhaps be expected at the outset. However, this is not the case; as a rare exception only a slight suggestion of a "floral" state, characterised by the two last leaf primordia being initiated simultaneously, not, as otherwise, singly, has been ascertained in *Eriophorum callitrix* during the second hibernation before the flowering.

In all species the reduction division in the pollen sacs takes place in the spring. In *Carex parallela* and *C. pedata* young P. M. C. have been observed at the setting-in of the winter. At this time the other species examined had not yet reached the P. M. C. stage, not even the morphologically much developed *Eriophorum* species. In the greater number of the *Carex* species and in *Elyna* the reduction division takes place immediately before the apex of the inflorescence is visibly protruded above the leaf sheaths. *C. misandra* and *Kobresia bipartita* do not reduce till the appearance of the inflorescence. *Carex Lachenalii* and *C. ursina* reduce at a very early stage, relatively long before the inflorescence becomes visible. *Eriophorum callitrix* and *E. polystachyum* do not reduce till immediately before the anthesis after the culm has become noticeably elongated. *E. Scheuchzeri*, however, reduces even before the inflorescence appears above the surface of the ground. (The more exact time of the reduction division has not been investigated in *Carex alpina*, *C. aquatilis stans*, *C. bicolor*, *C. capitata*, *C. glareosa*, *C. microglochin*, *C. pseudolagopina*, and *C. sparsiflora*.)

According to investigations made at Eskimonæs in the spring of 1935, as early as May 31st the floral organs of *Carex pedata* and *Carex supina* in snow-free localities were considerably more advanced in development than the plants examined in the winter stage. In *Elyna Bellardi*, likewise from a snow-free locality, no noticeable growth could be ascertained so far. Thus the species do not seem to awake from their dormant state at the same time, even though they grow under the same temperature conditions.

### *Gramineae.*

Lit.: Holm 1922, Raunkiær 1895—99, Resvoll 1917.

Twenty-seven species (and varieties), about two-thirds of which are hemicryptophytes and about one-third geophytes. One species, *Pleuropogon Sabinei*, is most correctly to be regarded as a helophyte.—Rhizome- and caespitose plants, with sympodial stem axes. Vivipary occurs in three species, the spikelets being transformed into bulbils (cf. Scholander

1934, p. 81 et seq.). Innovation shoots are initiated either intra- or extravaginally. As usual extravaginal shoots have a number of scale leaves besides the prefolium. In *Puccinellia angustata* only, whose shoots must be referred to the extravaginal type, the prefolium alone is often developed as a scale leaf. In most species either intravaginal or extravaginal shoots occur, only a few species having both types of shoot. The construction of the shoot is usually less regular than in the *Cyperaceae*, though with some exceptions; thus *Dupontia Fisheri* has an exceedingly regular construction.

Shoot dimorphism occurs in several species; in vigorous plants, in particular, "short shoots" without or with only limited possibilities of rejuvenescence may be formed in addition to the normal innovation shoots. They are to be regarded as floral terminal stages. They are but little conspicuous in tufted species with intravaginal shoots, while in species with extravaginal shoots they are conspicuous morphologically, appearing as erect shoots (cf. RAUNKIÆR l. c.) with a smaller number of scale leaves than the rhizome shoots. Fairly often the short shoots are capable of forming new short shoots of the same type. In rarer cases only the short shoots give rise to fresh normal innovation shoots. Shoot dimorphism with a distinct separation of the two shoot types is found in *Agropyrum violaceum*, *Calamagrostis neglecta*, *Festuca rubra*, *Hierochloe alpina*, and *Trisetum spicatum*. Shoot dimorphism without a sharp distinction between the two types is found in *Poa arctica*.

Of other forms of shoot dimorphism the following may be mentioned: *Poa Hartzii* exceptionally develop extravaginal shoots from the lower leaf axils, which shoots normally flower after a year's longer development than the usual intravaginal ones. *Puccinellia angustata* very often forms ascending shoots from the lower leaf axils, but as a rule they die after some (up to six) years' vegetative development without a final flowering.

A shoot dimorphism in some degree resembling that found in *Carex scirpoidea* is often suggested in *Puccinellia Vahliana*: floral side shoots, mostly with a 3—4-years' development, are furthered in growth at the expense of the mother shoot, which most frequently dies vegetatively after a number of years (up to seven years have been ascertained).

*Puccinellia phryganodes* develops 1) vegetative above-ground runners with proleptic rosettes in the leaf axils, and 2) floral shoots of normal appearance. The shoot type seems here to be determined by the influence of the external factors, the runner stages being associated with localities which are regularly flooded. In dry localities runners are often entirely lacking. Runners may be transformed into short-jointed floral shoots and the reverse. Flowering may occur after one year's short-jointed stage, at the earliest, mostly, however, much later.

Finally a curious case of shoot dimorphism in a somewhat wider sense in *Poa alpina* may be mentioned, two fundamentally different forms of the vegetative rejuvenescence of the plant occurring here: 1) Rejuvenescence from the upper leaf axils; the shoot generations often have a many-years' vegetative development. The Innovation shoots, as a rule only a number of one or two, are developed proleptically in the flowering year immediately at the base of the culm (cf. Pl. 3, Fig. 30), in which way the short-jointed shoot-chain is continued directly, so that the old culm bases are apparently situated laterally on the erect mesocorm. 2) Rejuvenescence from the lower leaf axils; lateral rosettes of the first and second order are formed in great number before the flowering of the mother shoot. Coherent older sympodial shoot axes do not, as a rule, occur, the lateral rosettes being, as it were, fixed to the mother axis by a constricted joint. The connection between the shoot generations easily break, and the new rosettes take root, and large, not organically united tufts will result. There is no doubt that before any actual root formation has taken place, casually detached rosettes frequently function as vegetative propagative organs. Plants with transitional forms between the two growth types are comparatively rarely found. Type 1 is chiefly associated with dry fjord regions, though it is not absent from the coastal tracts. Type 2 seems to be found exclusively on wet soil in the coast regions. Thus there seems to be a marked correlation between the type of development and the external factors. Whether it is also, or perhaps in an essential degree, genetically conditioned, cannot be decided at present. Transitional forms between the two types are evidently more frequent in *var. vivipara* than in the normally fructifying form(s). A viviparous pure Type 1 occurs, but less frequently than Type 2 and transitional forms.

The duration of the development of the individual shoot generations of the *Gramineae* is subject to greater modifications than in the *Cyperaceae*. In all species the scale-leaf stage, if such a stage occurs at all, normally lasts for a year in all species except in *Calamagrostis arundinacea*, in which it very frequently continues during one or two more years with the development of a corresponding larger number of scale-leaves. However, in the great majority of species the duration of the rosette stage, which ends in flowering, is variable, but in rare cases only it exceeds five years, the flowering year included. Only in *Arctagrostis latifolia*, *Calamagrostis arundinacea*, and *Poa glauca* is the duration of the green stages constant. The two first-named species have one year's development of rosette leaves before the flowering year; however, in *Arctagrostis* the rosette year is wanting in rare cases in specially vigorous plants, so that green leaves are only developed in the flowering year, that is to say, chiefly culm leaves. This course of development is the

only one found in *Poa glauca*. In these species weak, non-flowering shoots die after the same number of years, functioning two summers or one summer respectively.

In all the other species one or several invigoration years with formation of rosette leaves may intervene. A special capacity for extending the vegetative stage with a subsequent flowering has been observed in *Poa alpina* (shoots up to ten years old) and *Trisetum spicatum* (up to nine years). Purely vegetative nutrition shoots rarely attain any great age. In the *Festuca* species, however, shoots up to eight years old have been ascertained. Only in *Puccinellia phryganodes* are they present in large numbers. In the last-named species such vegetative shoots of an age of up to 15 years (excluding preceding runner years, if any) have been observed.

The number of green leaves developed every year during the vegetative stages of the shoot is fairly constant (apart from very weak vegetative shoots, which succumb early). The great majority of species develop three or four leaves; only in *Deschampsia brevifolia* and *Poa abbreviata* does the number fall to 2(—3), and only in *Poa alpina* does it rise to 5, though only towards the end of the development of the shoot. The last-named species is the only one in which the number of leaves increases noticeably from year to year, viz. from 3 to 5, during the invigoration stages. However, in *Puccinellia phryganodes* vigorous above-ground runners may develop up to about eight leaves yearly; the axillary buds are even often developed proleptically into small leaf rosettes.

In the flowering year 1—4 foliage leaves will develop, mostly two or three. They are either culm leaves or 1—2 rosette leaves and 2—1 culm leaves.

A noticeable periodicity of the leaf size may often be observed, the last leaf developed during the growth season not attaining the same length as the remaining ones. In *Poa abbreviata*, which lacks a seasonal periodicity of leaf size, a two-year growth and function of the leaf at the transition between the years' growths have been ascertained, the upper half of the leaf developing and functioning one year, the lower half next year. *Poa alpina* alone has, as a rule, winter-green leaves with a functioning period lasting far into the next growth season.

In a number of species the vegetative innovation is subject to a regular annual periodicity. In species with a more or less proleptic development of the innovation shoots the periodicity has been interrupted, so it seems to be due to a mere chance at which stage the young buds and shoots hibernate. An entirely continuous proleptic bud development, with a complete absence of periodicity in the shoot sequence, is found in *Deschampsia brevifolia*, *Phippsia algida*, and *Puccinellia Vahliana*. A very frequent proleptic development along with a normal

development is found in *Poa abbreviata*, *Poa alpina*, *Puccinellia phryganodes*, *Festuca brachyphylla var. supina*[1]), and somewhat less frequently in *Festuca brachyphylla var. brevifolia*[1]), *Festuca vivipara*, *Poa Hartzii*, *Poa pratensis*, *Puccinellia angustata*, *Trisetum spicatum*, *Agropyrum violaceum*, and *Festuca rubra*. In the three last-named species the proleptically developed shoots chiefly become short shoots. Only in *Phippsia algida* has it been ascertained that proleptically developed shoots may flower the same year. However, here, too, floral primordia have been formed the preceding year, the vegetative bud even one year earlier.

The floral organs of the hibernation stage are as a rule but slightly developed. Actual anthers and a more or less distinct ovary, though still without stigmata, are normally only formed in *Hierochloe alpina* (Pl. 3, Fig. 19), *Pleuropogon Sabinei* (Pl. 3, Fig. 23), and, together with less advanced stages, in *Phippsia algida* (Pl. 3, Fig. 21), *Deschampsia brevifolia* (Pl. 3, Fig. 10), *Puccinellia Vahliana* (Pl. 4, Figs. 8—9), and *Poa alpina* (growth type 2). A somewhat less advanced development, anthers and ovary being only suggested, but often poorly recognisable as such, is more frequent and is usually met with in *Alopecurus alpinus* (Pl. 3, Figs. 4—6), *Arctagrostis latifolia* (Pl. 3, Fig. 7), *Dupontia Fisheri* (Pl. 3, Figs. 12—13), *Festuca brachyphylla v. brevifolia* (Pl. 3, Fig. 15), *Poa abbreviata* (Pl. 3, Figs. 24—25), *Poa arctica* (Pl. 3, Fig. 33), *Puccinellia angustata*, *Trisetum spicatum* (Pl. 4, Fig. 12). A still lower degree of development, with the inflorescence indicated only as a pinnate primordium, is normal in *Agropyrum violaceum* (Pl. 3, Fig. 1), *Calamagrostis arundinacea* (Pl. 3, Fig. 9), *Calamagrostis neglecta*, *Festuca brachyphylla*, the main species and *var. supina* (Pl. 3, Fig. 16), *Festuca rubra* (Pl. 3, Fig. 17), *Poa pratensis* (Pl. 4, Figs. 2—3), *Poa alpina* (growth type 1) (Pl. 3, Fig. 30), *Poa glauca* (Pl. 3, Fig. 34), *Poa Hartzii* (Pl. 4, Fig. 1), *Puccinellia phryganodes* (Pl. 4, Fig. 7). However, in most species the floral hibernation stage is but little constant, so that inflorescence primordia may often be observed whose stage of development differs considerably from the normal one, both in respect of earlier and of later development. Completely aperiodical in regard to floral development are *Deschampsia brevifolia*, *Puccinellia Vahliana* (Pl. 4, Figs. 8—11), *Poa alpina* (growth type 2), and *var. vivipara*, likewise *Phippsia algida*, in which, however, certain stages of development are more frequent than others. *Puccinellia angustata* (Pl. 4, Figs. 4—6) and *Trisetum spicatum* (Pl. 4, Figs. 12—15) also sometimes show a fairly strong tendency towards aperiodicity. The lack of periodicity in the formation of the floral organs is in addition distinctly manifested by the frequent occurrence of destroyed inflorescences and by the appearance of retarded culms late in the summer. Thus in *Deschampsia brevifolia* the majority of shoots often end with a destroyed inflorescence, in *Puccinellia Vahliana*

[1]) Cf. p. 74.

often up to half the number. These inflorescences have as a rule been arrested in growth at a stage of development which is more or less farther advanced than the "normal" hibernation stage. Thus there is hardly any doubt that there is a maximal degree of development beyond which the flower buds do not tolerate hibernation. Accordingly it seems to be quite accidental what shoots are at the most favourable stage of development, viz. those whose floral primordia have not exceeded the maximal size for hibernating, but which are yet so far advanced in development that a flowering in due time is ensured, which alone affords a possibility for the ripening of the fruits.—In this connection it is remarkable that the "inflorescences" in the viviparous form of *Poa alpina* are capable of hibernating at all stages of development, while the normal form has a distinct maximum limit to its successful hibernation (cf. Pl. 3, Figs. 28 and 31). The other two viviparous *Gramineae* within the area, *Festuca vivipara* and *Poa alpigena var. colpodea*, are, however, "florally" periodical, with a rather low degree of development in the winter state.

As regards the period of development for the inflorescences it can be ascertained with certainty that the primordial stage of the florally aperiodical species extends over two growth seasons before the flowering year, at any rate for inflorescences with a normal time of flowering (cf. Pl. 3, Figs. 10—11, 21—22, 27, 29). A biennial primordial stage is further found in *Arctagrostis latifolia* (Pl. 3, Figs. 7—8) and *Dupontia Fisheri* (Pl. 3, Figs. 12, 14). A just distinct "floral" cone of growth in the last stage but one of hibernation is evidently found normally, or at any rate often, in *Alopecurus alpinus*, *Hierochloe alpina* (Pl. 3, Figs. 18—20), *Pleuropogon Sabinei*, *Poa alpigena var. colpodea*; and fairly often, but hardly always, in *Poa abbreviata*. In about half the number of species occurring within the area the cone of growth does not become distinctly floral till the summer before the flowering, that is to say, the floral primordial stage extends only over one period of growth; namely in *Agropyrum violaceum*, the *Calamagrostis* species, all the *Festuca* species, *Poa pratensis*, *Poa glauca*, *Poa Hartzii*, *Poa alpina* (growth type 1), *Puccinellia phryganodes*. *Puccinellia angustata* (Pl. 4, Figs. 4, 6) and *Trisetum spicatum* (Pl. 4, Figs. 12, 14, 15) have evidently mostly a one-year, but hardly rarely a two-year floral primordial stage.

The reduction division takes place in all species in the spring, but at very different morphological stages of development in the different species. According to the time for the reduction division in the anthers the species examined may be divided into three groups:

1) The reduction division takes place before the inflorescence protrudes, while the inflorescence is still concealed between the leaf sheaths:

*Dupontia Fisheri*, *Festuca brachyphylla cum varr.*, *Hierochloe alpina*, *Phippsia algida*, *Poa abbreviata*, *Puccinellia angustata*, *Puccinellia phryganodes*, *Puccinellia Vahliana*, *Trisetum spicatum*. In *Puccinellia angustata* the reduction division takes place at an extraordinarily early date, while the floral parts are still quite small.

2) The reduction division takes place simultaneously with or immediately after the inflorescence has become visible above the sheath: *Poa alpina*, *Poa arctica*, *Poa Hartzii*.

3) The reduction division takes place long after the protruding of the panicle, after the uppermost joint of the culm has become more or less elongated: *Alopecurus alpinus*, *Arctagrostis latifolia*, *Calamagrostis arundinacea*, *Festuca rubra*, *Poa pratensis*, *Poa glauca*. In all the species of group 3 the formation of pollen (summer of 1935) was more or less defective. The contents of the anthers developed normally until the P. M. C. stage, after which the sporogenous tissue was destroyed. In *Calamagrostis arundinacea* practically no pollen was formed, and in *Arctagrostis* pollen was only formed in the minority of cases. Among the species within group 2 destruction of the content of the anthers was likewise frequent in *Poa Hartzii*. In *Poa arctica* all the plants examined with a normal formation of soboles contained pollen, while in all caespitose plants examined the anther content was destroyed at the P. M. C. stage. (The lack of pollen formation in *Poa arctica var. caespitans* has further been ascertained by NANNFELDT (in lit.))[1]). None of the species within group 1 showed destruction of pollen.

(The time for reduction division (and possibility of destruction of sporogenous tissue) has not been investigated in the following species: *Agropyrum violaceum*, *Calamagrostis neglecta*, *Deschampsia brevifolia*, *Pleuropogon Sabinei*.)

Pollen mother cells in the hibernation stage have only been found in *Phippsia algida*.

On May 25th, 1935, *Hierochloe alpina* and *Puccinellia angustata* were observed to be in distinct growth in snow-free localities, with floral primordia noticeably more developed than in the hibernation stage; *Hierochloe* in the same place in reduction division on June 3rd; *Phippsia* in a favourably exposed locality, which happened to be snow-free, in growth on May 25th; *Poa abbreviata* and *Festuca brachyphylla* distinctly in growth on June 2nd.

### *Juncaceae.*

Lit.: Cf. RAUNKIÆR 1895—99, RESVOLL 1917.

The family comprises seven species, representing two genera, *Juncus* and *Luzula*, which are highly different in shoot construction.

[1]) Cf. J. A. NANNFELDT in Symbolae Botanicae Upsalienses IV: 4. Uppsala 1940.

1) The *Juncus* species are geophytes; the wintering organs, however, have developed somewhat differently in the various species; *J. arcticus* has a rather thickened rhizome, *J. biglumis* has a combined rhizome- and bulb-formation, *J. castaneus* has slender soboles with terminal tubers, and *J. triglumis* has a combined rhizome-, tuber-, and bulb-formation. During hibernation the shoot apices are protected by hard scarious scale leaves or by withered basal parts of the foliage leaves of the preceding summer. The construction of the shoot shows a nearly mathematical regularity. Shoot dimorphism does not occur. The duration of the development of the shoot generations is constant. If the shoot is too weak for flowering, it withers after the same number of years as shoots which end by flowering. In *J. biglumis* and *J. triglumis* the year's growth is limited to one shoot generation; each generation has a development of green leaves during two growth seasons, thus a rosette year precedes the year of flowering. *J. arcticus* has a yearly growth of 1—4 shoot generations, *J. castaneus* 1—3 generations; both species have green leaves in the flowering year only, and all shoot generations of the year's growth develop to nearly the same stage the preceding summer. The oldest (proximal) of the shoot generations in question, however, is as a rule somewhat more advanced in development than the youngest (distal) ones.

The two-year green phase for *J. biglumis* and *J. triglumis* on the one hand and the one-year phase for *J. arcticus* and *J. castaneus* on the other do not indicate a corresponding accordance in the developmental time of the shoot reckoned from its formation as bud (primordium) to its floral termination. *J. arcticus* and *J. biglumis* agree in regard to the time for the formation of the innovation buds, the buds in these species being initiated very early, so the principal bud of the second order is distinctly initiated within the principal bud of the first order, the development of the shoot thus (normally) taking four years in *J. biglumis* and three years in *J. arcticus*. A four-year development may also be established in the last-named species, viz. in weaker sympodes producing only one generation annually, for here the first traces of a principal bud of the third order can be ascertained. However, in vigorous sympodes with several shoot generations annually the bud stage of the last ones of each batch is shortened, so that here the total development takes two years. In *J. triglumis* and *J. castaneus* the innovation buds are initiated very late. A principal bud of the second order is not (or only exceptionally) visible; thus the development of the shoot normally takes three years in *J. triglumis* and two years in *J. castaneus*. In *J. castaneus*, in particular, the late formation of buds is notable, the 2—3 shoot generations developed each year being formed consecutively. This shows very plainly that the growth is subject to a period-

icity manifested by an arrest of growth in the individual shoot generations, apparently independently of the external conditions. In the other species also the growth shows a distinct autonomous periodicity.

In *J. arcticus* the stem and the stem-like involucral leaf constitute the only assimilating organ. In *J. castaneus* the production of foliage leaves amounts to four, all of which develop in the year of flowering. In the vegetative rosette year *J. biglumis* and *J. triglumis* usually develop four foliage leaves, the last one, however, is but slightly developed. The growth of partially developed leaves is not continued in the succeeding year. In *J. biglumis* as a rule one foliage leaf, and in *J. triglumis* usually three leaves are developed in the flowering year.

The floral development in the hibernation stage is fairly constant, but differs greatly in the various species. *J. biglumis* has as a rule well developed flower buds with developed anthers and ovary enclosed in the perianth (Pl. 4, Figs. 17—18); however, sometimes younger stages are found. In *J. arcticus* the floral parts may exceptionally be in incipient differentiation (Pl. 4, Fig. 16), but mostly only the inflorescence axes are just recognisable. In *J. triglumis* the inflorescence axis is only suggested as a broad cushion-shaped formation with incipient bracts (Pl. 4, Figs. 21—22). In *J. castaneus* the cone of growth is normally still, as far as can be seen, purely vegetative during the hibernation (Pl. 4, Fig. 20); only exceptionally can it be recognised as "floral" (Pl. 4, Fig. 19). In the *Juncus* species the inflorescence is apparently initiated laterally at the base of the primordial involucral leaf.

Thus in the *Juncus* species the chief part of the formation and development of the floral organs takes place in the year of flowering, except in *J. biglumis*, which is the only one in which the floral primordial stages extend over the greater part of the growth season preceding the flowering.

Reduction division in spring and summer. Investigations on the time for the reduction division in the anthers carried out in the summer of 1935 were not entirely satisfactory, as staining of the nuclei with aceto-carmine was impossible. *J. biglumis* develops pollen while the flowers are still concealed between the leaf sheaths, but with the involucral leaf projecting. *J. triglumis* does not develop pollen till the culms have attained almost their full length. As late as July 20th *J. arcticus* had no pollen in nearly fully developed flower buds of a length of 4—5 mm on fairly tall stems. In *J. castaneus* P. M. C. were observed in brown inflorescences projecting above the leaf sheaths. Evidently the development had been arrested there. In flower buds and flowers in the female stage with the stigmas visible pollen had not yet developed by the middle of July.

2) The *Luzula* species are hemicryptophytes. *L. nivalis* and *L. spicata* are densely caespitose, while *L. confusa* is more loosely caespitose with ascending underground shoots. Shoot structure: The vegetative construction is rather irregular, in all essentials resembling that of the *Gramineae*. The shoot development must be termed extravaginal, the prefolium being short and all shoots beginning with scale leaves. Incomplete shoot dimorphism is suggested in *L. nivalis* and *L. spicata*, rejuvenation shoots from the upper part of the shoot generations often having a large prefolium and a more rapid development. Shoot dimorphism is most frequent in plants growing in comparatively dry localities with a dense sod, rejuvenescence from the upper leaf axils being here especially marked, while the development of shoots from the lower leaf axils, if such are found at all, is very slow. Thus the shoot dimorphism is of precisely the same type as that found in *Poa alpina*. Proleptic shoot development, however, does not seem to take place in the *Luzula* species. The rejuvenation buds are always formed in the axils of green foliage leaves and normally unfold the succeeding year. In the first year of growth both scale leaves and foliage leaves are formed in *L. nivalis* and *L. spicata*, while only scale leaves are formed in *L. confusa*. In the latter species the scale leaf stage is not rarely biennial; thus a distinct horizontal rhizome with a corresponding greater number of scale leaves is formed.

The number of years with foliage leaves is not constant, but depends on the vigour of the shoot. The upper shoots in *L. nivalis* and *L. spicata* have mostly only two green years including the flowering year, that is to say, a three-year development, while the basal shoots in these species have mostly a four or five years' development. *L. confusa* has the slowest development, mostly four years with foliage leaves, and as the bud plus the scale-leaf stage extends over 2—3 years, its development is most frequently 6—7 years, but it may be eight years, too. Purely vegetative, not flowering, shoots rarely attain the same age as flowering ones. Weak shoots, especially issuing from the lower leaf axils, frequently occur, but as a rule they die after the lapse of one or two years, and their production of leaves is inconsiderable.

The yearly production of leaves during the invigoration stages is as a rule four in *L. confusa*, mostly five in *L. spicata*, less constant in *L. nivalis*, varying between three and five. In *L. confusa* leaves at the transition between the annual additions have a typical two years' growth, as in *Carex nardina*. The same probably takes place, though to a less extent, in *L. nivalis*, in which the basal parts of the leaves last developed remain green during the winter. In *L. spicata* the growth is not extended beyond the first growth season, so in old shoots the years' growths are distinctly marked by a seasonal periodicity in the size of the leaves. In *L. nivalis* two leaves are as a rule developed in the

year of flowering, in *L. confusa* three, and in *L. spicata* four leaves; the last leaf is in all cases a stem leaf of small size. The number of leaves in the year of flowering is in close correlation with the floral stage of development during the last wintering. *L. nivalis* has the most well developed floral primordia, the anthers are distinctly initiated, and the same applies to the ovary, which, however, is as a rule not closed at the apex (Pl. 4, Figs. 26—29). Very frequently less developed inflorescence primordia are found, too, this species, in contrast to the other two, being fairly aperiodical in vegetative as well as in floral development. Only in the rapidly growing shoots issuing from the upper leaf axils is the floral primordial stage actually annual. In the lower shoots the floral primordial stages of inflorescences developed "in time" dates back to the end of the growth season before the last one. *L. confusa* has a strictly periodical floral development so that even the wintering stage is much the same in plants in snow-free localities with a long growth period and in such in localities with a prolonged snow-covering and a short growth period. The floral development is less advanced than in *L. nivalis* (in a "normal" wintering stage). The distal part of the bracts is developed as bundles of long fringes, which cover and project far beyond the relatively slightly developed axillary clusters, whose individual flowers are hardly recognisable (cf. Pl. 4, Figs. 23—25). The floral primordial stage extends over one growth season only. In *L. spicata* the floral axes during the wintering before the year of flowering are only indicated as an articulated, rather undifferentiated tall cone of growth (cf. Pl. 4, Figs. 30—31). Thus in case of a normal flowering the floral cone of *L. nivalis* and *L. spicata* is initiated at the end of the growth season, but the time interval between this and the flowering is fairly precisely one year longer in *L. nivalis* than in *L. spicata.*

The reduction division takes place at approximately the same morphological stage of development in the three species. Owing to the much recurved position of the basal leaves in *L. nivalis* and *L. spicata* the inflorescence early becomes visible and is of a dark colour. Here the reduction division in the anthers does not take place till some time after the appearance of the inflorescence. In *L. confusa* the inflorescence long remains enclosed within the erect sheathing parts of the leaves; the reduction division takes place almost simultaneously with the appearance of the inflorescence.

### *Juncaginaceae.*

Lit.: Cf. RAUNKIÆR 1895—99, p. 23 et seq.

Only one species, *Triglochin palustre*, which is a geophyte. Sympodial growth. The hibernation organ is a bulb with one (or two) scales. The old roots and all the organs except the bulb die at the end of the

growth season. The bulb hibernates without roots. The roots of the next growth year are just recognisable as a whorl of primordia.

Shoot dimorphism: 1) The most vigorous and often the only innovation shoot develops in the axil of the uppermost foliage leaf. It is spot-bound, and in the first growth year produces 1—3 foliage leaves plus 1(—2) starch-filled bulb scales without blades; in the second growth year 3(—4) foliage leaves plus the inflorescence. 2) In vigorous plants an augmentation shoot is, in addition, formed in the axil of the bulb scale. In the first growth year this shoot produces a stolon with about four scale leaves plus the bulb. The development during the second growth year is like that of the main shoot. One shoot generation is developed annually. The development of shoots always takes three years, the bud being formed in the axil of not unfolded leaves. The shoots are constantly developed proleptically, so that two shoot generations are always visible during the growth periods. The yearly leaf production is mostly 5—6, distributed over two shoot generations.

The development is strictly periodical. Weaker, not flowering shoots die after the second year of growth like the flowering ones. In such shoots a very small rudiment of an inflorescence axis is present at the base of the innovation shoot.

During the wintering the inflorescence of the succeeding year is recognisable as such. The individual flowers are formed as broad disk-shaped primordia, but the floral parts are not recognisably differentiated (Pl. 5, Fig. 1).

The precise date of the reduction division has not been investigated.

### *Liliaceae.*

Lit.: PORSILD 1920a.

Two species of the *Tofieldia* genus. Caespitose hemicryptophytes with sympodial shoots.

*T. coccinea* has a typical rejuvenescence from the axils of the second but one pair of leaves below the scape. The shoot axes remain fresh several generations back. Adventitious roots issue only from older shoot generations, the shoot apices being therefore often raised above the surface of the ground to the chamaephyte position. In *T. palustris* rejuvenescence often takes place from the lower part of the shoot generations, the most vigorous rejuvenation shoots, however, issue from the axils of the uppermost pair of leaves below the scape. Adventitious roots arise from the last flowering shoot generation, while the older shoot generations are soon destroyed, so that the shoots of older tufts become without any organic connection. The plant is thus a typical hemicryptophyte. The shoot development in both species is typically

intravaginal, the large prefolium being the only actual scale leaf. Proleptic shoot development does not occur.

In *T. coccinea* the development of the shoot as a rule takes seven or eight years, only quite exceptionally a shorter time; the vegetative invigoration stage may, however, be considerably prolonged. Flowering shoots with up to eighteen years' development were observed. Purely vegetative shoots do not normally occur. *T. palustris* has a six to twelve years' development, eight or nine years being the rule. Weak, purely vegetative shoots, especially from the lower part of the shoot generations, frequently occur; their lifetime varies greatly, viz. from two to fifteen years.

In *T. coccinea* the annual leaf production in the vegetative invigoration years is constantly two; the growth is slow, and all leaves do not attain their full size till after the course of two growth seasons (in addition to one year's primordial state). The arrest of growth in winter is mostly manifested morphologically by a joint-like constriction in the leaf. The leaves function altogether for four years (two years in addition to the growth years), the lowest leaves on the shoot, however, as a rule only three years. *T. palustris* develops three leaves annually, though only two in the two first growth years of the shoot generations. At any rate the leaf at the transition between the years' shoots has a two years' growth. This species, like *T. coccinea*, remains green during the winter, but the leaves do not function more than two growth seasons. Only two small stem leaves are developed in the year of flowering. In *T. coccinea* even the blade of the lowermost of these has developed the preceding year.

The floral primordial stage lasts only one year, although the floral development is much advanced during the last wintering. The scape is somewhat elongated, but it is enclosed, together with the inflorescence, between the leaf sheaths. The flower buds are almost fully developed, the anthers and the ovary are distinctly formed. In *T. coccinea* (Pl. 5, Fig. 2), which is the most advanced in development, the ovules are distinctly initiated, while in *T. palustris* (Pl. 5, Fig. 3) they are hardly recognisable.

Reduction division in the spring, immediately before the inflorescence appears above the leaf sheaths.

### *Potamogetonaceae.*

Lit.: Cf. RAUNKIÆR 1895—99, p. 80 et seq.

Only one species, *Potamogeton filiformis*. Hydrophyte. Wintering organs are rootless stem tubers consisting of two naked, starch-filled, swollen internodes plus the terminal bud.

The whole flowering shoot as a rule bears eleven leaves, the first six of which are scale leaves, the last five foliage leaves. The first three scale leaves develop and perish the year before the flowering (belong to the mother plant). The internodes between the 2nd and the 4th scale leaves are the wintering organ filled with nutrition, the fourth and fifth scale leaves surround the terminal winter bud. In the axils of the last scale leaf and the first four foliage leaves purely vegetative leaf shoots develop, the lowermost ones of which, at any rate, again produce leaf shoots of the second order. Thus the number of foliage leaves will be large, 30—50, mostly 35—45. Plants with less than 30 foliage leaves do not usually flower; even in vigorous plants only the main shoot flowers. Vegetative as well as flowering plants die after the end of the growth season with the exception of the fresh wintering organs, which are initiated in a number of about one to four, mostly two, according to the vigour of the plant. The wintering organs represent the terminal part of lateral shoots (stolons) of the second and third or even of the fourth order from the axils of the scale leaves.

During the wintering the primordial development is much advanced. The whole plant of the succeeding year is actually formed in the wintering bud, even lateral shoots of the second order are visible as distinct buds; that is to say, that the development of the shoot in a general sense takes two years. The flower spike is distinctly formed, the individual flowers appear as disk-shaped formations with the first indication of differentiation of the floral parts (Pl. 5, Fig. 4).

Reduction division in the summer, date not investigated.

## *Dicotyledones.*

### *Choripetalae.*

#### *Betulaceae.*

Only one species, *Betula nana*. Deciduous dwarf bush, chamaephyte. Wintering buds with bud scales, which are actually the stipules of the primordial leaves of the bud. Lateral shoots have two prefolia of the same appearance and function as the bud scales.

Shoot dimorphism with sharp distinction between vegetative long shoots and floral dwarf shoots. The long shoots have monopodial growth. The (1—)2 lowermost leaf primordia of the year's shoot, which are but slightly protected during the wintering, do not develop. About seven green leaves are developed. The lowermost axillary buds either do not unfold or produce weak dwarf shoots with some years' vegetative growth before flowering, the middle ones producing female catkins, the upper ones male catkins. The uppermost axillary bud, situated near the ter-

minal bud, produces a long shoot like the latter. However, variations may sometimes occur, all or most of the lateral buds producing either male catkins only or female catkins only. The dwarf shoots normally have no elongation of the internodes; as a rule they produce three leaves annually. Otherwise the male and the female dwarf shoots behave differently. The male dwarf shoots have mostly a three-year development, including the bud stage, but only one year with green leaves. No leaves are developed in the flowering year. The catkin winters naked and fully developed. The whole dwarf shoot mostly dies after flowering; however, not rarely it forms fresh dwarf shoots from the leaf axils. Sometimes the development is prolonged by one (or several) vegetative years. The female dwarf shoots normally flower the year after the elongation of the mother shoot, so that already in the first year of growth a flowering catkin plus three foliage leaves are developed. Very often, however, one or several growth years with the formation of 2—3 leaves annually intervene. Normally fresh dwarf shoots are formed in the leaf axils, so that whole complexes of branches arise, consisting of sympodially connected dwarf shoots. Such dwarf shoot sympodes are mostly not purely female. Prolepsis does not take place, but vigorous dwarf shoot sympodes may flower every year. In certain cases dwarf shoots may after several years continue directly in long shoots; similarly, long shoots may sometimes produce mere dwarf shoots, of the terminal bud as well as of the lateral buds.

The differentiation into long shoots and dwarf shoots takes place during the bud stage. During the wintering, buds which are to form long shoots enclose the leaf production of the succeeding year in the form of large primordia plus 2—3 quite small ones nearest the growing point. Thus here the primordial stage extends over one growth season only, apart from the lowermost leaves of the year's shoot. Buds destined to form dwarf shoots likewise enclose the yearly leaf production, viz. three, as large leaf primordia plus 2—3 quite small ones. Thus the primordial stage of the dwarf shoots must be said to extend over more than one year even though it does not extend over two whole growth seasons.

The floral primordial development is noteworthy in so far as it is entirely different for the male and the female catkins. The male catkins pass the winter fully developed with pollen formed (cf. Pl. 5, Fig. 5). The reduction division takes place in August. The primordial stage does not extend beyond this growth season, and the floral development proceeds at a very rapid rate towards the end of the summer. The female catkins, which flower the succeeding spring simultaneously with the fully developed male catkins, are singularly little developed during the wintering (cf. Pl. 5, Fig. 6). The catkin scales are formed, but the

ovary is only recognisable as a low ring-shaped pad (cf. Pl. 5, Fig. 7). The development of the female catkins must accordingly take place very rapidly in the spring.

The facts that the female floral primordia normally begin their development in the lateral buds of the mother shoot already in its year of elongation, while the development of the male primordia does not commence till next year, and that the leaf production is alike for the male and the female dwarf shoots, would seem to suggest that the male development is retarded one year as compared with the female one. Brother and sister shoots develop embryo-sac and pollen within the same growth season, but copulation takes place between sexual cells of which the male ones are one generation older than the female ones.

### *Callitrichaceae.*

Lit.: SEIDELIN 1910.

One species, *Callitriche verna*. Summer annual therophyte. The primary root completes its growth very early, and its functions are taken over by adventitious roots arising from the nodes. All the foliage leaves support flowers except the lowermost pair, which in vigorous plants supports short side branches, likewise with flowers in the leaf axils. Main stem with altogether 5—10 pair of leaves. Total length of plant ($^1/_2$—)1—3 cm.

In the only known locality within the area the plant grew in damp soil. The first 4—5 pair of leaves were distinctly water leaves; the desiccation had accordingly taken place during the growth period.

Ripe fruits in the lower leaf axils about the middle of July, 1931.

### *Caryophyllaceae.*

Lit.: HOLM 1922, RESVOLL 1917, WARMING 1920.

Hemicryptophytes and herbaceous chamaephytes. The subfamily *Silenoideae*, comprising five species, has more or less well delimited wintering buds; the cone of growth and floral primordia are protected by the closely packed leaves of the bud. Bud scales lacking entirely. The most compact winter buds are found in *Silene acaulis* and *Melandryum triflorum* (Fig. 18, p. 201). In *Viscaria alpina* no actual bud is formed, but the still green sheath parts of older leaves protect the undeveloped leaves. The subfamily *Alsinoideae* comprises 13 species. *Honckenya* holds a special position among them, its rejuvenation shoot beginning with scale leaves enclosing the bud during the wintering. None of the other species form winter buds, and the shoot apices have almost the same appearance all the year round. In some species the

young, not unfolded, leaves do not even closely surround the shoot apex, so the cone of growth is entirely unprotected. In the majority the young leaves are only loosely joined, more closely, however, in *Stellaria longipes*, the termination of the shoot forming a closed bud. The primordial axillary buds are quite open, the growth beginning with two papillary formations, the first pair of leaves, even before the cone of growth of the shoot itself becomes visible.

The axial parts are built up of sympodes in all species except the *Sagina* species and *Minuartia biflora*, which have a monopodial growth in connection with a strict shoot dimorphism, with differentiation into vegetative shoots with unlimited longitudinal growth and floral short shoots without innovation. In *Sagina caespitosa* and *Minuartia biflora* the vegetative axis is branched, while in *Sagina intermedia* the primary axis remains unbranched. In species with sympodial growth a different form of shoot dimorphism is sometimes found, but it is less marked; thus in *Stellaria longipes*, which forms vegetative long shoots and floral short shoots; however, sooner or later the long shoots assume the character of short shoots, and flower. The long shoots are partly subterranean scaly runners, which may have more than one year's subterranean growth and may be branched; but sooner or later the shoot apices will bend upwards and continue in an above-ground shoot. The long shoots are in part above-ground even from the beginning. Their yearly leaf production is then much larger than that of the short shoots, viz. 5—10 pairs as against 3—4, and often new vegetative leaf shoots also develop proleptically from the axils. A more or less distinct leaf dimorphism is here associated with the shoot dimorphism. The leaves of the long shoots are long and relatively narrow; those of the short shoots are short and broad. Plants in unfavourable habitats do not form long shoots. In addition to the above-mentioned shoot types this species develops short axillary shoots with short internodes; these shoots easily get detached and serve as vegetative propagation organs.

Suggestions of a similar shoot dimorphism may be observed in *Cerastium alpinum* and *Cerastium Regelii*. Here the "long shoots" are evidently only specially vigorous shoots which grow exceptionally rapidly. In *Cerastium alpinum* these shoots terminate the growth year with a retarded flower or with a highly developed flower bud, which is either destroyed in the course of the winter or flowers early in the spring after wintering. These "long shoots" as a rule develop proleptic side shoots, which very early, even before the first pair of leaves are fully expanded, begin to form floral primordia. These few-leaved short shoots normally flower the succeeding summer.

In *Cerastium Regelii* vigorous long shoots have often one or two runner-years, after which the great growth year follows. It is interesting

to note that in *Cerastium Regelii* these shoots are the only shoots which flower, and that the flowering is not, as in *Cerastium alpinum*, shifted to an abnormal season; for the floral primordia hibernate as in normal shoots of *C. alpinum*, though at a more advanced stage of development. The ordinary, less vigorous shoots of *C. Regelii* do not, as a rule, flower; their apices are loosened and shed (see below p. 103).

The development of the shoot in species with sympodial growth mostly extends over 3—5 years. However, the time of development is not constant, it may be prolonged by one or several growth periods. In *Silene acaulis* flowering shoot generations of an age of up to 15 years have been noted. Weak vegetative shoots as a rule die after a couple of years. *Honckenya* is of a type of growth which is common in temperate regions but rare in the Arctic. The development of the shoot extends over two years, a scaly bud being formed in the first year which next year develops into the leaf- and flower-bearing shoot. The whole green part of the shoot dies at the end of the growth season. The rejuvenescence takes place from the lowermost leaf axils. However, the time of development may be prolonged, for the scale-leaf stage may, at any rate, continue up to three years with formation of a fresh set of scale leaves every year.

In the *Silenoideae* the sequence of the shoot development is more or less periodical, in *Silene acaulis* as in *Honckenya* even strictly periodical, in accordance with the fact that special winter buds develop in this species. In the sympodial *Alsinoideae* the succession of shoots is rather aperiodical, wintering taking place at all stages of development. In *Minuartia stricta*, however, the succession of shoots is as a rule periodical. The lack of periodicity in the succession of shoots is associated with the frequent proleptic shoot development. Thus prolepsis does not take place in the *Silenoideae*, or only exceptionally in vigorous plants; nor does it take place in *Minuartia stricta* and probably only rarely in *Cerastium Regelii*. But prolepsis is fairly frequent in *Arenaria ciliata*, *Cerastium alpinum*, *Cerastium trigynum*, and *Minuartia rubella*. In *Cerastium trigynum* the numerous proleptically developed shoots often only develop into lateral rosettes of short duration, that is to say, pure nutrition shoots. Some species have a constant proleptic development of all shoots, viz. *Minuartia Rossii*, *Stellaria humifusa*, *Stellaria longipes*. By prolepsis the buds are initiated already while the subtending leaves are in the primordial stage; this is especially pronounced in *Minuartia Rossii*, where the primordia of lateral shoots are formed simultaneously with the corresponding subtending leaves.—The three monopodial species differ in regard to the periodicity of the consecutive development of the floral shoots: *Sagina caespitosa* has a periodical succession of shoots without prolepsis, and the floral shoot development extends over two

years; *Minuartia biflora* sometimes shows prolepsis; however, this does not, or only apparently, alter the period of development of the floral shoots, which normally lasts three years. *Sagina intermedia* has a constant proleptic development of the floral shoots. The parallel development of the floral axis and the corresponding subtending leaf in this species gives rise to the curious phenomenon that the shoots developed in the axils of the first leaves of the yearly growth have one year's shorter development than those developed in the axils of the last leaves of the year (all pairs of leaves normally subtend floral axes, cf. Pl. 5, Fig. 26). Thus lateral shoots of two different age classes flower almost simultaneously every year, namely a lowermost (outermost) series with a four-year (apparently three-year), and an uppermost (innermost) with a three-year (apparently two-year) development. As the leaves of the main axis function two years (excluding the primordial year), the flowering shoots of the uppermost series are always subtended by green leaves, the lowermost series, however, by withered leaves.

The annual growth in *Caryophyllaceae* amounts to from two to six pair of leaves, three and four being commonest. The number is fairly constant for the species within the *Silenoideae*; even if the shoot development continues for several years, the annual leaf production is only slightly increased from year to year. This, however, is the case to a greater extent in the species within the *Alsinoideae*. Normally the whole annual augmentation is formed as primordia the year before expansion. However, this does not apply to the long shoots of *Stellaria longipes* and *Cerastium alpinum*, in which only part of the annual augmentation is initiated the year before. The same is often the case for *Honckenya peploides* and, *mirabile dictu*, *Minuartia Rossii*. The annual growth of this species may amount to seven pair of leaves, but the number of pairs in a primordial stage hardly exceeds three. The examined plants of this species, so rare within the area, are from Ymer Ø, an isolated occurrence indicating the southern limit of the species in East Greenland, so very possibly these plants have a development which is abnormal for the species. The plants have chiefly a procumbent growth and long internodes, while within its main area of distribution the species exhibits a typical short-jointed pulvinate growth. In certain respects the plants examined resemble abnormally deformed plants, which other species, e.g. *Minuartia rubella*, may develop in highly manured localities.

In *Honckenya*, the *Melandryum* species, and *Silene acaulis* the leaves function in one year, and wither at the end of the growth season. Unlike the other *Silenoideae*, *Viscaria alpina* passes the winter in a green state, and its leaves evidently function during the greater part of the growth season after wintering. In the other species (the *Alsi-*

*noideae* with the exception of *Honckenya*) the leaves function two years and have a lifetime of three years: the first year is the usual primordial stage, in the second year the growth of the leaves is terminated, but the internodes are as a rule not elongated. During the succeeding wintering this stage of a number of species show much incurved and succulent leaves resembling veritable green bulbs—most markedly in *Arenaria ciliata* and *Stellaria humifusa*—and serving as reservoirs of stored up nourishment. In the third year the elongation of the internodes takes place, in so far as it does take place at all, the leaves are emptied of their stored up nourishment, and in the course of the summer they lose their turgor and wither. However, the transition between the three stages is always quite gradual. To some species this rule only applies with certain reservations: in *Stellaria longipes* and *Cerastium trigynum* the functioning period of the leaves is actually shorter. It is true that *Stellaria longipes* seems to pass the winter in a green state, but the leaves wither as early as the beginning of the succeeding growth season. In *Cerastium trigynum* the actual primordial stage and the foliage leaf stage of the first year are, as it were, united in an elongated bud with closely-set half-developed green leaves. Thus fully developed leaves do not winter; accordingly the shortening takes place at different stages of development in the two species.

The order of development of the floral primordia exhibits a fairly close parallelism with that of the vegetative development. In the vegetatively periodical species the floral development also is periodical, and in such species all the flower buds are in about the same phase of development during the wintering. This is the case with the *Melandryum* species (cf. Pl. 5, Figs. 15—17), *Silene acaulis* (Pl. 5, Fig. 27), and *Minuartia stricta* (Pl. 5, Fig. 21). In the other, more or less aperiodical, species, in which flower buds in fairly different phases of development may be found, one stage, often the relatively most advanced stage, is most strongly represented numerically ("normal stage"). However, in *Stellaria humifusa* the floral development seems often to be entirely aperiodical (cf. Pl. 5, Figs. 28—30). It applies to the wintering flower buds that such as have developed pollen in the anthers will not develop further. Large buds without pollen in the anthers continue their development but the contents of the anthers are destroyed, whereas the ovules have a normal appearance and are probably capable of functioning and developing seed provided pollination takes place. Still smaller wintering buds give rise to normal bisexual flowers. Entirely similar conditions are found in *Cerastium alpinum* (cf. Pl. 5, Figs. 9—12) and *Minuartia rubella*. In these species, however, there is, as a rule, a considerable difference in size between the largest wintering buds and buds of "normal size". The largest buds (cf. Pl. 5, Fig. 9) must here no doubt be regarded

as retarded from the preceding summer. To both species it applies that pollen-bearing buds, which are constantly destroyed during the wintering, are of very common occurrence and that the flowers first expanded in the spring are purely female, the contents of the anthers having been destroyed. However, often some few anthers, especially of the flowers developed a little later, show a normal formation of pollen. In *Cerastium alpinum* it is chiefly buds at the apex of long shoots which flower early in the spring. In this species there is no absolute difference between these retarded buds and the "normal" ones, and the species shows a fairly continuous flowering. In *Minuartia rubella*, however, the flowering is not continuous; there may be a distinct spring flowering of retarded buds from the preceding year, succeeded by a period without flowering, until the actual normal flowering begins. Retarded bud stages are perhaps even more frequent in *Stellaria longipes* than in the species just mentioned, but in this species they are all destroyed in the course of the winter. Flowering in the spring does not take place at all. Only "normal" buds develop flowers in this species, and the flowering sets in rather late in the summer. Shoots with closely-set withered leaves, which apparently represent one shoot generation, often on dissection are seen to consist of a sympodium of several shoot generations whose individual parts terminate in a destroyed flower bud.

*Minuartia Rossii* seems to be aperiodical in regard to floral development. That much advanced bud stages may continue their development after wintering, appears from the fact that flowering shoot generations only expanded one pair of leaves in the flowering year or none at all. Flower buds which were to winter were found at all stages of development. In this species and in the likewise entirely aperiodical *Stellaria humifusa* the floral primordial development no doubt often extends over more than one growth period, so that the flower buds winter twice. In all the other species the duration of the floral primordial stage, at any rate normally, is one year, and the flower buds winter once. Exceptions are *Viscaria alpina* and in certain cases *Honckenya peploides*. In *Viscaria* (cf. Pl. 6, Figs. 3—4) the cone of growth is hardly recognisably floral during the last wintering, though all leaves, the stem leaves also, are in a primordial stage. The floral primordial development has accordingly been advanced to the flowering year proper. *Honckenya* develops two kinds of shoots (which, however, may possibly not always be sharply distinguished), partly such as pass the winter with four pair of foliage primordia plus a floral primordium (Pl. 5, Fig. 14) in addition to bud scales, and they are the more frequent, partly such as winter with about five pair of foliage leaf primordia plus a vegetative cone of growth. Both kinds of buds develop flowering shoots; in the latter type about eight pair of leaves and one or several flowers develop on the

main axis; further, side branches may be formed, and these, too, will flower. Thus not only the floral, but also part of the vegetative primordial development has advanced to the flowering year.

For the more or less periodical species we may—summarily—distinguish between the following "normal" wintering stages:

1) Cone of growth not yet floral (cf. Pl. 6, Fig. 4): *Viscaria alpina*, *Honckenya peploides* (in part).

2) Floral primordium shaped like a five-sided crown. First whorl of anthers distinct, calyx and ovary not developed (cf. e.g. Pl. 5, Fig. 8): *Arenaria ciliata*, *Honckenya peploides* (in part), *Sagina caespitosa*, *Cerastium trigynum*(?), *Stellaria longipes* (most frequently).

3) Calyx developed (in the *Silenoideae* actually only the calyx teeth), flower bud closed, anthers ±stalked, ovary initiated but no ovules (cf. e.g. Pl. 5, Figs. 21 and 27); *Cerastium alpinum*, the *Melandryum* species, *Minuartia rubella* (sometimes young ovules), *Minuartia stricta*, *Silene acaulis*, *Stellaria longipes* (largest buds).

4) Ovules present, ovary, however, as a rule not closed[1]) (cf. e. g. Pl. 5, Figs. 13, 19): *Cerastium Regelii*, *Minuartia biflora*, *Sagina intermedia*.

Markedly aperiodical are (cf. above): *Minuartia Rossii*, *Stellaria humifusa*.

The reduction division, in all species taking place in the spring, sets in at a fairly early stage of development while the flower buds are still quite small and before any elongation of the flower stalks has taken place. The majority of species commence growth very early in the spring or after the melting of the snow. Thus for instance *Melandryum affine* in a snow-free locality was in reduction division as early as May 27th, 1935.

Special forms of vegetative reproduction are found in *Cerastium Regelii*, *Minuartia Rossii*, and *Stellaria longipes*. *Stellaria longipes* does not develop seeds[2]). This seems to be due to the fact that the great majority of the plants are female. It is true that anthers are present, but they are destroyed at an early date. Among thousands of populations of this common species observed on Clavering Ø in 1935 bisexual plants were only found in two cases; they were recognisable even from a distance owing to their longer, more flatly expanded petals. The bisexual popula-

[1]) *Arenaria*, *Cerastium*, and *Stellaria* have distinctly axial placentae, the "carpels" are initiated as a ring-shaped pad, which only at a late stage grows up so as to enclose the ovules.—In the *Silenoideae*, *Sagina*, and *Minuartia* the originally locular ovary is initiated before the ovules.

[2]) GELTING's remark on this species: "Produces mature seeds" (1934, p. 55) must refer to an exception.

tions flowered too late to enable me to ascertain whether fructification would take place.—Vegetative reproduction by short-jointed, easily discharged axillary shoots (cf. Porsild 1932, p. 29).

In *Cerastium Regelii* and *Minuartia Rossii* flowering individuals are relatively rare. They have a lively vegetative reproduction by broken-off shoot apices, which are capable of taking root. In *Cerastium Regelii* the breaking off takes place by an active process, as a rule it is localised after the seventh or eighth pair of leaves of the shoot. An especially vigorous innovation bud is formed in the leaf axil immediately below the place of detachement.—In *Minuartia Rossii* the discharge of shoot apices (and shoot fragments without a primary growing point) is more irregular, and is possibly due to a general fragility of the axes.

### *Crassulaceae.*

One species, *Sedum roseum*. Hemicryptophyte with thick, perennial, often branched rootstock with unlimited monopodial growth. The main axes bear only scale leaves, seven of which are usually formed every year. The two lowermost ones subtend innovation buds, which, however, only in vigorous plants develop into new monopodial main axes. The next four scale leaves subtend buds, which the succeeding year give rise to above-ground floral shoots. Only in very vigorous plants will they all develop, but mostly only the lowermost one or ones develop. During the wintering stage of development the apical bud of the main axis is enclosed by the uppermost withered scale leaf. The bud is small and entirely concealed among the large, rounded, floral lateral buds. The last-named buds are provided at the base with about five fresh scale leaves, which enclose the whole floral shoot, whose numerous leaves and richly flowering cyme are distinctly formed. In addition to the five scale leaves these shoots bear 30—45 foliage leaves, the number varying according to the vigour of the shoot. Shoots with less than about 30 foliage leaves do not flower, and accordingly develop into purely vegetative nutrition shoots. These aerial shoots function only in one growth season, and often wither at an early date even before the end of the summer. Thus the development is strictly periodical. The scale leaves of the main axis only remain fresh one year beyond the primordial year. The primordial development of the above-ground shoots extends over one growth season only, the wintering bud of the main shoot having only axillary buds indicated in the lowermost two leaf axils; these buds do not form above-ground shoots but fresh main axes.

As will be seen, the annual leaf production is very considerable. In very vigorous main axes it may, however, be further increased, since

from the axils of the lowermost scale leaves of the floral shoots there may develop shoots (proleptically)—up to three, mostly two—of the same appearance as the relative mother shoot and simultaneously with the latter. Likewise, new lateral main axes of the same order as the floral shoots may proleptically produce above-ground flowering shoots from the lowermost leaf-axils. However, the anticipated shoots have, as usual, one year's primordial development, which thus conincides with the corresponding development of the relative mother axes.

The total size of the wintering inflorescence primordia varies greatly according to the vigour of the shoot, but the floral developmental phase is about the same in all cases (cf. Pl. 6, Figs. 5—6): the central flower of the mostly three-flowered elementary inflorescences have anthers and carpels differentiated; however, the carpels are not closed, and ovules not visible. The buds of higher orders are as a rule much less developed. Male and female flowers have the same appearance in the wintering stage, the differentiation according to sex setting in later. The sex organs not capable of functioning are retained as distinct rudiments.

Reduction division takes place in the spring. Favourably exposed plants were forming pollen as early as on May 28th, 1935.

### *Cruciferae.*

Lit.: HOLM 1922, RESVOLL 1917.

Twenty-two species, hemicryptophytes and mesocorm-chamaephytes. Mesocorm thick and fleshy in *Braya purpurascens* and *Eutrema Edwardsii*, likewise, though to a less extent, in *Braya linearis*. The same applies to the short main axes in *Lesquerella* and *Cochlearia*. In most species the shoot apices are open, with continuous development of green leaves; they are therefore of nearly the same appearance all the year round. Flower buds which have passed the youngest stages winter without protection of any kind. Only *Eutrema Edwardsii*, *Arabis arenicola*, *Braya linearis*, and *Braya purpurascens* winter without any green leaves. However, the two first-mentioned species have more or less open buds, *Eutrema* even so much that the young flower buds of floral shoots are entirely unprotected, since the lowermost internode of the stem may have been elongated somewhat before the wintering (see Fig. 19, p. 201). Only in the two last-mentioned species do the undeveloped leaves join so as to form an actually closed bud, though often only partially in *Braya linearis*. In all the species of the family the leaf primordia are provided with axillary leaf-like formations, stipulary scales, and in the not winter-green species, in particular, the latter have an abundant secretion of mucus. This is especially remark-

able in *Arabis arenicola* and *Eutrema*, that is to say, in the species with the most open buds.

Shoot structure: *Lesquerella arctica* has a short, thick, nearly always unbranched main axis with continued monopodial growth. The floral shoots issue laterally from the leaf axils. All the other species form sympodes with rejuvenation exclusively, or at any rate principally, from the uppermost leaf axils. The type of development of the shoot generations is distinctly the three year type: bud—rosette—flower. In *Arabis arenicola*, however, the first two stages normally coincide, the principal bud here forming one year later than in all the other species. The typical three-year development was noted in all the species except *Cardamine pratensis*, but it is not always the most frequent. On the whole the rosette stage of weaker shoots may be arbitrarily prolonged; however, a particularly prolonged shoot development is not frequent except in a few *Draba* species and in *Cardamine pratensis*, which is evidently never capable of accomplishing a development of short duration. In *Arabis arenicola*, *Braya linearis*, and *Braya purpurascens*, however, a prolongation of the vegetative stage does not seem to take place; fairly weak non-flowering shoots are arrested in their growth, like the floral ones, after the lapse of three years. The termination of the shoot is probably actually always floral, as is often recognisable by a very small (floral) rudiment at the base of the innovation shoot issuing from the uppermost leaf axil. Otherwise purely vegetative shoots practically do not occur. "Superfluous" unfolded buds as a rule die after developing some few leaves and without rejuvenation.

The annual leaf production differs greatly in the different species. *Cardamine bellidifolia* and *Eutrema Edwardsii* show the lowest production with an annual augmentation of three and four leaves per shoot; among the highest are *Lesquerella arctica* and *Cochlearia officinalis* with about 15 leaves in plants of average vigour. In *Lesquerella* the annual number of leaves may rise to about 20, in *Cochlearia* even to 30 in especially vigorous plants. Actually the leaf production of a number of species may exhibit even higher figures within a growth season, as one further shoot generation may develop within the same growth season. In this respect *Braya humilis* is no doubt the most extreme example (see below).

In the individual species also both the annual number of leaves developed in the invigoration years and the number of leaves per shoot generation vary in an exceptionally high degree. The figures given in Table 7 (p. 170 et seq.) indicate the average of a large number of cases investigated. Only *Cardamine bellidifolia* and *Eutrema Edwardsii* show an approximate constancy in this respect. In a few species the annual number of leaves increases considerably from year to year if the develop-

ment extends over several years. It would seem that no formation of flower buds takes place before the shoot attains a certain annual leaf production. This, for instance, is very marked in *Cardamine pratensis*, which very rarely flowers within the area.

In the great majority of species the developmental sequence of the shoot is regular and periodical. The primordia of the innovation buds are formed simultaneously with those of the flower buds, and they open and form rosette leaves the succeeding year, viz. in the flowering year of the mother shoot. The new rosettes always develop in the axils of green leaves formed in the same year. Thus prolepsis constantly occurs. Only in highly desiccating localities may the sprouting of some few species be retarded one year. However, in *Eutrema* the rosette is formed in the axil of the last leaf of the preceding year, but the rhythm of development is otherwise the usual one. In the summer-green species the leaves as a rule wither in the early autumn. Even in species with open buds whose outer leaves may have attained a certain development before the winter sets in, there is a very distinct border-line between withering and winter-green leaves. In the winter-green species the transition from primordia to fully developed leaves is quite gradual, and the actual growth of the leaf extends over two growth periods. Absolutely fully developed leaves probably winter to a small extent only, and if so, they only function during the first part of the succeeding growth period, and wither continually; thus in *Arabis alpina*, *Cardamine bellidifolia*, *Cardamine pratensis*, *Lesquerella arctica*. In *Cochlearia*, all the *Draba* species, and probably also in *Braya humilis* and *Braya Thorild-Wulffii* the leaves wither more in groups. This is especially distinctly seen in the *Draba* species of the *alpina* group (*D. alpina*, *D. Bellii*, *D. Gredinii*, and *D. micropetala*), whose leaves at the beginning of the winter are either entirely withered or fresh, succulent, and full of nutritive matter. In these species of *Draba* the outermost wintering leaves are evidently fully developed. In *Draba cinerea*, *D. daurica*, *D. lactea*, *D. crassifolia*, and *Cochlearia* the fully developed leaves wither. In *Cochlearia*, it is true, apparently fully developed leaves persist during the winter, but if so, the petiole continues the growth the succeeding year. *D. nivalis*, *D. fladnizensis*, and *D. subcapitata* behave like *Draba cinerea*, but in these species there is a noticeable difference in size between the innermost withering and the outermost wintering leaves. A similar decrease of the leaf size in groups is sometimes recognisable in *Braya humilis* and *Braya Thorild-Wulffii*.

As regards the sequence of floral development there is nearly always a sharp distinction between fairly strictly periodical and almost entirely aperiodical species. The great majority of species are florally periodical. Three species are aperiodical, viz. *Braya humilis*, *Braya Thorild-Wulffii*,

and *Draba crassifolia.* Of the other species as a rule only *Cochlearia officinalis* and *Draba cinerea* now and then show deviations from the entirely periodical development; thus flowering in the autumn (proanthesis, WITTROCK 1883) may sometimes take place in vigorous plants.

It would seem that the periodicity of many species is stabilised by a special order of the shoot sequence, an especially few-leaved floral generation taking the place of the principal bud; the floral primordia of this generation are initiated almost simultaneously with those of the mother shoot, and its flowering likewise begins at the same time as that of the mother shoot. Thus the inserted regulation shoot attains two years' development and only develops leaves in the flowering year. The new innovation buds are initiated in the usual way in the uppermost leaf axils of the regulation shoot simultaneously with the flower buds of the shoot, and the development goes on in the usual way as if nothing extraordinary had happened. Regulation shoots are frequently found in the following species: *Arabis alpina*, *Braya linearis*, *Braya purpurascens*, *Cardamine bellidifolia*, *Draba cinerea*, *Draba lactea*, *Draba micropetala*, *Draba crassifolia*, rarely in *Draba fladnizensis* and *Draba subcapitata.*—It is questionable whether the term "regulation shoot" is fully justified. At any rate it would seem that this kind of shoots are not in all cases able to prevent a continued floral development in the autumn of the most vigorous plants of *Draba cinerea*; and in *Draba crassifolia* the "regulation shoots", which are here formed in great numbers, seem to have no regulating influence at all, the shoot generations developing into flowering and fructification continuously until the winter frost sets in.

A peculiar fact as regards the periodical occurrence of regulation shoots may often be observed in *Draba cinerea* and *Draba lactea*, whose most frequent form of shoot development is the typical three-year development: often the normal formation of flower buds fails to take place even in vigorous first-year rosettes. The vegetative stage continues, being thus increased by one year. In the second rosette year, then, not only flower buds are formed in the main shoot, but also in a number of primordial regulation shoots. The abundant flowering of the next year may then be succeeded by a similar (two-year) vegetative development, which is again followed by abundant flowering. It would seem that for some reason or other the normal formation of flower buds is suspended, to manifest itself even more profusely when it sets in again after the lapse of one more year. At any rate the simultaneous development of two flowering shoot generations will mean a substantial investment of energy, and in accordance with this, regulation shoots do not, as a rule, occur in two consecutive years.

In the aperiodical *Braya* species, more especially in *Braya humilis*,

often two or even sometimes three flowering shoot generations are developed yearly (except in very dry localities). The number of leaves of the summer shoot generations—though it varies greatly—is not, as

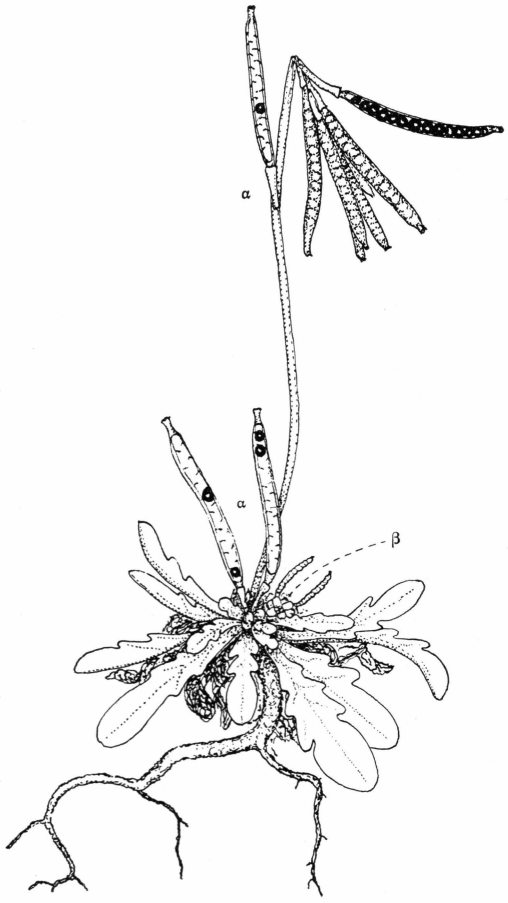



Fig. 11. *Braya humilis* in its wintering condition (Ella Ø, c. 15th September, 1931). To the left ($\alpha$), the withered scape with ripe siliques. The plant is actually acauline, the lowermost two siliques being basal. The elongated scape is the axis of the inflorescence. To the right ($\beta$) a young inflorescence with two slightly developed siliques. In the course of the succeeding summer it assumes the same appearance as the scape shown to the left; for the stem itself does not elongate if the plant winters in a flowering or incipiently fructifying state. c. $^1/_1$. Del. O. HAGERUP.

in the regulation shoots, noticeably smaller than in the wintering rosettes. Two successively developed shoot generations here flower consecutively, not simultaneously as in regulation shoots, so that it really seems like a reflorescence. At the same time as the first shoot generation bears ripe siliques, the next generation is in flower, while the third generation may have developed buds. Often it seems a mere

chance how far the plant advances in development before it is arrested by the frost. In the inflorescences developed later in the summer elongation of the stem fails entirely to take place, so that the lowermost flowers or siliques are situated directly on the basal axis like the rosette leaves. *Braya humilis* occupies a unique position among all the seminiferous species of the area in that inflorescences or infructescences at any stage of development may survive the winter and continue their development in the succeeding growth season. If an inflorescence has commenced flowering (and fructification) in the autumn, a considerable elongation of the middle parts of the raceme will take place after the wintering; these parts will become stem-like with large intervals between the siliques, while the lowermost siliques remain attached to the main axis or the extreme lowermost part of the "stem" (cf. Fig. 11). In *Braya Thorild-Wulffii* flowers which have opened in the autumn do not produce fruits, but the uppermost part of the inflorescence may develop normally after wintering.

Autumnal reflorescence, no rare phenomenon in *Draba cinerea*, can easily be ascertained the following summer, for the part of the inflorescence which has flowered in the autumn does not elongate. Thus the whole fruiting raceme or only its lowermost part may remain compact, forming an umbel. The autumnal flowers develop siliques, which, however, only contain destroyed seed primordia. It has been impossible to decide with certainty, whether a *Draba crassifolia* flowering in the autumn will be able to fructify; it does not seem probable.

The life duration differs greatly in the different species. It could be ascertained that young plants (not to be mistaken for seedlings) of short-lived species are much more frequently met with than of such as attain a great age. The invigoration stages before the first flowering are likewise relatively short in the short-lived species.

Least durable is *Cochlearia*, which is most frequently hapaxanthic, having a lifetime of 3—5 years; four years' development seems to be commonest (cf. GELTING 1934, p. 66). However, it is not rarely pollacanthic (Fig. 12), as vegetative buds may be initiated in the upper leaf axils. The phenomenon seems especially to occur in vigorous plants whose flower shoots attain anticipant flowering in the autumn. The flowering main stem will then be destroyed by the frost, whereas leafless daughter scapes may develop from the base, as also shoots from the uppermost rosette leaf axils, equipped with some leaves at the base. Below (outside) these, purely vegetative rosettes may appear; they will not flower again till after an invigoration stage of 3—4 years with a constantly increasing annual number of leaves, just like the seed plants. The process may repeat itself several times, so that a thick fleshy and branched mesocorm is formed.

*Braya humilis* has often a rather limited life duration; only where the plant is regularly overlain by a thin layer of loose material does the life duration seem to be "unlimited". Young plants will often flower



Fig. 12. Pollacanthic specimen of *Cochlearia officinalis* in summer state. (Clavering Ø, July 1935). c. $^5/_4$. Del. O. HAGERUP.

in their second year of life. The rate of growth may be impressive; thus for instance the following data were ascertained for a plant at the end of its second growth season: First year of life: cotyledons + seven rosette leaves; augmentation in the second year of life: 22 rosette leaves + fruiting raceme + five daughter shoots each with about 20 (15—25) rosette leaves, the largest with siliques, the smallest with flower buds with pollen in the anthers; each of these daughter shoots of the first

order with several lateral shoots of the second order, each with 7—9 half-developed leaves and young inflorescences of the "normal" wintering size, and in their uppermost leaf axils visible innovation buds for lateral shoots of the third order. That is to say, one summer's production from the same second-year root was six flower stems with partial fructification, about 120 fully developed leaves, about 15 young inflorescences (developed to about the P. M. C. stage) and (at least) 150 half-developed rosette leaves, indeed an enormous production. For the sake of completeness it should be added that the plant was collected in an entirely natural habitat, in peaty soil mixed with sand. The plant was indeed one of the most vigorous ones. The production is not unique, but decidedly above the mean.

*Draba fladnizensis* often dies after a few years. The most vigorous young plants flower in their second growth year. The first year such plants have about 16 fully developed leaves in addition to the cotyledons; in the second year a similar number of leaves + the inflorescence are developed. *Draba crassifolia* is likewise short-lived, and is probably sometimes hapaxanthic. It often flowers the second year.

As an example of a long-lived species I may mention *Draba Bellii*. This species is especially well suited for a determination of age, for the withered leaves are very durable and remain attached to the old stems. A "young plant" flowering for the first time was examined. It was almost pillar-shaped. The continually increasing size of the leaves gave the leaf-bearing mesocorm the shape of a top (an inversed cone). The lowermost annual series of leaves had been destroyed, but apart from them a total of 295 leaves could be counted from the base of the plant to the flower scape. As the plant, at any rate in its youngest stages, hardly produced ten leaves annually (the normal number for older shoots), its absolute minimum age will be about 35 years, or more probably 40 years. The plant in question was not derived from a poor locality, for well developed, abundantly flowering older plants with much branched mesocorms grew in the same place. Thus the age of these plants should evidently be counted in centuries!

*Lesquerella arctica*, which on a direct observation seems a durable plant, is not especially long-lived. This is probably in some degree due to the fact that it lacks the power of shoot rejuvenescence. The most vigorous plants are already noticeably weakened after about ten years' flowering and die after a few years. Weak plants with a small yearly growth, however, seem to hold their own much longer. Under favourable conditions young plants seem to be able to flower in the third or fourth year.

*Eutrema Edwardsii* no doubt attains a very high age, judging from the inconsiderable yearly increase in the thickness of the mesocorm and

the perennial tap-root. Its age is undeterminable, however, because leaves and leaf bases are very soon entirely destroyed. The first flowering hardly takes place till after ten years' vegetative invigoration, as a rule probably much later.

The floral primordial development is limited to the growth season preceding the flowering year, even in species in which the formation of pollen takes place before the wintering. The floral development during the wintering stage varies greatly in the different species, extending over all phases. According to the degree of development the species can be arranged into the following groups, beginning with those which are the least advanced. The developmental stage mentioned is that of the lowermost largest buds of the inflorescence. However, the difference in the developmental stage of the buds within the same inflorescence is mostly much smaller than the difference in size would seem to suggest.

1) Cone of growth during wintering apparently vegetative. Floral primordial development advanced to the flowering year proper: *Arabis arenicola.*

2) Flower buds not distinctly formed, anthers just recognisably differentiated as arched bodies on the receptacle. Ovary not differentiated: *Braya linearis* (Pl. 6, Fig. 11), *Cardamine pratensis* (Pl. 6, Figs. 17—18).

3) Flower buds distinctly developed, primordial ovules just visible or sometimes lacking: *Braya purpurascens* (Pl. 6, Figs. 12—13), *Cardamine bellidifolia* (Pl. 6, Figs. 15—16), *Draba fladnizensis* (Pl. 6, Figs. 24—25), *Draba nivalis* (Pl. 7, Figs. 1—2).

4) Flower buds somewhat larger, though the P. M. C. stage is hardly reached, ovules distinct: *Arabis alpina* (Pl. 6, Fig. 7), *Draba alpina*, *Draba Gredinii*, *Draba daurica* (Pl. 6, Fig. 23), *Draba subcapitata* (Pl. 7, Figs. 3—4), *Eutrema Edwardsii* (Pl. 7, Fig. 5).

5) Flower buds nearly fully developed, pollen mother cells frequent, pollen exceptionally present: *Braya humilis* (Pl. 6, Figs. 8—9) and *Braya Thorild-Wulffii* (very irregular); *Cochlearia officinalis* (Pl. 6, Figs. 19—20), *Draba cinerea*, *Draba lactea* (Pl. 6, Figs. 26—27), *Draba Bellii* (Pl. 6, Figs. 21—22), *Lesquerella arctica* (cf. Pl. 7, Figs. 7—8). In the latter species the largest buds mostly contain pollen, but they do not develop further. In addition all younger stages occur, the development of the axillary floral axes proceeding continually along with the subtending leaves. The axillary shoots of the later developed leaves of the year's growth are always much retarded in development. In accordance with this the flowering of vigorous plants with many floral shoots (up to seventeen have been ascertained) often extends over such a long period

that the first shoots have almost ripe siliques at the same time as the last ones flower (false reflorescence).

6) Flower buds fully developed, pollen formation in the autumn: *Draba micropetala* (Pl. 6, Fig. 28), relatively constant, though sometimes the reduction division does not take place till the spring. *Draba crassifolia*, very irregular, but the pollen stage doubtless the most frequent during the wintering.

The *Cruciferae* commence their action of life very early in the spring. *Draba cinerea* and *Lesquerella arctica* generally developed pollen in the days of May 25—30th, 1935, and *Braya purpurascens* was likewise (exceptionally) met with in reduction division in a specially warm habitat. *Draba daurica* and *Draba fladnizensis* were in reduction division in the first days of June, *Draba subcapitata* and *D. nivalis* a little later. *Eutrema Edwardsii*, which usually occurs in damp soil, was in pollen formation a few days after the melting of the snow, on June 5th. At the same time *Draba lactea* and the *Eriophorum* species, growing in the same place, had not yet shown any signs of life. As far as can be judged, *Eutrema* belongs to the species which begin their growth at the very lowest temperatures even before the uppermost layers of the soil have thawed. It is likewise astonishing how soon *Draba micropetala* commences growth after the melting of the snow, but hardly at such low temperatures as *Eutrema*.

*Cardamine pratensis* shows a lively vegetative propagation by the formation of embryonic plants on the leaves.

### *Hippuridaceae.*

Lit.: Seidelin 1910.

One species, *Hippuris vulgaris*. Rooted hydrophyte with horizontal elongated rhizome, submerged about 10 cm in the mire. The rhizome is built up of sympodes, whose individual joints consist of the first internode of each shoot generation. In moderately vigorous plants four shoot generations are developed annually, in weaker plants two or three.

If four generations are formed a year, the first ones are the most vigorous, and the first two often the only flowering ones. Each develops about 35—40 whorls of leaves. The lowermost c. 10 whorls consist of scale leaves, the remaining ones of foliage leaves, the lower whorls of which have four leaves, the upper six leaves. The leaves of about the twentieth whorl subtend flowers; generally only about five whorls produce fruits. The last two shoot generations as a rule remain purely vegetative and have hardly more than 15 whorls of foliage leaves. Roots are not formed till the green foliage leaves develop.

The generations, up to four in number, which develop within the same summer pass the winter in almost the same phase of development: about ten of the lowermost internodes are elongated, so that the apex of the shoot reaches the "surface of the soil", while the following leaves enclose the cone of growth. As far as about the 25th internode the leaves are still just recognisable as such, then follow about ten whorls of verruciform primordia (cf. Pl. 7, Fig. 9). Floral primordia hardly visible. The principal bud (on the last erect wintering shoot) encloses the succeeding three generations in a primordial state. Accordingly the shoot generations are at the outset formed in series, as if a single shoot generation were formed annually. Thus the shoot development is entirely of the three-year type. In weaker lateral sympodes the principal bud comprises a corresponding smaller number of shoot generations in the primordial stage.

*Oenotheraceae.*

Two species. Hemicryptophytes with sympodial growth. In *Chamaenerium latifolium* a perennial, somewhat woody, branched or irregularly knotty pseudorhizome (NILSSON 1885) of old shoot bases. Vegetative propagation by long subterranean runners, about whose nature and structure nothing can be stated[1]). In *Epilobium arcticum* no coherent sympodes are formed, as the oldest shoot generation and its roots die at the same time as the aerial shoot withers at the end of the summer.

Shoot development in both species taking three years. Wintering organs, however, widely different. In *Chamaenerium latifolium* the winter buds are large, often above-ground, scaly, enclosing the whole shoot of the succeeding year. In the axils of the scale leaves, functioning as bud scales, the first traces of next year's principal bud is present with distinctly formed prefolia. Buds are likewise found in the axils of the lower foliage leaf primordia, which buds develop proleptically into few-leaved nutritive leaf shoots in the flowering year. Flower buds, though but slightly developed, are found in the upper leaf axils. *Epilobium arcticum* winters with a rosette of green leaves—as a rule six—which, however, wither early in the next growth season. In the centre of the rosette next year's stem is present in a primordial state, entirely unprotected, though the flower buds are loosely enclosed by the young stem-leaves. In the axils of the lowermost rosette leaves the innovation buds are found, as a rule with two pair of leaf primordia, which consist largely of a mucro formation not developing further (Pl. 17, Fig. 13). The whole foliage leaf is later developed intercalarily.

Rosette leaves are lacking in *Chamaenerium*. The number of stem

[1]) By mistake the investigation material was not brought home. Nor has it been possible to find information about this question in the literature.

leaves and flowers varies greatly with the vigour of the shoot. The number of rosette leaves in *Epilobium arcticum* is fairly constantly six, the number of the stem leaves (generally 7) varies but slightly. Very rarely more than one flower is developed, the lowermost of the initiated buds. Non-flowering shoots are frequent in both species. In unfavourable summers the flower buds of *Epilobium arcticum* are as a rule destroyed.

Shoot succession: vegetative as well as floral development accomplished periodically in both species.

Floral development during wintering rather inconsiderable, though most advanced in *Epilobium arcticum* (Pl. 7, Fig. 12); in this species the anthers are distinctly formed, while in *Chamaenerium* they are hardly differentiated (cf. Pl. 7, Figs. 10—11). Ovules not yet visible in any of the species in the urn-shaped receptacle.

*Chamaenerium latifolium* awakes rather late from its winter dormance. The reduction division in this species takes place rather late, when the flower buds are highly morphologically developed, about 5 mm long and already freely visible in the axils of the subtending foliage leaves.

In *Epilobium arcticum* the reduction division probably takes place at a comparatively early date. A single flower bud, examined on June 18th, 1935, had P. M. C. They were peculiarly large as compared with the size of the anthers, but on the other hand only six were found in each loculus.

### *Papaveraceae.*

The only species, *Papaver radicatum*, is a mesocorm-chamaephyte. In many respects it shows close agreement with the *Cruciferae*. The axial parts consist of much branched, often bifurcate, sympodes with typical rejuvenescence from the upper leaf axils. Wintering buds open, but the cone of growth and youngest primordial organs protected by the broad joining bases of fresh and withered leaves. All fully developed leaves wither in the autumn, and there is a very sharp limit between the withering and the wintering, half-succulent, starchy leaves, although the boundary line is not indicated by the size or degree of development of the leaves. The boundary line runs through that part of the shoot in which the leaves are half-developed. The uppermost one or two withering leaves are suddenly arrested in their growth and evidently emptied of nutritive substances. By their smaller size and especially by the scanty development of the strengthening elements these early withering leaves distinctly mark the border-lines between the years' shoots even on very old mesocorms, on which only the scarious leaf-bases remain. The fresh, half-developed, leaves which winter unprotected continue their growth the succeeding year.

The type of shoot development is the three-year development, as in the *Cruciferae*, but the vegetative rosette stage is often prolonged, as in the latter, by one or two years, so that the development extends over four or five years. The innovation buds are initiated in the same year as the flower bud and immediately below the latter. They open the following year in the axils of the green foliage leaves. There is thus a constant prolepsis. The development of the innovation buds in the year in which they are initiated is strangely irregular, ranging from quite small ones with only a couple of leaf primordia to very large buds with green leaves spreading at the top and with up to twelve leaf primordia. In accordance with this, a greatly varying number of leaves develop in the succeeding, first rosette year, viz. as many as the number of primordia of the buds of the preceding year. Sometimes the bud does not open in the flowering year of the mother shoot, as in some cases the bud is not initiated till that year. In case the shoot development extends over more than three years, the yearly number of leaves in the vegetative invigoration years is mostly about eight. The number of leaves developing in the flowering year is as a rule 5—6, though extremely variable, ranging from one to nine.—The facts stated above should merely be regarded as an expression of lacking periodicity in the sequence of shoot development. Compared with this it is astounding that the floral degree of development is nearly always the same during the wintering. The flower buds have the same size whether situated immediately above an innovation bud with twelve or with two leaf primordia, and the flower bud is likewise in about the same stage of development whether a few or many leaf primordia are left, to expand simultaneously with the flower. Another fact should be mentioned which may contribute to an explanation of the striking contrast between the vegetative and the floral course of development: On examining old sympodes, one often comes across flower buds whose growth has ceased at a stage a little larger than the normal wintering stage. These buds appear to originate from years with a very sparse leaf production, that is to say, probably from cold summers or summers with a (locally) late melting of the snow. In spite of this the innovation shoot often exhibits a particularly abundant leaf production and flowering the succeeding year; that is to say, many leaf primordia and even a flower bud have been initiated in the unfavourable year.

The explanation of the apparently abundant storing of nourishment in an unfavourable year might be that the nutritive substances are simply removed from the destroyed flower bud and employed in the building up of the succeeding one (corresponding to the aforementioned sharp distinction between early withering leaves on the one hand and half-developed wintering leaves filled with nutritive substances on the

other hand). This in connection with the lack of agreement between the vegetative and floral periodicity seems to show that the flower buds—as in the case mentioned above—are always initiated at a relatively early date of the growth season and continue their development until a certain phase, while the vegetative growth goes on continually as long as the temperature conditions permit. The mode of development demonstrated seems in all cases to ensure a profitable capital investment for the plant, since flowering at an irregular time under the prevalent climatic conditions will always be a doubtful undertaking.

In apparent contrast with the consistent floral periodicity demonstrated is the fact that the species not rarely shows reflorescence, a few flowers appearing at a time when the plant bears fairly large capsules. However, these flowers originate from few-leaved lateral rosettes on the shoots with normal flowering. In spite of their late flowering they as a rule contrive to produce a daughter rosette in the usual way, sometimes even with a flower bud. However, examination of a comprehensive plant material has shown that the retarded flowers are initiated the preceding year, though they are rather far behind in development during the wintering (cf. Pl. 7, Figs. 14 and 16). We are here concerned with regulation shoots entirely like those found in the *Cruciferae*, only with the difference that the two shoot generations initiated in the same year do not flower simultaneously as is the case in the *Cruciferae*. The reflorescence is then not to be regarded as a case of proanthesis.

During the wintering state the flower buds are about 2.5 mm long and short-stalked. The anthers are formed, but only slightly developed (Pl. 7, Fig. 14). The formation of the ovary has begun, but it is open at the tip. On growth of the dissepiments towards the centre the lumen of the ovary is star-shaped viewed from above (Pl. 7, Fig. 15). Ovules are lacking, or hardly recognisable.

Reduction division takes place relatively long after the beginning of the growth in the spring; size of the bud about 7 mm.

### *Polygonaceae.*

Lit.: Holm 1922, Resvoll 1917.

The family comprises four species within the area, belonging to three biologically different groups.

1) *Oxyria digyna* and *Rumex Acetosella* are hemicryptophytes with sympodial growth. The perennial axial parts, the pseudo-rhizome, are built up of the shoot bases bearing rosette-leaves. In *Oxyria* it is thick and rooty, very long-lived, in *Rumex Acetosella* it is somewhat woody, stem-like, and less durable. Older pseudorhizomes of this species gradually make their way to the chamaephyte position, as a consequence

of the elongation of the rosette internodes. The type of shoot development is the three-year development, with the chief rejuvenescence from the axils of the uppermost rosette leaves. In such cases the rejuvenating rosettes are situated in the axils of the rosette leaves of the mother shoot in the flowering year of the latter. Not rarely rejuvenescence also takes place from the lower part of the shoot generation. The vegetative rosette stage is often prolonged, a four- and five-year development occurring along with the three-year development. A four-year development is often more frequent than a three-year development. In *Oxyria*, chiefly in older vigorous plants, subterranean runners may be found whose longitudinal growth seems normally to be limited to one growth season, after which the development continues as in the ordinary rosette shoots. In the elongated part the runners are provided with scale leaves. As a rule they spring from the lower part of the shoot generations, and probably often originate from old "dormant" buds. In *Rumex Acetosella* adventitious shoots in abundance are developed from the roots. These shoots require a fairly large number of invigoration years before flowering.

The annual production of leaves (rosette leaves) amounts to about six in *Oxyria* and about seven in *Rumex Acetosella*. All the green parts of the plant wither in the autumn. The winter buds are closed, concealed in the ochrea of the outermost leaf and, besides, surrounded by the older withered leaf bases.

The order of development, vegetative as well as floral, is largely aperiodical in *Oxyria*. A highly varying number of leaves are developed in the flowering year, 1—8 having been ascertained, though mostly about four (+ a stem leaf). The smaller the number of leaves, the more lively the floral development before the wintering. Floral primordia winter in all stages of development up to the P. M. C. stage. In those most advanced the primordial development extends over two growth seasons (cf. Pl. 7, Figs. 17—18). In spite of the aperiodical development, autumnal proanthesis hardly seems to take place. The reduction division begins late, rather shortly before the flowering, after the stem has been partially elongated.

In *Rumex Acetosella* the order of development is approximately periodical. The production of leaves in the flowering year is almost constantly four rosette leaves (+ two small stem leaves). The phase of development of the floral organs during wintering varies comparatively little. Male flowers with perianth and anthers just formed, that is to say very far from the P. M. C. stage. Female flowers evidently relatively less advanced, formation of ovary hardly begun (Pl. 7, Fig. 21). The time of reduction division not investigated.

2) *Polygonum viviparum.* Stem-tuber-geophyte with unbranched monopodial main axis and floral lateral axes. In older plants the main

axis gradually dies away behind after a functioning period of 10—20 years. In spite of the continued apical growth the growing point is always kept a few centimetres below the surface of the ground, the growth of the short-jointed rhizome constantly taking place in a downward direction, the cone of growth itself pointing downwards. Annual number of leaves on the main axis 3—6 in flowering plants. If the addition is less than three leaves, no floral side shoots are normally formed. Number of floral side branches 1—3 annually. In most cases only one is developed, corresponding to an addition of 3—4 leaves on the main axis. The buds developing into the floral shoots are formed in the axils of the uppermost one or two foliage leaves; next year the developed shoots will accordingly stand immediately outside the green leaves of the main axis. An additional floral shoot may develop above the other ones, in the axil of the lowermost (outermost) green leaf, but only in very vigorous plants. This shoot then has a proleptic development. The primordial development, however, is parallel for all shoots, and hardly extends over more than one growth season, lateral buds being formed rather far back from the cone of growth of the main axis.

The primordial development of the leaves of the main axis extends over two growth seasons, at any rate in weak plants with an inconsiderable production of leaves, in vigorous plants hardly over more than one. The unequal rate of development of the organs in weak and vigorous plants is demonstrated by the fact that the number of primordia in this species, unlike what is usually the case, is fairly constant irrespectively of the annual production of leaves.

The floral shoots bear two actual stem leaves and at the base a bladeless leaf, whose much developed ochrea encloses the shoot during wintering. The ochreae have an abundant secretion of mucus on their inner sides, so that all organs in the primordial stage are embedded in a jelly-like mass of mucus.

All the green parts of the plant wither in the early autumn. The order of development of the floral shoots as well as of the leaves of the main axis is strictly periodical and seasonally limited.

In their bud state during wintering the floral shoots have a length of 2—2.5 cm. In the flower buds the anthers are just recognisably differentiated, the ovary has not yet formed (Pl. 7, Fig. 20). The bulbils, formed in the upper part of the spike, commence as small obovoid bodies (Pl. 7, Fig. 19). The reduction division in the anthers takes place at the time when the spike penetrates the ochrea.

Young plants arising from bulbils pass through a great number of invigoration years before their first flowering. Yearly growth through several years only one small leaf.

3) *Koenigia islandica*, summer-annual therophyte. Moderately

vigorous plants have one stem leaf (in addition to the cotyledons), which supports a branch. The branch and the main stem each of them bear at the apex an inflorescence consisting of closely packed glomerules, and supported by 3(—4) green leaves. Much reduced individuals are of common occurrence: the lateral branch is frequently lacking, and the stem leaf may then be absent. Finally the number of glomerules with appertaining subtending leaves is reduced. The extreme lower limit is reached when the inflorescence becomes one-flowered at the same time as the number of subtending leaves is reduced to one. In such reduced plants the cotyledons are actually the only assimilation organs of any importance.

### *Ranunculaceae.*

Lit.: HOLM 1922, JESSEN 1911, RESVOLL 1917.

In addition to *Thalictrum alpinum* the family is represented within the area by the *Ranunculus* genus only, comprising eight species. These fall naturally into two groups: 1) the hemicryptophytic and 2) the hydrophytic species.

The first group, the hemicryptophytes, comprises *R. affinis*, *R. auricomus*, *R. glacialis*, *R. nivalis*, *R. pygmaeus*, and *R. sulphureus*. These species show great morphological and biological agreement, though in several respects *R. glacialis* occupies a special position. The axial parts constitute a vertical rhizome, as a rule but little branched, more or less thickened, built up of short sympodial joints. The rhizome gradually dies away behind after a functional period of about ten years, in *R. affinis* mostly only 6—8 years, in *R. auricomus* about 15 years. Rejuvenescence always takes place from the axils of the uppermost one or two rosette leaves. The wintering buds are more or less closed, though the slightly developed blade of the outermost leaf often projects from the bud, which is otherwise protected by the broad, frequently still fresh leaf base of the last leaf of the preceding summer. In *R. nivalis* the protection of the bud is more effective than in the other ones, the leaf sheaths of this species being closed; the sheath of the last developed leaf covers the bud completely like a cap. The sheaths of the withered leaves, however, are often destroyed in the course of the winter. In *R. glacialis* the two outermost leaves of the bud are scale leaves with rudimentary lamina; this, however, is not recognisable until the unfolding of the bud next spring, since the buds do not differ fundamentally from those of the other species during the winter.

The type of shoot development is the three-year one, when the innovation bud is initiated at the same time as the flower buds and open simultaneously with the flowering of the mother shoot in the axils of

the rosette leaves of the particular year. Thus there is a constant prolepsis. In cases where more than one innovation bud is developed, the unfolding of the weaker second bud is often retarded one year. The rosette stage may be prolonged one or two years, rarely more. In *R. glacialis* and *R. nivalis* a four-year development is just as frequent as a three-year development, and in *R. sulphureus* a four-year development is the most frequent. Only in *R. affinis* have deviations from the above-mentioned mode of development been ascertained in vigorous plants; thus two flowering shoot generations may develop the same year, but the flowering of the last one is then retarded. Thus we find here the entirely same type of "regulation" shoots as mentioned above under *Papaver radicatum*. Often the development of the shoot generations will then be: no flowering takes place the year after the two flowerings, while the next year there will again be two flowerings (as in *Draba cinerea* and *D. lactea*).

The progress of development of shoots and flowers is approximately periodical in all species except in *R. glacialis*, where it is to some extent aperiodical. Thus one to five foliage leaves may develop in this species in the first rosette year, and there is an entirely corresponding variation in leaf development in the flowering year. That is to say, the group or groups of scale leaves within the leaf succession of a shoot generation may intervene at any place. This in connection with the likewise—though less—variable number of leaves of the intervening vegetative rosette years and the fact that the floral wintering stage is variable, too, clearly shows that the plant grows continually, only with the interruptions implied by the annual climatic rhythm. The intervention, at the beginning of the year, of the scale leaves functioning as bud scales does not speak against this assumption, for they are probably not differentiated as such till the spring, simply because the lamina of the leaf does not develop further, probably owing to the cold of the winter.

The annual production of rosette leaves ranges from three to about five in the different species. The number is nearly constant in each species, except in *R. glacialis*, where it varies more.

During the wintering the flower buds are in a much advanced stage of development in all species. In outer morphological respects they are to be regarded as fully developed; in the species with the characteristic black felt-like hairiness of the calyx this is fully developed. However, the degree of development varies somewhat in all the species; most in *R. pygmaeus*, apart from *R. glacialis*, which, as stated above, is fairly aperiodical as regards the floral development also. The highest degree of development is reached by *R. nivalis* (Pl. 7, Figs. 26—27) and *R. pygmaeus* (Pl. 8, Fig. 1), as is also shown by the fact that sometimes all the rosette leaves of the shoot may be found to be developed the year before the flowering. The largest buds have reached the P. M. C.

stage, which stage is probably reached by the largest buds of all the species with the exception of *R. affinis*, which always seems to be somewhat behind the others (cf. Pl. 7, Fig. 22). (Of *R. auricomus* only plants collected on August 1st have been examined. Judging from the degree of development of the plant and from its production of leaves (one leaf) in the flowering year it must be assumed that in the wintering stage it is at least on a level with *R. affinis*). RESVOLL (1917, p. 92) states that *R. nivalis* (Scandinavia) winters with the pollen developed. However, in no case was I able to ascertain pollen in plants in the wintering stage in Northeast Greenland, either in this or in any of the other species

In spite of the advanced development before the wintering, the floral primordial development does not generally extend over more than one growth season Apart from *R glacialis* (cf. Pl. 7, Fig. 24), whose floral development doubtless in certain cases extends to the second growth period preceding the flowering, judging from the number of leaf primordia, cones of growth noticeably flattened "florally" have only in a few cases been observed in *R. pygmaeus* during wintering (cf. Pl. 8, Fig. 2). Such cones of growth must then be assumed to produce the most advanced buds next wintering.

The reduction division takes place in the spring, almost immediately after the melting of the snow, at any rate in the most advanced buds, at the time when the junctions of the winter bud begin to loosen.

The second group, the hydrophytes, comprises only two species, *R. hyperboreus* and *R. trichophyllus*. The latter sometimes develop land forms in localities in which, it is true, thaw-water may gather in the spring, but which dry up entirely in the course of the summer. It has been ascertained with certainty that the plant tolerated wintering in such a locality even without a constant snow-covering (Ella Ø, locality snow-free in February). *R. hyperboreus* frequently, perhaps most frequently, occurs in wet moss carpets. In both species the vegetative construction is entirely the same in land and water forms, with the difference that the internodes are much shortened in the land forms.

The wintering organs are simple shoots issuing from the axils of the leaves of the summer. They develop 2—4 leaves before the winter sets in; in *R. hyperboreus* they are rosette-like or with the lowermost internode elongated, while in *R. trichophyllus* they have long internodes. In *R. trichophyllus* all fully developed or half-developed leaves wither, in *R. hyperboreus* half-developed, often fairly long-stalked leaves remain fresh, succulent, and filled with starch. In *R. hyperboreus* a root is often formed before the wintering, while the wintering organs of *R. trichophyllus* are rootless. Next year the shoot continues its growth, forming

3—4 leaves and a terminal flower, while new wintering shoots are formed in the leaf axils. Further branching does not take place. Only quite exceptionally is a floral two-leaved shoot formed in the uppermost leaf axil in *R. trichophyllus*; this shoot may flower in the late summer. The wintering shoots are as a rule only detached passively by the destruction of the mother stem.

The shoot development accordingly takes two years. However, the new shoot generation may at times be present in the shape of quite small, just visible primordial formations in the axils of the not yet expanded leaves of the wintering shoots. If so, the lowermost innovation shoots actually have a "three-year" development.

All the leaves of the flower stem are present as primordia at the apex of the wintering organ, but the cone of growth is as a rule of a purely vegetative appearance (cf. Pl. 7, Fig. 25). Thus the floral primordial development is advanced to the flowering year.

The reduction division takes place while the flower buds are still quite small, enclosed in the uppermost leaf sheath.

*Thalictrum alpinum.* Hemicryptophyte with sympodial growth and long-lived axial parts—persisting up to about fifteen years—consisting of irregularly alternating erect short-jointed and horizontal long-jointed sections, whose delimitation does not necessarily coincide with that of the shoot generations but with that of the years' growths. The erect sections may represent one or several years' shoots, the horizontal sections only one year's shoot (actually only one half of a year's shoot). The erect years' shoots bear three scale leaves (bud scales) + (2—)3 foliage leaves, and normally terminate in an inflorescence or a new apical bud with bud scales and leaf primordia. The horizontal year's-shoots (subterranean stolons) bear a varying number of scale leaves (often about four) and terminate in a wintering bud, as in the rosette shoots. Only the rosette shoots develop directly from the wintering buds, whereas the runners are summer shoots, which represent the direct continuation of the axis of the leaf-bearing shoot, and in the last instance are nothing but axial parts with elongated internodes between the normal leaf-bearing shoot and its apical bud.

It would seem that the light factor may be decisive for the formation of stolons. If the wintering bud has been covered by a scanty layer of sand at the breaking up of the frost, the leaves appear above the new surface of the soil, while the shoot apex continues as a horizontal stolon. If a stolon is uncovered or happens to grow into the light during its growth, the scales of the stolon may develop into foliage leaves. The differentiation between aerial shoots and stolons may vary in other ways also, which might indicate that only slight external influences are required to change the habit of the shoot.

The most rapid shoot development apparently takes two years: first year: a scaly winter bud; second year: a leaf rosette and flowering. Actually, however, it takes three years, the bud formation having commenced a year before during the preparations of the mother shoot for wintering as a scaly principal bud. In most cases, however, the development is prolonged some few years, always with a year's growth of three scales + (2—)3 foliage leaves. A development lasting up to twelve years has been observed. When the shoot flowers, the sympode is continued by a principal bud (rarely two), formed in the axil of the uppermost scale leaf or the lowermost foliage leaf, with unfolding the succeeding year. Side branching of the rhizomes takes place in a corresponding way from the still vegetative year's-shoots, at the same time as the apical growth of the mother axis is continued. Proleptic development of "regulation" shoots with retarded flowering was observed in a single case.

In spite of their coriaceous character the leaves are not wintergreen.

Floral primordial development lasting one year, wintering stage slightly advanced. Flower axis and bracts formed, but the floral organs proper hardly differentiated (Pl. 8, Fig. 4). Time of reduction division not investigated.

*Rosaceae.*

Lit.: JESSEN 1913, RESVOLL 1917.

The family is chiefly represented by the genus *Potentilla* with seven species[1]), to which must be added *Sibbaldia procumbens*, which agrees entirely with the *Potentillae* in vegetative construction, more especially with *P. Crantzii*. The life-form represented by this group must be said to be the transition between H and Ch. Otherwise the family comprises only *Dryas*, a low dwarf bush, Ch.

1) *Dryas octopetala*[2]). Axial parts built up of sympodes. Rejuvenescence always from the axils of the uppermost foliage leaves. However, buds from the lower parts of the shoots often unfold, but develop only short-living few-leaved and small-leaved vegetative shoots. The shoot development is slow, mostly extending over six or seven years; even in vigorous plants less than five years have not been ascertained. Flowering shoots with up to about twenty years of development have been found. During the first two years hardly more than two leaves annually are formed, after which the annual number of leaves increases to four

[1]) *Potentilla stipularis* not investigated owing to lack of material.

[2]) In the investigation no account was taken of *Dryas integrifolia* (see p. 74). According to JESSEN (1913) the two *Dryas* species do not differ essentially in their rough morphology.

in the last one or two years before flowering. Two or three foliage leaves are developed in the flowering year. The innovation buds are initiated the same year as the flower buds. Their further development varies, but in vigorous shoots one or two small foliage leaves may be formed in the same year (prolepsis). Mostly the first foliage leaves are developed the succeeding year (the flowering year of the mother axis). The wintering buds (shoot apices) are open; half-developed leaves winter and continue the growth next year (cf. JESSEN l. c. Fig. 26, p. 64); the individual years' shoots are therefore hardly recognisable by differences in the size of the leaves. Withered leaves are not shed. *Dryas* is often reported to be evergreen (for literature cf. JESSEN l. c. p. 65). GELTING (1934, p. 99) states about the area dealt with here: "The plant is evergreen, and the life-time of the individual leaves seems to be from two to three years." I cannot confirm this, as all fully developed leaves seem to wither in the autumn.

The order of development of the floral organs is periodical, flower buds usually wintering in approximately the same phase of development (Pl. 8, Figs. 5—6). Anthers are formed, though they are far from the P. M. C. stage. Carpels but slightly developed. The floral primordial development is limited to one growth season before the flowering. Reduction division takes place about a fortnight after "leafing", even before the flower buds have become visible.

2) The species of the *Potentilla* group have an unlimited monopodial main axis and lateral floral axes with a functional period of one year. The main axis is short, erect, with very closely-set leaves in all the species except *Potentilla Crantzii* and *Sibbaldia procumbens*, which have a prostrate growth and slightly elongated internodes. In the species with erect main axes there is no branching of the older axes, no vegetative buds being usually formed after the first flowering has taken place. The basal innovation buds capable of forming new main axes often remain during a number of years in a permanent bud state with development of about two new "bud scales" every year. However, most of them never develop into leaf-bearing shoots. Branching from the base is most lively in *P. emarginata* but is likewise frequent in *P. pulchella*. In *P. nivea*, *P. rubricaulis*, and *P. rubella* there is very often only one main axis, all the lateral "shoots" remaining in the permanent bud state. *Potentilla Crantzii* and *Sibbaldia*, too, have chiefly branching from the base, though sometimes from the higher leaf axils, since vegetative buds alternating with floral ones may constantly form in these species.

The growth is slow. Both young plants and secondary main axes of older plants do not develop floral shoots till after a number of years. A young plant of *P. nivea* from a favourable locality was at least 15

years old before flowering for the first time. The addition in length of the main axis of older plants of *P. nivea* only amounts to 1—3 mm annually. Judging from the length of the axes plants of an age of 75—100 years are of common occurrence. In *P. rubella* the differential development proceeds much more rapidly than in the other erect species. Secondary main axes flower already after 2—3 years, and the monopodial side shoots are restricted to the 3—4 lowermost leaf axils.

The yearly production of leaves on main axes with floral shoots seems to be constant to a certain extent except in *P. Crantzii*, where it may vary from four to eight. The number of leaves otherwise varies from three in *Sibbaldia* to about seven in *Potentilla pulchella*. It is remarkably low, only about four, in *P. rubella*, considering that the occurrence of the species is limited to fairly favourable localities both as regards exposure and supply of water.

The number of the floral axes as a rule varies more according to the vigour of the plant than does the number of the leaves. The floral shoots may be initiated periodically, as only a limited number of the leaves of the year's shoot subtend such shoots. In such case the floral shoots are more rarely destroyed during the development. Such a periodical development takes place in *P. nivea*, *P. rubricaulis*, *P. Crantzii*, and *Sibbaldia procumbens*. In other cases the floral shoots are formed continuously in all or in most leaf axils of the main axes; destroyed floral shoots, arrested in their growth at different stages of development, are in such cases of frequent occurrence. Such an aperiodical floral development is found in *P. emarginata* and *P. rubella*. A position between the two types is occupied by *P. pulchella*.

The shoot apices pass the winter in different stages. In *P. nivea* and *P. rubricaulis* the winter buds are rather compact and well delimited, as all more or less expanded leaves wither in the autumn. The buds of *P. pulchella* are somewhat looser and hardly so well defined. In *Sibbaldia* and *Potentilla Crantzii* leaves whose laminae are in incipient unfolding in the autumn persist during the winter; their buds are large and loosely closed. Even more open buds are found in *P. rubella*, the extreme point being reached by *P. emarginata*, of which the central parts of the rosette, the half-developed leaves, normally winter, to continue their growth next spring.

The buds of the floral shoots of the succeeding year are formed at different distances from the apex of the main axis in the different species. In *P. nivea*, *P. rubricaulis*, and *Sibbaldia* they are initiated in the axils of the latest expanded leaves of the year, and in accordance with this fact the flowering shoots are situated immediately outside the central green leaf rosette in the axils of withered leaves. In *P. pulchella* they are situated nearer the apex of the shoot, and their primordia are chiefly

formed in the axils of non-expanded leaves; accordingly the majority of the flowering shoots stand in the axils of the outermost green rosette leaves, the lowermost, however, as a rule immediately outside the rosette leaves. In *P. Crantzii*, however, the floral shoots are situated farther from the apex, being chiefly limited to the central part of the preceding year's growth. In *P. emarginata* floral shoots often develop in all the leaf axils of the main axis, and in *P. rubella* they always do so. In *P. rubella* the development of the shoots is lively in the central part of the year's growth of the main axis, while the lowermost and uppermost shoot or shoots are as a rule arrested in development sooner or later. Finally, the uppermost floral shoots of *P. emarginata* spring from the axils of green rosette leaves; however, the place of the flowering shoots within the green rosette is not in the same degree as in *P. pulchella* a result of the displacement of the floral axes towards the apex, but is evidently chiefly due to the limit of the green leaves being shifted backwards as a consequence of the continued growth of the half-developed leaves after wintering.

The primordial development of the floral axes is chiefly limited to the growth season preceding the flowering, though in species whose floral development is well advanced during the last wintering (*P. Crantzii*, *P. emarginata*, *P. rubella*) the formation of the first stages takes place two years before the flowering.

There is a certain correlation between the degree of floral development during the wintering and the place of the floral shoots in relation to the apex of the monopodial axis; the farther back they are situated, the more advanced are they in development. An especially advanced stage of development is often exhibited by *P. Crantzii*, whose floral shoots even frequently show incipient expansion of the leaves before wintering. In the flowering year the lowermost leaf or leaves are therefore often withered. If so, the flower buds proper are but slightly protected during the winter. The anthers are formed, though the P. M. C. stage is hardly reached. The carpels show incipient formation of the style, and the ovules are often just recognisable (cf. Pl. 8, Figs. 7—8). *P. nivea* and *P. rubricaulis* show a much less advanced stage of development; yet the anthers are formed, but the carpels are but slightly developed (cf. Pl. 8, Figs. 13—14). *P. pulchella* is even considerably less developed (Pl. 8, Fig. 15), and in *Sibbaldia* the anthers are hardly, and the carpels not at all, differentiated (Pl. 8, Fig. 16).

In the aperiodical species *P. emarginata* and *P. rubella*, all stages, from buds with pollen and downwards, are sometimes to be found (cf. Pl. 8, Figs. 9—12). Whether buds with pollen develop after wintering, cannot be decided with certainty. At any rate the flowers first expanded are often remarkably black in the centre because the carpels and the

receptable have withered. In such cases the anthers may (apparently) be normally developed, while in other cases the anthers, too, are destroyed. Possibly there is a maximal limit to the development which cannot be exceeded without destroying the flower buds or the whole shoot. Floral shoots whose elongation has commenced noticeably before the wintering do not continue their growth the succeeding year. Mostly, however, the development is not entirely aperiodical in these species. The most advanced stages are lacking, or there is a certain difference in size between "retarded autumnal shoots" and the first shoots of spring, a difference which at any rate in *P. emarginata* may be further marked by a leaf between the two years' series being without axillary buds. Certain forms of the polymorphic *P. nivea*, especially from damp soil, may show similar signs of aperiodicity.

Reduction division in the spring at the time when the flowering stems begin to elongate or immediately before.

### *Salicaceae.*

Lit.: RESVOLL 1909, 1917.

Two species of the *Salix* genus. Deciduous dwarf bushes, chamaephytes. The vegetative construction differs. The woody stems of *S. arctica* are wholly above-ground, built up of sympodes, those of *S. herbaceae* partly under-ground (runners) partly above-ground. As long as the shoots are subterranean, the growth continues monopodially; when they have reached the surface of the ground, after the lapse of one or several years, the growth becomes sympodial.

*S. arctica* shows a marked shoot dimorphism: 1) Vegetative long shoots, which are constantly destroyed at the apex, as the last primordia of the bud do not develop further. The long-shoot sympodes, which alone form the persistent trunk of the plant, continue from the uppermost leaf axil. 2) Floral short shoots, issuing from the lower leaf axils of the long shoots. These shoots have a functioning period of one year and wither and are shed after flowering or ripening of the fruits. This form of shoot dimorphism does not occur in *S. herbacea*. The catkin is here terminal on the usual shoots, which constitute part of the persistent stems. Continuation of the axial parts is effected in the usual way by shoots issuing from the axils of the leaves. Non-flowering year's-shoots are destroyed at the apex, precisely as the long shoots of *S. arctica*. The persistent stems are always built up of sympodially connected joints, that is to say, in entirely the same way in flowering and non-flowering sympodes. The subterranean runners bear scale leaves and may continue their growth monopodially, at any rate during three years. They often issue side branches, which, like the mother shoot, sooner or later continue in aerial shoots.

The above-ground wintering buds have one hood-shaped closed bud scale formed of the coalescent prefolia. In *S. herbacea* the subterranean shoot apices are without protection, in appearance like the rhizomes of many herbaceous dicotyledons.

The yearly production of leaves, here meaning the number of leaves per shoot generation, is in *S. arctica* for long shoots 4—6 (4 being especially frequent) for floral shoots 2—3. Above-ground year's-shoots of *S. herbacea* have 2—3 leaves, two would seem to be the most frequent. Above-ground branches of this species often exhibit a very limited longitudinal growth, for instance: a branch 2 cm long comprising nine year's-shoots with two leaves each. Thus in this case the year's growth is only about 2 mm.

In all aerial shoots the development apparently takes two years (including the bud stage); actually, however, it takes three years, the first primordial development (growing point and prefolia) already commencing in the leaf axils of the wintering buds (Pl. 8, Fig. 20). But the primordial development of the catkins does not extend beyond the growth season preceding the flowering. Floral shoots wintering in the bud stage have fully developed catkins with long-haired scales. In both species the anthers are formed as such, but without any, or at any rate without any distinct, P. M. C. Ovary closed, ovules developing (cf. Pl. 8, Figs. 17—19). *S. herbacea* (Pl. 8, Fig. 21) seems to be somewhat less advanced in development than *S. arctica.*

Reduction division takes place in the spring, in *S. arctica* at the time when the catkin has reached about half of its full length. For *S. herbacea* the time has not been closely determined.

### *Saxifragaceae.*

Lit.: Holm 1922, Lindmark 1902, Resvoll 1917, Warming 1909.

Thirteen species of the genus *Saxifraga*, of other species only *Chrysosplenium tetrandum*. The species are either hemicryptophytes or chamaephytes. They exhibit an abundant variety of morphological and biological characters, they will therefore be dealt with in groups here according to their vegetative construction, as follows:

Group 1. *Saxifraga aizoides*, *S. Nathorsti*, *S. oppositifolia.*
Group 2. *Saxifraga caespitosa*, *S. tricuspidata*,
Group 3. *Saxifraga flagellaris.*
Group 4. *Saxifraga Hirculus.*
Group 5. *Saxifraga hieraciifolia*, *S. nivalis*, *S. nivalis tenuis*, *S. stellaris comosa.*
Group 6. *Saxifraga cernua*, *S. rivularis*, *Chrysosplenium tetrandrum.*

Group 1. *S. aizoides. S. Nathorsti, S. oppositifolia.* Winter-green chamaephytes, the last-named species with a perennial tap-root, the first-mentioned species with adventitious root formation, main root and axial parts long-living, about 20 years. In this as in other respects *S. Nathorsti* is intermediary, sometimes with adventitious roots. Sympodes without any definite constructional order. Rejuvenescence often from the base of the shoots, but otherwise arbitrary. The species agree entirely with the *Alsinoideae* in outer morphology, leaf development, and wintering state. Leaves functioning two growth seasons, transition from primordia to fully developed leaves perfectly even, for most leaves the growth extends over two growth years. No recognisable boundary between the years' growths. Shoot apices in wintering state open, without bud protection of any kind. *S. oppositifolia* often shows shoot dimorphism, though not very radical, as long shoots may form which at last flower. These shoots have especially long internodes and bear short floral shoots which, like the usual flowering shoots, are capable of forming innovation shoots from the axils of the leaves. However, many die after flowering and fructification.

The development of the shoots never takes less than four years, often more. The number of leaves during the vegetative years increases from year to year. Evidently no formation of flower buds takes place till the leaf production characteristic of each species within one growth season has been reached, viz. c. 15, c. 10, and c. 8 for *S. aizoides*, *S. Nathorsti*, and *S. oppositifolia* respectively, for long shoots of the last-named species almost twice the number, for short shoots often a smaller number. The short shoots often develop proleptically, and the subtending leaves wither one year earlier than in normal shoots (similarly as in *Cerastium alpinum*). Besides, prolepsis occurs occasionally in *S. Nathorsti*, but not in *S. aizoides*, in which rejuvenescence often proceeds very slowly; often the actual growth of the innovation shoots from the base of the mother shoot generation does not begin till the flowering year of the latter.

In accordance with the type of growth there is hardly any recognisable morphological periodicity in the vegetative construction. In *S. oppositifolia*, however, the shoot development is periodical to a certain degree. The floral development of this species is likewise periodical, in *S. aizoides* it is more or less aperiodical, and in *S. Nathorsti* it is as a rule almost entirely aperiodical. During wintering the flower buds are covered by the last, not expanded leaves. In their wintering state the buds of *S. oppositifolia* are fully developed, and anthers and petals are deeply coloured (cf. Pl. 9, Figs. 12—14). The anthers probably as a rule contain P. M. C., but the ovules are not fully developed. In plants from localities which become snow-free at an early date pollen evidently never occurs,

whereas pollen is not rarely found in plants from snow-patches. Such buds with pollen may possibly be retarded from the preceding summer. More probably, however, we are here concerned with special biotypes, all the more so since the species is highly polymorphic and has a wide ecological amplitude. Buds in the same phase of development as the normal ones of *S. oppositifolia* are frequently found in *S. Nathorsti*, but, in addition, very often buds with pollen as well as all younger stages. Accordingly the flowering of this species extends over the greater part of the summer. In *S. aizoides* the flower buds are but slightly developed. Only in the largest buds (Pl. 9, Fig. 1) are the anthers just differentiated, but a broadened cone of growth with an incipient or no differentiation of the floral parts is most commonly found (Pl. 9, Fig. 2). The floral development hardly extends beyond the growth season preceding the flowering in any of the species.

Group 2. *S. caespitosa*, *S. tricuspidata.* Chamaephytes with a perennial tap-root and without any formation of adventitious roots. Rejuvenescence from the uppermost leaf axils. Vegetative buds initiated simultaneously with the flower buds, opening next year. Leaf development and wintering chiefly as in Group 1. Leaves of *S. caespitosa* thin, withering early in the second year of function; in *S. tricuspidata* leathery and stiff, functioning period three years (excluding the primordial stage).

The development of the shoot takes four years or more. The yearly number of leaves increases in the course of time to about 10 in *S. caespitosa* and about 12 in *S. tricuspidata.* Order of development for vegetative shoots and flower buds in *S. caespitosa* is mostly aperiodical, in *S. tricuspidata* almost periodical. Flower buds of *S. tricuspidata* in wintering state somewhat varying, in the largest the anthers are differentiated, and open ovaries are present; first bulging of the ovules on placenta visible. Buds, somewhat less developed, occur too. The flower buds are extremely unprotected, the leaves around the shoot apex being much recurved. *S. caespitosa* may have flower buds in very different stages of development, from the P. M. C. stage downwards (cf. Pl. 9, Figs. 3—6). Pollen-bearing buds were not observed. The floral primordial development takes one year in *S. tricuspidata*, whereas in *S. caespitosa* it takes two years for the most advanced buds, one year for the others. The two-year floral development is reflected in a remarkable way in the vegetative construction of the plant, the shoots with highly developed floral stages having two series of innovation shoots. The first series is initiated in the usual way, at the beginning of the primordial development of the flower buds, in the axils of the half-developed leaves at a certain distance from the cone of growth. As the development of the flower bud extends over one more growth season, the vegetative buds

first formed unfold that year at the same time as a new series is formed in the axils of the now half-developed leaves. The last-mentioned series unfolds in a normal manner in the flowering year. The number of foliage leaves on the main axis in the flowering year is in close correlation with the developmental degree of the flower buds during the wintering. If the buds are large, only a few leaves are developed, and the uppermost innovation shoots have a very vigorous development; if the buds are small, a large number of leaves develop on the flowering axis, while the innovation shoots attain a slight development only (similarly as in *Ranunculus glacialis*).

Group 3. *Saxifraga flagellaris*. Chamaephyte with rosettes which flower once; from the leaf axils of the rosettes there issue slender, leafless, above-ground flagellae, which form new rosettes at the apex. Apart from the fact that the shoot generations are separated and live independently after the formation of adventitious roots, the plant shows great resemblance in several respects to *S. caespitosa*; as in the latter, the leaves wither early in the second year of function. In most cases rosette-bearing flagellae are formed in the flowering year only; the flagellae are subtended by the withering leaves; that is to say, not till the year in which the flower buds are initiated will axillary vegetative buds be produced (cf. Pl. 9, Figs. 8—9).

Floral wintering stages vary as in *S. caespitosa*. The investigation material was too insufficient to allow of a direct demonstration of a two-year primordial development of the largest buds (the youngest floral stages, the first wintering stage, not observed). However, a comparison with *S. caespitosa* suggests that two consecutive floral winterings may occur, for plants may occasionally be met with which form flagellae the year before flowering, and whose formation of flagellae continues in the higher leaf axils in the flowering year (cf. *Saxifraga caespitosa*). GELTING's statement (1934, p. 122) that the species flowers at different times of the summer, agrees with the aperiodical development.

Shoot development (actually development of individuals) very slow. Flowering rosettes younger than five years not observed (i. e. six years' development including the bud stage). A nine or ten years' development is the most frequent; plants twelve years old have been ascertained with certainty. Still older plants, whose age, however, could not be more precisely determined, sometimes occur. Yearly number of leaves increasing from six to about twelve; the latter number of leaves seems to be necessary for flowering.

Group 4. *Saxifraga Hirculus*, hemicryptophyte. The axial parts, short erect rhizomes, are formed of sympodes with adventitious root

formation. The rhizomes die off behind after a functioning period of 10—15 years. All the green parts of the plant wither in the autumn. The wintering buds are well defined, with the young leaves closely packed, of the same type as those of the *Melandryum* species. Rejuvenescence almost exclusively from the upper leaf axils. In agreement with the late formation of the flower buds, the invigoration buds do not become visible till the flowering year and they do not unfold till the year after the flowering of the mother shoot. The shoot development takes 3—7 years, most frequently four or five years. The yearly number of leaves in the vegetative years is nearly constant, though increasing from about 6 to about 8. Order of development for floral as well as vegetative organs periodical. The floral development during the wintering is inconsiderable. The floral organs are but slightly differentiated, the calyx and the first whorl of anthers being just recognisable in those most advanceed in development (cf. Pl. 9, Figs. 10 and 11).

Group 5. *Saxifraga hieraciifolia*, *S. nivalis*, *S. nivalis tenuis*, *S. stellaris comosa*. Rosette-hemicryptophytes with short erect rhizomes composed of sympodes with adventitious roots. In *S. stellaris comosa* no rhizome is formed, as the older axial parts are very soon destroyed; in the other species the rhizome dies off behind after a number of years, in *S. hieraciifolia* after 10—15 years; in *S. nivalis* (incl. *var. tenuis*) after 15—20 years. Rejuvenescence always takes place from the uppermost leaf axil or axils. The innovation buds are initiated simultaneously with the flower buds, and in *S. stellaris comosa* and *S. nivalis tenuis* they develop rosette leaves in the flowering year of the mother shoot. In *S. hieraciifolia* the innovation bud increases in size in the flowering year, but does not generally unfold till next year. Both types are represented in *S. nivalis* (the main species). The time of the unfolding evidently depends on whether the mother shoot develops a few or many leaves in the flowering year, the smaller the number on the mother shoot, the greater the number on the daughter shoot. The leaves pass the winter in a green state, but wither in the course of the succeeding summer. *S. hieraciifolia*, however, is not actually winter-green as the others; only the leaves last developed persist during the winter, but they wither very early next summer. The shoot development is relatively rapid, as a rule it takes three years, though in *S. hieraciifolia* at least four years. The annual number of leaves is 4—8, being lowest in *S. nivalis tenuis* and highest in *S. hieraciifolia*. In *S. stellaris comosa* the growth of the majority of leaves is often continued over two years, many partially developed rosette leaves subsisting during the winter. The shoot sequence in the *S. nivalis* forms and in *S. stellaris comosa* is rather aperiodical, as the limits of the years' growths may be inserted at an

arbitrary place in the succession of leaves of the shoot generations. *S. hieraciifolia*, however, is as a rule periodical.

The floral development is much advanced during the wintering, P. M. C. however, hardly formed. The forms of *S. nivalis* are the most advanced, var. *tenuis* being as a rule a little farther advanced than the main species. However, their phase of development is not very constant, younger stages being frequently found. *S. hieraciifolia* is somewhat less advanced in development, but more constant. In *S. stellaris comosa* the inflorescence axes as a rule bear only viviparous buds (Pl. 9, Fig. 16), while only the most vigorous plants form a single flower at the apex. Such flower buds were not examined in their wintering stage. The bulbil clusters pass the winter at fairly different, evidently causal stages of development. The plant is "florally" as well as vegetatively aperiodical. The bulbils seem to survive the winter, no matter in what phase of development they are.

Group 6. *Saxifraga cernua*, *S. rivularis*, *Chrysosplenium tetrandrum*. Hemicryptophytes. Morphologically as well as biologically it is a fairly heterogeneous group, whose extreme forms, *Saxifraga cernua* and *Chrysosplenium*, however, are associated in certain respects with *Saxifraga rivularis*, which appears in two forms, one of which, var. *purpurascens* LANGE (1880, p. 62), lacking runners, resembles *S. cernua*, while the other, with runners, comes nearer to *Chrysosplenium*.

The axial parts consist of sympodially united rooted joints, whose lifetime extends over a relatively small number of years. Innovation buds are found in all leaf axils. As a rule the greater number of them are developed, the uppermost ones producing the most vigorous shoots.

*Chrysosplenium* exhibits the most primitive structure. The vegetative axial parts are thin, long-jointed, horizontal rhizomes, creeping among damp moss or other loose material. All leaves are developed as foliage leaves, the most shaded, however, sometimes having a small-sized blade. The shoot development extends over 3—4 years. The sequence of the development of leaves and shoots is continual, that is to say aperiodical, in vigorous shoots with a gradual transition to proleptic shoot development. The shoot apices are the same summer and winter; the growth of the individual leaves often extends over two growth seasons.

*Saxifraga cernua* has a short erect main axis. All shoots commence (first year of growth after the bud stage) with a set, four or less, of scale leaves, which are thick and filled with nutritive matter, the first year's shoot being thus almost a small bulb. The bulb winters, serving as a reservoir of nourishment, and is emptied during the continued growth next spring. In the uppermost innovation shoot, which is the most vigorous, foliage leaves plus a new series of bulb scales for wintering

will then be formed. In the weaker lateral shoots foliage leaves are as a rule not formed till the third growth year; for in the second growth year only a larger bulb is formed in continuation of the old one, which is, in turn, emptied of nutritive substances. During the following years alternately foliage leaves, which wither in the autumn, and bulb scales, which persist during the winter, are formed. In the first two growth years the shoots receive their nutrition from the mother plant, later on a formation of adventitious roots may take place. While the bulb shoots are still receiving their nutrition from the mother shoot, they may form lateral bulbs of the second order. Thus young bulb shoots in large numbers arise. They are easily detached and, in the same way as the bulbils from the axils of the upper stem leaves, serve in the propagation of the plant (the species evidently never produces seeds). The development of the uppermost shoot, including the bud year, as a rule takes four years, of the lateral shoots hardly less than seven years and often more. Exceptionally the principal (uppermost) bud has only a three years' development, since vigorous plants may develop foliage leaves already in the first growth year before the wintering bud is formed. In that case the shoot generation accordingly starts with foliage leaves.

In *S. rivularis* the erect main axis is built up like that of *S. cernua*, with the difference that only foliage leaves are developed. The innovation shoots are of two kinds: 1) The uppermost shoot (the principal innovation shoot) forms foliage leaves already in the flowering year of the mother shoot. 2) The lower buds form a rhizome in the first growth year, with about three somewhat succulent scale leaves and with a bud at the apex. This bud develops rosette leaves next year, precisely as the principal innovation shoot the year before. Sometimes, when the plant grows in very loose material, the rhizomes may develop foliage leaves instead of scale leaves, and the similarity to *Chrysosplenium* is then remarkable. The above-mentioned mode of development applies to the main species, whose occurrence within the area is chiefly limited to relatively dry shore lagoons with an abundant moss vegetation. Far commoner, however, is *var. purpurascens*, which does not form runners. The construction of the shoots is precisely the same as that of the main species, except that the internodes between the scale leaves of the lateral shoots do not elongate; so in the first growth year a bud with thick scale leaves is formed directly on the main axis. Like the corresponding runner shoots of the main species it develops foliage leaves in the second growth year. Thus the development of the lateral shoots takes at least one year more than that of the principal shoot. The resemblance in the vegetative construction between the last-mentioned form and *S. cernua* is evident. The exceptional three-year development of the innovation shoot of *S. cernua* with direct formation of foliage

leaves in the first growth year corresponds entirely to the normal development of the upper shoot of *S. rivularis*, the development here likewise taking three years.

Functioning period of the leaves: In *S. cernua* foliage leaves wither in the autumn, and scale leaves formed one year wither next year. Considering that in *S. cernua* the foliage leaves within the year's shoot are situated below, and the scale leaves destined to winter above, it will be seen that the lifetime of the leaves of *S. rivularis* is entirely similar: The leaves developed first within a growth season in this species wither in the autumn, while those developed last persist during the winter and wither rather early next summer. Thus for instance the leaves of the innovation shoot remain fresh during the winter, while its subtending leaf, likewise expanded in the same summer, withers. *Chrysosplenium* behaves in a similar way. The greater number of the leaves remain green during the winter, but wither early next summer.

The yearly number of (foliage) leaves per shoot in the species of this group is inconsiderable, three or four. The yearly production of leaves of the sympodes constituting part of two consecutive shoot generations is highest in *S. rivularis*, being up to six leaves.

The order of floral development in *Chrysosplenium* is fairly aperiodical while it is periodical in *S. cernua* and *S. rivularis*. In *S. rivularis* few-leaved regulation shoots with a somewhat retarded flowering may sometimes be met with. The flower buds of all three species are very slightly protected during wintering. In both the *Saxifraga* species the phase of development is fairly much advanced, *S. cernua* being evidently as a rule a little ahead of *S. rivularis*; however, the P. M. C. stage is hardly reached in any of the species (cf. Pl. 9, Figs. 7 and 15). *Chrysosplenium* frequently shows a wintering stage in which the earliest flowers of the cymules contain pollen (cf. Pl. 8, Fig. 22). Inflorescences containing pollen throughout seem to be more frequent than those entirely without pollen. Considerably less advanced stages of development are not lacking (cf. Pl. 8, Figs. 23—25), but numerically they are more sparsely represented. The development proceeds at a rapid rate, and the floral primordial stage, even of the most advanced inflorescences, hardly exceeds that of the last summer before the flowering.

*Chrysosplenium tetrandrum* is the only species within the *Saxifragaceae* which normally has an extensive pollen formation in the autumn. In *Saxifraga Nathorsti* and especially in *S. oppositifolia*, however, it is rather an exception. Otherwise the formation of pollen takes place in the *Saxifragaceae* early in the spring and summer. Reduction division occurs at a time when the flower stem has just commenced to be elongated; in *S. stellaris comosa*, however, much later. Occasional buds from partially elongated stems, which were examined, had not by far reached the

stage for reduction division. A non-closed bud, c. 2 mm broad, at the apex of an almost fully developed stem, examined on July 17th, 1935, contained pollen and P. M. C. In other species also, for instance in *S. cernua* and *S. rivularis*, the flower buds are not, or only incompletely, closed during the development (cf. for instance Pl. 9, Figs. 5 and 15).

### *Sympetalae.*

### *Campanulaceae.*

Lit.: Holm 1932.

Two species of the genus *Campanula*, agreeing in all essentials in their vegetative construction. Hemicryptophytes with a perennial thick tap-root, from whose crown, in older plants, there issue horizontal root-like and perennial rhizomes, which especially in *Campanula rotundifolia* may be fairly widely branched and give rise to a whole clone, still exclusively or chiefly receiving its nutrition from the main root. The main axes (which in older plants are accordingly of a higher order) have closely packed leaves and unlimited monopodial growth with erect floral shoots issuing from the axils of the leaves. The rhizomes, which during the growth are very thin and provided with scale leaves, always issue from old axial parts and arise from old "dormant eyes". At the base they are mostly provided with a collar of old scale leaves (bud scales). Their longitudinal growth is completed in the course of one summer. The apical bud may sometimes form a foliage leaf the same year, but as a rule it winters near the surface of the soil and after wintering produces rosette leaves. On vigorous main axes floral shoots may form in the second rosette year, though as a rule later. Until the appearance of the first floral shoots the two species behave in all essentials alike, whereas they differ in their continued development.

*C. rotundifolia* develops about four (3—5) rosette leaves a year. The development of leaves takes place continually until it is arrested by the frost (if drought has not interrupted the growth at an early date). Floral shoots are formed in all leaf axils. The lowermost shoots of each growth season are situated below (outside) the green rosette leaves, that is to say, in the axils of the last rosette leaves of the preceding year, the uppermost shoot or shoots in the axils of the first rosette leaves of the present year. The lowermost shoot is often weaker than the succeeding one; the last one or ones as a rule do not attain full development before being destroyed by the frost. Thus the order of development of the floral shoots is continuous like that of the leaves. It clearly depends exclusively on the degree of development at the time when the frost sets in whether a floral shoot is killed as the last shoot of the year

or is developed after wintering as the first one next year. Not rarely the first floral shoot has a different appearance, as the greater number of the internodes do not elongate. Nearly all the stem leaves are gathered in a rosette-like way near the base; at the same time they obtain a shape differing from the normal shape of stem leaves but reminding one of that of the basal leaves, while only the uppermost internodes of the stem will elongate, even out of all proportion, like a "leafless" scape. There is hardly any doubt that such shoots mark the maximal winter phase of development on which a successful wintering depends. Non-appearance of the elongation of the internodes as a consequence of the influence of the frost in stems or inflorescence axes which have passed the winter in an overoptimal phase of development, is well known from other species; it is for instance very frequent in the *Cruciferae*. The number of leaves of the floral shoots is large, mostly 20—25, not rarely about 30. Only about 12—18 are present as primordia during the wintering, and the cone of growth is always purely vegetative (cf. Pl. 9, Fig. 17). Accordingly not only the flower but also the last 10—15 stem leaves are not initiated till the flowering year.

*C. uniflora* forms only foliage leaves on the monopodial main axis as long as this is still too weak to develop floral shoots. The first year a floral shoot appears it is often so weak that it does not flower, and the main axis then as a rule still bears foliage leaves. Later on the main axis only develops scale leaves, in whose axils the leaf-bearing floral shoots are developed. Three or four, as a rule only three, scale leaves are formed annually. Buds are formed in all leaf axils, but the developmental sequence of floral shoots is periodical, so that the axillary bud in the uppermost one or two is not developed beyond the first primordial stage. Occasionally the last leaf on the main axis, which does not subtend any shoot, develops as a foliage leaf. The rosettes grow very old, but at last they grow weaker and in the last years of their life again form foliage leaves, while the floral shoots degenerate or are entirely suppressed. At the same time a rejuvenescence takes place from the lower part of the axis, one of the dormant buds among the remnants of old floral shoots unfolding into a new monopodial axis, which, as usual, develops rosette leaves in the first year only, but scale leaves and floral shoots later on. This form of rejuvenescence does not seem to take place in *C. rotundifolia*, and very likely cannot take place at all, as probably all axillary products on the flowering main axes unfold at once. On the other hand, the formation of rhizomes from the old rootstock (and from the old runners of a lower order) is more lively in *C. rotundifolia* than in *C. uniflora*. The floral shoots of *C. uniflora* bear 8—10 leaves. The periodicity in the sequence of development is marked, the apical bud of the main axis and the primordia of next year's floral

shoots showing almost a hibernal appearance as early as in the summer when the plant flowers. In the wintering stage the primordia of the floral shoots project beyond the apices of the subtending scale leaves, all the stem leaves are initiated, and the same applies to the flower, which has even distinctly formed corolla and anthers (Pl. 9, Fig. 18). The hypogynous ovary may be closed at the apex, united so as to form a process (the style) in the centre of the flower. Formation of ovules not yet commenced.

In both species reduction division does not take place till the stem has been partially elongated and the flower bud is plainly visible.

*Compositae.*

Ten species, seven of which are hemicryptophytes, three mesocorm-chamaephytes. The stem axes are always built up of sympodes. All or the greater number of the leaves are basal, gathered in a rosette.

A number of species show a certain, though far from complete, agreement in vegetative construction, in that rejuvenescence only, or at any rate chiefly, takes place from the axils of the uppermost rosette leaves. The innovation buds unfold in the flowering year of the mother shoot, often from the axils of green leaves developed the same year, sometimes also, or exclusively, from the axils of one year old withered leaves. These species are: *Antennaria alpina*, chamaephyte with elongated mesocorm and lively formation of adventitious roots; the three *Erigeron* species, of which *E. compositus* is a chamaephyte with a tap-root and perennial branched main axes; *E. unalaschkensis* and *E. uniflorus* are hemicryptophytes, in which the older axes die off and which have a lively formation of adventitious roots; finally, the four *Taraxacum* species, which are hemicryptophytes with a persistent tap-root and a short, thick, root-like mesocorm. None of the eight species mentioned have developed special organs to protect the winter buds, and none of them are actually winter-green. In the two chamaephytes, *Antennaria alpina* and *Erigeron compositus*, partially expanded leaves do indeed winter in a green state, but they do not continue their growth next summer. *Erigeron unalaschkensis* and *Taraxacum arcticum*, too, which are always covered with snow during the winter, may be "winter-green". Here as in many snow-patch plants, we are merely concerned with leaves which have developed late and which are preserved in a fresh state below the snow, though they may properly be said to wither at the end of the winter rather than at the beginning of the summer; they hardly continue to function after the wintering. In the other species the leaves wither in the autumn, and the winter buds are well defined. In *Taraxacum phymatocarpum* and *T. pumilum* the wintering buds are

surrounded by durable basal parts of the withered leaves from earlier years.

The shoot development of the *Taraxacum* species takes three years, of the other species mostly four years or more. However, all species may have a three-year development. The annual number of leaves in the *Taraxacum* species is fairly constant, while in the *Erigeron* species and especially in *Antennaria* it varies greatly.

Only in *Erigeron compositus* is a distinct minimum of yearly leaf production required, if floral primordia are to be formed. If the innovation shoot of this species is so vigorous that at least ten leaves are expanded in the first growth year, a primordial flower bud will form in that year, and the development will thus take three years. Less vigorous shoots continue the rosette stage the following year or years until the production of leaves within a single growth season amounts to ten (or more). On examination of old shoot-chains it is seen that a particularly large number of shoots end in a destroyed flower head in a stage of development as a rule somewhat more advanced than, or sometimes equivalent to, the "normal" wintering stage (cf. Pl. 9, Fig. 26). It is noteworthy that in such cases the innovation shoot most frequently (apparently) has a three-year development, that is to say, the number of leaves rises to at least ten even in the first growth year. The sequence of development for the vegetative shoot formation as well as for the flower buds is largely aperiodical, and there can hardly be any doubt that the destroyed flower heads are such whose rate of development has not harmonised sufficiently with the rhythm of the climate. They seem to be retarded flower heads, whose growth, however, has been arrested at some time or other before the winter sets in. That the destroyed heads are hardly such as have been destroyed by the frost of the winter on account of a too early development, appears from the fact 1) that the flower buds are normally formed rather late in the autumn, and 2) that in shoots with destroyed heads the innovation buds do not, as a rule, open in the normal year, but not till the following year. Thus, as stated above, the rapid development of the innovation shoot in the first growth year seems to be a natural consequence of the phenomenon that the growth—one year too late, it is true—may begin immediately next spring, starting from a bud stage which is more advanced in development than is normally the case. The floral primordial development seems never to go farther back than to the summer before the flowering, even hardly farther back than to the latter part of the summer.

*Antennaria alpina* has likewise a partially aperiodical order of development of its organs. However, destroyed inflorescences evidently do not occur. The floral development during the wintering is somewhat

varying, as a rule but little advanced (Pl. 9, Fig. 20). The flowers are only indicated as projections on the receptacle of the inflorescence. In plants growing in soil with a relatively prolonged snow-covering a two years' primordial development of the floral organs may apparently occur (cf. Pl. 9, Fig. 19), manifested in the same way as in *Saxifraga caespitosa* (p. 131) by the fact that the innovation shoots do not sprout in the flowering year, as would normally occur, but the year before, and that only a very small number of rosette leaves (2—3 as against normally 6—12) are developed in the flowering year. The inflorescence must accordingly have wintered (last time) in a much advanced stage. The shoot development extends over a different number of years. Plants growing in fairly damp soil have as a rule a (3—)4 years' development of the shoot, in drier localities generally about six years. Curiously enough the annual production of leaves is as a rule larger in dry-soil plants with their long-living shoot generations than in plants on damp soil with their rapid shoot development. Flowering shoots older than about seven years were not observed. In shoots which do not flower within a period of 5—7 years the cone of growth is destroyed, evidently without passing into a floral state.

*Erigeron unalaschkensis* and *E. uniflorus* have in the main a periodical development of their organs. The flower-heads of *E. unalaschkensis* are fairly well advanced in development during the wintering. The anthers are formed in the flowers, and the hypogynous ovary shows a distinct lumen. There is a marked difference between ray flowers and disk flowers (cf. Pl. 9, Figs. 27—28). *E. uniflorus* shows a somewhat less advanced development. In accordance with this the innovation buds of this species are enclosed in the winter bud, and they do not unfold till the following year in the axils of the green rosette leaves, sometimes, however, not till the next year again. In *E. unalaschkensis* the vegetative innovation buds are situated below the actual winter bud and are developed in the flowering year outside the green mother rosette.

In the *Taraxacum* species the development of the organs is periodical, though somewhat less so in *T. arcticum* than in the other species. *T. arcticum*, *T. phymatocarpum*, and *T. brachyceras* form a beautiful series as regards the formation and development of the floral primordia. *T. arcticum* is much advanced in development during the wintering, the heads are already fairly large, the individual flowers contain anthers and a closed ovary (cf. Pl. 10, Figs. 5—6). *T. phymatocarpum* is somewhat less advanced (cf. Pl. 10, Figs. 9—10), and in *T. brachyceras* the heads are only present as primordial receptacles, and in certain cases the first recognisable signs of the floral stage of the growing point do not appear till the spring preceding the flowering. As far as could be gathered

from the rather sparse material, *Taraxacum pumilum* occupies a remarkable intermediary position between *T. phymatocarpum* and *T. arcticum*; as regards the production of leaves as well as in most morphological characters it bears the greatest resemblance to *T. phymatocarpum*, while as regards the floral development it is in accordance with *T. arcticum* (cf. Pl. 10, Figs. 11—12).—In the *Taraxacum* species the annual number of leaves is fairly constant, that is to say, it is almost the same in weaker and more vigorous shoots within the same species, being c. 9 in *T. arcticum* and c. 12 in the other species. The number of flower heads, however, varies according to the vigour of the shoot. In weak shoots only one termimal head is formed, while in more vigorous shoots heads are further formed in the axils of the uppermost leaves above the innovation bud, often with one or two foliage leaves at the base of the scape. More than three heads on the same shoot are very rarely formed. It would seem that by the formation of several heads the plant consumes its surplus of energy so that a too early growth, which would break the periodicity, is prevented. A further means of ensuring the periodic course of development was observed in vigorous plants of *T. phymatocarpum*, actual regulation shoots being inserted in the shoot chain, as in many *Cruciferae*. In this way the plant contrives to develop two consecutive flowering shoot generations in the same summer, even often with several heads each. The insertion of the regulation shoot is effected as follows: The innovation shoot, which, as normally, unfolds simultaneously with the flowering of the mother shoot, develops only half the number of leaves (six as against normally 12), and ends with the heads, which flower at about the time that the heads of the mother shoot are fructifying, or a little later. The six-leaved shoot (the regulation shoot) again in its turn forms an innovation bud with a similar small number of leaf primordia and with primordial flower heads. Its leaves do not unfold, or unfold very little, that year. The wintering bud, which comprises the whole or the greater part of the new short shoot, both as regards the number of leaf primordia and the floral development, then exhibits the same character as the normal 12-leaved shoots which unfold half the number of their leaves in the first growth year. In this way the surplus of energy is released for the time being and the development may continue in the normal way. The order of development just described was observed in the last year's shoot of preserved plants. Thanks to the long persistent leaf bases, the two consecutive short shoot generations intervening between the normal ones can easily be demonstrated on older shoots, too. That such regulation shoots are of frequent occurrence in *T. phymatocarpum* further appears from an observation made on Ymer Ø at the beginning of August, 1932, viz. that at that time this species quite commonly bore ripe and flowering

heads at the same time. As far as could be judged from the sequence of shoot generations in *T. pumilum*, regulation shoots of the same character may occur in this species, too, whereas they were not observed in *T. arcticum* (and *T. brachyceras*; material available for examination sparse).

The remaining two species of the family, *Arnica alpina* and *Matricaria inodora*, each differs in various respects from those already mentioned, and they will therefore be treated separately.

*Arnica alpina.* Hemicryptophyte. Subterranean, more or less horizontal, thickened sympodial rhizome with very short internodes. The rhizome dies off behind after functioning for many years. The winter buds are better protected in a morphological respect than in any other species within the area. Quite a brush of stiff, very durable hairs is found in all the leaf axils. Together with the old leaf remnants these hairs form a tunic around the bud. The fresh bud itself consists of two outer hood- or cuff-shaped sheaths formed by the intergrowth of the partners of the outermost two pair of leaves. Inside each of the sheaths there is a thick layer of hairs from the axils of the leaves. In general two pairs of actual foliage leaves are developed yearly, though often in addition a third pair, which is smaller and often only partially unfolded. In addition to the two scale leaf sheaths, two pair of stem leaves are formed in the flowering year, sometimes also a pair of basal leaves. The development of the shoot extends over an extremely variable number of years, from three to twenty or more. In a single case even a two years' development was ascertained; in such cases the shoot only develops leaves in the flowering year. A three years' and especially a four and five years' development is frequent in plants growing in extensively manured soil below bird cliffs. Plants from "normal" (unmanured) habitats have as a rule a very prolonged shoot development. The rhizomes of the plant have a very different appearance in weak and in vigorous plants. In all cases buds are as a rule formed in the axils of all pairs of leaves. In vigorous plants (1—)2 buds are developed as distinct principal buds in the flowering year, one from each of the "cuffs" of the last series. These buds unfold next year, forming vigorous rosettes, which flower after the lapse of a few years and continue the rhizome. Less advanced buds also unfold now and then, but they give rise to much weaker shoots. In weak plants flowering after a number of invigoration years, a recognisable principal bud is never formed; all the buds are extremely small, and it cannot be seen which will continue the growth the succeeding year. They give rise to very weak rosettes, which, it is true, form only one pair of actual foliage leaves in the first couple of years, but which comparatively soon attain the normal yearly number of leaves. On

the other hand, the leaves are of minimal size. The rhizome, which grows in a horizontal direction, is at first extremely thin, increasing slowly in thickness from year to year until after some 15—20 years or more it attains the same dimensions as those of vigorous plants, after which flowering sets in. It is worth noting that the flowering stem, when developed, is almost just as vigorous as in plants growing in favourable localities. The development may then start afresh. The whole rhizome and its roots, which are thick but only present in a comparatively small number, and the axillary buds remain fresh during all these years, even till the flowering. The annual growth in length is inconsiderable, thus for instance a rhizome twenty years old measured only 6 cm. It would seem that the rhizome and its roots store spare food in increasing quantities year by year until flowering takes place. The final fate of the old rhizome could not be traced with certainty on the basis of the material brought home, the attachment of the shoot generations being so thin and delicate that in older rhizomes the connection behind was always broken. It seems most probable that the whole of the old rhizome dies after having produced the weak innovation shoots.

The organic development is strictly periodical throughout. The foliage leaves wither already in the late summer. In the wintering state the flowers of the central head have formed, with young anthers (cf. Pl. 9, Figs. 21—22). Lateral heads are only present as arched receptacles; primordia of such are constantly formed, but are very rarely developed in the flowering plant.

*Matricaria inodora.* The plant is most frequently hapaxanthic, but also often pollacanthic (see Fig. 13). It has, however, a limited lifetime; more than three consecutive flowering shoot generations have not been observed. Perennial tap-root; older plants have often in addition vigorous adventitious roots issuing from the thick, fairly succulent mesocorm. Such older plants are typical mesocorm chamaephytes. The development takes at least four years, more frequently five years, before the first flowering. The main axis forms 6—8 rosette leaves yearly. Weaker plants as a rule form no lateral rosettes and flower only once. More vigorous plants form buds in the axils of the rosette leaves of the second year, which buds develop into side rosettes next year. Very often the main axis and the lateral axes flower at the same time, and the plant is then hapaxanthic in this case also. If the lateral axes do not flower the same year as the main axis, the plant becomes pollacanthic, and the development may likewise continue by forming new lateral shoots of the same order from the higher leaf axils, or by the formation of lateral shoots of the second order. Even plants which flower several times hardly attain a greater age than about ten years. Leaf-bearing shoot

apices pass the winter in an open state. The expanded leaves are destroyed by the frost, and often the apices of the very young leaves, which unfold next year, are destroyed, a phenomenon not observed in any other species within the area. The organic development is largely aperiodical. Flower



Fig. 13. Pollacanthic specimen of *Matricaria inodora* (Kap Hedlund, c. 73° N. lat., July 1932). c. $^1/_1$. Del. O. Hagerup.

heads which have advanced so much in the autumn as to be visible, are destroyed by the frost like the surrounding leaves and leaf apices, and very often flowering plants are observed in which the lateral axes only have developed while the central head developed earlier in the autumn has been destroyed during the wintering. Retarded flowering heads are of frequent occurrence right to the winter sets in. During the wintering heads in all stages of development may be met with (cf. Pl. 10, Figs. 1—4); the most frequent seems to be a stage with a flatly broadened head

receptacle and the involucre just indicated. Heads whose flowers are present as hardly differentiated cylindrical formations, seem to be the largest ones which survive the winter (cf. Pl. 10, Figs. 1—2). Heads are developed entirely open. At no time do involucral leaves entirely cover the disk of the head.

In all the *Compositae* reduction division occurs in spring and summer. *Arnica*, the *Erigeron* species, and *Matricaria* reduce relatively late, after the heads have attained a diameter of 5—8 mm and the elongation of the stem has commenced. The reduction division of the *Taraxacum* species takes place at a time when the spheroid heads are becoming cylindrical. The elongation of the scape has not yet begun. In *Antennaria* the time of the reduction division has not been investigated.

### *Empetraceae.*

Lit.: HAGERUP 1927, MENZ 1909.

One species, *Empetrum nigrum*, represented only by the hermaphroditic form *var. hermaphrodita* (*Empetrum hermaphroditum* HAGERUP). Evergreen procumbent dwarf bush, chamaephyte. Formation of adventitious roots insignificant. Monopodial growth, with the years' shoots distinctly delimited morphologically. Leaves in 4-leaved whorls, each year's shoot with two whorls of scale leaves, which function as bud scales, and most frequently five whorls of foliage leaves. The uppermost whorl subtends vegetative buds, the middle whorls on the year's shoot subtend flower buds, which flower next spring. Shoots with less than three whorls of foliage leaves do not form flower buds. Thus lateral shoots do not form flower buds till their third or fourth year's shoots. The vegetative buds rest at least one year before unfolding. The leaves as a rule function six years (wither in the course of the sixth summer). The flower buds winter fully developed with pollen, entirely unprotected (cf. Pl. 10, Fig. 21). Reduction division and formation of pollen take place in August. As a rule there are only 1—3 anthers, sometimes anthers are entirely lacking, and if so, the flower is purely female. The whole succeeding year's shoot is formed in the wintering bud, but the axillary products are not visible. The flower buds are accordingly developed in the course of one summer.

### *Ericaceae.*

Lit.: HAGERUP 1928, HAGLUND 1905, WARMING 1908 a.

The family comprises six species, all dwarf bushes, chamaephytes. In five of the species the stems are built up of sympodes, in one species,

*Cassiope tetragona*, of monopodial shoots. Two species are only green in the summer, viz. *Arctostaphylos alpina* and *Vaccinium uliginosum*. The remaining four species are evergreen. The functioning period of the leaves, however, differs greatly in the different species. In *Rhododendron lapponicum* the leaves function in two growth seasons, in *Cassiope hypnoides* in three, in *Phyllodoce coerulea* in four, and in *Cassiope tetragona* in about five growth seasons (including the growth season in which the leaves wither). The number of the successive year's-shoots with green leaves during the wintering is thus always the functioning years indicated less one. The wintering buds are very differently equipped. *Arctostaphylos*, *Vaccinium*, and *Rhododendron* have actually distinct winter buds with bud scales. The *Cassiope* species entirely lack bud scales, while *Phyllodoce* occupies an intermediate position, the outermost leaves of the winter bud being of a scaly shape. They turn green, however, but their functioning period is one or two years shorter than that of the actual foliage leaves. However, these scale leaves hardly play any great role in the protection of the bud, and the leaf primordia in the winter bud of this species are, as in *Cassiope tetragona*, closely joined by a resinous glandular secretion. Despite the lack of bud scales in *Cassiope tetragona*, the boundaries between the years' shoots are recognisable, the first pair of leaves in each year's shoot being always a very little smaller than the others. This pair of leaves, which covers the bud during the wintering, terminates the growth in the autumn, and should perhaps rather be regarded as the last pair of leaves of the preceding year's shoot. In *Cassiope hypnoides* only every form of protection of the bud is lacking. The transition from the youngest leaf primordia to the entirely expanded leaves is here quite gradual, and the boundary between the years' shoots is not marked at all.

Adventitious roots are absent in *Rhododendron* and *Phyllodoce*, but present in the other species, where they may give rise to a vegetative propagation of older plants, especially in *Cassiope hypnoides* and *Arctostaphylos*. In *Cassiope tetragona* vegetative propagation plays no role.

In spite of the differences in the shoot construction of the species, it clearly presents itself as variants of one and the same type, which may perhaps be termed the *Bicornes* type. *Cassiope hypnoides*, however, forms an exception; its vegetative construction falls entirely outside that of the other species.

*Bicornes*-shoot structure. The schematic representation (Fig. 14) shows at the same time the similarity and the differences in the shoot construction of the species within the *Ericaceae* and of *Empetrum*, which bears close resemblance to these species. Characteristic of the type are the lateral flowers. Only in *Empetrum* and *Cassiope* is this lateral position

of the flowers immediately conspicuous, as in these species the main axis continues the growth. In the other species the inflorescence is terminal, the main axis terminating the growth simultaneously with the flowering. The further development of the plant is taken over by lateral shoots, which, except in *Vaccinium*, grow monopodially, often during a great number of years, until the next flowering takes place. Only in *Vaccinium* is the apex of the year's shoot destroyed, no matter whether or not the shoot is floral.

The transition between the monopodial and the sympodial growth type is shown with extraordinary distinctness with *Phyllodoce* as an intermediary link. Above the lateral flowers the main axis of this species continues into a shoot apex with four or more entirely developed leaves and a greater number of leaf primordia. However, the shoot apex dies, and rejuvenescence takes place by lateral shoots issuing from the main axis below the inflorescence, forming like an umbel. The apex of the main axis is most reduced in *Rhododendron*, in which it is only recognisable during the first developmental phases of the flower buds (see Pl. 10, Fig. 19).

As regards the place of the innovation buds in relation to the flower buds during the wintering the reader is referred to Fig. 14. Here it should merely be pointed out that in *Arctostaphylos* and *Phyllodoce* the whole inflorescence and the innovation buds are enclosed in the same winter bud, which is the terminal bud of the relative main axis. In *Arctostaphylos* the unfolding of the innovation buds takes place in the flowering year (prolepsis), in *Phyllodoce* the vegetative buds increase but slightly in size that year, while the first actual year's-shoot is not developed till next year[1]) In *Rhododendron* the flower buds are enclosed in the terminal bud of the main axis, the innovation buds are situated below the terminal bud. Precisely the same displacement of the innovation buds to a position below the winter bud of the main axis is found in *Empetrum* as compared with *Cassiope tetragona*. In *Vaccinium* the displacement towards a separation of floral and vegetative organs during the wintering is carried still farther, the individual flower buds, like the innovation shoots, being each of them enclosed in special scaly winter buds situated laterally to the mother axis, which gives an immediate impression of a thorough shoot dimorphism shown by the development of vegetative long shoots and one-flowered short shoots without foliage leaves.

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[1]) An examination of plants from South Greenland shows that here the innovation shoots always unfold simultaneously with the flowering of the mother shoot. If so, the species agrees entirely with *Arctostaphylos*. The delayed unfolding in the plants of Northeast Greenland must then be assumed to be caused by the unfavourable growth conditions at the northern limit of the species.

*Vaccinium* (like *Cassiope tetragona*) has normally a yearly flowering. The shoot development always takes three years (vegetative shoot + the lateral flowers, being referred to the same shoot generation similarly as in the other species), including the bud stage. In the other sympodial species a shoot development taking less than four years was not observed in any of the species, but as a rule the development takes a longer time, 10—15 years' development being fairly frequent. In species whose winter buds are protected by bud scales, series of scale leaves and foliage

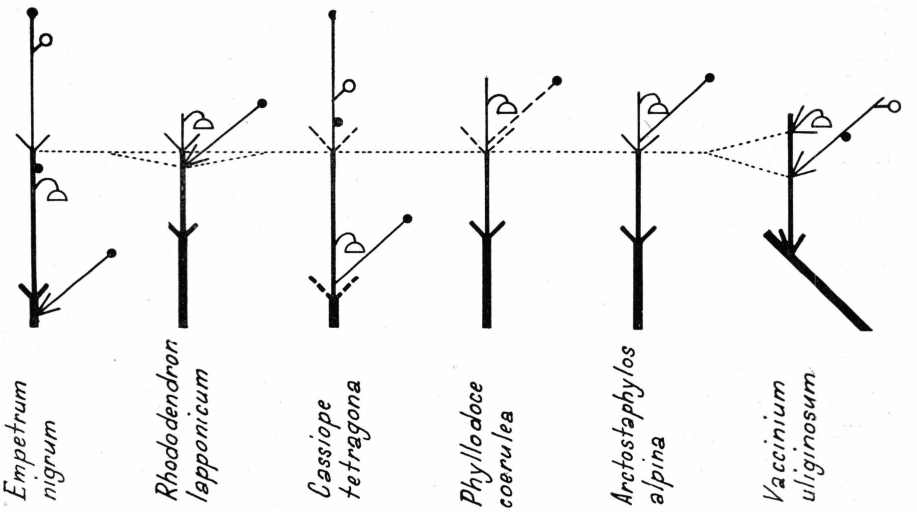



Fig. 14. Schematic representation of the *Bicornes* shoot construction of the *Ericacea* and *Empetrum* of Northeast Greenland. Year's-shoots two years old shown in heavy line, one year old shoots in moderately heavy line, growth of the present summer in thin line. The dotted line indicates the boundary between the last two year's-shoots. Flowers expanded in the present summer indicated as bells (semicircles). Flower buds to expand the succeeding summer indicated by a white circle, vegetative buds by a black circle (cf. further the text).

leaves are, of course, formed alternately, while species without bud scales form foliage leaves only. *Cassiope tetragona* as a rule forms eight pair of leaves annually (in moderately vigorous flowering shoots). If the year's shoot forms less than seven pair of leaves, flowering does not, as a rule, take place. Thus lateral shoots do not seem to form flowers till on their fourth year's shoot, at the earliest. *Vaccinium* forms 4—8, as a rule 6, foliage leaves annually. A year's shoot with less than four foliage leaves does not as a rule form flower buds. *Arctostaphylos* and *Rhododendron* often have an almost constant yearly number of foliage leaves, c. 5—6(—7) in both species, during several years before the flowering. The year before the formation of flower buds the number generally

increases to seven. In *Phyllodoce* the number of leaves increases from year to year, and flower buds are as a rule only formed when the yearly production attains 25—30 leaves. In this species the foliage leaves of the last year's shoot unfold in the flowering year, while in all the other species the production of foliage leaves in the flowering year is associated with the innovation shoots.

*Cassiope hypnoides*. In contrast to all the other species, this species has terminal solitary flowers. The shoot construction is sympodial, each shoot generation terminating with a flower. The branching is irregular, the unfolding and development of the lateral shoots showing no certain correlation with the flowering of the mother shoot. The lateral buds (only a minority unfold) are initiated in groups at the base of the years' shoots, and the innovation shoots are therefore always situated at least at a year's shoot's length from the flowering shoot apex. The last year's shoot dies after the flowering and fructification of the shoot, which, however, does not take place till a year after the expansion of the shoot, the fully developed flower bud wintering in the shoot apex only covered by the last few leaves, which are broad and membranous. There is a partial differentiation between long shoots and short shoots, both kinds, however, terminate with a flower. The long shoots, whose period of development is 5—12 years including the vegetative bud year and the flowering year, are prostrate and put out adventitious roots from their proximal parts. The short shoots, whose development as a rule takes 4—5 years (growth 2—3 years), are situated laterally on the long shoots. They are erect, and often die entirely after the fructification, but not rarely they form innovation shoots (i. e. the same type as *Saxifraga oppositifolia*). The number of leaves of the years' shoots increases from year to year, and the floral state commences when the annual number of leaves reaches c. 30.

In the *Ericaceae* the floral development is as a rule much advanced during the wintering. *Cassiope tetragona* (Pl. 10, Fig. 15), *Rhododendron lapponicum* (Pl. 10, Fig. 18), and *Cassiope hypnoides* (Pl. 10, Fig. 14) have fully developed flowers with pollen. The reduction division and the formation of pollen take place in August. The other three species have reduction division in the spring. As regards their phase of development during the wintering they form a graduated series, *Arctostaphylos* being the most advanced in development (Pl. 10, Fig. 13). The anthers seem to have young P. M. C. Next follows *Phyllodoce*, which is also fairly well advanced in development; though it has not yet reached the P. M. C. stage (Pl. 10, Fig. 17). Farthest behind is *Vaccinium*, though anthers and ovary are formed, but seed primordia are only visible as verruciform projections on the placenta (Pl. 10, Fig. 20).

The organic development is strictly periodical in all the species

with the exception of *Cassiope hypnoides*. In this species flower buds at a much younger stage of development than the normal one may sometimes be found during the wintering. But nothing can be said about the further fate of such buds; the species is of such rare occurrence within our area that observations on the duration of the flowering time are lacking.

Even in the species with formation of pollen in the autumn the whole floral development from and including the first primordial stages is restricted to the same summer. In *Cassiope tetragona*, however, it is possible—though with some difficulty—already in the autumn to ascertain some small verruciform projections in the axils of the leaf primordia of the winter bud, which, judging from their position, are the first traces of the lateral floral axes which are to flower two calendar years later (cf. Pl. 10, Fig. 16).

### *Gentianaceae.*

Three species, all hapaxanthic hemicryptophytes.

*Gentiana tenella* is biennial (Fig. 15 A). Examination of herbarium material in the Arctic collections of the Botanical Museum, Copenhagen, has shown that the species is biennial in all the other localities in Greenland, too.

In the only locality within the area *Gentiana nivalis* is triennial (Fig. 15 D). Examination of herbarium material from South and West Greenland shows that there the species is partly annual (Fig. 15 B) partly biennial (Fig. 15 C), whereas triennial plants have not been observed in these localities.

*Gentiana detonsa* is likewise only known from one locality within the area, and that merely as withered, one year old (or older) specimens. As the lifetime of these plants can hardly be determined with certainty, I had to draw my conclusions from age determinations made on plants from other (all more southern) Greenland localities; in these localities the species occurs partly as biennial partly as triennial. It must be assumed that the Northeast Greenland plants are triennial.

In flowering plants of *G. detonsa* and *G. tenella* the leaves of the preceding year or years have withered. In flowering plants of *G. nivalis* the leaves of the first year have withered, while the rosette of the second year has not entirely withered but is of a brownish colour. The leaves of this species are more durable than those of the other two, being fairly thick and leathery. Its basal leaves no doubt pass the winter in a green state and function the first part of the next summer, which can hardly by the case in the other two species.

The production of leaves of the three species, besides the cotyledons, is as follows for the individual years: *G. tenella* 2 + 4 pair of leaves;




Fig. 15. *Gentiana tenella* and *Gentiana nivalis*. The individual years' growths indicated by the numbers 1, 2, and 3. All figures $^3/_2$. Del. O. HAGERUP.

A: *G. tenella*, from Maanedalen on Traill Ø, (72°45′ N. lat.) c. 1st July, 1932. The withered rosette leaves of the preceding summer are seen at the base of the stem. B—D: *G. nivalis*. B: annual plant from South Greenland, Kingua, Tasiusak (61°45′ N. lat.), leg. N. HARTZ. Cotyledons still fresh during the flowering. C: biennial plant from West Greenland, Holstensborg (66°56′ N. lat.), leg. E. WARMING & TH. HOLM. The two lower leaves have survived from the preceding summer. D: triennial plant from Northeast Greenland, Traill Ø, Maanedalen (72°45′ N. lat.). The entirely withered remnants of the first year's leaf rosette are seen at the base. The largest of the remaining basal leaves have survived from the preceding summer (second growth year).

*G. nivalis* 1 + 3 + 4 pairs, *G. detonsa* 2 + 3 + 3 pairs. These numbers of leaves, which seem to be relatively constant, apply to one-flowered

individuals. In case the plant branches in the flowering year, the number of leaves is increased that year, in *G. tenella* and *G. detonsa* as a rule by one pair for each flower, in *G. nivalis* as a rule by two pairs. Vigorous plants of *G. nivalis* show a greater tendency to branching than the other two species. However, the number of flowers hardly exceeds 5—6 even in the most vigorous plants.

Germination no doubt takes place in the spring. Observations as to whether flower buds are initiated the summer before the flowering are not available. At any rate, the floral development prior to the wintering can hardly have gone beyond the first few stages, if the cone of growth winters at all in a floral state.

### *Lentibulariaceae.*

Lit.: HEIDE 1908.

One species, *Pingvicula vulgaris*, found only once within the area. (Investigation material from the area of Scoresby Sund). Hemicryptophyte with all the leaves gathered in a rosette. Unbranched sympode. The basal axis soon dies off behind, so that only two shoot generations are alive at the same time. Rejuvenescence takes place from the uppermost leaf axil by a large bulb-like wintering bud. Flower buds are not initiated till the spring—as a rule in a number of three—on the cone of growth, which is large, obtusely pyramidal. In most cases only one of these buds is developed.

In the flowering year 5—6 foliage leaves are always developed. At the beginning of the winter, however, the principal bud has about twice the number of leaf primordia. From this it must be inferred that the lowermost (outermost) half of these alone function as reservoirs of nourishment and as bud scales during the wintering. These outermost leaves of the bud are evidently destroyed very soon after being emptied of nutritive matter in the spring; for it is impossible to discover any trace of them when the plant flowers.

It should be noted that all the leaves of the wintering bud from the outside towards the interior are of the same character; thus the initials of the glandular hairs are formed. It would therefore seem to be due to external conditions which of them are developed into foliage leaves. HEIDE's (l. c.) division of the species into an arctic type, in which the principal bud does not develop foliage leaves in the year of formation, and a temperate type, in which the first leaves of the bud are developed as foliage leaves before the wintering, is therefore hardly justified. The two different types of development should no doubt merely be regarded as phenotypical deviations caused by the climate. Another fact that favours this view is that plants from South Greenland may some-

times develop a couple of leaves on the principal bud before the wintering.

The leaves wither in the early autumn. The cone of growth is not distinctly floral before wintering (cf. Pl. 11, Fig. 1). Thus the whole floral development is limited to the flowering year alone.

### *Plumbaginaceae.*

One species, *Armeria vulgaris*, represented by *var. sibirica*[1]). Hemicryptophyte (sometimes transition to mesocorm-chamaephyte) with perennial tap-root and only slightly branched, short and thick, sympodial mesocorm. Rejuvenescence from the uppermost leaf axils. The innovation buds are initiated simultaneously with the flower buds and unfold (proleptically) simultaneously with the flowering of the mother shoot. Curiously enough, almost always two buds unfold; these form leaf rosettes with a very variable number of leaves. The lowermost of these rosettes always dies after the growth of this one summer, while the uppermost alone continues the stem. Branching of the axis is effected by three buds unfolding and forming the rosettes of the first year; the lowermost of these then dies, while the uppermost two continue the growth, forming two almost equally vigorous main axes. The time of development of the individual shoot generations varies greatly, 2—7 years having been ascertained, though a 3—4 years' development is by far the most frequent. The yearly addition in height of the mesocorm is inconsiderable. Thus for instance ten successive shoot generations, representing the growth of fourteen years, measured 30 mm. In this case the yearly growth was accordingly c. 2 mm. The plants grow very old. A "young" plant, which flowered for the first time, was at least eleven years old. The yearly production of leaves amounts to about ten, but varies greatly. The development of leaves takes place continuously. The boundaries between the years' growths are hardly indicated by any difference in the size of the leaves. The state of the shoot apex does not differ essentially in winter and in summer. The greater number of the leaves of the preceding summer winter as green leaves, but all the fully developed leaves wither very early next summer. The partially developed leaves continue their growth and do not wither till the end of the summer.

The organic development is aperiodical, distinguished 1) by the extremely variable number of leaves in the first growth year of the shoot and in the flowering year, 2) by the wintering of the floral organs

[1]) *Armeria scabra* (Willd.) Ivers. *subsp. labradorica* (Wallr.) Ivers.—JOHS. IVERSEN in Kgl. Danske Vidensk. Selsk. Biol. Medd. XV, 8. København 1940.

in highly different phases of development (cf. Pl. 11, Figs. 2—4), 3) by the flowering being poorly delimited as to time, and finally, 4) by the presence of many abortive flower heads, destroyed in different stages of development, as will be seen on examination of older shoot-chains.

The leaves are initiated about one year before expanding. The floral primordial stage seems hardly to extend beyond the last growth season before the flowering, since, judging from the number of leaf primordia, even young wintering floral primordia will have reached such a degree of development in the course of the following summer that a new wintering will not be possible. The upper limit of the development of the flower heads during the wintering could not be more exactly fixed. A stage in which the head with involucral bracts has a diameter of 2—3 mm and the anthers and calyx have just commenced to differentiate in the individual flowers, must be regarded as a favourable and fairly frequent wintering stage (Pl. 11, Fig. 2). The effective floral wintering stage may thus be said not to be much advanced. The reduction division takes place relatively late. At the time the scape begins to elongate, the flower buds show a fairly low degree of development, less advanced than the large involucre would seem to suggest. The reduction division does not take place till immediately before the involucre begins to open.

### *Polemoniaceae.*

Lit.: Holm 1922.

One species, *Polemonium boreale*, hemicryptophyte. Sympodial growth. The axial parts consist partly of a horizontal long-jointed rhizome, partly of short-jointed, often branched pseudorhizomes of limited life duration. Two kinds of shoots: 1) Long subterranean runners provided with scale leaves, springing from the distal part of older runners. The longitudinal growth of the runners seems as a rule to be limited to one summer, the tip turning towards the surface of the ground. Next summer, or perhaps even the same summer, a leaf rosette begins to develop. After an invigoration stage extending over a different number of years, according to the vigour of the shoot, flowering takes place. The rosette axis then continues with 2) innovation shoots springing from the axils of the uppermost rosette leaves. These shoots are short-jointed, and their structure and development agree with the rosette part of the runners. After a few shoot generations the rejuvenescence from the rosette leaf axils ends, and at the same time or often at an earlier date the pseudorhizomes rejuvenate, as a rule from the base, by the unfolding of "dormant" buds. The basal shoots have a collar of

old scale leaves at the base, which shows the continuous formation of new scale leaves by the "dormant" buds. Sooner or later the whole shoot complex dies after the lapse of a number, often a fairly great number, of years. The runners are of the same (or longer?) duration of life than the pseudorhizomes, and they increase in thickness in the course of the years. New runners are not formed till the mother generation has been consolidated through the stationary activity during a number of years. They are always produced by "dormant" buds on old rhizomes.

The time of development for the above-ground shoot generations is often three years, but it is very often prolonged by the intervention of a further number of rosette years up to at any rate six years. The sequence of development of the vegetative as well as the floral organs is irregular, and the annual production of leaves likewise varies greatly. Vegetative buds are initiated simultaneously with the flowering of the mother shoot. In the first rosette year as a rule 2—3 leaves, but sometimes up to six leaves are formed. Not rarely the bud just opens, but fails to expand any leaves at all before wintering. In the vegetative rosette years as a rule 3—6 leaves yearly are developed, though at times up to ten leaves. In the flowering year from three to eleven basal leaves have been observed in addition to the two stem leaves. If the number of leaves is large, the development of the stem is much retarded.

All the green parts of the plant are killed by the winter frost. The wintering buds are open, or at any rate not with closely packed leaves. All leaves which have just commenced to expand, do not continue their growth after the wintering. The years' growths are always terminated by partially expanded leaves, which distinctly shows that the growth continues steadily until it is interrupted by the winter frost.

The floral wintering stages vary greatly in their degree of development (cf. Pl. 11, Fig. 5). The reduction division takes place in the spring.

As will be seen from the above, the plant is aperiodical throughout. Stems, destroyed before the time, occur, but apparently less frequently than is usual in entirely aperiodical species, and this in spite of the failing frost resistance of the above-ground organs. However, the material available for examination was too inconsiderable to allow of a final decision of this problem.

### *Primulaceae.*

Lit.: MATHIESEN 1916.

One species, *Primula stricta*[1]). Hemicryptophyte. Sympodial growth. No actual rhizome is formed, as each shoot generation dies already at the ripening of the fruits.

The wintering bud has four broad bud scales, which are closely joined. Inside the bud scales the bud contains nine leaves and the terminal inflorescence. In addition the innovation bud, formed with altogether nine leaf primordia, is found in the uppermost leaf axil immediately below the inflorescence. This is the whole leaf production of the succeeding year. The innovation bud unfolds simultaneously with the flowering of the mother shoot, so that the development of the leaves, though it is distributed with one half to each of the two consecutive shoot generations, takes place continuously during the summer. The leaves wither early, before the winter frost sets in, and at the same time the winter bud is fully formed. Thus the development of the organs is strictly periodical. The innovation shoot develops roots simultaneously with the expansion of the leaves.

The flower buds are well advanced in development during the wintering (cf. Pl. 11, Figs. 6—7). All the organs of the flower are formed, the ovary is closed, entirely filled with the globular placenta. The style is shaped like an open tube. Formation of pollen takes place in the spring.

### *Pyrolaceae.*

Lit.: WARMING 1908a.

One species, *Pyrola grandiflora.* Hemicryptophyte (cf. p. 187). All the shoots arise as subterranean long-jointed runners with scale leaves. Sooner or later the apex of the runner turns towards the surface of the ground and continues in the above-ground aerial shoot, which is normally unbranched and flowers once. Weak above-ground shoots die in a vegetative state after a number of years. Adventitious roots issue from the axils of the scale leaves of the runners.

The development of the runners is entirely aperiodical. The longitudinal growth is not limited to definite growth seasons, and the same shoot generation may continue the growth horizontally during two and probably sometimes during three growth seasons. The runners are often much branched, and side branches are formed both before and

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[1]) The material available for examination was very sparse. The description of the wintering organs is based on the examination of one individual.

after the mother axis passes into the above-ground stage. Often the side branches of the runners simply grow in a vertical direction from the outset, forming above-ground shoots, in other cases the direction of growth is at first horizontal and later vertical. Runners in all stages of development may be met with during the winter. The years' growths are not, or hardly, marked by the relative position of the scale leaves. Up to about ten scale leaves per annum are developed; the yearly growth in length differs greatly, up to c. 25 cm has been noted. Runners of the same shoot generation of a length of up to 50 cm were observed. On the ascending part of the runner the scale leaves grow larger and are situated at close intervals, the last ones functioning as bud scales at the surface of the soil. The above-ground stage starts with one foliage leaf in the first year. The succeeding years 2(—3) scale leaves, the bud scales, and a slowly increasing number of foliage leaves are formed, often only one or two leaves yearly being formed for a number of years. Even after the number of three has been attained, a year's-shoot with only one leaf not rarely intervenes. Such year's-shoots with a smaller number of leaves probably mark unfavourable summers. Only when at least three foliage leaves have been formed in at least two consecutive years will the shoot apex become floral. No foliage leaves are developed in the flowering year. Only the scale leaves of the above-ground shoots in certain cases subtend buds. These buds rarely unfold, probably chiefly if the apex of the main shoot is damaged so that its continued growth is interrupted. A shoot development below six and above thirteen years was not ascertained. Older shoots hardly occur, as weak shoots which have not contrived to flower within a certain limited number of years die without passing into a floral state. A 7—8 years' development is the most frequent for flowering shoots. The foliage leaves function 3—5 summers, most frequently four.

The organic development of the above-ground shoots is generally periodical, though the flower buds do not always winter in precisely the same stage of development. A frequent wintering stage is distinguished by a relatively large, broadened receptacle with the outermost two sepals formed (actually the prefolia) (cf. Pl. 11, Fig. 10). Sometimes both the corolla and the antipetalous anthers, besides all five lobes of the calyx, are recognisably differentiating (Pl. 11, Figs. 8—9).

The time for the reduction division was not investigated. According to HAGERUP (1928, p. 7) the reduction division takes place in the anthers when the flower bud measures 3 mm in diameter (c. 1st July).

### *Scrophulariaceae.*

Lit.: Holm 1922, Mathiesen 1921, Resvoll 1917.

Five species, viz. three *Pedicularis*, one *Veronica*, and one *Euphrasia*. All the species differ from each other in vegetative construction. Even the three *Pedicularis* species represent just as many types. All the species of the family will therefore be dealt with separately.

*Pedicularis hirsuta.* Hemicryptophyte with perennial tap-root and sympodial, often branched mesocorm. Rejuvenescence from the upper rosette leaf axils, and especially in old plants also rejuvenescence from the base. The lifetime of the plant, however, is often fairly limited. The shoot development takes 3—6 years, generally four years. The wintering buds have 3—5 bud scales, which are distinctly metamorphosed foliage leaves with a broad sheath and often with a rudimentary lamina. The protection of the bud is but little effective, the junction of the leaves of the winter bud being too loose; and the bud scales, too, are not closely jointed. During the wintering the buds are loosely surrounded by persistent withered leaf bases. Vegetative buds are formed in the axils of the uppermost foliage leaves of each series. Thus they pass the winter outside the apical bud of the mother axis, and are protected by a pair of small scale-like leaves, which in contrast to all the succeeding series of bud scales may subtend vegetative buds; these buds as a rule remain dormant during a number of years, but may unfold later, gradually as the older sympodes are weakened at the top. In case of rejuvenescence from the upper part of the rosette the buds unfold the year before the flowering of the axis, from the axils of the withered foliage leaves of the preceding year. The yearly production of rosette leaves is extremely variable according to the vigour of the shoot. Often only a few leaves are formed the first year, after which the number increases year by year. The flower buds are not initiated until the growth season in which the shoot is vigorous enough to expand six (as a rare exception five) foliage leaves. In vigorous shoots with a shorter development the number of leaves in the last rosette year may increase considerably, even up to twelve. No basal leaves are formed in the flowering year. During the last wintering bud scales in a number of 6—8 are present, the last ones of which move up the stem during the development. In addition the stem bears 5—8 foliage leaves below the inflorescence, whose 15—20 flowers are likewise subtended by green leaves. A young plant which flowered for the first time was 6—7 years old.

*Pedicularis flammea.* Spot-bound hemicryptophyte, with short erect sympodial rhizome, which soon dies off behind so that only two shoot generations are alive at the same time. Rejuvenescence from the

upper part of the rosette. The adventitious roots are thick and spongy like the axial parts. In contrast to all the other herbaceous plants of the area it is deciduous. On account of the crescent-shaped leaf scars and the compact closed bud at the apex of the rhizome the year's shoot in the wintering stage bears a peculiar resemblance to a short branch of a deciduous tree (cf. Fig. 17A, p. 199). The number of the bud scales of vigorous buds is constantly eight; weaker buds have fewer bud scales. They are of a very hard consistency and very closely packed, closing hermetically around the bud (cf. Fig. 17). The vegetative buds are always initiated in the axils of the innermost bud scales. Thus the innovation buds are protected in the apical bud of the main axis during the winter and immediately develop foliage leaves on unfolding next year. As a rule only one or two buds of the uppermost series unfold. Thus the unfolding takes place in the flowering year. The development of the shoot takes 3—7 years, generally four years. The yearly production of foliage leaves is inconsiderable, mostly only two, though sometimes up to five. The greatest number of leaves is most frequently found in the last invigoration year in originally weak shoots with a development extending over many years. The most vigorous shoots with only a three years' development as a rule form only two foliage leaves in the only year in which rosette leaves in such cases develop. The main axis develops no rosette leaves in the flowering year, and no actual stem leaves either. In fact, the plant is acauline, flower buds being initiated in the axils of any of the leaves situated above the bud scales. Very rarely flowers and capsules are developed in the lowermost leaf axils; if so, the lowermost capsule is situated immediately above the bud scales. The flower buds of the lowermost 3—5 leaf axils are normally destroyed at a very early stage of development. Already during the wintering these buds are as a rule less advanced in development than the succeeding ones, and the destroyed buds in nearly the same phase of development are found on the flowering plant (cf. Pl. 11, Fig. 13). They must accordingly have ended their growth before the wintering. The lowermost leaves are as a rule larger than the succeeding ones, which subtend developed flowers, and the corresponding internodes are further elongated during the postfloration, which lends to the plant the appearance of possessing an actual stem and stem leaves.

*Pedicularis lapponica.* Hemicryptophyte (cf. p. 187). In its vegetative construction the plant in an astounding degree resembles *Pyrola grandiflora*, in company with which it generally grows. The axial parts consist partly of subterranean, long-jointed, much branched, thin and fragile runners with scale leaves, partly of hemicryptophytic, short-jointed, shoots with development of rosette leaves, from whose axils flowering shoots or sympodes issue.

Rejuvenescence always takes place by runners springing from older runners. The length of the runners, their number of internodes, and their time of development vary greatly. The longitudinal growth may continue at any rate during two years, though often for a shorter time and in certain cases it only extends over part of one growth season. After the tip of the runner has turned towards the surface of the ground, the development of rosette leaves begins. Then always (2—)3 scale leaves are formed yearly, which function as bud scales, and in addition three foliage leaves, though in the first year only 1—2 foliage leaves. The development of the subterranean runners is entirely aperiodical, manifested i. a. by the circumstance that the transition to the rosette axis at the surface of the soil is now marked by a series of scale leaves, now by a series of foliage leaves. It must be assumed that runners reaching the surface at the beginning of the growth season will form foliage leaves and subsequently the wintering bud, while such as reach the surface in the course of the summer will only form a wintering bud.

The rosette axis forms buds in the axils of the midmost or the uppermost two scale leaves of each series. Only a small number of these buds, often only one, develop into floral shoots. The bud is initiated and winters as in *P. flammea*, viz. in the interior of the apical bud of the rosette axis, but does not develop foliage leaves next year as in *P. flammea*. No leaves are formed, but the bud increases immensely in size and at the next wintering consists of four bud scales enclosing the whole flower stem of the succeeding year. Thus the floral lateral axes have a three years' development. The rosette axis may develop several floral daughter shoots, but much more frequently the flower stems appearing later are side shoots of a higher order issuing from the uppermost bud scale or scales of the floral shoot first formed. The development always takes three years, and the sympodes of floral side axes thus flower every year. They have not been found to have more than three shoot generations. The lifetime of the hemicryptophytical axial parts is very limited; no such "plants" older than 6—7 years were noted. Rejuvenescence from the base does not seem to take place, and the whole "plant" dies. The floral shoots bear 5—10 stem leaves, the uppermost of which in most cases support small two-leaved rosettes. The subtending leaves of the flowers are small and are hardly of any importance for the assimilation.

It will be noted that the leaf production of *P. flammea* and *P. lapponica* is remarkably small as compared with that of *P. hirsuta*. It seems natural to conclude from this that the two first-mentioned species are to a greater extent than the last-named one prepared for a heterotrophic nutrition.

The organic development of the *Pedicularis* species, with the exception of the runners of *P. lapponica*, is periodical, though less strictly so in *P. hirsuta* than in the other two, which i. a. is manifested in the somewhat varying floral development during the wintering of this species. In all the species the flower buds contain primordia of calyx, anthers, and ovary (cf. Pl. 11, Figs. 11—17), but the development is evidently normally slightly less advanced in *P. hirsuta* and *P. flammea* than in *P. lapponica*. However, there are no great differences. The primordial development itself of the flower buds is limited to the last summer before the flowering.

In *P. hirsuta* and *P. flammea* the reduction division takes place at the incipient growth and appearance of the inflorescence. The length of the flower buds is c. 2—3 mm. When the stem began to elongate, *P. lapponica* bore buds of c. 1.5 mm length. At that time P. M. C. were not yet recognisable.

*Veronica alpina.* Hemicryptophyte, whose perennial axial parts consist of prostrate or half-subterranean, rooted, somewhat elongated sympodes. The individual joints function at any rate for five years. The shoot development takes three years: The first year is the bud stage. The second year 3—4 pair of leaves are developed, which may most precisely be termed scale leaves or quite small foliage leaves with long internodes and axillary buds. This year's growth constitutes the perennial axial part. In the third year the flowering stem is developed, which bears c. 7 pair of leaves and 5—10 flowers. At the same time new scale leaf shoots, with buds for the next shoot generation in the leaf axils, are formed from the lower persistent part of the shoot. Root formation takes place from the proximal part of the shoot in the flowering year.

The shoot apices are entirely unprotected during the winter. Only four pairs of leaf primordia are found during the wintering, that is to say, that not only the flowers, but also about half the number of the stem leaves proper are not initiated still the flowering year. Hence RESVOLL's statement (1917, p. 210), "Blomsteranlæggene . . . kun litet utviklet høsten forut" (flower primordia . . . but slightly developed the preceding autumn), for which MATHIESEN (1921, p. 378) has: "the flowers are already formed during the autumn of the first year", was not confirmed.

*Euphrasia latifolia.* Summer-annual therophyte. The cotyledons are succeeded by two stem leaves, which—very occasionally—may support few-flowered inflorescences in the most vigorous plants. Normally no axillary shoot is developed. The two stem leaves are succeeded by the inflorescence. The subtending leaves of the flowers resemble the stem leaves and constitute the most important assimilation organ of the

plant. Their number is as a rule 8—10, but varies from 3—12. The number of the developed flowers is always lower, a greater or smaller number of the flower buds being destroyed at an early date. This applies especially to the lower ones, for which reason the number of stem leaves is apparently greater. Starved forms with much reduced inflorescences are very frequently met with. Even if only one flower is developed, the total number of leaves does not seem to fall below five, viz. two stem leaves plus three leaf-like bracts.

Table 7. Survey of a number of biologic-morphological characters of the

| | (1) Distributional type | (2) Life-form | (3) Thawing type | (4) Kind of shoot | (5) Developmental time of shoot (generation): years | (6) Flowering (of sympode) every $n^{th}$ year: n | (7) Years with development of fol. leaves (of standard shoot) |
|---|---|---|---|---|---|---|---|
| *Carex alpina* | SS | H | II | .. | **4**(3)—5 | 2 | 2 |
| — *aquatilis stans* | N | G | II—III | LU<br>S | 6—**7**—8<br>5—**6** | (2—)3<br>.. | 5<br>4 |
| — *atrofusca* | NN | H | II(—III) | .. | 4—**5**—6 | 2 | 3 |
| — *bicolor* | SS | H | II | .. | **5** | 2 | 3 |
| — *capillaris* | S | H | I | .. | **3**(2)—5 | 1 | 2 |
| — *capitata*[1] | SS | H | II | .. | **5**(6)—7 | 2 | 3 |
| — *glareosa* | S | H | II—III | .. | **5**—6 | 2 | 3 |
| — *incurva* | M | G | II—III | .. | 3—**4**—8 | 1 | 3 |
| — *Lachenalii* | SS | H | II—III | .. | **5**—6 | 2 | 3 |
| — *microglochin* | SS | G | II | .. | **3**(4) | 1 | 2 |
| — *misandra* | N | H | I—III | ..<br>VE | **5**(4)—8<br>4—**5**—6 | 1<br>.. | 4<br>4 |
| — *nardina* | C | H | I | ..<br>SE | 4—**5**<br>3—**4** | 1<br>.. | 4<br>3 |
| — *parallela* | NS | G | II | .. | **4**(5)—5 | 1 | 3 |
| — *pedata* | SS | H | I | .. | 4—**5**(4)—6 | 2 | 4 |
| — *pseudolagopina* | NS | H | III | .. | 4—**5** | 2 | 3 |
| — *rariflora* | SS | G | III | .. | **6**—7 | 2 | 4 |
| — *rigida* | S | G | II—III | .. | **6**—7 | 2 | 4 |
| — *rupestris* | M | G | I | .. | 7—**9** | 2(—3) | 5—6 |
| — *saxatilis* | M | G | III | .. | **5**(6)—7 | 1 | 3 |
| — *scirpoidea* | SS | G | II | L<br>SEA | **3**(4)<br>**2**(3) | (1)<br>.. | 2<br>1 |
| — *sparsiflora* | NS | G | I—II | .. | 6—**8**—11 | 3 | 5 |
| — *subspathacea* | S | G | II—III | LU<br>S | **5**(4)—6<br>**4**—5 | 1<br>(3) | 3<br>2 |
| — *supina* | SS | G | I | LU<br>S<br>SE | **7**—9<br>**4**—6<br>**3** | (4)<br>1—2<br>.. | 4<br>3<br>2 |
| — *ursina* | SS | H | III | .. | **4** | 2 | 3 |
| *Elyna Bellardi* | C | H | I | ..<br>SE | 5—**6**<br>**6**(7) | 2<br>.. | 5<br>5 |
| *Eriophorum callitrix* | NS | H | II—III | .. | 5—**7**(8)—8 | 3 | 4[5] |

[1]) *Carex arctogena* H. Sm. — H. SMITH in Acta Phytogeogr. Suecia XIII, p. 191. Uppsala 1940.

lowering plants of Northeast Greenland. For explanation of the table, see p. 181.

| (8) Number of leaves per standard shoot | | (9) | (10) | (11) | (12) | (13) | (14) | |
|---|---|---|---|---|---|---|---|---|
| Scale leaves | Foliage leaves | Yearly number of fol. leaves of vegetative shoot | Yearly number of fol. leaves of sympode | Wintering type of leaves | Wintering type of buds | Wintering floral type | Number of consecutive winterings of floral primordia | |
| 3 | 9 | (4—)5 | 5 | s | p | 5 | 1 | *Carex alpina* |
| c. 12 | 18 | 5 | 6 | s | p | 5 | 1+ | — *aquatilis stans* |
| c. 8 | 15 | 5 | .. | | | | | |
| 6 | 10 | 4 | 5 | s | p | 5 | 1+ | — *atrofusca* |
| 6 | 10 | 4 | 5 | s | p | 6 | 1 | — *bicolor* |
| 1 | 8 | 5 | 8 | s | p | 6 | 1 | — *capillaris* |
| 6 | 5 | 2 | 2 | w | u | ap | (1—)2 | — *capitata*[1]) |
| 5 | 7 | 3 | 4 | s | p | 6 | 1 | — *glareosa* |
| 7 | 11 | 4 | 11 | s | p | ap | 1(—2) | — *incurva* |
| 4 | 8 | 3 | 4 | s | p | 6 | 1 | — *Lachenalii* |
| 8 | 6 | .. | 6 | s | p | 5 | 1 | — *microglochin* |
| 1 | 11 | 4 | 11 | (w) | u | 6 | 1 | — *misandra* |
| 1 | c. 15 | .. | .. | .. | .. | .. | .. | |
| 1 | 11 | 3 | 11 | s | p | 6 | 1(+) | — *nardina* |
| 1 | 8 | 3 | .. | | | | | |
| 5 | 8 | 3 | 8 | s | p | 6 | 1 | — *parallela* |
| 4 | 12 | (3—)4(—5) | 6 | s | p | 6 | 1 | — *pedata* |
| 5 | 8 | 3 | 4 | s | p | 6 | 1 | — *pseudolagopina* |
| 11 | 16 | (4—)5(—6) | 8 | s | p | 6 | 1 | — *rariflora* |
| 8 | 18 | 5 | 9 | s | p | 5 | 1 | — *rigida* |
| c. 30 | 14 | 3 | 7 | s | p | 6 | 1 | — *rupestris* |
| 6 | 8 | 3 | 8 | s | p | 5 | 2 | — *saxatilis* |
| 6 | 7 | 4 | 7 | s | p | 6 | 1 | — *scirpoidea* |
| 4 | 3 | .. | .. | .. | .. | 6 | 1 | |
| 5—10 | 18 | 4 | 6 | w | u | 5 | 1 | — *sparsiflora* |
| 10—12 | c. 12 | 5 | 12 | s | p | 5 | 1 | — *subspathacea* |
| 8 | c. 7 | 5 | .. | | | | | |
| 20—40 | 18 | 5 | | .. | .. | .. | .. | |
| 5 | 13 | 5 | c. 8 | s | p | 3 | 1 | — *supina* |
| 3 | 9 | .. | | s | p | 3 | 1 | |
| 4 | 11 | 4 | 5 | s | p | 5 | 1 | — *ursina* |
| 1 | 8 | 2 | 4 | s | p | 6 | 1+ | *Elyna Bellardi* |
| 1 | 8 | 2 | .. | | | | | |
| 4 | c. 12 | 3 | 4 | s | p | 6 | 1(+) | *Eriophorum callitrix* |

Table

| | (1) Distributional type | (2) Life-form | (3) Thawing type | (4) Kind of shoot | (5) Developmental time of shoot (generation): years | (6) Flowering (of sympode) every $n^{th}$ year: n | (7) Years with development of fol. leaves (of standard shoot) |
|---|---|---|---|---|---|---|---|
| *Eriophorum polystachyum triste* | NN | G | II—III | .. | 4—**7**—10 | 3 | 4[5] |
| — *Scheuchzeri* | C | G | III | .. | **5**—6 | 2 | 3[4] |
| *Kobresia bipartita* | M | H | II | ..<br>S(E)<br>VE | **5**(4)<br>**5**<br>2—**3**—4 | 2<br>..<br>.. | 4<br>4<br>2 |
| *Agropyrum violaceum* | SS | H | I | ..<br>S(A) | **4**—5<br>**4**(3) | 2<br>1 | 3<br>3 |
| *Alopecurus alpinus* | N | G | II—III | .. | **4**—5 | 1 | 3 |
| *Arctagrostis latifolia* | NN | G | II | .. | (3—)**4** | 1 | 2 |
| *Calamagrostis arund. purpurasc.* | S | H | I | ..<br>L(U) | **4**—6<br>6 | 1<br>.. | 2<br>2 |
| — *neglecta* | S | G | III | LU<br>S(E) | **6**(7)—7<br>5—6 | 2<br>.. | 4<br>4 |
| *Deschampsia brevifolia* | NN | H | II—III | .. | **4**—5 | 2 | 3 |
| *Dupontia Fisheri* | NS | G | III | .. | 4—**5** | 1 | 3 |
| *Festuca brachyphylla* | C | H | I—II | .. | **3**—4 | 1 | 2 |
| — — "*v. brevifolia*"[1] | NN | H | II | ..<br>A | 3—**4**<br>2(3) | 1<br>.. | 3<br>2 |
| — — "*v. supina*"[1] | NN | H | II—III | ..<br>A | 3—**4**<br>2(3) | 1<br>.. | 3<br>2 |
| — *rubra* | SS | G | II | LU<br>SA | **4**<br>2(3) | 1<br>.. | 3<br>2 |
| — *vivipara* | N | H | I—III | .. | 3—**5**—7 | 1 | 4 |
| *Hierochloe alpina* | C | G(H) | I—II | LU<br>S | 4—**5**—6<br>**4**—5 | 2<br>1 | 3<br>3 |
| *Phippsia algida* | C | H | III—IV | .. | 4—**5**(4) | 2 | 3 |
| *Pleuropogon Sabinei* | NN | HH | III | .. | **4**—6 | 1 | 2 |
| *Poa abbreviata* | NN | H | I | .. | **4**(3)—5 | 1 | 3 |
| — *alpigena colpodea* | NN | G | II—III | .. | **4**—7 | 1 | 2 |
| — *alpina* (type 1) | SS | H | I—II | .. | 4—**5**(4)—8 | 3 | 4 |
| — — (type 2) | SS | H | II—III | .. | 3—**4**—5 | 2 | 3 |
| — — *vivipara* | SS | H | II—III | .. | 3—**4**—6 | 2 | 3 |
| — *arctica* | N | G | II—III | LU<br>S | 3—**4**—7<br>3 | 2<br>2 | 2<br>2 |
| — *glauca* | C | H | I | .. | **3** | 1 | 1 |

[1]) Cf. p. 74.

(continued).

| (8) Number of leaves per standard shoot | | (9) | (10) | (11) | (12) | (13) | (14) | |
|---|---|---|---|---|---|---|---|---|
| Scale leaves | Foliage leaves | Yearly number of fol. leaves of vegetative shoot | Yearly number of fol. leaves of sympode | Wintering type of leaves | Wintering type of buds | Wintering floral type | Number of consecutive winterings of floral primordia | |
| 11 | 16 | 4 | 5 | s | p | 6 | 1 | *Eriophorum polystachyum triste* |
| c. 10 | 10 | 3 | 5 | s | p | 6 | 1 | — *Scheuchzeri* |
| 1 | 12 | 3 | 6 | s | p | 4 | 1 | |
| 1 | c. 10 | 3 | .. | s | p | 4 | 1 | *Kobresia bipartita* |
| 1 | c. 5 | 3 | .. | .. | .. | .. | .. | |
| 2 | 8 | 3 | | | | | | |
| 1 | 9 | 3 | c. 7 | s | p | 3 | 1 | *Agropyrum violaceum* |
| 6 | 6 | 3 | 6 | s | p | 4 | 1+ | *Alopecurus alpinus* |
| 7 | 6 | .. | 6 | s | p | 4 | 2 | *Arctagrostis latifolia* |
| 7 | 6 | .. | 6 | | | | | |
| 14 | 6 | .. | .. | s | p | 3 | 1 | *Calamagrostis arund. purpurasc.* |
| 11 | 11 | 3(—4) | 6 | | | | | |
| 1(—2) | 11 | 3(—4) | .. | s | p | 3 | 1 | — *neglecta* |
| 1 | 4—7 | 2(—3) | 3 | s | p | ap | 2 | *Deschampsia brevifolia* |
| 5 | 12 | 4 | 12 | s | p | 4 | 1+ | *Dupontia Fisheri* |
| 1 | 6 | 3 | 6 | s | p | 3 | 1 | *Festuca brachyphylla* |
| 1 | 7 | 3 | 7 | | | | | |
| 1 | 5 | .. | .. | s | p | 4 | 1 | — — "*v. brevifolia*" [1] |
| 1 | 7 | 3 | 7 | | | | | |
| 1 | 3(—5) | .. | .. | s | p | 3 | 1 | — — "*v. supina*[1]" |
| 4 | 11 | 4 | 11 | s | p | 3 | 1 | |
| 1 | 3(—5) | .. | .. | .. | .. | .. | .. | — *rubra* |
| 1 | 11 | 4 | 11 | s | p | 3 | 1 | — *vivipara* |
| 5 | 8 | 3 | | | | | | |
| 1(—2) | 8 | 3 | c. 7 | s | p | 5 | 1+ | *Hierochloe alpina* |
| 1 | c. 9 | 4(—5) | c. 10 | (s) | p | ap | 2 | *Phippsia algida* |
| 5 | 7 | 3 | 7 | s | p | 5 | 1+ | *Pleuropogon Sabinei* |
| 1 | 6 | 2(—3) | 6 | s | p | 4 | 1(+) | *Poa abbreviata* |
| 5—7 | 7 | 3(—4) | 7 | s | p | 3 | 1+ | — *alpigena colpodea* |
| 1 | c. 12 | 3 → 5 | 4 | w | u | 3 | 1 | — *alpina* (type 1) |
| 1 | 7—9 | 4—5 | 4 | w | u | ap | (1—)2 | — — (type 2) |
| 1 | 8—11 | 3 → 5 | c. 5 | w | u | ap | 2 | — — *vivipara* |
| 4—5 | 7—8 | 3—4 | 4 | | | | | |
| 2—3 | 6 | .. | .. | s | p | 4 | 1 | — *arctica* |
| 3 | 3(—4) | .. | 3 | s | a | 3 | 1 | — *glauca* |

Table 7

| | (1) Distributional type | (2) Life-form | (3) Thawing type | (4) Kind of shoot | (5) Developmental time of shoot (generation): years | (6) Flowering (of sympode) every $n^{th}$ year: n | (7) Years with development of fol. leaves (of standard shoot) |
|---|---|---|---|---|---|---|---|
| *Poa Hartzii* | NN | H | I | .. | **3**—6 | 1 | 2 |
| — *pratensis* | S | G | I—II | .. | **5**—6 | 2 | 2 |
| *Puccinellia angustata* | N | H | I | .. | **4**(3)—5 | 1 | 3 |
| — *phryganodes* | C | H | II—III | .. | 3—**4**(3)—11 | (2) | 3 |
| | | | | V | .. | .. | .. |
| — *Vahliana* | NN | H | III | .. | **3**(2)—4 | 1 | 2 |
| *Trisetum spicatum* | C | H | III | .. | **4**—9 | 2 | 2(—3) |
| | | | | A | 3(4) | 1 | 2(—3) |
| *Juncus arcticus* | SS | G | II—III | .. | (2—)**3**(—4) | 1 | 1 |
| — *biglumis* | C | G | III—IV | .. | **4** | 1 | 2 |
| — *castaneus* | M | G | II | .. | **2**(3) | 1 | 1 |
| — *triglumis* | S | G | II | .. | **3** | 1 | 2 |
| *Luzula confusa* | C | H | I—IV | .. | 4—**6** | 2 | 4 |
| | | | | LU | **7**—8 | 3 | 4 |
| — *nivalis* | N | H | III—IV | .. | 4—**5** | 2 | 4 |
| | | | | S | **3**—4 | 1 | 2 |
| — *spicata* | SS | H | I—II | .. | **4**—6 | (1—)2 | 3 |
| | | | | S | 3 | 1 | 2 |
| *Triglochin palustre* | SS | G | II—III | .. | **3** | 1 | 2 |
| | | | | U | 3 | (1) | 5 |
| *Tofieldia coccinea* | M | H | I—II | .. | 7—**8**—18 | 5 | 7 |
| — *palustris* | SS | H | II | .. | 6—**8**—12 | 6 | 7 |
| *Potamogeton filiformis* | SS | HH | III | .. | **2** | 1 | 1 |
| *Betula nana* | SS | Ch | I | VM | ∞ | .. | .. |
| | | | | F♂E | **3** | .. | 1[2] |
| | | | | F♀ | **2**— | (1) | 1 |
| *Callitriche verna* | SS | Th | (II) | .. | **1** | (1) | (1) |
| *Arenaria cil. pseudofrigida* | M | Ch | I | .. | **3**(2)—5 | 1 | 2 |
| *Cerastium alpinum* | C | Ch | I—III | .. | **3**(2)—10 | 1 | 2 |
| | | | | L | 3(2) | (1) | 2(1) |
| — *Regelii* | NN | Ch | IV | S(V) | **4**—6 | .. | 3 |
| | | | | L | 4(3) | .. | 2 |

[1]) Bulb scales. [2]) Including axillary nutrition shoots. [3]) Cotyledons. [4]) Up to 3 shoot generations a year.

(continued).

| (8) Number of leaves per standard shoot | | (9) | (10) | (11) | (12) | (13) | (14) | |
|---|---|---|---|---|---|---|---|---|
| Scale leaves | Foliage leaves | Yearly number of fol. leaves of vegetative shoot | Yearly number of fol. leaves of sympode | Wintering type of leaves | Wintering type of buds | Wintering floral type | Number of consecutive winterings of floral primordia | |
| 1 | 4 | 3 | 4 | s | p | 3 | 1 | *Poa Hartzii* |
| 7 | 11 | 4 | 6 | s | p | 3 | 1 | — *pratensis* |
| 1(—3) | 8 | 3 | 8 | s | p | 4(ap) | 1(—2) | *Puccinellia angustata* |
| 1 | 12 | 4 | 6 | (s) | p | 3(ap) | 1 | — *phryganodes* |
| .. | .. | 5—8 | .. | (s) | p | .. | .. | |
| 1 | (4—)6 | 3 | 6 | (s) | p | ap | (1—)2 | — *Vahliana* |
| 3 | 7 | 3 | 4 | s | p | 4(ap) | 1(—2) | *Trisetum spicatum* |
| 2 | 7 | .. | .. | | | | | |
| 8 | 1 | .. | 1—3[4]) | s | a | 3 | 1 | *Juncus arcticus* |
| 4 | 4 | 3 | 4 | s | p | 6 | 1(+) | — *biglumis* |
| 8 | 4 | .. | 4 | s | a | 2 | 0 | — *castaneus* |
| 4 | 6 | .. | 6 | s | p | 3 | 1 | — *triglumis* |
| 5 | 15 | 4 | 7 | s | p | 4 | 1 | *Luzula confusa* |
| 10 | 15 | 4 | 5 | s | p | 4 | 1 | |
| 3 | 12 | (3—)4 | 6 | (w) | u | ap | 1+(-2) | — *nivalis* |
| 3 | 6 | (4—)5 | 5 | (w) | u | (ap) | 1 | |
| 3 | 12 | 5 | c. 8 | s | p | 3 | 1 | — *spicata* |
| 2 | 10 | 5 | | | | | | |
| 0+1[1]) | 5—7 | .. | 6 | s | a | 4 | 1 | *Triglochin palustre* |
| 4+1[1]) | 3 | .. | .. | .. | .. | .. | .. | |
| 1 | 13 | 2 | 2—3 | e | u | 6 | 1 | *Tofieldia coccinea* |
| 1 | 17 | 3 | 3 | w | u | 5 | 1 | — *palustris* |
| (6) | (5) | .. | 30—50[2]) | s | a | 4 | 1 | *Potamogeton filiformis* |
| (2) | 7 | .. | | s | a | .. | .. | *Betula nana* |
| (2) | 3 | .. | 10 | s | a | 6 | 1 | |
| (2) | 3 | 3 | | s | a | 4 | 1 | |
| 2[3]) | 10—20 | .. | c. 16 | s | a | 1 | 0 | *Callitriche verna* |
| 0 | 16 | 8 | 16 | w | u | 4 | 1 | *Arenaria cil. pseudofrigida* |
| 0 | 12 | 6 → 8 | 12 | w | u | 5(ap) | 1 | *Cerastium alpinum* |
| 0 | c. 20 | .. | .. | w | u | (6—7 (ap)) | (1) | |
| 0 | c. 16 | 4(—6) | .. | w | u | .. | .. | — *Regelii* |
| c. 8 | c. 16 | .. | .. | w | u | 6(ap) | 1 | |

Table 7

| | (1) Distributional type | (2) Life-form | (3) Thawing type | (4) Kind of shoot | (5) Developmental time of shoot (generation): years | (6) Flowering (of sympode) every $n^{th}$ year: n | (7) Years with development of fol. leaves (of standard shoot) |
|---|---|---|---|---|---|---|---|
| *Cerastium trigynum* | SS | Ch | II | .. | 2—**3**(2)—5 | 2 | 2 |
| *Honckenya peploides* | M | H | II | ..<br>.. | **2**<br>**2** | 1<br>1 | 1<br>1 |
| *Melandryum affine* | N | H | I | .. | (2—)**3**—4 | 1(—2) | 2 |
| — *apetalum* | N | H | III | .. | 4—**6**—7 | 3(—4) | 5 |
| — *triflorum* | N | H | I | .. | 3—**4**—5 | 2 | 3 |
| *Minuartia biflora* | S | Ch | II—III | VM<br>FE | ∞<br>(2—)**3**(—4) | ..<br>.. | ..<br>2 |
| — *Rossii* | NN | Ch | (III) | .. | **2**—? | 1 | 2 |
| — *rubella* | C | Ch | I—III | .. | **3**(2)—6 | 1 | 2 |
| — *stricta* | M | Ch | II | .. | **3**—5 | 1 | 2 |
| *Sagina caespitosa* | SS | Ch | (III) | VM<br>FE | ∞<br>**2** | ..<br>.. | ..<br>1 |
| — *intermedia* | C | H | III—IV | VM<br>FE<br>FE | ∞<br>**2**(3)<br>**3**(4) | ..<br>..<br>.. | ..<br>1<br>2 |
| *Silene acaulis* | C | Ch | III | .. | 3—**4**—15 | 3 | 3 |
| *Stellaria humifusa* | S | Ch | II—III | .. | 3—**4**(3)—6 | 2 | 3 |
| — *longipes* | N | Ch | I—IV | ..<br>L | **3**(2)—5<br>.. | 1<br>.. | 2<br>.. |
| *Viscaria alpina* | SS | H | II | .. | **4** | 2 | 3 |
| *Sedum roseum* | SS | H | I | VM<br>FE | ∞<br>**2** | ..<br>.. | ..<br>1 |
| *Arabis alpina* | SS | Ch | II | ..<br>R | 3—**4**<br>2 | 2<br>.. | 3<br>1 |
| — *arenicola* | SS | H | (I) | .. | **2**—3 | 1 | 1 |
| *Braya humilis* | M | H | I—II | .. | 2—**3**—4 | 1 | 2 |
| — *linearis* | M | H | I | ..<br>R | **3**<br>2 | 1<br>.. | 2<br>1 |
| — *purpurascens* | NN | H | I—II | ..<br>R | **3**<br>2 | 1<br>.. | 2<br>1 |
| — *Thorild-Wulffii* | NN | Ch | I | .. | 2—**3** | 1 | 2 |
| *Cardamine bellidifolia* | N | Ch | III—IV | ..<br>R | **3**—5<br>2 | 1<br>.. | 2<br>1 |

[1]) Often in addition axillary shoots.

(continued).

| (8) Number of leaves per standard shoot | | (9) | (10) | (11) | (12) | (13) | (14) | |
|---|---|---|---|---|---|---|---|---|
| Scale leaves | Foliage leaves | Yearly number of fol. leaves of vegetative shoot | Yearly number of fol. leaves of sympode | Wintering type of leaves | Wintering type of buds | Wintering floral type | Number of consecutive winterings of floral primordia | |
| 0 | c. 26[1]) | .. | 14 | (s) | u | 4 | 1 | *Cerastium trigynum* |
| 8 | 8[1]) | .. | c. 16 | s | a | 3 | 1 | *Honckenya peploides* |
| 8 | —16 | .. | | s | a | 1 | 0 | |
| 2 | 14 | 6 | 14 | s | p | 5 | 1 | *Melandryum affine* |
| 2 | 30 | (4—)6 | 10 | s | p | 5 | 1 | — *apetalum* |
| 2 | 24 | 6(—8) | 12 | s | p | 5 | 1 | — *triflorum* |
| .. | 4—6 | .. | 8(—10) | (w) | u | .. | .. | *Minuartia biflora* |
| 0 | 8 | .. | | (w) | u | 6 | 1 | |
| 0 | 8—14 | .. | c. 10 | w | u | ap | 1—2 | — *Rossii* |
| 0 | c. 14 | 6 | 14 | w | u | 5(and 6) | 1 | — *rubella* |
| 0 | 10(—12) | 4—6 | 10 | w | u | 5 | 1 | — *stricta* |
| .. | c. 8 | .. | 14 | w | u | .. | .. | *Sagina caespitosa* |
| 0 | 4—8 | .. | | w | u | 4 | 1 | |
| .. | c. 8 | .. | | w | u | .. | .. | |
| 0 | 6 | .. | 14 | w | u | —6 | 1 | — *intermedia* |
| 0 | 10 | .. | | w | u | —6 | 1 | |
| 0 | 30 | 10 | 10 | s | p | 5 | 1 | *Silene acaulis* |
| 0 | c. 16 | (4—)8(—10) | 8 | w | u | ap | 1(—2) | *Stellaria humifusa* |
| 0 | 12(—16) | 6(—8) | 8 | s | p | 4(ap) | 1 | — *longipes* |
| .. | .. | 10—20 | .. | .. | .. | .. | .. | |
| 0 | 32 | 10 → 12 | 16 | w | u | 2 | 1 | *Viscaria alpina* |
| 7 | 0 | .. | 30—45 | .. | .. | .. | .. | *Sedum roseum* |
| 5 | 30—45 | .. | | s | a | 5 | 1 | |
| 0 | 24—30 | c. 10 | c. 12 | w | u | 6 | 1 | *Arabis alpina* |
| 0 | 10—14 | .. | .. | .. | .. | .. | .. | |
| 0 | 8—10 | 8—10 | c. 10 | s | p | 2 | 1 | — *arenicola* |
| 0 | 15—20 | c. 10 | c. 20 | w | u | ap | 1 | *Braya humilis* |
| 0 | c. 15 | .. | c. 15 | s | u | 4 | 1 | — *linearis* |
| 0 | 2—5 | .. | .. | .. | .. | .. | .. | |
| 0 | 13—15 | .. | c. 14 | s | p | 5 | 1 | — *purpurascens* |
| 0 | 6 | .. | .. | .. | .. | .. | .. | |
| 0 | 12—14 | .. | c. 13 | w | u | ap | 1 | — *Thorild-Wulffii* |
| 0 | 6 | 3 | 6 | w | u | 5 | 1 | *Cardamine bellidifolia* |
| 0 | 3 | .. | .. | .. | .. | .. | .. | |

Table 7

| | (1) Distributional type | (2) Life-form | (3) Thawing type | (4) Kind of shoot | (5) Developmental time of shoot (generation): years | (6) Flowering (of sympode) every n$^{th}$ year: n | (7) Years with development of fol. leaves (of standard shoot) |
|---|---|---|---|---|---|---|---|
| *Cardamine pratensis* | S | H | II—III | .. | ≥**5** | ? | 4 |
| *Cochlearia officinalis var.* | C | H | II—III | .. | 3—**4**—5 | (3—)4 | 4 |
| *Draba alpina* | N | Ch | III | .. | **3**—5 | 1 | 2 |
| — *Bellii* | NN | Ch | I—II | .. | 3—**4**—5— | 2 | 3 |
| — *cinerea* | N | Ch | I | ..<br>R | **3**—5<br>2 | 1<br>.. | 2<br>1(—2) |
| — *crassifolia* | SS | H | II | ..<br>R | **3**<br>2 | 1<br>.. | 2<br>1(—2) |
| — *daurica* | M | Ch | I | .. | 3—**4**—7 | 2 | 3 |
| — *fladnizensis* | NS | Ch | I | ..<br>R | **3**—4<br>2 | 1<br>.. | 2<br>1(—2) |
| — *Gredinii* | NS | Ch | III | .. | **3**—6 | 1 | 2 |
| — *lactea* | N | Ch | III—IV | ..<br>R | **3**—5<br>2 | 1<br>.. | 2<br>1(—2) |
| — *micropetala* | NN | Ch | IV | ..<br>R | **3**—6<br>2 | 1<br>.. | 2<br>1(—2) |
| — *nivalis* | S | Ch | I | .. | 3—**4**—10 | 2 | 3 |
| — *subcapitata* | NN | Ch | I | ..<br>R | **3**—4<br>2 | 1<br>.. | 2<br>1(—2) |
| *Eutrema Edwardsii* | NN | H | II | .. | **3**(4)—5 | 1 | 2 |
| *Lesquerella arctica* | NN | Ch | I | VM<br>FE | ∞<br>**2**(3) | ..<br>.. | ..<br>1 |
| *Hippuris vulgaris* | S | HH | III | .. | **3** | 1 | 1 |
| *Chamaenerium latifolium* | C | H | II | .. | **3** | 1 | 1 |
| *Epilobium arcticum* | SS | H | III | .. | **3** | 1 | 2 |
| *Papaver radicatum* | N | Ch | I—III | ..<br>R | **3**—5<br>2 | 1<br>.. | 2<br>1 |
| *Koenigia islandica* | S | Th | III | .. | 1 | (1) | 1 |
| *Oxyria digyna* | C | H | III—IV | ..<br>U | 3—**4**—5<br>4—**5** | 2<br>.. | 3<br>3—4 |
| *Polygonum viviparum* | C | G | I—III | VM<br>FE | ∞<br>**2**(3) | ..<br>.. | ..<br>1 |
| *Rumex Acetosella* | SS | H | I | .. | **3**—4 | 1 | 2 |
| *Ranunculus affinis* | M | H | I | ..<br>R | **3**—4<br>2 | 1<br>.. | 2<br>1 |

[1]) Cotyledons. [2]) Up to 3 shoot generations a year. [3]) Including axillary nutrition shoots.

(continued).

| (8) Number of leaves per standard shoot | | (9) | (10) | (11) | (12) | (13) | (14) | |
|---|---|---|---|---|---|---|---|---|
| Scale leaves | Foliage leaves | Yearly number of fol. leaves of vegetative shoot | Yearly number of fol. leaves of sympode | Wintering type of leaves | Wintering type of buds | Wintering floral type | Number of consecutive winterings of floral primordia | |
| 0 | 35 | 6 → 15 | ? | w | u | 4(ap?) | 1 | *Cardamine pratensis* |
| (2)[1] | c. 65 | 8 → 20 | c. 15 | w | u | 6(ap) | 1 | *Cochlearia officinalis var.* |
| 0 | c. 15 | c. 10 | c. 15 | w | u | 6 | 1 | *Draba alpina* |
| 0 | c. 25 | c. 10 | c. 13 | w | u | 6 | 1 | — *Bellii* |
| 0 | c. 18 | c. 12 | c. 18 | w | u | 6(ap) | 1 | — *cinerea* |
| 0 | 6 | .. | .. | .. | .. | .. | .. | |
| 0 | c. 13 | c. 10 | c. 15 | w | u | 7(ap) | 1 | — *crassifolia* |
| 0 | 1—8 | .. | .. | .. | .. | .. | .. | |
| 0 | c. 25 | 8 → 10 | c. 13 | w | u | 6 | 1 | — *daurica* |
| 0 | c. 17 | c. 11 | c. 17 | (w) | u | 5 | 1 | — *fladnizensis* |
| 0 | 1—5 | .. | .. | .. | .. | .. | .. | |
| 0 | c. 13 | c. 8 | c. 13 | w | u | 6 | 1 | — *Gredinii* |
| 0 | c. 13 | c. 8 | c. 13 | w | u | 6 | 1 | — *lactea* |
| 0 | 6 | .. | .. | .. | .. | .. | .. | |
| 0 | c. 9 | c. 6 | c. 9 | w | u | 7 | 1 | — *micropetala* |
| 0 | c. 5 | .. | .. | .. | .. | .. | .. | |
| 0 | c. 24 | c. 9 | c. 12 | w | u | 5 | 1 | — *nivalis* |
| 0 | c. 17 | c. 11 | c. 17 | (w) | u | 6 | 1 | — *subcapitata* |
| 0 | 5—7 | .. | .. | .. | .. | .. | .. | |
| 0 | 11 | 3 → 4 | 11 | s | u | 6 | 1 | *Eutrema Edwardsii* |
| .. | 10—20 | .. | c. 20 | w | u | .. | .. | *Lesquerella arctica* |
| 0 | 5 | .. | | .. | .. | —6 | 1 | |
| c. 24 | c. 180 | .. | c. 500[2] | s | p | 3 | 0(—1) | *Hippuris vulgaris* |
| c. 10 | c. 20 | .. | c. 40[3] | s | a | 4 | 1 | *Chamaenerium latifolium* |
| .. | c. 13 | .. | c. 13 | w | u | 5 | 1 | *Epilobium arcticum* |
| 0 | c. 12 | c. 8 | c. 12 | s | u | 4 | 1 | *Papaver radicatum* |
| 0 | 4 | .. | .. | .. | .. | 3 | 1 | |
| (2)[1] | 1—**6**—10 | .. | 6 | s | a | 1 | 0 | *Koenigia islandica* |
| 0 | c. 12 | 6 | 6 | s | a | (ap) | (1—)2 | *Oxyria digyna* |
| 5 | c. 16 | 6 | .. | .. | .. | .. | .. | |
| .. | (2—)3(—6) | .. | 5 | s | a | .. | .. | *Polygonum viviparum* |
| 1 | 2 | .. | | .. | a | 5 | 1 | |
| 0 | 7 | 7 | 7 | s | a | 4 | 1 | *Rumex Acetosella* |
| 0 | 7 | (4—)5 | 7 | s | p | 5 | 1 | *Ranunculus affinis* |
| 0 | 4 | .. | .. | .. | .. | 4 | 1 | |

Table 7

| | (1) Distributional type | (2) Life-form | (3) Thawing type | (4) Kind of shoot | (5) Developmental time of shoot (generation): years | (6) Flowering (of sympode) every $n^{th}$ year: n | (7) Years with development of fol. leaves (of standard shoot) |
|---|---|---|---|---|---|---|---|
| *Ranunculus auricomus* | SS | H | I—II | .. | **3**—4 | 1 | 2 |
| — *glacialis* | M | H | III | .. | 3—**4**(5)—6 | 2 | 3 |
| — *hyperboreus* | C | HH | III | .. | **2**(3) | 1 | 2 |
| — *nivalis* | M | H | III | .. | 3—**4**(5)—5 | 2 | 3 |
| — *pygmaeus* | S | H | III | .. | **3**(4)—4 | 1 | 2 |
| — *sulphureus* | M | H | III | .. | 3—**4**—5 | 2 | 3 |
| — *trichophyllus* | S | HH | III | .. | **2** | 1 | 2 |
| *Thalictrum alpinum*[1] | SS | H | I—II | .. | **2**(3)—c. 12 | 1 | 1 |
| *Dryas octopetala* | N | Ch | I | .. | 5—**6**—c. 15 | 5 | 5 |
| *Potentilla Crantzii* | SS | Ch | II | VM<br>FE | ∞<br>**2**(3) | ..<br>.. | ..<br>1(—2) |
| — *emarginata* | N | Ch | I—III | VM<br>FE | ∞<br>**2**(3) | ..<br>.. | ..<br>1(—2) |
| — *nivea* | N | H | I | VM<br>FE | ∞<br>**2** | ..<br>.. | ..<br>1 |
| — *pulchella* | N | Ch | I | VM<br>FE | ∞<br>**2** | ..<br>.. | ..<br>1 |
| — *rubella* | NS | H | II | VM<br>FE | ∞<br>**2**(3) | ..<br>.. | ..<br>1(—2) |
| — *rubricaulis* | NN | H | I—II | VM<br>FE | ∞<br>**2** | ..<br>.. | ..<br>1 |
| — *stipularis* | NS | H | .. | VM<br>FE | ∞<br>**2** | ..<br>.. | ..<br>.. |
| *Sibbaldia procumbens* | SS | Ch | II | VM<br>FE | ∞<br>**2** | ..<br>.. | ..<br>1 |
| *Salix arctica* | C | Ch | I—III | V<br>FE | **2**(3)<br>**2**(3) | ..<br>.. | 1<br>.. |
| — *herbacea* | S | Ch | II | V<br>F | **2**(3)<br>**2**(3) | ..<br>(1) | 1<br>1 |

[1]) As regards runners, see p. 123.

(continued).

| (8) Number of leaves per standard shoot | | (9) | (10) | (11) | (12) | (13) | (14) | |
|---|---|---|---|---|---|---|---|---|
| Scale leaves | Foliage leaves | Yearly Number of fol. leaves of vegetative shoot | Yearly number of fol. leaves of sympode | Wintering type of leaves | Wintering type of buds | Wintering floral type | Number of consecutive winterings of floral primordia | |
| 0 | 5 | 3 | 5 | s | p | 5 | 1 | *Ranunculus auricomus* |
| 2·2 | c. 12 | 4 | 6 | s | (a) | 6(ap) | 1—2 | — *glacialis* |
| 0 | 6 | .. | 6 | s | u | 2 | 0 | — *hyperboreus* |
| 0 | 8 | 4 | 4 | s | p | 6 | 1+ | — *nivalis* |
| 0 | 5 | 3 | 5 | s | p | 6 | 1+ | — *pygmaeus* |
| 0 | 9 | (3—)4 | 5 | s | p | 6 | 1 | — *sulphureus* |
| 0 | 6—8 | .. | c. 7 | s | p | 2 | 0 | — *trichophyllus* |
| 3 | 3 | 3 | 3 | s | a | 3 | 1 | *Thalictrum alpinum*[1]) |
| 2 | 16 | 2 → 4 | 3 | s | u | 5 | 1 | *Dryas octopetala* |
| ..<br>(1) | (4—)6(—8)<br>3—4 | ..<br>.. | 9 | s<br>s | u<br>u | ..<br>6 | ..<br>1 | *Potentilla Crantzii* |
| ..<br>(1) | (4—)5(—6)<br>2—3 | ..<br>.. | 7 | s<br>s | u<br>u | ..<br>ap | ..<br>1 | — *emarginata* |
| ..<br>(1) | (5—)6(—7)<br>2—4 | ..<br>.. | 9 | s<br>.. | p<br>.. | ..<br>5 | ..<br>1 | — *nivea* |
| ..<br>(1) | c. 7<br>2 | ..<br>.. | 9 | s<br>.. | p<br>.. | ..<br>4 | ..<br>1 | — *pulchella* |
| ..<br>(1) | (3—)4(—5)<br>3 | ..<br>.. | 7 | s<br>s | u<br>u | ..<br>ap | ..<br>1 | — *rubella* |
| ..<br>(1) | c. 5<br>2—3 | ..<br>.. | 7 | s<br>.. | p<br>.. | ..<br>5 | ..<br>1 | — *rubricaulis* |
| ..<br>.. | ..<br>.. | ..<br>.. | ..<br>.. | ..<br>.. | ..<br>.. | ..<br>.. | ..<br>.. | — *stipularis* |
| ..<br>(1) | 3(—4)<br>2 | ..<br>.. | 5 | s<br>.. | u<br>.. | ..<br>3 | ..<br>1 | *Sibbaldia procumbens* |
| 2<br>2 | 5(—6)<br>2—3 | ..<br>.. | c. 7 | s<br>s | a<br>a | ..<br>5 | ..<br>1 | *Salix arctica* |
| 2<br>2 | 2—3<br>2—3 | ..<br>.. | 2—3 | s<br>s | a<br>a | ..<br>5 | ..<br>1 | — *herbacea* |

Table 7

| | (1) Distributional type | (2) Life-form | (3) Thawing type | (4) Kind of shoot | (5) Developmental time of shoot (generation): years | (6) Flowering (of sympode) every $n^{th}$ year: n | (7) Years with development of fol. leaves (of standard shoot) |
|---|---|---|---|---|---|---|---|
| *Chrysosplenium tetrandrum* ... | NS | H | II | .. | **3**(2)—4 | 1 | 2 |
| *Saxifraga aizoides* ..... | SS | Ch | II | .. | **4**—5 | (3) | 3 |
| — *caespitosa* ..... | C | Ch | I—III | .. | (3—)4—**6**—7 | 4 | 5 |
| — *cernua* ..... | C | H | III—IV | .. | (3—)**4**—c. 7 | 2 | 2 |
| — *flagellaris* ..... | NN | Ch | III | .. | 6—**9**—c. 12 | 7 | 8 |
| — *hieraciifolia* ..... | NS | H | II | .. | **4**—5 | 2 | 2 |
| — *Hirculus* ..... | NN | H | III | .. | 3—**4**—7 | 3 | 3 |
| — *Nathorsti* ..... | NS | Ch | II | .. | 4—**5**—6 | (4) | 4 |
| — *nivalis* ..... | C | H | I—II | .. | **3**—4 | 1 | 1—2 |
| — — *tenuis* ..... | C | H | III—IV | .. | **3**—4 | 1 | 2 |
| — *oppositifolia* ..... | C | Ch | I—II | ..<br>L | 4—**5**—10<br>5 | (3)<br>.. | 3(—4)<br>4 |
| — *rivularis* ..... | S | H | III—IV | ..<br>U | **3**—4<br>**4**—5 | 1<br>.. | 2<br>2 |
| — *stellaris comosa* .... | N | H | III—IV | .. | **3**—4 | 1 | 2 |
| — *tricuspidata* ..... | M | Ch | (I) | .. | 3—**4**—6 | 2 | 3 |
| *Campanula rotundifolia* ..... | SS | H | I | VM<br>FE | ∞<br>**2** | ..<br>.. | ..<br>1 |
| — *uniflora* ..... | M | H | I | VM<br>FE | ∞<br>**2** | ..<br>.. | ..<br>1 |
| *Antennaria alpina* ..... | S | Ch | II | .. | 3—**4**—7 | 2 | 3 |
| *Arnica alpina* ..... | M | H | I | .. | 3—**4**—c. 20 | (3) | 3 |
| *Erigeron compositus* ..... | C | Ch | I | .. | 3—**4**—6 | 2 | 3 |
| — *unalaschkensis* ..... | SS | H | II—III | .. | **3**—c. 10 | 1 | 2 |
| — *uniflorus* ..... | C | H | I | .. | 3—**4**—5 | (2—)3 | 2 |
| *Matricaria inodora* ..... | SS | Ch | II | .. | 3—**5** | (5) | 5 |
| *Taraxacum arcticum* ..... | NN | H | III | .. | **3**—? | 1 | 2 |
| — *brachyceras* ..... | SS | H | II | .. | **2**(3)—? | 1 | 2 |

[1]) Cotyledons.

(continued).

| (8) Number of leaves per standard shoot | | (9) | (10) | (11) | (12) | (13) | (14) | |
|---|---|---|---|---|---|---|---|---|
| Scale leaves | Foliage leaves | Yearly number of fol. leaves of vegetative shoot | Yearly number of fol. leaves of sympode | Wintering type of leaves | Wintering type of buds | Wintering floral type | Number of consecutive winterings of floral primordia | |
| 0 | (4—)5(—8) | 4 | 5 | (w) | u | 7(ap) | 1(—2) | *Chrysosplenium tetrandrum* |
| 0 | c. 30 | 6 → 15 | (c. 10) | w | u | 3(ap) | 1 | *Saxifraga aizoides* |
| 0 | 40—45 | 6 → 10 | c. 10 | w | u | ap | 1(—2) | — *caespitosa* |
| 2·4 | 9 | 3 → 4 | c. 5 | s | a | 6 | 1 | — *cernua* |
| (0) | 75—80 | 6 → 12 | c. 11 | w | u | ap | 1—2 | — *flagellaris* |
| 0 | c. 13 | 8 | 6 | (s) | u | 5 | 1 | — *hieraciifolia* |
| 1(—2) | c. 24 | 6 → 8 | 8 | s | p | 4 | 1 | — *Hirculus* |
| 0 | c. 32 | 6 → 10 | c. 8 | w | u | ap | 1 | — *Nathorsti* |
| 0 | 5 | 5 | 5 | w | u | 6 | 1 | — *nivalis* |
| 0 | 4 | 4 | 4 | w | u | 6 | 1 | — — *tenuis* |
| 0 | c. 24 | 6 → 8 | c. 8 | w | u | 6 | 1 | — *oppositifolia* |
| 0 | c. 40 | c. 14 | .. | w | u | 6 | 1 | |
| 0 | 6 | 3 | 6 | (w) | u | 5 | 1 | — *rivularis* |
| 3—4 | 6 | 3 | 6 | (w) | u | 5 | 1 | |
| 0 | c. 7 | 4 | 7 | w | u | ap | 1(—2) | — *stellaris comosa* |
| 0 | c. 30 | 8 → 12 | c. 15 | e | u | 5 | 1 | — *tricuspidata* |
| .. | 4 | .. | c. 25 | s | p | .. | .. | *Campanula rotundifolia* |
| (c. 2—4) | 20—25 | .. | | s | p | 1 | 0 | |
| 3(—4) | 0 | .. | c. 9 | (s) | (p) | .. | .. | — *uniflora* |
| (0) | 8—10 | .. | | s | p | (4—)5 | 1 | |
| 0 | 28—34 | 10—12 | c. 15 | (s) | u | 3(ap) | 1(—2) | *Antennaria alpina* |
| 3·4 | 14 | 4 → 6 | c. 4 | s | a | 5 | 1 | *Arnica alpina* |
| 0 | c. 25 | 6 → 10—12 | c. 12 | s | u | 4 | 1 | *Erigeron compositus* |
| 0 | c. 20 | 6(—8) | c. 20 | s | p | (4—)5 | 1 | — *unalaschkensis* |
| 0 | c. 26 | 7—10 | c. 13 | s | p | 4 | 1 | — *uniflorus* |
| (2)[1]) | c. 36 | 4 → 6—8 | c. 7 | s | u | ap | 1 | *Matricaria inodora* |
| 0 | 9 | .. | 9 | s | p | 5(ap) | 1 | *Taraxacum arcticum* |
| 0 | 10—15 | .. | c. 15 | s | p | (3) | 1 | — *brachyceras* |

Table 7

| | (1) Distributional type | (2) Life-form | (3) Thawing type | (4) Kind of shoot | (5) Developmental time of shoot (generation): years | (6) Flowering (of sympode) every $n^{th}$ year: n | (7) Years with development of fol. leaves (of standard shoot) |
|---|---|---|---|---|---|---|---|
| *Taraxacum phymatocarpum*... | NN | H | I | ..<br>R | **3**—4—?<br>2 | 1<br>.. | 2<br>1 |
| — *pumilum* ..... | NN | H | (I) | .. | 3—? | 1 | 2 |
| *Empetrum nigrum*..... | S | Ch | II | VM<br>FE | ∞<br>2 | ..<br>.. | ..<br>0[1] |
| *Arctostaphylos alpina*..... | SS | Ch | I | .. | **4**—**6**—10 | 4 | 4[5] |
| *Cassiope hypnoides*..... | SS | Ch | II | .. | 4—**5**—c. 12 | (3—4) | 3[4] |
| — *tetragona*..... | N | Ch | II | VM<br>FE | ∞<br>2(3) | ..<br>.. | ..<br>0[1] |
| *Phyllodoce coerulea* ..... | SS | Ch | I—II | .. | **4**—**9**—16 | 7 | 7 |
| *Rhododendron lapponicum* .... | S | Ch | I | .. | 5—**6**—15 | 4 | 4[5] |
| *Vaccinium uliginosum* ..... | S | Ch | I—II | V<br>FE | **2**<br>**2** | ..<br>.. | 1<br>0[1] |
| *Gentiana detonsa*..... | SS | H | II | .. | (**3**) | (3) | 3 |
| — *nivalis* ..... | SS | H | II | .. | **3** | (3) | 3 |
| — *tenella*..... | SS | H | II | .. | **2** | (2) | 2 |
| *Pinguicula vulgaris*..... | SS | H | II | .. | **2**(—?) | 1 | 1 |
| *Armeria vulgaris var.*[2]) ..... | M | H | I—II | .. | (2—)**3**—4—7 | 2 | 3 |
| *Polemonium boreale*[3])..... | NS | H | II | .. | **3**—6 | 1 | 2 |
| *Primula stricta* ..... | SS | H | II | .. | **3**(—?) | 1 | 2 |
| *Pyrola grandiflora*..... | M | H | I—II | .. | 6—**8**—13 | .. | (5[6]—)<br>6[7] |
| *Euphrasia latifolia* ..... | SS | Th | I—II | .. | **1** | (1) | 1 |
| *Pedicularis flammea* ..... | S | H | I—II | .. | 3—**4**—7 | 2 | 3 |
| — *hirsuta* ..... | N | H | I—III | .. | 3—**4**—6 | 2 | 3 |
| — *lapponica*..... | SS | H | II | VM<br>F | ≦8<br>**3** | ..<br>.. | ..<br>1 |
| *Veronica alpina*..... | SS | H | II | .. | **3** | 1 | 1 |

[1]) Cotyledons. [2]) Cf. p. 154. [3]) As regards runners, see p. 155.

(continued).

| (8) Number of leaves per standard shoot | | (9) | (10) | (11) | (12) | (13) | (14) | |
|---|---|---|---|---|---|---|---|---|
| Scale leaves | Foliage leaves | Yearly number of fol. leaves of vegetative shoot | Yearly number of fol. leaves of sympode | Wintering type of leaves | Wintering type of buds | Wintering floral type | Number of consecutive winterings of floral primordia | |
| 0 | 12 | 12 | 12 | s | p | 4 | 1 | *Taraxacum phymatocarpum* |
| 0 | 6 | .. | .. | .. | .. | .. | .. | |
| 0 | 10—13 | .. | c. 12 | s | p | 5 | 1 | — *pumilum* |
| 8 | 20 | .. | 20 | e | a | .. | .. | *Empetrum nigrum* |
| 4 | 0 | .. | | .. | .. | 7 | 1 | |
| 5·6 | c. 26 | 7 | 7 | s | a | 6 | 1 | *Arctostaphylos alpina* |
| 0 | c. 70 | 10 → 30 | c. 25 | e | u | 7 | 1 | *Cassiope hypnoides* |
| .. | 16 | .. | 16 | e | a | .. | .. | — *tetragona* |
| 2 | 0 | .. | | .. | .. | 7 | 1+ | |
| (0) | c. 140 | 10 → 30 | c. 25 | e | a | 6 | 1 | *Phyllodoce coerulea* |
| 6·3 | c. 24 | 5—7 | c. 6 | e | a | 7 | 1 | *Rhododendron lapponicum* |
| 6 | 4—8 | .. | c. 6 | s | a | .. | .. | *Vaccinium uliginosum* |
| 8 | 0 | .. | | .. | a | 5 | 1 | |
| 2[1]) | c. 16 | 4 → 6 | c. 6 | s | u | 2? | 0? | *Gentiana detonsa* |
| 2[1]) | c. 16 | 2 → 8 | c. 6 | w | u | 2? | 0? | — *nivalis* |
| 2[1]) | c. 10 | 4 → 8 | c. 6 | s | u | 2? | 0? | — *tenella* |
| 6 | 6 | .. | 6 | s | a | 2 | 0 | *Pinguicula vulgaris* |
| (1) | c. 25 | c. 10 | c. 12 | w | u | ap | 1 | *Armeria vulgaris var.*[2]) |
| 0 | c. 10 | (3—)4(—10) | c. 10 | s | u | ap | 1 | *Polemonium boreale*[3]) |
| 4 | 18 | .. | 18 | s | a | 6 | 1 | *Primula stricta* |
| x+7·2 | c. 13 | 1 → 3 | 2 | e | a | 4 | 1 | *Pyrola grandiflora* |
| 2[1]) | (5—)10(—14) | .. | c. 10 | s | a | 1 | 0 | *Euphrasia latifolia* |
| c. 16 | c. 16 | 2(—5) | c. 8 | s | a | 5 | 1 | *Pedicularis flammea* |
| c. 10 | c. 32 | 3 → 6—8 | c. 16 | s | a | 5 | 1 | — *hirsuta* |
| 2—3 | 3 | .. | 5—10 | s | a | .. | .. | — *lapponica* |
| 4 | 7 | .. | | s | a | 5 | 1 | |
| 6—8 | 12—14 | .. | c. 14 | s | u | 1 | 0 | *Veronica alpina* |

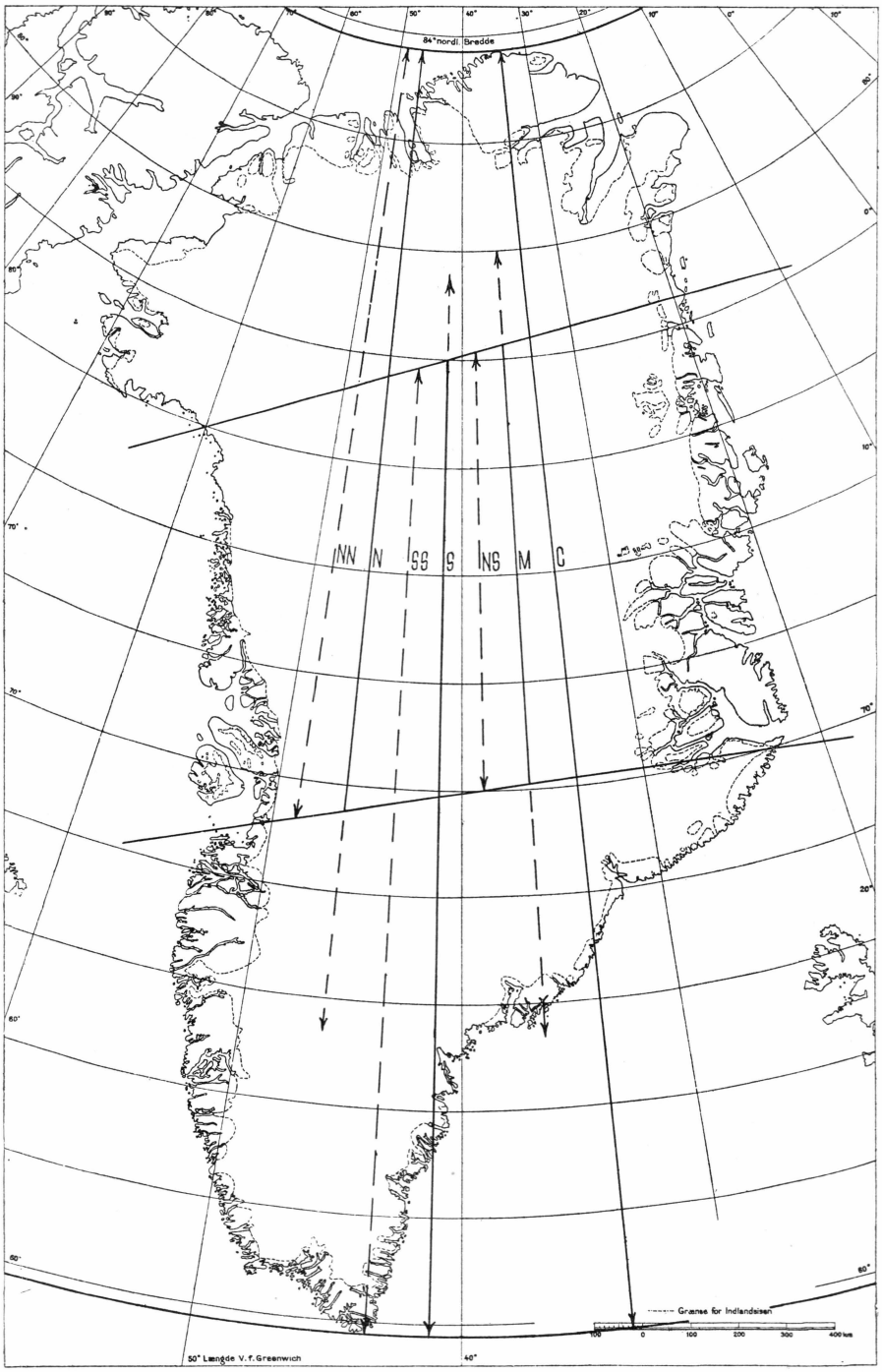



Fig. 16. Map of Greenland illustrating the Greenland areas of the various distributional groups (schematically).

## Explanation of Table 7.

Column (1) indicates the distributional type of the species within Greenland. The species are divided into seven groups, whose distribution is illustrated in the map Fig. 16.

**SS**: Species with a distinct northern limit within the area, and whose northern limit in West Greenland does not run north of 75°30′ N. lat. (Melville Bugt), but without a southern limit as defined below under NN.

**NN**: Species which in East Greenland have their southern limit in the Scoresby Sund area (70°09′ N. lat.) or north of it, and which are not found in West Greenland south of Jakobshavn Gl. (69°10′ N. lat.), but which have no northern limit as defined above under SS.

**NS**: Species having a northern limit as defined above under SS and a southern limit as defined above under NN.

**S**: Species without any distinct northern or southern limits as defined above under the groups SS and NN, extending southwards to the southernmost point of Greenland, but not around the north of Greenland.

**N**: Species which have no distinct northern or southern limits as defined above under the groups SS and NN, and which extend around the north of Greenland, but do not spread to the southernmost point of Greenland.

**M**: Species which have no distinct northern or southern limits as defined above under SS and NN, but which do not extend either north or south around Greenland.

**C**: Species without northern or southern limits within Greenland, that is to say, circumgreenlandic species.—(See further p. 184).

Column (2) indicates Raunkiær's life-forms of the species (Raunkiær 1907). **Ch**: Chamaephyte. **H**: Hemicryptophyte. **G**: Geophyte. **HH**: Helo- or Hydrophyte. **Th**: Therophyte.—(Cf. further p. 185).

Column (3) indicates the thawing types of the species. The Roman numerals I—IV indicate the thawing type for the ecosystem or ecosystems in which the species is naturally included. In accordance with Table 6 (pp. 56—59) they indicate as follows:

**I**: Snow-covering normally ceases on June 1st at the latest.
**II**: Snow-covering normally ceases between June 1st and June 15th.
**III**: Snow-covering, or ice-cover of fresh waters, normally ceases between June 15th and July 1st.
**IV**: Snow-covering does not normally disappear till after July 1st.—(Cf. further p. 187).

Column (4) concerns species with shoot dimorphism (polymorphism), differentiation between long shoots and short shoots, vegetative and floral shoots, etc. **L** means long shoots, **S** short shoots; these designations are applied in cases where both long shoots and short shoots are floral. **V**: vegetative shoots. **F**: floral shoots. **M**: monopodial axes. **E** (ephemeral) shoots without rejuvenescence. **A**: anticipated shoots (as compared with the normal shoots of the species). **U**: subterranean rhizomes or stolons (in contrast to erect shoots). **R**: regulation shoots (Cf. p. 107).

Column (5) indicates the time of development of the shoots (shoot generations) reckoned in years, i. e. growth years, including the year of initiation (bud stage) and the flowering year. If the time of development of the shoots varies, the

limits for the duration of the development are indicated as far as possible. The shoot type as regards the course of development (standard shoot, see p. 190) used as type for the number of leaves, etc., in the succeeding columns ((6) (7) (8) and (10)) are in heavy type. Unlimited duration of monopodial axes indicated by ∞. —(Cf. further p. 189).

Column (6) shows the interval between consecutive flowerings within the same shoot chain under a continuous standard development: flowering every $n^{th}$ year. In cases of shorter or longer shoot development than that of the standard shoot (Column (5)) the interval between the flowerings are shortened or prolonged respectively by a corresponding period (number of years).

Column (7) indicates the number of years with development of foliage leaves (and flowers) per standard shoot. If no foliage leaves are developed in the flowering year, the number of years with foliage leaves + the flowering year are added in square brackets. (If the duration of the shoot differs from that of the standard shoot, the number of seasons with leaf development is altered correspondingly). Monopodial axes are not dealt with in this column.

Column (8) indicates the number of leaves per standard shoot: scale leaves and foliage leaves. By foliage leaves is understood basal leaves + stem leaves and inflorescence bracts, if they are of such a character and size that they must be supposed to participate materially in the assimilation as foliage leaves. Bracts without assimilative importance are disregarded. (If the developmental time of the shoot differs from that of the standard shoot, the number of leaves is increased or reduced by the number of foliage leaves per year indicated in the next column). The yearly number of leaves of monopodial axes is indicated in this column.—(See further p. 191).

Column (9) shows the yearly production (number) of foliage leaves per shoot in the invigoration years preceding the flowering year. Monopodial axes are not dealt with in this column.—(See further p. 193).

Column (10) indicates the yearly production (number) of foliage leaves of the unbranched sympode on continual development of standard shoots. For species with seperate vegetative and floral axes, the yearly number of leaves for the vegetative axes + one floral shoot is given.—(See further p. 193).

Column (11) indicates the wintering state of the leaves. The species are divided into three groups as follows: **s**: summer-green, **w**: winter-green, **e**: evergreen.—(See further p. 197).

Column (12) indicates the condition of the shoot apices (buds) during wintering: **a**: active bud protection, **p**: passive bud protection, **u**: unprotected buds.—(See further p. 200).

Column (13) indicates the floral wintering stage as follows:

**1**: Cone of growth purely vegetative during wintering. A number of leaf primordia in addition to the floral primordia are formed in the flowering year proper.

**2**: Cone of growth generally of a vegetative appearance during the wintering. All leaf primordia as a rule formed. Floral primordia are formed in the flowering year proper.

**3**: Cone of growth not of a purely vegetative appearance. Inflorescence axis, however, without distinctly differentiated floral primordia.

**4**: The floral parts in incipient differentiation; only anthers and calyx recognisable as slightly differentiated processes.

**5**: Calyx and anthers at any rate distinctly formed. Ovary developing, not yet closed. Ovules lacking or only incipient verruciform formations on the placenta. Flower buds relatively small.

**6**: Flower buds roughly developed morphologically. Anthers sometimes with P.M.C. Ovary as a rule closed, with distinct, though not fully developed ovules. Flower buds large.

**7**: Flower buds fully developed. Anthers with fully developed pollen.

**ap**: Floral development aperiodical. Flower buds at all or most of the aforementioned (3—7) phases of development during wintering.

An (ap) added to the numerical designations indicates that the floral development is partially aperiodical, though the developmental stage indicated by the main designation is the most frequent.—(See further p. 202).

Column (14) indicates the number of winterings of shoot apices (cones of growth) in a "floral" (i.e. not purely vegetative) condition. A + added indicates that one more wintering often takes place. If so, the cone of growth during its first wintering is at a stage of development just recognisably at the transition from the purely vegetative to the "floral" stage. — (See further p. 207).

## Interrelations of developmental and biological characteristics and their relations to distributional and thawing types.

In the succeeding pages a summary will be given of the developmental-morphological and biological characteristics and their plant-geographical importance on the basis of the data laid down in Table 7.

(1) Distributional groups. Referring to the explanation of the table above it should be noted that the SS-species are typical southern species within the area, the NN-species are northern, while S, N, and especially C comprise species which are widely distributed in Greenland as compared with M and NS, the distribution in a north-south direction of the species belonging to these two groups being fairly limited. The M-species are lacking in the southern and northern parts of Greenland. The NS-species have an extremely limited range; within Greenland no less than twelve of the thirteen species are restricted to the area of Northeast Greenland dealt with here.

The reason why I considered the distribution of the species in West Greenland of decisive importance for the division into groups is, 1) as regards the fixation of the northern limit of the southern species, that the northernmost parts of the area dealt with here are comparatively poorly investigated, and doubts may therefore arise as to whether the northernmost localities known for a species actually indicate its approximate northern limit. If, therefore, the northern limit of a species according to the finds known is situated within our area, but the species has also been found in the relatively well investigated Thule area of the west coast (north of 75°30′ N. lat.), the northern limit of the species in East Greenland must be regarded with a certain reservation. Such species are therefore not referred to the SS (respectively the NS) group. 2) As regards the fixation of the southern limit of the northern species the motive has been to keep the group division clear of the specially East Greenland climatic boundary, Blosseville Kyst, south of Scoresby Sund (BÖCHER 1933 a), or, in other words, to base the division into groups more on latitudes. On the east coast of Greenland a comparatively large number of species have a distinct southern limit in the area of Scoresby Sund, while on the west coast they are found much farther south (south of 69°10′ N. lat.). Such species are not referred to the NN (respectively NS) group. (For the distribution of the species in West Greenland, see OSTENFELD 1926[1])). It appears from Tables 8 and 9 that the SS group is by far the most numerously represented, com-

[1]) As regards various species the list has been corrected according to our present knowledge of the occurrence of the species.

Table 8. The absolute distribution of the Northeast Greenland flora within the geographical distributional groups and life-forms.

| | Ch | H | G | HH | Th | Total |
|---|---|---|---|---|---|---|
| SS | 11 | 29 | 7 | 1 | 2 | 50 |
| NN | 8 | 14 | 3 | 1 | .. | 26 |
| S | 8 | 7 | 5 | 2 | 1 | 23 |
| N | 10 | 10 | 3 | .. | .. | 23 |
| NS | 3 | 7 | 3 | .. | .. | 13 |
| M | 4 | 13 | 4 | .. | .. | 21 |
| C | 7 | 16 | 4 | 1 | .. | 28 |
| Total... | 51 | 96 | 29 | 5 | 3 | 184 |

Table 9. The percentage distribution of the Northeast Greenland flora within the geographical distributional groups and life-forms.

| | Ch | H | G | HH | Th | Distributional Groups |
|---|---|---|---|---|---|---|
| | % | % | % | % | % | % |
| SS | 22.0 | 58.0 | 14.0 | 2.0 | 4.0 | 27.2 |
| NN | 30.8 | 53.8 | 11.5 | 3.9 | .. | 14.1 |
| S | 34.8 | 30.4 | 21.7 | 8.7 | 4.4 | 12.5 |
| N | 43.5 | 43.5 | 13.0 | .. | .. | 12.5 |
| NS | 23.1 | 53.8 | 23.1 | .. | .. | 7.1 |
| M | 19.0 | 61.9 | 19.1 | .. | .. | 11.4 |
| C | 25.0 | 57.1 | 14.3 | 3.6 | .. | 15.2 |
| Life-form... | 27.7 | 52.2 | 15.8 | 2.7 | 1.6 | .. |

prising more than one-fourth of all the species. As might be expected, the NS group is the smallest group, comprising c. 7 per cent. of the total number of species. The remainder of the species are distributed fairly equally over the other five groups with c. $^1/_8$ of the total number on each group.

(2) Life-forms. GELTING (1934) has treated at length the life-form problem in relation to the flora of Northeast Greenland. As pointed out by GELTING, an exact determination of the life-forms of the arctic plants is difficult. But in my opinion the difficulty has very different causes from those suggested by GELTING when he says (l. c. p. 289): "Sometimes a species varies so little in outer morphology that all its individuals belong to the same life-form class . . . .other species vary so much in outer morphology that the different individuals may belong to different life-form classes, which variation may be designated class

change." (As regards the class change problem, cf. further ALLORGE 1921, HAGERUP 1930, GRAM 1935). I cannot see that the arctic species vary more in outer morphology than for instance the Danish species. The difficulty in determining the life-form of the arctic plants may be largely found in their small absolute size. It is obvious that when the whole above-ground plant measures only some 5 cm, and many plants do not even attain that size, it would indeed be asking too much to expect that the wintering buds of the geophytes should be situated at any great depth below the surface of the soil or that the chamaephytes should be able to raise their buds to any great height above the surface. Nobody has ever talked about class change because the Danish hemicryptophytes, as for instance *Arabis hirsuta* or *Potentilla minor*, winter with their innovation buds elevated $^1/_2$ cm above the surface of the soil, though this is very often the case. These two species are easily comparable with the arctic *Drabae* and *Potentillae* respectively; the similarity of *Potentilla minor* to *P. Crantzii* is especially great. Nevertheless I designate the arctic *Drabae* and *Potentilla Crantzii* chamaephytes in accordance with GELTING. My reason for this is largely the fact that the surface of the soil in the Arctic is two-dimensional to a much greater extent than is the case in temperate regions. On account of the abundant accumulation of dead leaves and the activity of the earth-worms in the temperate regions, the "surface of the soil" here actually has a third dimension. The winter buds of typical mesocorm plants as e. g. *Arabis hirsuta* and *Potentilla minor* will quite passively be embedded in this mouldy layer of decaying plant remains termed by us the surface of the soil, and thus they become passive hemicryptophytes. In the Arctic the case is different; owing to the inconsiderable fall of leaves and the lack of any activity of earth-worms the surface of the soil is here a more exact concept. By the yearly growth of the rosette axes—however inconsiderable it may be—the mesocorm plants are in the course of time forced upwards into the chamaephyte position, especially in places exposed to the wind, where precisely those species are abundantly represented which GELTING accuses of class change. It is not the failing outer morphology of the plants, but their small size in connection with the distinct limitation of the surface of the soil which is the principal cause of the difficulties encountered in the Arctic, where we are confronted with the task of grouping the plants according to principles worked out in an entirely different climatic area. The above-mentioned conditions compel us to make our measuring methods more exact than the life-form system in its original shape will allow of. GELTING has reduced his scale and has taken the consequences—as regards the chamaephytes. His erection of the group *chamaephyta mesocormatosa* is an exceedingly happy choice. But as regards the geophytes—his

placing of *Juncus castaneus* and *Triglochin palustre* among the hemicryptophytes seems to me to lack foundation. At any rate they may with equal right as for instance *Polygonum viviparum*, which is generally recognised as a geophyte, be referred to the geophytes. As regards *Juncus biglumis* and *Juncus triglumis* the life-form is more problematic. I refer them to the geophytes even though the small size of the plants makes the position of the buds very much approach the hemicryptophyte level.

The life-form of the two species, *Pyrola grandiflora* and *Pedicularis lapponica*, which agree in vegetative construction (cf. pp. 157 and 160), may be disputed. The vegetative rejuvenescence always takes place from subterranean runners, as in the geophytes, The hemicryptophytic floral shoots have a limited life duration and produce no vegetative reproductive shoots. If the floral shoots had only one year's vegetative invigoration stage before the flowering, the species would have to be referred to the geophytes on the same grounds as those on which RAUNKIÆR referred the *Rubus* species to the hemicryptophytes (1907, p. 57), viz. the fact that the continued existence of the individual does not depend on the wintering of the above-ground shoot. As the hemicryptophytic floral shoots of the species mentioned require a several years' invigoration stage before flowering, not only would the flowering be prevented by a destruction of the rosette shoots during the winter, but at the same time the storing up of nourishment on which the continued life of the individual depends would in the course of a very few years be reduced to the critical minimum. These species are therefore rightly to be referred to the hemicryptophytes, despite the wintering of the vegetative shoot apices at the geophyte level.

If we consider the life-form spectra of the different distributional groups, which must naturally be compared with the spectrum for the flora of the area as a whole, the most concpicuous features will be (cf. Tables 8 and 9) that the NN group has no remarkably high Ch percentage, that the therophytes are lacking in the groups with a northern distribution, that the SS species have a low Ch percentage and a high H percentage, and that the groups M and NS, that is to say, the groups that are the most characteristic of our area, being but slightly distributed or not found at all outside the area, likewise have a low Ch percentage, while they have a high H and G percentage. In connection with the relatively high G percentage for the area as a whole demonstrated by GELTING, this can only confirm GELTING's characterisation (l. c. p. 321) of Northeast Greenland as a geophyte-chamaephyte area within the arctic chamaephyte zone (RAUNKIÆR 1911).

(3) Thawing groups. (cf. Table 6, p. 56). In Table 7 the species are listed as belonging sometimes to a definite thawing group, sometimes

to two or more groups according to the different ecological amplitude of the species as regards the factor considered. An actual proof of the correctness of the records for the melting of the snow cannot of course be given here. For the time being the author must be responsible for them.

In all numerical computations of the distribution of the species within the thawing groups each species within each thawing group was regarded as a unit, or in other words: not the species as such, but their "places" in the thawing scale form the basis of the computations.

Table 10 shows the percentage distribution of the thawing "places" within the individual distributional groups. Here, too, the frequency of the individual groups must of course be viewed in relation to the distribution of the total number of "places" within the thawing groups, as appears from the bottom line of the table. The unequal distribution of the places over Groups I—IV is connected with the fact that the number of species is always low for the localities where the snow melts latest. Group II, for instance, has a high number of species, whereas Group IV has an inconsiderable number. It will appear from the table that the SS species chiefly belong to Group II, to a small extent to Group III, while Group IV is not represented at all within the SS species. The NN species are very equally distributed over the first three thawing groups and accordingly have a relatively small content of II species. The same applies to the N and C species, which on the other hand have a maximum in III and IV. The NS and M groups comprise a comparatively high number of II and I species respectively. Thus the southern species are chiefly associated with the ecosystems thawing moderately early, while the northern and widely distributed species are to a greater extent associated with the ecosystems thawing late. Species with small areas (NS and M) are chiefly associated with the ecosystems which become free of snow at an early date.

In the same way Table 11 gives the distribution of the thawing groups within the individual life-forms. Ch is abundantly represented by I species, is accordingly chiefly associated with the early snow-free ecosystems. H is "normally" distributed over the thawing groups, it is accordingly, from a statistic point of view, independent of the duration of the snow-covering. G is concentrated in Groups II and III; the geophytes accordingly show a correlative connection with a rather late thawing. Th has its maximum in II. According to the nature of their habitat, HH is only represented by III species.

(4) As regards shoot dimorphism (polymorphism) the reader is referred to the explanation of Table 7 on p. 181 and the treatment of the individual species in the special part.

Table 10. The percentage distribution of the thawing types over the geographical distributional groups within the flora of Northeast Greenland.

| | I | II | III | IV | Number of "places" |
|---|---|---|---|---|---|
| | % | % | % | % | % |
| SS | 27.3 | 61.8 | 10.9 | .. | 55 |
| NN | 31.3 | 31.3 | 31.3 | 6.2 | 32 |
| S | 21.9 | 37.5 | 37.5 | 3.1 | 32 |
| N | 30.2 | 23.3 | 34.9 | 11.6 | 43 |
| NS | 14.3 | 57.1 | 28.6 | .. | 14 |
| M | 46.2 | 34.6 | 19.2 | .. | 26 |
| C | 28.3 | 24.5 | 34.0 | 13.2 | 53 |
| Norm. (All "places") .. | 29.0 | 37.7 | 27.4 | 5.9 | .. |

Table 11. The percentage distribution of the thawing types over the individual life-forms.

| | I | II | III | IV | Number of "places" |
|---|---|---|---|---|---|
| | % | % | % | % | % |
| Ch | 35.6 | 34.2 | 23.3 | 6.9 | 71 |
| H | 30.6 | 36.6 | 26.1 | 6.7 | 131 |
| G | 13.3 | 46.7 | 37.8 | 2.2 | 44 |
| HH | .. | .. | 100.0 | .. | 5 |
| Th | 25.0 | 50.0 | 25.0 | .. | 4 |
| Norm. (All "places") .. | 29.0 | 37.7 | 27.4 | 5.9 | .. |

(5) Duration of the development of the shoots (shoot generations). In a number of species the duration of the development of the shoots is constant, but in the majority it varies within wide limits. In several cases it is only possible within a certain interval to state what duration of the shoot development is the most frequent, as it often depends in a high degree on external conditions. Sometimes the duration of the development of the shoot is difficult to determine exactly, even in the concrete cases; for chiefly in species with a more or less aperiodical shoot sequence the buds may be formed continually, so that the transition between anticipated and not anticipated shoots become quite gradual. As regards such species the duration of the developmental type which is estimated to be the most frequent is indicated in Table 7 (in heavy type), and the (supposed) deviating type is given in parentheses. In

species which normally have a proleptic shoot development the deviating type shows a year's prolongation of the bud stage. And conversely, in species in which the proleptic shoot must be regarded as the deviating one, its bud stage is shortened by one year as compared with the normal shoot.

For statistical purposes it is of interest to operate with a definite type of shoot development for each species; for this type I employ the term "standard shoot". The developmental type of most frequent occurrence was naturally chosen as the standard shoot in so far as such a type could be found. If this was not possible, the type of shoot whose development indicates the mean value of the duration of shoot development in the species, determined on the basis of an examination of a (random) number of shoots, was selected as standard shoot. The standard shoot will accordingly in all cases be a perfectly valid illustration of the course of shoot development of the particular species.

Tables 12 and 13 show the percentage distribution of the duration of the development of "standard shoots" within the different distribution- and thawing-groups. As will be seen, the three-year development is the most frequent. A special preponderance for any of the individual groups within the two series is hardly recognisable. Nor is the monopodial growth type essentially associated with any definite group. It proves, however, that the S and SS groups show a greater tendency towards a short development of the shoot than the other groups. It should be pointed out here that in the calculation of the duration of the shoot development of hapaxanthic species the seed stage is—perhaps not very logically—excluded. Finally it should be pointed out that for species with a sympodial growth and regularly alternating vegetative and floral shoots (e. g. *Vaccinium uliginosum* and *Salix arctica*) the duration of the shoot development is reckoned to be: the total duration of a vegetative + a succeeding floral shoot (cf. further the remarks on Fig. 14 under *Ericaceae* p. 147 et seq.).

(6) The time interval between the flowerings within the same sympode. The statements in Table 7, which refer to the standard shoot, are chiefly of theoretical interest in the species whose shoot duration is not constant. Shoots of different duration of development here often alternate irregularly within the same sympode, sometimes, however, more or less regularly (see e. g. *Draba*, p. 107, and *Ranunculus affinis*, p. 121).

(7) The number of years with development of foliage leaves per shoot (standard shoot). On comparison with the shoot duration (5) the numerical values (Table 7) also serve as a measure of the duration of the bud or runner stage (cf. also (14): rate of growth, p. 207).

Table 12. The percentage distribution of the time of development of standard shoots over the distributional groups within the flora of North-east Greenland.

| | Sympodial axes | | | | | | | | | Monopodial axes |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 year | 2 years | 3 years | 4 years | 5 years | 6 years | 7 years | 8 years | 9 years | ∞ |
| | % | % | % | % | % | % | % | % | % | % |
| SS ..... | 4.0 | 12.0 | 32.0 | 18.0 | 14.0 | 4.0 | 2.0 | 2.0 | 2.0 | 10.0 |
| NN ..... | .. | 3.8 | 42.3 | 34.6 | 3.8 | .. | 3.8 | .. | 3.8 | 7.7 |
| N..... | .. | .. | 34.8 | 21.7 | 13.0 | 8.7 | 4.3 | .. | .. | 17.4 |
| S ..... | 4.3 | 8.7 | 26.0 | 21.7 | 13.0 | 13.0 | .. | 4.3 | .. | 8.7 |
| NS..... | .. | .. | 30.8 | 15.4 | 23.1 | .. | 7.7 | 7.7 | .. | 15.4 |
| M..... | .. | 10.0 | 25.0 | 35.0 | 10.0 | .. | 5.0 | 5.0 | 5.0 | 5.0 |
| C ..... | .. | 3.6 | 32.1 | 32.1 | 14.3 | 10.7 | .. | .. | .. | 7.1 |
| Norm. (All species) ... | 1.6 | 6.0 | 32.8 | 25.1 | 12.6 | 5.5 | 2.7 | 2.2 | 1.6 | 9.8 |

Table 13. The percentage distribution of the time of development of standard shoots over the thawing groups.

| | Sympodial axes | | | | | | | | | Monopodial axes |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 year | 2 years | 3 years | 4 years | 5 years | 6 years | 7 years | 8 years | 9 years | ∞ |
| | % | % | % | % | % | % | % | % | % | |
| I..... | 1.4 | 2.8 | 34.7 | 22.2 | 11.1 | 8.3 | 2.8 | 2.8 | 2.8 | 11.1 |
| II..... | 2.1 | 6.4 | 31.9 | 23.4 | 16.0 | 3.2 | 4.3 | 3.2 | 1.1 | 8.6 |
| III..... | 1.4 | 5.6 | 29.2 | 29.2 | 15.3 | 6.9 | 4.2 | .. | 1.1 | 6.9 |
| IV ..... | .. | .. | 53.3 | 26.7 | 6.7 | 6.7 | .. | .. | .. | 6.7 |
| Norm. (All "places").. | 1.6 | 4.7 | 33.2 | 24.9 | 13.8 | 6.0 | 3.6 | 2.0 | 1.6 | 8.7 |

(8) The total number of leaves per shoot (standard shoot). The number of leaves chiefly depends on the duration of development when the latter is variable. This dependency is found in certain genera and families with a periodical shoot development, even with such a regularity that the age of the shoots can be determined by a simple determination (counting) of the number of leaves, which for a number of shoots will arrange themselves in groups at regular intervals, indicating the yearly number of leaves developed.

The number of leaves stated in Table 7 refers to the standard shoot. As regards the species with a monopodial growth the yearly number of leaves on the main axis + the number of leaves of a floral shoot have been employed in the statistical treatment here. As these species correspond biologically to sympodial species with a three years' shoot duration and yearly flowering (proleptic shoot development), this procedure might justify a direct comparison of all the species in regard

Table 14. The average number of leaves per shoot generation (standard shoot) in the different species[1]), grouped according to their type of distribution.

| | SS | NN | S | N | NS | M | C |
|---|---|---|---|---|---|---|---|
| Number of fol. leaves per shoot.. | 18.7 | 14.6 | 13.6 | 13.9 | 13.0 | 13.8 | 13.3 |
| Number of scale leaves per 100 fol. leaves..... | 19.5 | 14.3 | 36.7 | 14.1 | 17.4 | 37.0 | 13.3 |

Table 15. The average number of leaves per shoot generation (standard shoot) in the different species[1]) arranged according to their thawing type.

| | I | II | III | IV |
|---|---|---|---|---|
| Number of fol. leaves per shoot ..... | 16.2 | 16.3 | 13.5 | 9.7 |
| Number of scale leaves per 100 fol. leaves | 21.5 | 20.4 | 20.8 | 19.9 |

to the number of leaves, irrespectively of whether they belong to the monopodial or the sympodial growth type. The results of this investigation are given in Tables 14 and 15. The first line indicates the average number of foliage leaves per shoot in the species within the group stated. The second line of the tables indicates the average number of scale leaves per 100 foliage leaves. It is true that the error in these figures are great owing to the dissimilarity of the material (the absolute number of leaves depends chiefly on the inherited constitution of the individual plant species); yet it seems to me that the tables reveal a certain regularity. Thus Table 14 shows that the SS species have a higher average number of leaves per shoot (generation) than the species of the other groups. The number of leaves per shoot generation or, as it may also be expressed, per flowering, is thus as a rule larger in species which in Northeast Greenland are near their northern limit than in the species within the same area which are not there near their northern limit of distribution. Table 15 shows a distinct maximum number of leaves per shoot for the first thawing groups, decreasing over III to a clear minumum in IV. That

[1]) *Hippuris* not included.

is to say, the number of leaves per flowering in the different species are in a certain direct proportion to the date of the thawing in the localities in which the various species are chiefly found. The second lines of the two tables show a certain variation in the average numerical scale leaf formation in the different groups, though without any marked tendency.

(9) The yearly leaf production of the individual shoot in case of vegetative invigoration years. This size can as a rule only be measured in shoots whose development extends over more than three years; for it has proved that in case of a development extending over several years the number of leaves in the first growth year and the flowering year are not directly comparable with the intermediate years. In many species, especially in the monocotyledons, the yearly number of leaves is surprisingly constant in the same species, even though the number of the invigoration years may vary according to the vigour of the shoot. In the dicotyledons the yearly number of leaves is often less constant and in a number of species it increases gradually from year to year, and flowering then often does not occur till a fairly constant number of leaves for each species is attained, developed within one and the same growth season. In such cases the increase in the number of leaves is indicated in Table 7 by an →, the highest number indicating the minimum of one year's growth of leaves required for flowering.

The yearly production of leaves on the vegetative shoot is of special interest compared with

(10) the yearly leaf production of the sympode. By this I mean the total yearly number of foliage leaves developed on the same "unbranched" sympode, irrespective of the number of shoot generations which contribute to the leaf production. It must be obvious that this size can be expressed as $\frac{\text{number of foliage leaves per shoot (8)}}{\text{number of years between each flowering (6)}}$ (in case of continuous development of standard shoots). The yearly leaf production of the sympode as a rule exceeds the yearly leaf production of the individual shoot during the invigoration stages; this is largely due to the fact that in most species there is more than one leaf-bearing shoot at the same time in the sympode. In most Monocotyledons and in some few Dicotyledons this is brought about by the innovation bud at the base of the mother shoot unfolding—and this from the axil of already withered subtending leaves—at a very early phase of the development of the mother shoot; the process may even repeat itself once or several times before the original mother shoot reaches its flowering stage. In most Dicotyledons and in a few Monocytoledons there is no pos-

Tables 16—17. The relation between yearly number of foliage leaves of the individual shoots during the invigoration year (years) and the yearly number of foliage leaves of the sympodes of *Cyperaceae* and *Gramineae*. Table 16 arranged according to the distributional groups, Table 17 according to the thawing groups.

Table 16.

| | SS | NN | S | N | NS | M | C |
|---|---|---|---|---|---|---|---|
| Number of species | 14 | 9 | 7 | 6 | 5 | 4 | 9 |
| Number of fol. leaves ot vegetative year's sh ot | 4.1 | 3.0 | 4.0 | 3.8 | 3.4 | 3.3 | 3.1 |
| Number of fol. leaves of sympode | 5.9 | 5.4 | 6.9 | 7.7 | 6.8 | 8.0 | 5.6 |
| $\frac{\text{Year's shoot}}{\text{Sympode}} \cdot 100$ | 76.0 | 57.8 | 62.7 | 57.3 | 57.5 | 41.7 | 62.1 |

Table 17.

| | I | II | III |
|---|---|---|---|
| Number of "places" | 18 | 30 | 28 |
| Number of fol. leaves of vegetative year's shoot | 3.5 | 3.7 | 3.7 |
| Number of fol. leaves of sympode | 6.7 | 6.0 | 6.5 |
| $\frac{\text{Year's shoot}}{\text{Sympode}} \cdot 100$ | 58.4 | 65.3 | 62.0 |

sibility for the existence of more than two leaf-producing shoot generations at the same time, the innovation bud being here situated in the upper part of the mother shoot immediately below the flower scape, and if so, it will as a rule unfold in the axils of the green subtending leaves in the flowering year of the mother shoot.

In Tables 16 and 17 a comparison is made between the yearly leaf productions of the still vegetative shoot and of the sympode in *Cyperaceae* and *Gramineae*. These families are especially well suited for such a comparison, partly because of their fairly uniform leaf production altogether, and partly on account of the protracted development of the shoots; this renders it possible to include nearly all the species in the comparison. The tables explain themselves. In the last line the number of leaves of the vegetative shoot is given in per cent. of that of the sympode, which for Table 16 fairly distinctly manifests a tendency of the southern groups of species, more especially the SS group, to concentrate the leaf production on a few shoots with a comparatively large number of leaves on each, in contrast to the northern and middle groups.

The individual thawing groups (Table 17) show only inconsiderable deviations (from the mean), though the concentration of the mass of

Tables 18—19. The relation between yearly number of foliage leaves of the individual shoots during the invigoration year (years) and the yearly number of foliage leaves of the sympode of Dicotyledons. Table 18 arranged according to the distributional groups, Table 19 according to the thawing groups.

Table 18.

| | SS | NN | S | N | NS | M | C |
|---|---|---|---|---|---|---|---|
| Number of species | 12 | 6 | 8 | 11 | 6 | 11 | 10 |
| Number of fol. leaves of vegetative year's shoot | 9.4 | 7.8 | 6.1 | 6.8 | 7.5 | 6.5 | 7.6 |
| Number of fol. leaves of sympode | 12.5 | 11.5 | 7.8 | 11.4 | 9.8 | 8.8 | 9.7 |
| $\frac{\text{Year's shoot}}{\text{Sympode}} \cdot 100$ | 79.4 | 69.0 | 82.1 | 59.5 | 83.3 | 77.3 | 77.7 |

Table 19.

| | I | II | III | IV |
|---|---|---|---|---|
| Number of "places" | 32 | 34 | 23 | 7 |
| Number of fol. leaves of vegetative year's shoot | 7.4 | 7.6 | 6.7 | 5.3 |
| Number of fol. leaves of sympode | 10.8 | 10.4 | 9.9 | 8.3 |
| $\frac{\text{Year's shoot}}{\text{Sympode}} \cdot 100$ | 69.9 | 76.7 | 70.3 | 65.1 |

leaves on fewer shoots is just recognisable in group II as compared with the other groups. The distribution of the leaves over the shoot generations is thus evidently—judging from the tables—more closely correlated with the geographical distributional type of the species than with their specific attitude towards the thawing (and snow covering) factor.

Tables 18 and 19 give the corresponding comparison for those Dicotyledons whose shoot duration is sufficient for a determination of the yearly number of leaves of the invigoration stage. (In cases in which the number (according to Table 7) is varying, the mean number has been employed). However, the material is too inconsiderable in view of its heterogeneity. From the figures given in the bottom line it will be seen that the variations here are smaller than in the Monocotyledons; still they point in the same direction: A concentration of the leaf mass on fewer shoots in the southern and central specific groups as compared with the northern species of the distributional series and within group II of the thawing series. It should be pointed out that the numerical expressions of the "distribution" of the leaf mass in certain species groups given here as compared with its "concentration" in other species

groups represent absolute minimum values, and that the differences are actually larger than the computed numerical differences would seem to suggest, the leaf production being computed for unbranched sympodes. For there is a marked correlative connection between the distribution of the leaf mass over several shoot generations (and proleptic shoot development) and a highly developed branching of the main axes on the one hand, and between the concentration of the leaf mass on a single shoot generation and a sparse branching of the main axis on the

Tables 20—21. Average yearly number of foliage leaves of sympode in all species[1]). Table 20 arranged according to the distributional groups, Table 21 according to the thawing groups.

Table 20.

| | SS | NN | S | N | NS | M | C |
|---|---|---|---|---|---|---|---|
| Number of fol. leaves of sympode.. | 10.8 | 9.0 | 8.3 | 8.0 | 10.0 | 9.4 | 8.8 |

Table 21.

| | I | II | III | IV |
|---|---|---|---|---|
| Number of fol. leaves of sympode ..... | 10.2 | 9.2 | 8.4 | 7.3 |

other hand. It will be difficult, however, to give a numerical expression to this connection, as the tendency to branch is in all cases highly dependent on the vigour of the plant. Finally it should be pointed out that a number of species with a short shoot-development and belonging mainly to the S and SS groups (cf. Table 12, p. 191) had to be excluded from the computations on account of the want of vegetative invigoration years. Precisely these (southern) species have a marked concentration of the production to the flowering year's-shoot proper. In the therophytes and the perennial species with a two years' shoot development the leaf production of the "sympode" is of course identical with that of the flowering year's-shoot. Viewed in the light of these facts it will be seen that the difference between the northern and southern species in regard to the place of the leaf mass is only incompletely expressed in Tables 16 and 18, in so far as the whole flora of the area is concerned.

Tables 20 and 21 illustrate the yearly leaf production of the sympodes of all the species in relation to distributional groups and thawing groups. Table 20 shows an exceedingly small oscillation in favour of the SS group. Thus the "effective" leaf production proper seems to be fairly independent of the distributional type of the species. Table 21, on the other hand, shows a distinct increase in the number of leaves

[1]) *Hippuris* not included.

along with a decreasing duration of the snow-covering. The normal leaf production of the specific groups are accordingly here to a certain degree directly proportional to the extent of that vegetation period which is characteristic of the localities in which the species of each group principally grow.

(11) The wintering state of the foliage leaves. The division into the three groups, summer-green, winter-green, and evergreen, is an expression of the functioning periods of the foliage leaves. In the summer-green plants the leaves function only in the summer in which

Table 22. The absolute and percentage distribution of the wintering leaf types within the Northeast Greenland flora. s: summer-green, w: winter-green, e: evergreen.

| Wintering leaf types | s | w | e |
|---|---|---|---|
| Number of species | 127 | 49 | 8 |
| Per cent. | 69.0 | 26.6 | 4.4 |

they expand. In the winter-green plants the leaves function to a smaller or greater extent during two growth seasons, the majority, however, hardly during two whole summers, as the wintering leaves as a rule wither in the course of the ensuing summer, though at different times in the different species. The distinction between summer-green and winter-green species is not sharp, all the more so since the wintering conditions may have a certain influence. In Table 7 transitional cases are given in parentheses. Thus (s) indicates that under favourable snow-covering conditions—especially if there has been a somewhat retarded development the preceding summer—the plant may occasionally be met with in the early summer bearing old foliage leaves which have survived the winter. A (w) indicates that in dry localities exposed to the wind the leaves do not remain green during the winter—as is normal for the species (in statistical computations such species are included in the individual groups according to the letters by which they are designated). In the evergreen plants the leaves function more than two summers. *Rhododendron lapponicum*, however, whose leaves are shed after a functioning period of two years, forms an exception. Yet this species naturally belongs to the evergreen plants on account of its periodical shedding of the leaves and their leathery consistency.

Table 22 illustrates the frequency of the three types within the flora of Northeast Greenland. Table 23 shows the distribution of the types

Table 23. The percentage distribution of wintering leaf types over the distributional groups.

| | s | w | e | Number of species |
|---|---|---|---|---|
| | % | % | % | |
| SS | 74.0 | 22.0 | 4.0 | 50 |
| NN | 69.2 | 30.8 | .. | 26 |
| S | 69.6 | 21.7 | 8.7 | 23 |
| N | 60.8 | 34.8 | 4.4 | 23 |
| NS | 61.5 | 38.5 | .. | 13 |
| M | 61.9 | 23.8 | 14.3 | 21 |
| C | 71.4 | 28.6 | .. | 28 |
| Norm. (All species) | 69.0 | 26.6 | 4.4 | .. |

Table 24. The percentage distribution of the wintering leaf types over the life-forms.

| | s | w | e | Number of species |
|---|---|---|---|---|
| | % | % | % | |
| Ch | 33.3 | 54.9 | 11.8 | 51 |
| H | 77.1 | 20.8 | 2.1 | 96 |
| G | 96.6 | 3.4 | .. | 29 |
| HH | 100.0 | .. | .. | 5 |
| Th | 100.0 | .. | .. | 3 |
| Norm. (All species) | 69.0 | 26.6 | 4.4 | .. |

Table 25. The percentage distribution of the wintering leaf types over the thawing groups.

| | s | w | e | Number of "places" |
|---|---|---|---|---|
| | % | % | % | |
| I | 67.6 | 25.7 | 6.7 | 74 |
| II | 68.4 | 25.5 | 6.1 | 96 |
| III | 70.7 | 29.3 | .. | 70 |
| IV | 40.0 | 60.0 | .. | 15 |
| Norm. (All "places") | 67.2 | 28.6 | 4.2 | .. |

within the individual distributional groups. The SS group has the highest percentage of summer-green plants of all groups and a low percentage of winter-green plants. Otherwise it is noticable that the evergreen plants are entirely lacking in the NN group as also in the C group. The NS

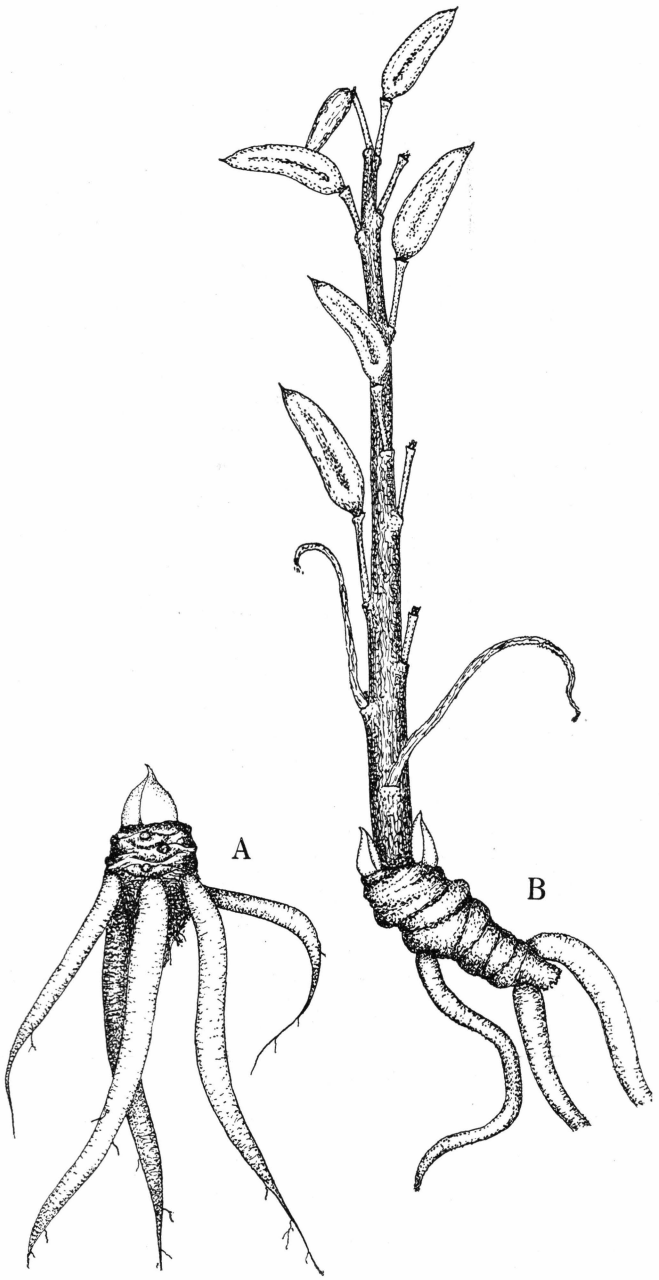



Fig. 17. *Pedicularis flammea* in wintering condition, as an example of winter buds with active bud protection. A: plant which will flower the succeeding summer. The winter bud contains the primordial inflorescence. B: plant which has flowered last summer. The small innovation buds are still purely vegetative, as the shoot requires an invigoration stage of one year or several years for flowering. c. $^3/_2$.
Del. O. Hagerup.

group has the highest percentage of winter-green plants, while M is especially rich in evergreen species. Table 24 shows the distribution of the types of wintering leaves over the individual life-forms. It exhibits nothing noteworthy except the well-known fact that winter-green and evergreen species are especially abundantly represented among the chamaephytes. Table 25 shows the distribution of the wintering leaf types within the individual thawing groups, and shows that the evergreen species are associated with early snow-free localities, while the winter-green species increase in number if the melting of the snow is retarded.

(12) The wintering state of the buds. The wintering buds are divided into three groups: 1) Species with active bud protection (a) (cf. Fig. 17). To this group I refer species whose wintering buds are protected by special organic formations of any kind whatever. In addition to species with actual bud scales I further refer to this group for instance the *Polygonaceae*, whose membranous ochreae function entirely like bud scales. Likewise *Ericaceae* with young leaves and leaf primordia cemented together but otherwise without any protection of the buds. Finally the therophytes must be referred to this group. 2) Species with a passive protection of the buds (p) (cf. Fig. 18). To this group belong all (summer-green) species whose wintering buds are formed of closely united leaf primordia, so that all the organs or organic parts which winter in a fresh state form a bud-shaped delimited whole when the withered leaf bases have been removed. For the sake of completeness it should be pointed out that such *Cyperaceae* and *Gramineae* in which the distal and proximal parts of certain leaves are developed each in its year, but in which the elongated free part of the leaf withers in the winter, have also been referred to this group. 3) Species without protection of the buds (u), (cf. Fig. 19). To this group belong all winter-green species and evergreen species which do not come under (a). Further, summer-green species, whose outermost fresh, more or less elongated leaf primordia are free in their distal part and thus do not contribute to the formation of an actual bud. In such species the shoot apex actually winters in precisely the same way as in the winter-green species, in which there is no fundamental morphologically manifested difference between the summer and the winter state.

Table 26 shows the frequency of the three different bud types within the flora of the area as a whole. Table 27 shows the distribution of the bud types within the distributional groups. From this it appears that the SS group has the highest representation of active bud protection of all the groups. In especially sharp contrast to this is the NN group, which entirely lacks species with active bud protection. The

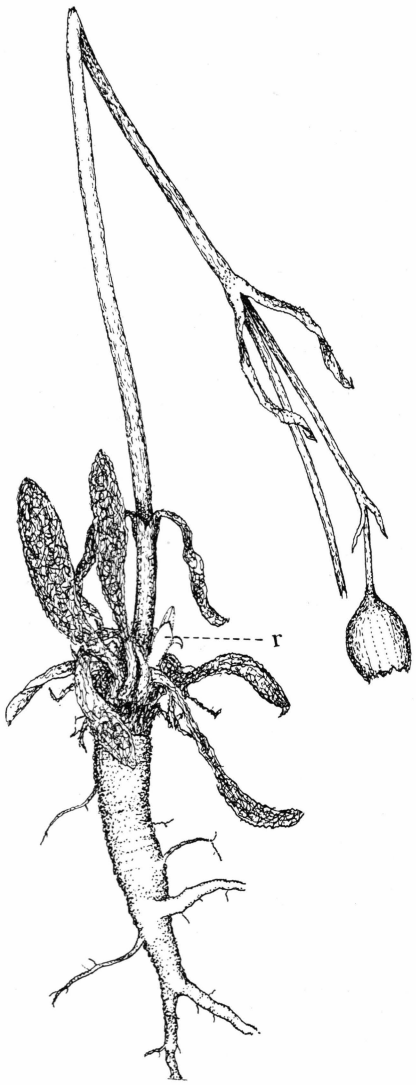



Fig. 18. *Melandryum triflorum* in wintering condition, as an example of winter buds with passive bud protection. r: the innovation bud, whose leaf primordia develop into foliage leaves the succeeding summer. The old withered leaves have been turned aside in order to make the bud visible. The bud requires an invigoration stage of several years for flowering. c. $^3/_2$. Del. O. HAGERUP.

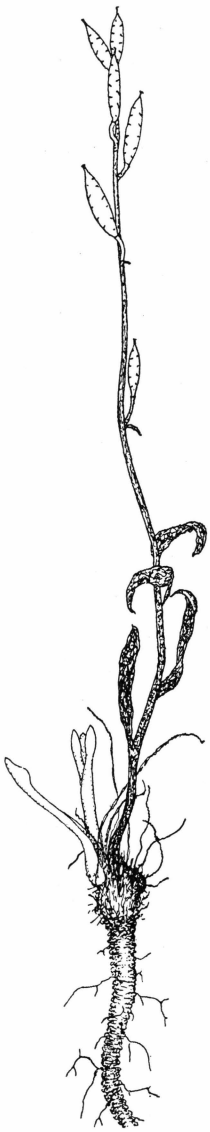


Fig. 19. *Eutrema Edwardsii* in wintering condition, as an example of unprotected winter buds. The flower stem of next year already partially elongated. The primordial inflorescence concealed below the head-like closed stem-leaf primordia. c. $^1/_1$. Del. O. HAGERUP.

Table 26. The absolute and percentage distribution of the wintering bud types within the Northeast Greenland flora. a: active bud protection, p: passive bud protection, u: no bud protection.

| Wintering bud type | a | p | u |
|---|---|---|---|
| Number of species | 33 | 80 | 70 |
| Per cent | 18.0 | 43.7 | 38.2 |

same contrast is exhibited by groups S and N, though in a less marked degree. It is further particularly remarkable that the NS group has the highest percentage of unprotected buds, and that—like the NN group—it lacks species with active bud protection. Table 28 illustrates the distribution of the bud types over the individual life-forms. From this it appears that the chamaephytes to a great extent lack bud protection. The passive bud protection increases rapidly from Ch over H to G. Active bud protection is not especially characteristic of any definite life-form (apart from the therophytes). Table 29 shows the distribution of the bud types within the thawing groups. The table reveals a surprisingly slight correlation between the character of the bud and the snow-covering. However, thawing groups I and II, which represent a sparse snow-covering, have relatively a somewhat richer representation of actively protected buds than groups III and IV. Group IV, which designates the most persistent snow-covering, shows a comparatively high percentage for unprotected buds.

(13) The developmental stages of the floral organs during wintering. On examination of the state of development of the floral organs during the wintering it was ascertained that as regards the greater number of species the flower buds of each individual species winter in approximately the same phase, that is to say, that the formation and development of the floral organs show a certain correlation with the seasonal periodicity of the climate, or, in short, that the floral development is periodical. In a minority—though comprising no inconsiderable number of species—there is no correlation between the periodicity of the climate and the order of formation of the floral organs. Here the transition from the vegetative to the floral stage takes place at different dates in the shoots of the same plant and seem to depend exclusively on the vigour or developmental stage of the shoot. The floral development of such plants must be termed aperiodical. The lack of floral periodicity is always correlated with a corresponding aperiodicity in the sequence of development of the vegetative shoot, while a certain aperiodicity may sometimes make itself felt in the shoot development with-

Table 27. The percentage distribution of bud types over the individual distributional groups.

| | a | p | u | Number of species |
|---|---|---|---|---|
| | % | % | % | |
| SS | 28.0 | 34.0 | 38.0 | 50 |
| NN | .. | 65.4 | 34.6 | 26 |
| S | 26.1 | 47.8 | 26.1 | 23 |
| N | 8.7 | 47.8 | 43.5 | 23 |
| NS | .. | 33.3 | 66.7 | 12 |
| M | 23.8 | 38.1 | 38.1 | 21 |
| C | 21.4 | 42.9 | 35.7 | 28 |
| Norm. (All species) | 18.0 | 43.7 | 38.2 | .. |

Table 28. The percentage distribution of bud types over the individual life-forms.

| | a | p | u | Number of species |
|---|---|---|---|---|
| | % | % | % | |
| Ch | 17.6 | 5.9 | 76.5 | 51 |
| H | 16.9 | 52.6 | 30.5 | 95 |
| G | 13.8 | 82.8 | 3.4 | 29 |
| HH | 20.0 | 60.0 | 20.0 | 5 |
| Th | 100.0 | .. | .. | 3 |
| Norm. (All species) | 18.0 | 43.7 | 38.2 | .. |

Table 29. The percentage distribution of bud types over the individual thawing groups.

| | a | p | u | Number of "places" |
|---|---|---|---|---|
| | % | % | % | |
| I | 20.3 | 44.6 | 35.1 | 74 |
| II | 21.6 | 36.1 | 42.3 | 96 |
| III | 13.3 | 53.3 | 33.3 | 70 |
| IV | 13.3 | 26.7 | 60.0 | 15 |
| Norm. (All "places") | 18.4 | 42.9 | 38.7 | .. |

out the periodicity of the floral development being therefore necessarily abandoned. Even in the periodical species, though with the exception of certain species with wintering pollen, the wintering stage, on examination of a large material, will always prove to vary somewhat,

and may to some extent be influenced by external conditions. The distinction between the periodical and the aperiodical species is far from sharp. In addition to entirely aperiodical species, such in which different stages are found during the wintering may be met with, though a certain stage of development is more frequent than the others. Many *Gramineae*, for instance, behave in this way. As regards the most irregular species of this type an (ap) is added in Table 7 to the designation of the developmental phase of most frequent occurrence. (Some of these doubtful species might perhaps with equal right be referred to the aperiodical species *s. str.*, for instance *Ranunculus glacialis*. Only the

Table 30. The wintering condition of the floral organs within the flora of Northeast Greenland (for the numerical designations of the developmental phases (floral type), see the explanation on p. 182).

| Wintering floral type ..... | 1 | 2 | 3 | 4 | 5 | 6 | 7 | ap |
|---|---|---|---|---|---|---|---|---|
| Number of species..... | 5 | 9 | 24 | 28 | 44 | 44 | 8 | 21 |
| Per cent. ..... | 2.7 | 4.9 | 13.1 | 15.3 | 24.0 | 24.0 | 4.4 | 11.5 |

entirely, or at any rate highly, aperiodical species are listed under the designation ap). In certain *Caryophyllaceae*, finally, two maxima of floral developmental stages may be demonstrated, the most advanced of which doubtless represents retarded buds from the preceding summer (see pp. 100—101).

On the basis of their floral development during the winter the species have been divided into seven groups (in the succeeding pages termed floral types), to which must be added an eighth group comprising the aperiodical species. As regards the definition of the group the reader is referred to the explanation of Table 7 (p. 182). Table 30 gives a summary of the floral development in the winter of the flora as a whole. As to this table it should be noted that group 2 is uncertain as regards three of the species, viz. the three *Gentiana* species, which I had no opportunity of investigating in their wintering condition. It would seem most probable, however, that they should be referred to this group, and in all the following computations also they are included as belonging to group 2. Table 31 shows the percentage distribution of the floral types over the distributional groups. It will appear immediately from the table that the floral development is rather plainly correlated with the distributional type of the species, the southern species, the SS group in particular, having a relatively large majority of species with an inconsiderable floral development, while the northern species centre round the groups

Table 31. The percentage distribution of floral types over the distributional groups.

| | Wintering floral types | | | | | | | | Number of species |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | ap | |
| | % | % | % | % | % | % | % | % | |
| SS | 8.0 | 12.0 | 20.0 | 10.0 | 18.0 | 20.0 | 6.0 | 6.0 | 50 |
| NN | .. | .. | 11.5 | 19.2 | 23.1 | 23.1 | 3.9 | 19.2 | 26 |
| S | 4.4 | 4.4 | 26.1 | 4.4 | 30.4 | 17.4 | 8.7 | 4.4 | 23 |
| N | .. | .. | 4.4 | 26.1 | 34.8 | 17.4 | 4.4 | 13.0 | 23 |
| NS | .. | .. | .. | 8.3 | 25.0 | 33.3 | 8.3 | 25.0 | 12 |
| M | .. | 4.8 | 4.8 | 23.8 | 23.8 | 28.5 | .. | 14.3 | 21 |
| C | .. | 3.6 | 10.7 | 18.0 | 21.4 | 35.7 | .. | 10.7 | 28 |
| Norm. (All species) | 2.7 | 4.9 | 13.1 | 15.3 | 24.0 | 24.0 | 4.4 | 11.5 | .. |

Table 32. The percentage distribution of floral types over the life-forms.

| | Wintering floral types | | | | | | | | Number of species |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | ap | |
| | % | % | % | % | % | % | % | % | |
| Ch | .. | .. | 5.9 | 13.7 | 23.5 | 29.4 | 11.8 | 15.7 | 51 |
| H | 2.1 | 6.3 | 13.7 | 15.8 | 24.2 | 23.2 | 2.1 | 12.6 | 95 |
| G | .. | 3.4 | 24.1 | 17.2 | 22.6 | 24.1 | .. | 3.5 | 29 |
| HH | .. | 40.0 | 20.0 | 20.0 | 20.0 | .. | .. | .. | 5 |
| Th | 100.0 | .. | .. | .. | .. | .. | .. | .. | 3 |
| Norm. (All species) | 2.7 | 4.9 | 13.1 | 15.3 | 24.0 | 24.0 | 4.4 | 11.5 | .. |

Table 33. The percentage distribution of floral types over the thawing groups.

| | Wintering floral types | | | | | | | | Number of "places" |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | ap | |
| | % | % | % | % | % | % | % | % | |
| I | 2.7 | 1.4 | 14.8 | 18.9 | 31.1 | 21.6 | 2.7 | 6.7 | 74 |
| II | 3.1 | 6.1 | 17.4 | 13.3 | 24.5 | 17.4 | 5.1 | 13.3 | 96 |
| III | 1.3 | 2.7 | 9.3 | 16.0 | 25.3 | 28.0 | .. | 17.3 | 70 |
| IV | .. | .. | .. | 13.3 | 13.3 | 40.0 | 6.7 | 26.7 | 15 |
| Norm. (All "places") | 2.3 | 3.4 | 13.4 | 15.6 | 25.9 | 22.9 | 3.1 | 12.4 | .. |

with highly developed floral organs. M and C have almost a "normal" distribution, though they completely lack species with wintering pollen. Such species, on the other hand, are chiefly represented in the southern groups and the NS group. Aperiodical species are chiefly represented among the northern groups, though they are found in the greatest numbers within the NS group, the specially Northeast Greenland species. Table 32 shows the distribution of the floral types within the individual life-forms. As regards floral development the life-forms form a series beginning with Ch with highly developed flower buds, continuing over H and G to HH with a constantly decreasing floral development, and ending with Th, which according to the nature of the case forms the extreme limit, since not only the development of the flowers, but of the whole plant takes place in the flowering year. Aperiodical species are most abundantly represented among the Ch, they are still fairly frequent among H, while G contributes with only one species. Table 33 shows the distribution of the floral types within the thawing groups. Thawing group I, the earliest snow-free species, shows an approximately "normal" distribution as regards the floral type. Otherwise there is a general tendency to an increased floral development from II to IV, that is to say, towards a retarded thawing. The aperiodical species show a continuous relative increase parallel with the retardation of the thawing. A comparison of the two tables, 31 and 33, however, would seem to suggest that the degree of floral development as a rule is more closely correlated with the distributional type of the species than with the time of snow-melting in the localities in which the individual species principally occur. Finally, Table 34 shows the correlation between the "winter-green" condition of the plants and their floral development, figured as the distribution of the floral types within the individual wintering groups. It will be seen that the floral types are distributed in almost a normal way within the summer-green group, while the winter-green, and in an even higher degree the evergreen plants, show a tendency to a high development of the floral organs in the wintering condition. It is especially pointed out that flower buds which winter in the pollen stage preponderate among the evergreen species, while the aperiodical species chiefly occur among the wintergreen species. The tendency of aperiodical species to remain green during the winter is no doubt even more general than is immediately evident from the table, certain summer-green aperiodical species being actually "winter-green" on account of an inherent tendency. Thus for instance in a marked degree *Matricaria inodora* and *Polemonium boreale*, whose leaves are clearly not subject to natural withering, but are killed by the frost. This phenomenon is to a certain degree illustrated by Table 35, which shows the relation between the floral types and the character of the winter buds; for it turns out that

Table 34. The percentage distribution of floral types over the leaf-wintering groups.

| | Wintering floral types | | | | | | | | Number of species |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | ap | |
| | % | % | % | % | % | % | % | % | |
| Wintering leaf types s ... | 4.0 | 5.6 | 17.5 | 19.1 | 26.2 | 19.9 | 0.7 | 7.1 | 126 |
| Wintering leaf types w ... | .. | 4.1 | 4.1 | 6.1 | 20.4 | 34.7 | 6.1 | 24.5 | 49 |
| Wintering leaf types e ... | .. | .. | .. | 12.5 | 12.5 | 25.0 | 50.0 | .. | 8 |
| Norm. (All species)..... | 2.7 | 4.9 | 13.1 | 15.3 | 24.0 | 24.0 | 4.4 | 11.5 | .. |

Table 35. The percentage distribution of floral types over the bud-wintering groups.

| | Wintering floral types | | | | | | | | Number of species |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | ap | |
| | % | % | % | % | % | % | % | % | |
| Wintering bud types a ... | 9.1 | 6.1 | 12.1 | 18.2 | 24.2 | 15.2 | 12.1 | 3.0 | 33 |
| Wintering bud types p ... | 1.3 | 2.5 | 21.3 | 17.5 | 28.5 | 23.8 | .. | 5.0 | 80 |
| Wintering bud types u ... | 1.4 | 7.1 | 5.7 | 10.0 | 18.6 | 28.6 | 5.7 | 22.9 | 70 |
| Norm. (All species)..... | 2.7 | 4.9 | 13.1 | 15.3 | 24.0 | 24.0 | 4.4 | 11.5 | .. |

aperiodicity is chiefly to be found in species with unprotected winter buds. In addition it appears from the table that the group with active protection of the buds is to a fairly great extent composed of species entirely lacking floral organs during the wintering and such species as bear flowers with pollen. The group with a passive protection of the buds has almost a "normal" floral distribution, while the group with unprotected buds shows some preponderance of highly developed flower buds.

(14) Rate of growth. This column in Table 7 indicates the number of winterings of growing cones which are recognisably "floral", that is to say, not purely vegetative. This character is closely correlated with the rate of growth, an expression of which is found in the period that elapses from the primordium, be it the primordium of a floral axis or a leaf primordium, is differentiated on the cone of growth to its full development. In the great majority of species the number of leaf primordia in the wintering buds is almost the same as the yearly number of leaves developed on the shoot. That is to say that in such cases the

leaves remain about one year in the primordial stage. The development of the floral organs and of the leaves are almost parallel, taking place at the same rate; and in the greater number of the species, more especially the species whose flower buds winter in more advanced phases of development, the floral organs begin to differentiate immediately in the spring or at any rate at a very early date of the growth season preceding the flowering year proper. In some species the number of leaf primordia exceeds the yearly production of leaves. This of course causes the primordial development to extend over more than one year, sometimes even up to two whole years. The most typical example is perhaps *Carex saxatilis*, whose number of leaf primordia is always about twice the number of leaves developed in a year, and the cone of growth is here distinctly "floral" at a date when the leaf primordia, already formed, amount to a number corresponding to the leaf production of a whole year plus that of the flowering year. *Arctagrostis latifolia* behaves in a similar way. In this species one year with formation of leaves normally precedes the flowering year. The "floral" axis is nevertheless differentiated in the autumn before the first foliage leaves of the shoot are expanded. The rate of growth of the aperiodical species is generally very slow. But a very rapid rate of growth is found in the therophytes, in which the greater number of the organs complete their development within one growth season. Some few perennial species also are distinguished by a rapid rate of growth, thus for instance *Veronica alpina*, in which the number of leaf primordia during the wintering only constitutes about half the number of the leaves produced the succeeding year. A rapid rate of growth often seems to be a character more prevalent in the southern than in the northern species.

All the organs of the plant seem to be governed by the same rate of growth. Thus it has been ascertained that species whose leaf and flower primordia develop slowly, likewise have a very slow development of the innovation shoots, so that the normal bud stage proper may extend over as much as two whole years (e. g. *Carex saxatilis*). Similarly, in species with a rapid floral development, where the floral development from and including the primordial stage takes place in the flowering year, we find a late formation and an especially rapid development of the vegetative buds. Thus in the course of the same growth season in which it is formed itself, the vegetative shoot primordium may develop either green leaves (e. g. in *Ranunculus hyperboreus* and *Ranunculus trichophyllus*) or subterranean runners (e. g. in *Juncus castaneus*). Cf. also (7), p. 190.

Flowering time. The observations on the flowering periods of the species recorded in Table 5 (pp. 51—53) are all derived from Clavering

Table 36. The distribution over the geographical distributional groups of the flora of Clavering Ø whose flowering times were observed (cf. Table 5, pp. 51—53), illustrating the reliability of the observations on flowering, as an expression of the flowering of the Northeast Greenland flora as a whole.

| | SS | NN | S | N | NS | M | C | Number of species |
|---|---|---|---|---|---|---|---|---|
| NE Greenland: Total number of species | 50 | 26 | 23 | 23 | 13 | 21 | 28 | 184 |
| Clavering Ø: Number of species observed in flower | 25 | 18 | 20 | 21 | 8 | 19 | 28 | 139 |
| Clavering Ø: Per cent | 50.0 | 69.2 | 87.0 | 91.3 | 61.5 | 90.5 | 100.0 | 75.6 |

Ø in the summer of 1935. Accordingly they have only reference to a limited number of the plant species of Northeast Greenland. Before I proceed to a discussion of the flowering time of the species on the basis of this observation material, it will be necessary to find out whether the species whose flowering periods were registered on Clavering Ø may be regarded as a valid representation of the flora of Northeast Greenland as a whole. The observations on flowering made on Clavering Ø comprise 139 of the 184 species of Northeast Greenland, or about 75 per cent. It appears from Table 36 that only about half the number of all the SS species are represented among them, whereas all the C species are represented. The representation of the other groups lies between these two extremes. Actually these numerical values give an approximate expression of the relative frequency of the distributional groups within Northeast Greenland as a whole. The circumgreenlandic species are undoubtedly the most frequent. The markedly southern (SS) species are the rarest; it should, however, be noted that a relatively large number of these species have their northern limit south of Clavering Ø. Despite the unequal representation of the different groups, it must be justifiable to regard the flora of Clavering Ø as that transverse section of the flora of Northeast Greenland which the position of the island would directly indicate.

It would seem that the relation between the flowering time of the species and their types of distribution, life-form, etc., can be most adequately figured graphically according to the method of GELTING (cf. p. 66). The abscissa indicates the time in 5-day periods from June 1st to July 30th. The ordinate indicates the percentage of species belonging to the particular group which has commenced its flowering at the date shown by the abscissa. The date for incipient flowering refers to the indications in Table 5.

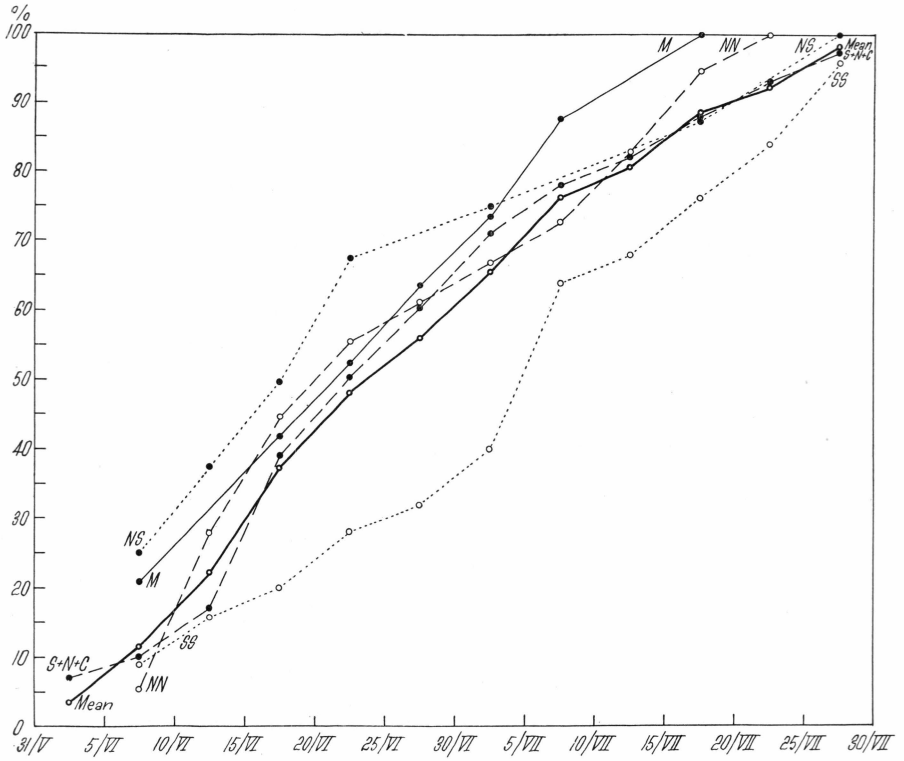



Fig. 20. Graphic representation of the rate of the first flowerings of the species, according to observations made on Clavering Ø in 1935, showing the distributional groups. Curve showing rate of the first flowering of all the species observed has been inserted ("mean"). The ordinate indicates the percentage of the total number of species observed within the respective groups which had commenced flowering at the date given by the abscissa.

Fig. 20 illustrates the chronological order of the first flowerings of the distributional groups. In addition to the flowering curves for the individual groups the "mean" curve for incipient flowering is drawn on the basis of the flowering of all the species observed en bloc. Groups S, N, and C have been included in one curve, as they conincide to such an extent that they cannot be represented separately in the same graph. It will be seen that in the first part of the spring the flowering rate of the NS group is generally more rapid than that of the other groups. The M group, too, flowers early, and actually late-flowering species are entirely absent here, which is shown by the curve taking a straight course. NN strongly approaches the "mean", though not in the same high degree as S, N, and C. The flowering curve of the SS group shows the most remarkable course. The species of this group on average flower considerably later than the species of the other groups. It is characteristic of the course of several of the curves that a comparatively violent

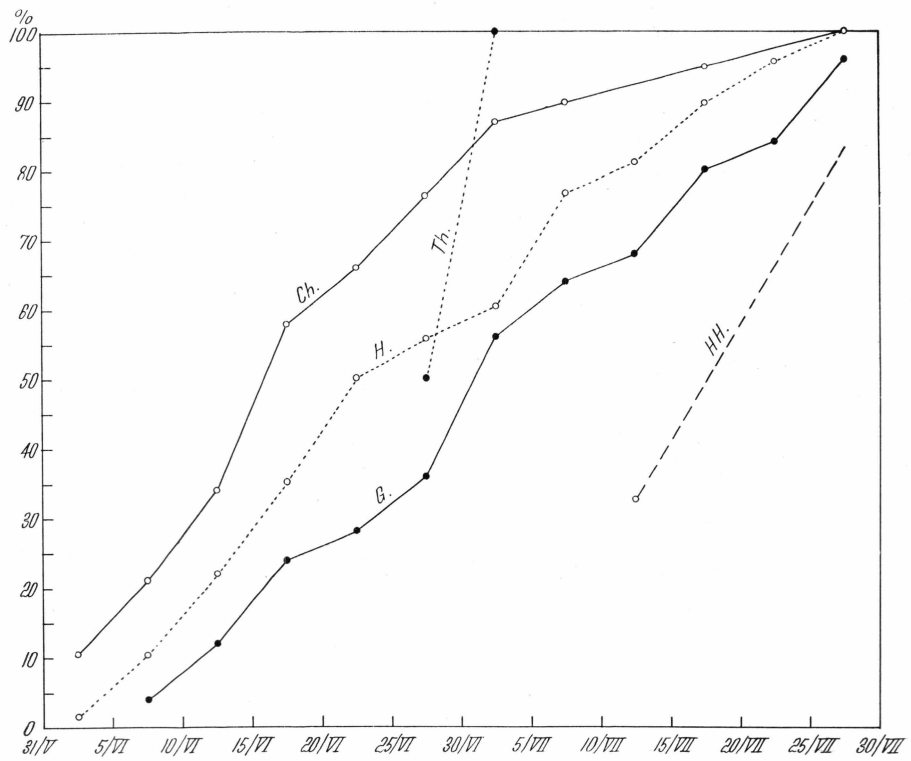



Fig. 21. Graphic representation of the rate of the first flowerings of the species, based on observations made on Clavering Ø in 1935. Life-forms. (For explanation, cf. Fig. 20, p. 210).

increase in the flowering occurs before and until about 50—60 per cent. of the species begin to flower, while after that time the rate of flowering grows slower. This increase occurs about 16—17 days later for the late-flowering SS group than for the early flowering NS group. A late flowering was likewise ascertained by Söyrinki (1938) in the southern species of the Petsamo-Lappmark flora.

Fig. 21 shows, in a similar way, the flowering of the different life-forms. From this it appears that the Ch species generally flower earliest. H flowers 5—10 days later, that is to say, the same percentage of H is not in flower till 5—10 days later. Somewhat later still comes G. The therophytes flower relatively early, while the hydrophytes flower late. Curiously enough Gelting (1934, p. 316), on the basis of observations made in the summer of 1932, likewise on the flora of Clavering Ø, arrived at the result that the geophytes flower earlier than the hemicryptophytes. It is hardly possible to say anything definite about the cause of this disagreement. Yet it may be due to the above-mentioned (p. 60) fact that the *Gramineae* flowered especially late in 1935 as

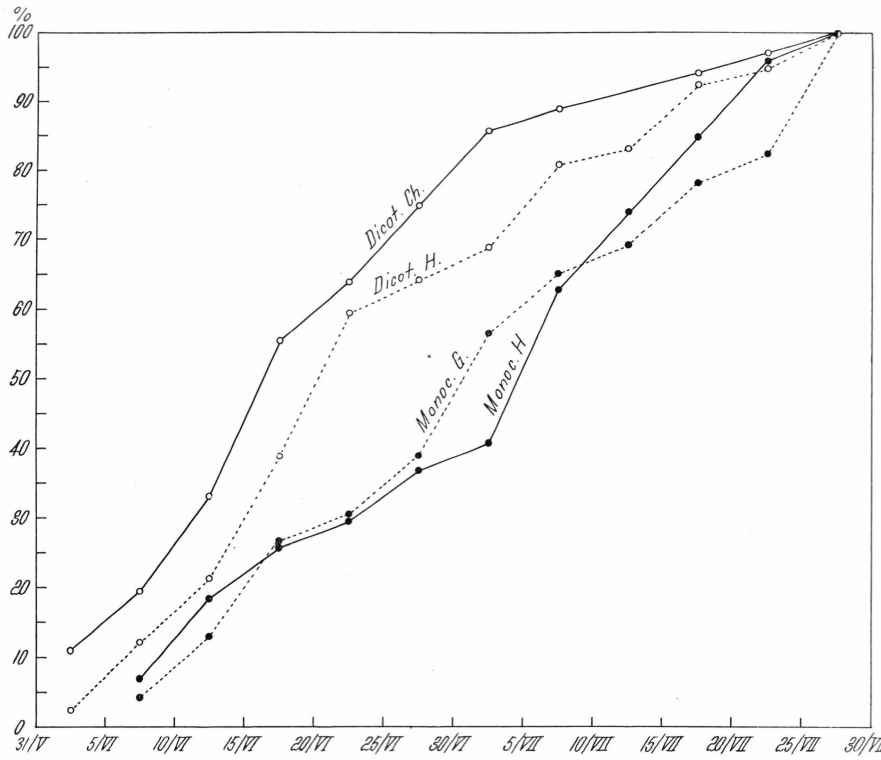



Fig. 22. Graph showing the rate of the first flowerings of the species, based on observations made on Clavering Ø in 1935. Dicotyledonous Ch, dicotyledonous H, monocotyledonous H, and monocotyledonous G. (For explanation, cf. Fig. 20, p. 210).

compared with 1932. The influence which this would have on the course of the flowering curves for hemicryptophytes and geophytes will be evident when it is taken into consideration that the *Gramineae* contribute about one-third to the total number of geophytes but only about one-sixth to the total number of hemicryptophytes. This consideration gives rise to the question whether the flowering time is not altogether a character to be regarded as purely systematical rather than as being in direct relation to the life-form (cf. HOLM 1895, and further ILLICHEVSKY 1925—27, STOJANOFF 1928). The reply to this question is suggested in Fig. 22, which presents a comparison between the flowering times of Monocotyledons and Dicotyledons. The hemicryptophytes are here employed as a kind of common denominator of life-forms and systematical groups, it being the only life-form which is comparatively well represented both among Monocotyledons and Dicotyledons. It appears from the figure that as regards the flowering time the dicotyledonous hemicryptophytes show more agreement with the dicotyledonous chamaephytes than with the monocotyledonous hemicryptophytes; and

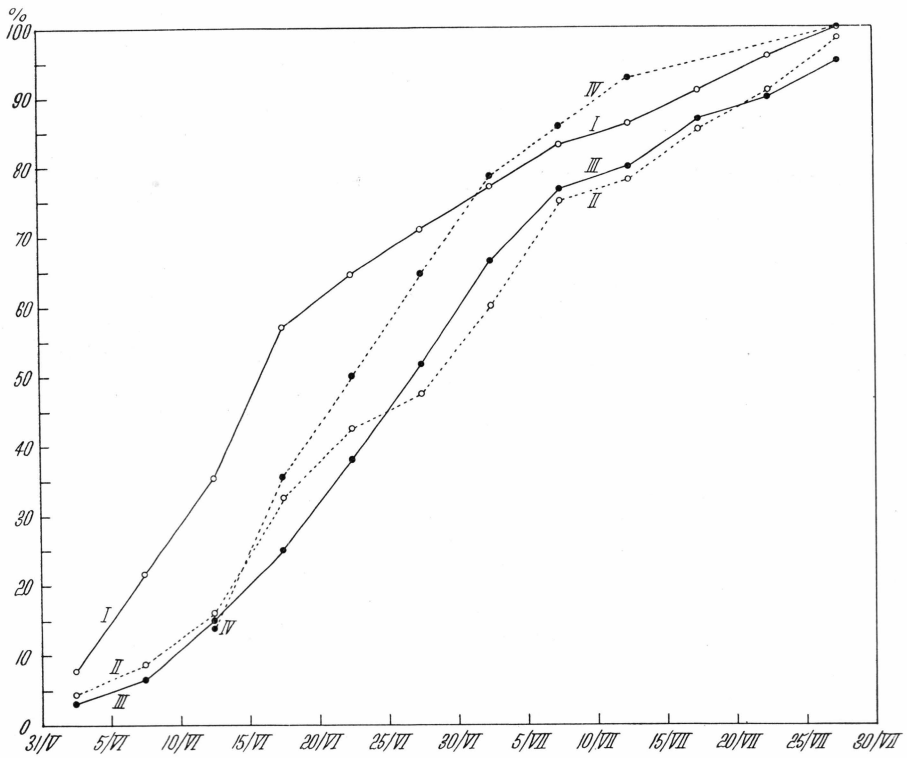



Fig. 23. Graph showing the rate of first flowering of species, based on observations made on Clavering Ø in 1935. Thawing groups. (For explanation, cf. Fig. 20, p. 210).

furthermore, that the monocotyledonous hemicryptophytes agree more closely with the monocotyledonous geophytes than with the dicotyledonous hemicryptophytes. The date of the incipient flowering thus seems to be less associated with the life-form as such than might be immediately evident from GELTING's figure (l. c. p. 316) and from Fig. 21 of the present paper, though the fact still remains, as demonstrated by GELTING, that the chamaephytes are distinguished by early flowering.

Fig. 23 illustrates the incipient flowering in relation to the thawing groups. The course taken by these flowering curves may perhaps seem astonishing at first sight, as it proves that thawing group IV distinctly precedes groups II and III as regards flowering. However, it should especially be noted that the thawing groups are a purely floristic concept, each comprising the species whose main occurrence is restricted to the particular thawing zones, and not the vegetation as such of the thawing zones. As the snow-patch plants generally belong to the commonest species, it is evident that the observations on incipient flowering refer to individuals occurring at the upper edge of, not to say entirely above, the snow-covering zone to which they naturally belong, and there-

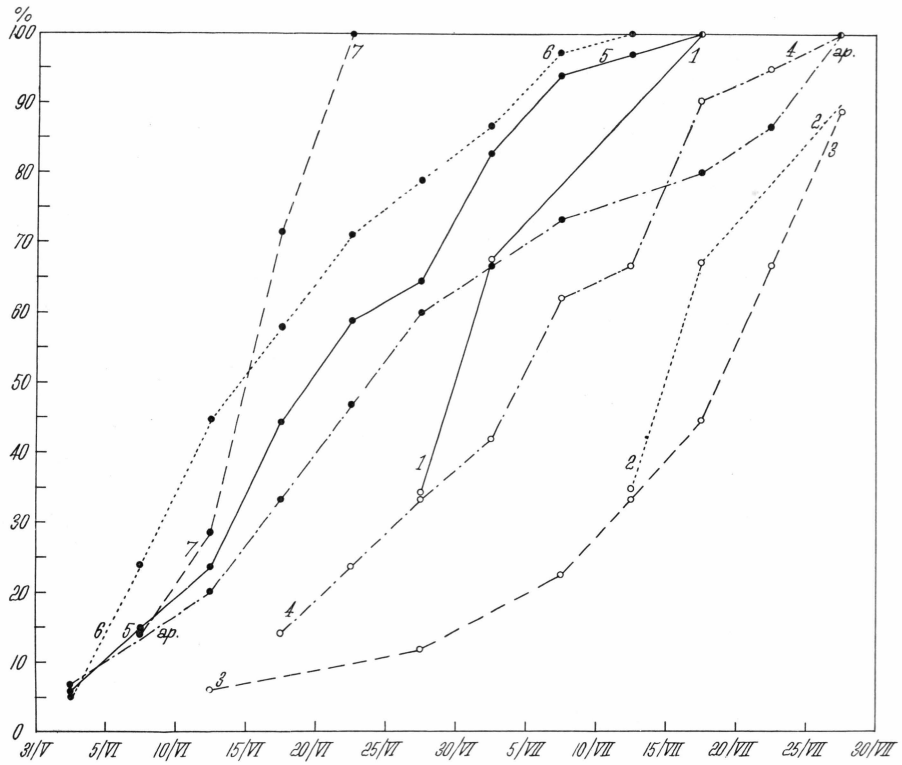



Fig. 24. Graph showing rate of first flowering of the species, based on observations made on Clavering Ø in 1935. Floral types. (For explanation, cf. Fig. 20, p. 210).

fore show an abnormally early flowering for these species. The possibility for a corresponding shifting upwards in the thawing zones with a consequent advanced flowering of course decreases when we come to snow-covering (thawing) groups III and II and is a priori impossible for group I. The result will of course be that the difference in the time of the first flowering of species belonging to different groups will be inconsiderable, much smaller than the chronological order of their actual flowering as such would justify (cf. Table 6, pp. 56—59).

The investigation of the incipient flowering of the thawing groups then chiefly axquires the theoretical interest that the incipient flowering noted for the various other groups, whether of distributional-geographical or of a biologic-morphological nature, is influenced to a comparatively small extent by the place of the particular groups or species in the thawing groups which have reference to the mass occurrence of the species in nature.

Fig. 24 illustrates the correlation between the floral development during the wintering and the first flowering; the date of the first flowering is figured in the usual way for each of the eight floral types separately

(see pp. 182—183). Groups 3—6 inclusive, in the dates for their first flowering directly reflect the developmental stage of the flower buds during the wintering, that is to say, when the growth starts in spring. The more developed the flower buds are, the earlier the flowering. The average difference in time for the first flowering of species with floral organs of developmental type 3 and such as have floral organs of developmental type 6 amounts to no less than about one month. Species with wintering pollen (floral type 7) flower remarkably early and simultaneously, though they do not contribute to the earliest vernal aspect. Species of floral type 2 and more especially species of type 1 fall outside the other groups, their flowering setting in disproportionately early. Thus the rate of development of these species is distinguished by an extreme rapidity, viewed in relation to the other groups. The curve for the aperiodical species runs obliquely to the others. That is to say, the rate of expansion within the species of the group is slow. In view of the fact that in the greater number of the species of this group part of the flower buds are always highly developed, corresponding to type 5 and often to type 6, the flowering on the whole sets in late. This must be correlated with the slow rate of growth in the species of this group, which is already indicated by the frequent two-year primordial development of the organs of these species (cf. p. 208).

## The plant geographical importance of developmental-morphological and biological characteristics.

The characteristics of the flora of Northeast Greenland pointed out in the present chapter were meant to supply a more detailed knowledge of such biological conditions as may be supposed to be of fundamental importance for an estimate of the regional and ecological plant geography of the area. Since important plant-geographical problems must be solved by comparison of the vegetation of different areas on common fundamental principles, the value of investigations like the present will depend on the material available for comparison from adjoining or more remote regions. Only as regards the life-form character is information at hand from different climates. Comparative studies of the floristic plant-geographical position of Northeast Greenland on the basis of life-form spectra have been made by GELTING (1934, p. 319 et seq.). Such studies as a rule result in the establishment of a "plant climate", whose plant-geographical importance—from a logical point of view—is not quite clear to me. The abstract life-form spectrum may no doubt be a valuable aid in the characterisation of the vegetation of an area and its individual vegetation types. But to an understanding of,

or more correctly to the explanation of, the vegetation of an area it contributes but little, all the more so since the actual biological meaning of the life-form is unknown. The life-form indicates the position of the vegetative wintering buds in relation to the surface of the soil during the resting period. To study a definite, biologic-morphological character during a well defined section of the life cycle of the plant, was the ingenious idea conceived by RAUNKIÆR. Every attempt to put anything more into the life-forms will merely create confusion and thus discredit the life-forms as an aid in plant-geographical research. This view, though not directly stated, is clearly expressed in HAGERUP'S "Étude des types biologiques de Raunkiær dans la flore autour de Tombouctou" (1930).

The most easily demonstrable reaction of the species to the constellation of external factors is manifested in their occurrence or non-occurrence. An investigation of the morphological, biological, and eco-systematical characteristics including the life-forms of the species at the limits of their range therefore seems to me to be one of the most important sources which is at the disposal of ecological and regional plant-geographical research for elucidating the reaction of the species to the environment. As a main result of the investigations dealt with in this chapter, I will summarise here the characteristics concerning the biological morphology of the individual species or groups of species which somehow or other, judging from a comparison with the other groups, seem to be correlated with the existing northern and southern limits of the distribution of species in Northeast Greenland.

Let us first consider the northern group (NN), whose species have their southern limit within the part of Northeast Greenland dealt with here or immediately south of it (the area of Scoresby Sund). As regards its life-form spectrum this species group differs but slightly from the "normal" of the area. However, the therophytes are entirely absent and, what is perhaps of the greatest interest, the chamaephytes, though abundantly represented, show a somewhat smaller percentage representation here than within the groups of species with a larger, and accordingly generally more southern, area in Greenland. The number of foliage leaves per shoot, that is to say per flowering, hardly differs from that of the more widely distributed species, and the yearly leaf production of the sympode does not differ perceptibly from the "normal"; but the species of the group show a relatively marked tendency towards a distribution of the leaf production at the same time over several shoots within one and the same sympode—though hardly more than the species with a larger southern distribution (the N group), which likewise extend to the north coast of Greenland. Evergreen species are entirely lacking, and the percentage of winter-green species is a little above the "normal" but not higher than in the N group. Active bud protection is not found

at all within the group; it contains a fairly high percentage of species with unprotected buds and a very high percentage of species with a passive bud protection. The floral development in the wintering stage is generally well advanced, aperiodical species are of frequent occurrence, and flowering sets in early. As regards snow-covering, the group is comparatively well represented in the ecosystems which become free of snow very early and rather late, but is rather sparsely represented in the ecosystems thawing at a moderately early date.

Turning now to the group of southern species (SS) which have their northern limit within Northeast Greenland, we shall see that the chamaephytes are rather sparsely represented here, while the hemicryptophyte percentage is above the "normal". The number of foliage leaves per shoot (i. e. per flowering) is considerably higher than in the other groups. The yearly leaf production of the sympode itself is not essentially higher than in the other groups, but the tendency to confine the leaf production to a few shoots (generally only one) within the same sympode is recognisable, though not especially marked as compared with the other southern species (the S group), which extend farther northward, but whose distribution extends to the southernmost point of Greenland. The group shows a high percentage of summer-green and a low percentage of winter-green species. Active bud protection occurs to a greater extent than in the other groups. Species with slightly developed floral organs during the wintering are very frequent, and aperiodical species are rare. Flowering as a rule sets in later than in any of the other groups. The species of the group principally occur in ecosystems with a moderately early melting of the snow.

As regards the characteristics dealt with here the NS group, which comprises the species whose distribution is chiefly limited to Northeast Greenland, agrees in the main with the northern species of the area, and often a tendency, suggested in the NN species, becomes more consistent in the species of this group. Thus, for instance, the percentage of aperiodical species is even higher in the NS than in the NN group, and the flowering likewise is remarkably early in the species of the NS group. It is almost as regards the life-form alone that agreement with the northern species is lacking to some extent, the Ch percentage being lower and the G percentage exceptionally high. In contrast to the northern species, with which they have their southern limit in common, but in accordance with the southern species, with which they have their northern limit in common, the special Northeast Greenland species chiefly occur in ecosystems with a moderately early melting of the snow.

In the above comparison between the markedly northern and markedly southern species of Northeast Greenland it will be noticeable

that the distributional type is directly correlated with a number of the characters whose distribution over the groups of species has been subjected to statistical treatment above.

The southern species often require the development of a relatively large number of leaves for each flowering, and likewise often a certain number of leaves developed on one and the same shoot within the same growth season in order that flower buds may form at all. If at the same time we note that these species concentrate the effective yearly leaf production on some few shoots (often only one), and that they grow in the most favourable localities (as regards exposure and moisture), at any rate one aspect of the biology of the plant as regards its northern limit will be clear. More unfabourable conditions of growth, which may further reduce the production of leaves, would result in the plant never developing beyond the vegetative stage. There is hardly any doubt that certain species reach their northern limit where the growth conditions are no longer sufficiently favourable to support the yearly vegetative development required if the species is to flower. Even if the vegetative development puts no obstacles in the way of the formation of the floral organs, the inconsiderable floral development during the wintering and the consequent late flowering will soon, if the growth period is further shortened, prevent the plant from producing ripe fruits even if flowering actually takes place.

Similarly, a consideration of the same characteristics in the northern species will in a satisfactory way render probable their power of holding their own under more unfavourable growth conditions, chiefly because of the short duration of the growth period. The necessary yearly minimum number of leaves per shoot required for the formation of floral organs is here very low. The yearly leaf production of the sympode, however, is not essentially lower than in the southern species, and thus often greatly exceeds the minimum. The discrepancy is eliminated by a distribution of the contemporaneous leaf production over two or more successive shoots within the same sympode (cf. also remarks on regulation shoots, e. g. in *Draba*, p. 107).

This tendency is carried to the extreme limit in the aperiodical species, which are precisely characteristic of the northern groups (cf. Table 31, p. 205). In these species there evidently exists no interdependence between the yearly leaf production of the shoot and the formation of the floral organs. A permanent failure to flower as a consequence of a deficient yearly growth (leaf production) does not, accordingly, occur in the same degree in the northern as in the southern species. In addition there is a well advanced floral development in the winter in the northern species, which conditions an early flowering—at any rate as compared with the date for the melting of the snow—by

which seed reproduction is ensured. The constitutional tendency towards a staccato development, which even under unfavourable growth conditions ensures to the plant a harmonious development, and under optimum conditions of growth renders a more frequent flowering possible, the flower-bud formation of the daughter shoot taking place simultaneously with the flowering of the mother shoot, seems to be one of the most important biological characteristics of high-arctic plants. The dense, short-jointed, more or less cushion-shaped growth-form of these plants is no doubt directly associated with this character and is hardly to be regarded as a direct adaptation to, or a consequence of, external agencies, but is more properly an indirect consequence of developmental-morphological peculiarities, which contribute to ensure the seed reproduction of the plant even if the growth period is considerably shortened. Thus the low and crowded growth form in the last instance becomes an "adaptation" to a short summer. The proleptic development of the innovation shoot, so common in the high-arctic plants but rather rare in those of the temperate regions (NILSSON 1885, p. 23), is clearly directly correlated with the above-mentioned peculiarity in the developmental morphology. GELTING (l. c., p. 291) says that cushion plants are chiefly found in dry soil free of snow in the winter and in particularly wet localities without a closed cover of vegetation (this chiefly means localities with late-melting snow: the snow-patches). I can fully confirm this. As stated above (cf. Table 10, p. 189), precisely the northern species are comparatively well represented within the early and late thawing groups, but more sparsely in the middle groups within the thawing scale.

Referring to the above discussion it should be pointed out here that the peculiarities in developmental morphology which are characteristic of the southern species on the one hand and of the northern species on the other hand, as it were predestine the species for the geographical distribution in Northeast Greenland peculiar to them, in so far as the northern limit of the southern species and the markedly northern occurrence of the northern species is concerned. On the other hand, the developmental morphology leaves us in the lurch as regards a more precise explanation of the southern limit of the northern species. This may indicate that northern and southern limits of species in Northeast Greenland are not of the same value. This supposition is moreover strongly supported by the fact that in the statistical computation of the correlative association of the individual biologic-morpholigical characters with the different distributional groups, a greater accordance will generally be found between Groups NN and N, with an approximately common northern limit (the species of these groups actually (in most cases) lack a climatic northern limit in Greenland) but different southern limits, than between the SS and S groups, which agree in their relatively

southern main distribution, but whose northern limits differ. The northern outposts of the southern species are characteristic by their relatively favourable growth conditions (favourable exposure and water supply, see below pp. 242—243). That the outpost species in such localities easily hold their own in the competition with the "indigenous" northern species, on account of their taller growth and more abundant foliage, is often immediately apparent (cf. ANDERSSON & BIRGER 1912, FRÖDIN 1915, 1917: Sydberg; i. e. Southern mountain slopes). Thus the southern species reach their absolute climatic northern limit. The southern limit of the northern species is hardly of a similar purely climatic character. As the most probable cause (apart from the possible constitutionel attitude of the species towards the temperature factor) of their disappearance towards the south their generally small absolute size may be mentioned as also the inconsiderable leaf production and foliage of the individual shoots, and perhaps in the first place their slow rate of growth, which will cause them to be outmatched in the struggle for room in competition with the southern species.

It is perhaps not superfluous to point out that the considerations set forth above concerning the distributional limits of species in relation to developmental-morphological data are clearly free from all metaphysical elements. Be this said as an introduction to a brief discussion of a few other characteristics of the species treated in the total tabellary and statistical summary above. I am here referring to such characteristics as to whose appropriateness we cannot (from our present knowledge of the physiology of the species) have any well-founded idea, and whose correlative association, elucidated statistically, with the distributional type of the species does not invite rational comments disengaged from teleology. The increase in the Ch percentage with increasing geographical latitude demonstrated by RAUNKIÆR can accordingly hardly be rationally explained, that is to say, the geographical limits of the species cannot be consistently correlated with the life-form. In short, we do not know what is hidden behind the life-forms.

The law of the increasing Ch percentage towards the north does not seem to have unlimited validity in Greenland. The groups whose species have their southern limit at Scoresby Sund or north of this sound have a lower Ch percentage than the southern and northern groups, which have a wide distribution within Greenland but are absent from the north coast of Greenland. This is in accordance with NORDHAGEN's (1928) demonstration of a decreasing Ch percentage for the greatest heights within the Sylene area of Scandinavia. As regards the snow-covering it has been established that in Northeast Greenland the Ch species are chiefly associated with the ecosystems which are free of snow in the winter or become free of snow at an early date. This is likewise

in accordance with observations made in other arctic and subarctic regions, for instance in East Greenland south of Scoresby Sund (Böcher 1933 b) and Iceland (Mølholm Hansen 1930).

Greenness in the winter is chiefly, and the evergreen state almost exclusively, associated with chamaephytism. Similarly, unprotected winter buds are more frequent in chamaephytes than in species of other life-forms.

A well advanced floral development during the growth period preceding the flowering year and an early flowering are generally more frequent in the chamaephytes than in the other life-form groups. Aperiodical species occur most frequently among the chamaephytes, though this type is also represented among the hemicryptophytes.

Thus it will be seen that from a statistical point of view there exists a certain correlation between chamaephytism and a number of extreme characters which are distinctive features of northern species. However, this, of course, in no way disagrees with the great abundance of hemicryptophytes in the extreme north, which has been pointed out above, the hemicryptophytes being always absolutely dominant numerically within all the distributional groups.

Similarly as the chamaephytes are correlated with "northern" characters, the other life-forms, arranged in the order H, G, HH, Th, show an increasing correlation with "southern" characters, that is to say, characters which irrespective of the life-form are characteristic of species with a southern distribution.

Like the life-form, the leaf and bud states of the species during wintering escape logical consideration. Here, as in the case of the life-form, we must be content with the simple ascertainment of the facts. Within Northeast Greenland winter-greenness is characteristic notably of the markedly northern species including the special Northeast Greenland species (the NS group). The evergreen species, however, are chiefly species with southern and middle-Greenland areas. Active bud protection is mainly found in species with a southern distribution, while not in a single of the absolutely northern (NN) and the specially East Greenland species (NS) are the wintering buds protected by special arrangements. The teleological explanation, that bud protection has been abandoned by the species farthest north, because even the most effective protective means would here be of no avail against the violent external agencies, is natural but of course without scientific interest. Strictly speaking the phenomenon is ununderstandable. But it is a fact. It should merely be noted here that the lack of bud protection to a certain extent runs parallel with the absence of periodicity. By far the greater number of aperiodical species are without bud protection of any kind, and conversely, an effective development of the protection of winter

buds is always associated with a consistent periodicity in the order of organic development. Thus the increase ascertained in the frequency of unprotected buds northward seems to indicate a tendency to abandon periodicity; and, as illustrated above, this may actually be a profitable, though in certain respects an uneconomic, adaptation to conditions which are dominated by the decrease of the growth period towards the critical minimum.

## Phylogeny of developmental characters. Examples of retarded and accelerated development.

In this place, finally, some facts should be pointed out, which are mainly of a theoretical interest, and which cannot fail to attract attention on a consideration of the species with wintering pollen. This "floral type" is represented by eight species in Northeast Greenland, viz. *Betula nana*, *Empetrum nigrum*, *Cassiope tetragona*, *Cassiope hypnoides*, *Rhododendron lapponicum*, all of which are woody plants, and *Draba crassifolia*, *Draba micropetala*, and *Chrysosplenium tetrandrum*, which are herbs. It is my impression that we are here confronted with two cases fundamentally different in a phylogenetic respect, one of which concerns the dwarf bushes, the other the herbs.

1) All the bushes are strictly periodical in their floral development (*Cassiope hypnoides*, however, sometimes shows a slight tendency towards aperiodicity). The formation of pollen takes place comparatively early and is as a rule completed by the middle of August. Proleptic shoot development does not occur in these species. On closer inspection of the developmental sequence of the shoots and floral organs in *Empetrum*, *Cassiope tetragona*, and *Rhododendron* (cf. *Ericaceae*, pp. 148—149) one receives the impression that the flowering has been postponed one year, in short, the original "plan" for the floral development was a flowering in direct continuation of the formation of pollen. As regards *Betula*, only the male catkins show a retarded vernal flowering after wintering in a fully developed state, while the female catkins develop in the "normal" way (cf. further *Betulaceae*, p. 94 et seq.). It must be admitted that there is no reason whatever to assume a different history as regards the floral development of the other *Bicornes* of Northeast Greenland, in which the pollen formation occurs in the spring. The *Salices*, which likewise have pollen formation in the spring, also resemble the *Bicornes* in their course of development; all these species have highly developed flower buds during their wintering though the pollen formation does not take place till the spring. The species in question belong to decidedly old families, and it is probably beyond any doubt that the conversion of

autumnal flowering to vernal flowering dates very far back. The problem is not a specially arctic one, but is of a general kind, the type being also represented in the temperate zone; but in a treatment of the developmental morphology of the arctic plants it appears in a new light, because the arctic flora exhibits undoubted cases of convergent development, in which the very same result has been attained in entirely different ways, as will be mentioned at greater length below. It should merely be pointed out first that in the case of *Cerastium alpinum—Cerastium Regelii* (see further pp. 97—98) we are confronted with a conversion from autumnal to vernal flowering *in statu nascendi.* In *Cerastium alpinum*, as also in *Minuartia rubella*, the normal little advanced flower buds are found in the spring at the beginning of the growth season, but in addition there occur some flower buds which have wintered in a highly advanced stage of development and flower early in the spring; these flowers are as a rule situated at the apex of long shoots. As far as could be ascertained (*C. Regelii* chiefly reproduces vegetatively and rarely flowers), the flowering of *C. Regelii* was solely due to flower buds of the last-named type occurring in *C. alpinum.* This is shown not only—and not mainly—by the developmental stage of the buds during wintering, but by their position at the apex of long shoots and by the developmental type of the latter as compared with the normal short shoots of more common occurrence. If we consider the occurrence of the two *Cerastium* species—*Cerastium Regelii*, in contrast to *Cerastium alpinum*, is a typical (northern) snow-patch plant—the phenomenon reveals itself as a profitable adaptation to "deteriorated" climatic conditions, manifested by a shortening of the duration of the growth period. The floral development of *Bicornes*, *Empetrum*, etc., viewed in the light of the *Cerastium* example, cannot fail to suggest that the change from autumnal to vernal flowering is correlated with a prehistoric change of climate, or, if it be preferred, deterioration of the climate. However, a further discussion of this problem is of course far beyond the scope of this work.

2) The three herbs, *Draba crassifolia*, *Draba micropetala*, and *Chrysosplenium tetrandrum*, have not, like the dwarf bushes, a strictly periodical floral development; this appears from the fact that buds whose pollen formation does not take place till the spring often occur in addition to the pollen-bearing buds, which, however, are the most frequent. In their developmental morphology these species merely represent the extreme points in the line of anticipated development of the successive shoot generations. Thus we are here concerned with an acceleration of the floral differentiation of the growing point, resulting in a flowering "in time", not, as in *Bicornes*, with retarded flower buds initiated "in time". In contrast to the woody plants, the herbs with pollen formation

in the autumn belong to relatively young families, and their peculiar floral development must here be regarded as a relatively recent "adaptation" to extreme growth conditions tending towards a shortening of the vegetation period. From a phylogenetic point of view this type is doubtless very dissimilar to the above-mentioned *Bicornes-Empetrum-Betula* type, whereas it is very closely related to the aperiodical type in this respect. Of the three species actually only *Draba micropetala* is fairly consistently periodical, while *Chrysosplenium* and especially *Draba crassifolia* form a direct transition to the purely aperiodical species.

# VI. SOME GERMINATION EXPERIMENTS

A very valuable work on the seed reproduction of the arctic-alpine vegetation of Petsamo-Lappland was recently published by SÖYRINKI (1938—39). The very extensive investigations in the field which form the basis of these researches have been supplemented by germination experiments. Thus SÖYRINKI found a rather satisfactory power of germination in the arctic plants from the investigated area. While the object of SÖYRINKI's experiments was to ascertain the germinating power as such, some germinating experiments on Northeast Greenland species carried out by me on Clavering Ø in the spring of 1935 had a different object, namely to try to find out the temperature requirements of the arctic plants for germinating at all.

The seed material for this experiment was collected in the course of September, 1934. Owing to the relatively late season at which the collection was made the seed employed in the great majority of cases was fully ripe, the samples collected consisting in most cases of the remaining contents of the capsules and other seed vessels. As regards some few early flowering species all the seeds had been shed, so that it was impossible to secure seeds of all the species growing around Eskimonæs. For this reason even certain common species could not be included in the experiment, thus for instance *Hierochloe alpina*, *Juncus biglumis*, *Arenaria ciliata*, *Erigeron compositus*. Other species, chiefly *Gramineae*, on removing the chaff of the seeds proved to have a very defective fructification, since even abundant samples of infructescences did not yield a single seed. Such species were: *Alopecurus alpinus*, *Arctagrostis latifolia*, *Calamagrostis purpurascens*, *Dupontia Fisheri*, *Festuca rubra*, *Poa pratensis*, *Poa alpina*, *Poa glauca*, *Puccinellia phryganodes*, *Carex parallela*, *Carex saxatilis*, *Carex subspathacea*. Furthermore *Tofieldia palustris*, *Salix herbacea*, *Saxifraga Hirculus*, and *Campanula rotundifolia*, in which species it was distinctly seen that the seeds had simply not contrived to ripen, at any rate not in the localities accessible to me during the collection. Finally it should be mentioned that *Saxifraga cernua* and *Saxifraga stellaris comosa*, which have an

abundant vegetative propagation, apparently never produce seeds in Northeast Greenland, even though they flower (the last-named species, however, only exceptionally); the same applies to *Stellaria longipes*. As regards the absence of seed production in *Carex parallela* the peculiarity may be emphasised that male plants are very rare on Clavering Ø, where the species is very near its northern limit, whereas female plants are abundant locally. It might therefore seem probable that the failing seed production is due to failing pollination and fertilisation. (For similar phenomena in *Stellaria longipes*, see p. 102).

The seed material collected was kept during the winter at the station of Eskimonæs at the ordinary (arctic!) room temperature. The germination experiments were prepared in the spring in the following way: After cleaning the seed it was packed up into capsules made of grey filter paper of the ordinary kind used for drying plants. As regards the greater number of the species seeds derived from several collections were mixed, each collection having often yielded only some few seeds. The paper capsules with the seeds were placed in the open snow-free field, pressed closely down on to the substratum by the aid of some frames with a net of twine made for the purpose. With a view to the control of the temperature conditions the seeds were laid out in the same place affected by solifluction as had been selected for thermograph observations of the temperature of the soil surface. For the germination experiments the slope of solifluction soil further had the advantage that the soil was damp, and that in the early spring it was watered by the slowly oozing thaw-water from the snow-fans situated at some distance above. When the seeds were laid out on May 20th—22nd, the soil was still completely frozen. During the subsequent incipient thawing of the surface the paper capsules remained damp, or during the largest influx of thaw-water even drenched. After the supply of surface water had stopped by the middle of June, the thin layer of moss and withered grass beneath the capsules caused them to be exposed to desiccation. In order to prevent this, the sod was removed, and the paper capsules were placed directly on the damp mineral soil. In spite of these precautions, drying by sun and wind could not be prevented in the long run, and the experiment must therefore be regarded as finished on July 1st. Registration of the stage of germination of the seed samples was made four times, the last time on July 1st: the wet capsule was cautiously opened, and after the state of the contents had been ascertained, it was put back in its place.

The immediate result will appear from Table 37, in which all the species included in the experiment are listed in alphabetic order. The four vertical columns indicate the four readings. A × indicates that germination (by which is meant the distinct piercing of the seed shell

Table 37. Result of germination experiments, made at Eskimonæs in the spring of 1935 (see the text on p. 226).

| | 7 June | 14 June | 23 June | 1 July |
|---|---|---|---|---|
| *Antennaria alpina* | .. | × | .. | .. |
| *Arctostaphylos alpina* | .. | .. | .. | .. |
| *Armeria vulgaris* | .. | .. | × | .. |
| *Arnica alpina* | .. | × | × | .. |
| *Betula nana**) | .. | .. | × | .. |
| *Braya humilis* | .. | .. | × | .. |
| — *purpurascens* | × | × | .. | .. |
| *Campanula uniflora* | .. | .. | .. | .. |
| *Cardamine bellidifolia* | .. | .. | × | .. |
| *Carex alpina* | .. | .. | .. | .. |
| — *atrofusca* | .. | .. | .. | .. |
| — *capillaris* | .. | .. | .. | .. |
| — *incurva* | .. | .. | .. | .. |
| — *Lachenalii* | .. | .. | .. | .. |
| — *misandra* | .. | .. | .. | .. |
| — *nardina* | .. | .. | .. | .. |
| — *pedata* | .. | .. | .. | .. |
| — *rariflora* | .. | .. | .. | .. |
| — *rigida* | .. | .. | .. | .. |
| — *rupestris* | .. | .. | .. | .. |
| — *scirpoidea* | .. | .. | .. | .. |
| — *supina* | .. | .. | .. | .. |
| — *ursina* | .. | .. | .. | .. |
| *Cassiope tetragona* | .. | .. | .. | .. |
| *Cerastium alpinum* | .. | × | × | × |
| *Chamaenerium latifolium* | × | .. | .. | .. |
| *Chrysosplenium tetrandrum**) | .. | .. | × | .. |
| *Cochlearia officinalis* | .. | × | .. | .. |
| *Draba cinerea* | .. | × | × | × |
| — *crassifolia* | .. | × | × | × |
| — *daurica* | × | × | × | × |
| — *fladnizensis* | × | × | × | × |
| — *lactea* | × | × | .. | .. |
| — *micropetala* | .. | × | × | .. |
| — *nivalis* | .. | × | × | .. |
| — *subcapitata* | .. | × | × | .. |
| *Dryas octopetala* | .. | × | × | .. |
| *Elyna Bellardi* | .. | .. | .. | .. |
| *Erigeron unalaschkensis* | .. | × | × | .. |
| — *uniflorus* | × | .. | .. | .. |
| *Eriophorum callitrix* | .. | .. | .. | .. |
| — *polystachyum* | .. | .. | .. | .. |
| — *Scheuchzeri**) | .. | .. | × | × |
| *Euphrasia latifolia* | × | .. | .. | .. |

*) Sparsely germinating.

Table 37. (continued).

| | 7 June | 14 June | 23 June | 1 July |
|---|---|---|---|---|
| *Eutrema Edwardsii* | .. | × | × | .. |
| *Festuca brevifolia* | .. | .. | .. | × |
| *Gentiana tenella**) | .. | × | .. | .. |
| *Juncus triglumis* | .. | .. | .. | × |
| *Kobresia bipartita* | .. | .. | .. | .. |
| *Koenigia islandica* | × | .. | .. | .. |
| *Lesquerella arctica* | × | × | × | .. |
| *Luzula confusa* | .. | .. | × | × |
| — *nivalis* | .. | .. | .. | .. |
| — *spicata* | .. | .. | × | .. |
| *Matricaria inodora* | × | .. | .. | .. |
| *Melandryum affine* | × | × | × | × |
| — *apetalum* | × | × | × | × |
| — *triflorum* | × | × | × | × |
| *Minuartia biflora* | .. | .. | × | × |
| — *rubella* | .. | × | × | .. |
| — *stricta* | .. | .. | .. | .. |
| *Oxyria digyna* | × | × | .. | .. |
| *Papaver radicatum* | .. | .. | .. | .. |
| *Pedicularis flammea* | .. | × | .. | .. |
| — *hirsuta* | .. | .. | .. | .. |
| — *lapponica* | .. | .. | .. | .. |
| *Phippsia algida* | .. | .. | × | × |
| *Poa abbreviata* | .. | .. | .. | × |
| — *arctica* | .. | .. | × | × |
| — *Hartzii* | .. | × | × | × |
| *Polygonum viviparum* | .. | (×) | .. | .. |
| *Potentilla Crantzii* | .. | .. | .. | .. |
| — *emarginata* | .. | .. | × | × |
| — *nivea* | .. | × | × | × |
| — *pulchella* | .. | × | × | × |
| — *rubricaulis* | .. | .. | × | × |
| *Puccinellia angustata* | .. | × | × | .. |
| — *Vahliana* | .. | × | × | .. |
| *Pyrola rotundifolia* | .. | .. | .. | .. |
| *Ranunculus affinis* | .. | .. | .. | .. |
| — *nivalis* | .. | .. | .. | .. |
| — *pygmaeus**) | .. | .. | .. | × |
| — *sulphureus* | .. | .. | .. | .. |
| *Rhododendron lapponicum* | .. | .. | .. | × |
| *Sagina intermedia* | × | .. | .. | .. |
| *Salix arctica* | × | .. | .. | .. |
| *Saxifraga aizoides* | .. | .. | .. | .. |
| — *hieraciifolia* | .. | .. | .. | .. |
| — *Nathorsti* | .. | .. | .. | .. |
| — *nivalis* | .. | × | × | × |

*) Sparsely germinating.

Table 37 (continued).

| | 7 June | 14 June | 23 June | 1 July |
|---|---|---|---|---|
| *Saxifraga oppositifolia* | .. | .. | × | × |
| — *rivularis* | .. | .. | × | × |
| — *stellaris comosa* | .. | (×) | .. | .. |
| *Sedum roseum* | .. | × | × | .. |
| *Silene acaulis**) | .. | .. | × | .. |
| *Stellaria humifusa* | .. | .. | .. | .. |
| *Taraxacum arcticum* | .. | × | .. | .. |
| — *phymatocarpum* | .. | × | .. | .. |
| *Tofieldia coccinea* | .. | .. | .. | .. |
| *Trisetum spicatum* | .. | .. | × | × |
| *Vaccinium uliginosum* | .. | .. | .. | .. |

*) Sparsely germinating.

by the radicle) was ascertained at the date stated above the column. No close determination (countings) of the intensity of the germination was made. Species which germinated very poorly are marked by an asterisk. In case the germination of a species is only indicated by a × in one of the columns, no continued germination was ascertained in the later readings. If the species is marked with a cross in more than one column, it means that more seeds had germinated since the preceding reading.

The list comprises 99 species in addition to *Polygonum viviparum* and *Saxifraga stellaris comosa*. As regards the last-named two species the experiment showed that bulbils kept together with the seed samples were capable of germinating when they were laid out in the spring. Of the 99 species a total of 62 species germinated, while 37 showed no signs of life. It should be noted that about half the number of the non-germinating species are *Cyperaceae*, of whose 19 species only one, viz. *Eriophorum Scheuchzeri*, germinated, though poorly. The failure to germinate does not of course mean that the seed was not capable of germinating, but it may be due to the unsuitability of the conditions for the germination of such species, or may simply be due to the fact that under natural conditions, too, the species in question germinate very slowly. Thus Söyrinki (l. c.) noted slow germination in a number of *Carex* species. Furthermore the *Ranunculaceae*, in particular, showed disinclination for germination (cf. also Kinzel 1926).

A specially vigorous, more or less complete germination was ascertained chiefly in the earliest germinating species (reading June 7th). The two therophytes *Koenigia* and *Euphrasia* showed practically a 100 per cent. germination. A similar complete germination was observed in *Chamaenerium latifolium* and *Salix arctica*. This is noteworthy as

regards *Chamaenerium*, because this species has a very effective vegetative propagation by runners, and as regards *Salix*, because in earlier investigations on the germination of *Salices* (e. g. HERIBERT NILSSON 1918) it has been doubted whether the seed was at all capable of preserving its power of germination for any length of time. SÖYRINKI (1938, p. 168 et seq.), however, basing his opinion on the finding of seedlings in nature before the dissemination of the present year, thinks that the willows of Lappland are in certain cases capable of germinating after wintering. As regards *Salix arctica* there can hardly be any doubt that germination of wintering seeds may take place to a great extent under natural conditions also.

Finally it deserves mention that *Poa Hartzii* showed excellent germination; for, ascertaining, on the basis of herbarium material, that this species failed to produce seeds, NANNFELDT (1935, p. 25 et seq.) expressed the supposition that the plant is of a hybrid nature. However, if one has seen this plant in nature, where it is even dominant in some places, one cannot doubt its rank as a species. In view of the fact that the seed production of this plant may in certain cases be even extremely sparse, as also in the other *Poae* (though with the exception of *Poa abbreviata*) and various other *Gramineae*, NANNFELDT's view is understandable. However, I shall not here enter into any further discussion of the individual species.

On the other hand, the germination of the species viewed in relation to their distributional type and their thawing type (see p. 181), will be dealt with at some length. Fig. 25 shows the germination of the individual distributional groups figured according to the same method as the flowering in Figs. 20—24 (cf. p. 210); it shows the percentage of germinating species within each group at the date marked on the abscissa. Thus the end of the curves to the right indicates the final percentage of germinating species at the close of the experiment. It appears from the figure that the southern species germinated more poorly than the northern ones—the more markedly southern (SS), the poorer the germination, the more markedly northern (NN), the more complete the germination (computed by species). Furthermore it will be seen that the germinating power is in a fairly great degree directly proportional to the (Greenland) area of the species. Group C, which comprises the circumgreenlandic species, has 2—3 times as high a percentage of germinating species as the M and NS groups, which have only a limited middle Greenland area. The characteristic distribution of the germinating power under the given experimental conditions can hardly be due to a mere chance, even though the numerical material, it must be admitted, is too sparse. It is true that the SS group is fairly abundantly represented among the *Cyperaceae*, which, regarded as a family, ger-

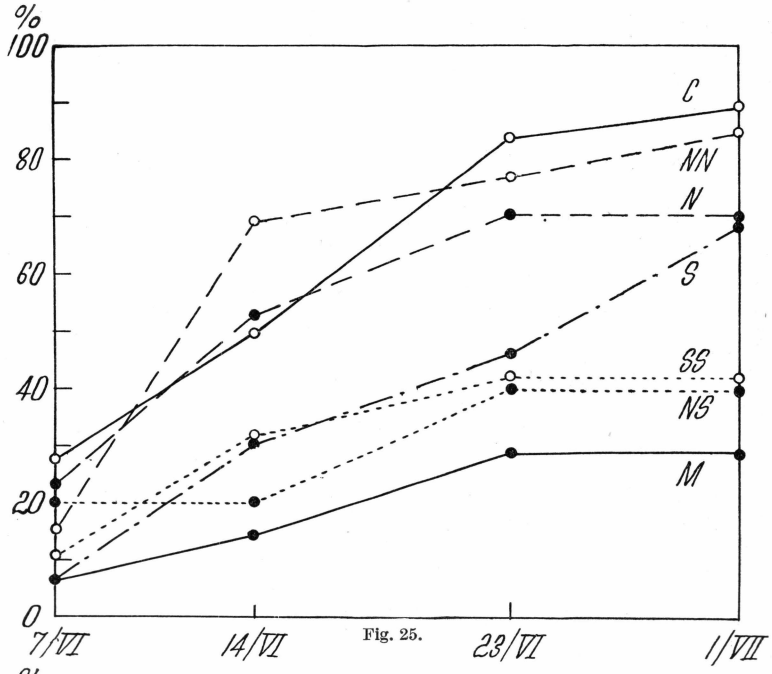



Fig. 25.

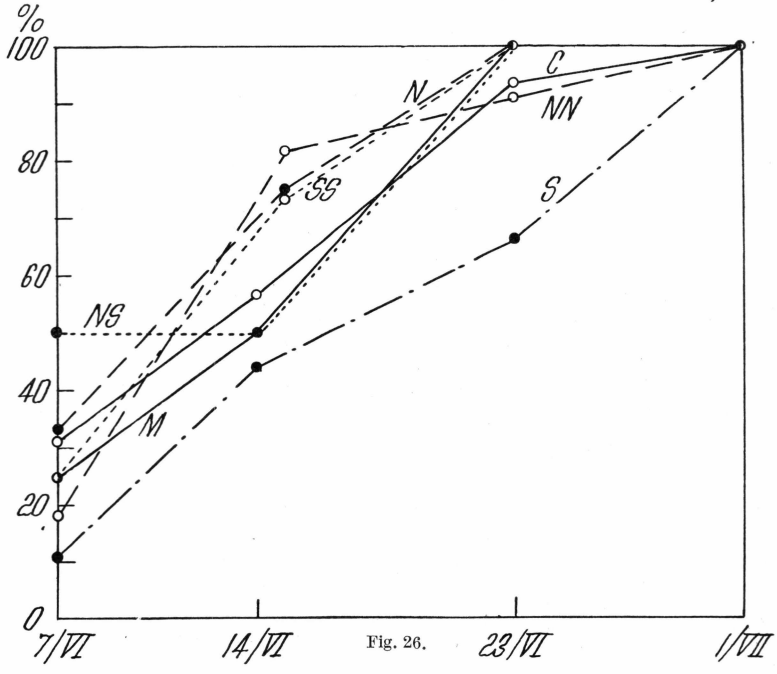



Fig. 26.

Figs. 25—26. Graph showing the germination frequency within the individual distributional groups. The ordinate indicates the percentage of germinated species at the date indicated on the abscissa. The germination percentage given in Fig. 25 is computed on the basis of the total number of the species included in the experiment within the respective groups. The germination percentage given in Fig. 26 is computed on the basis of the number of species germinating before July 1st within the respective groups.

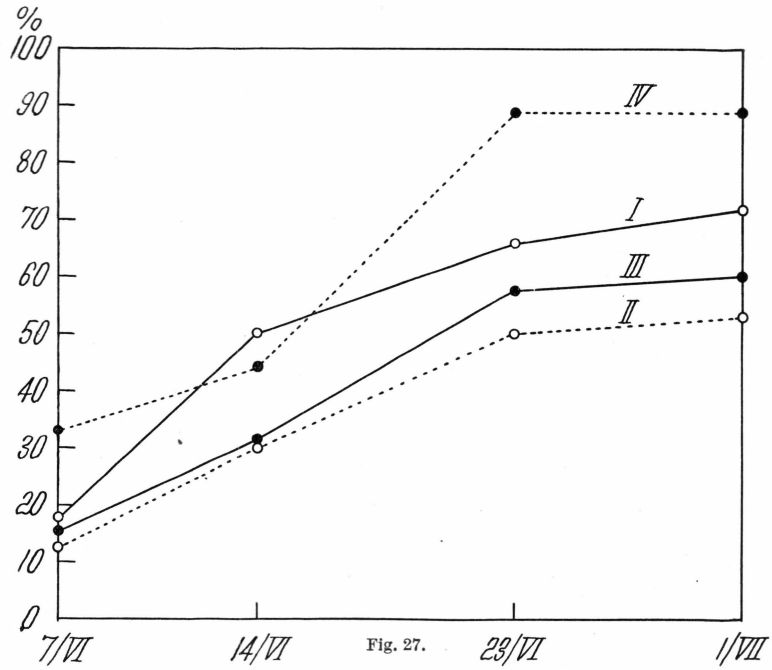



Fig. 27.

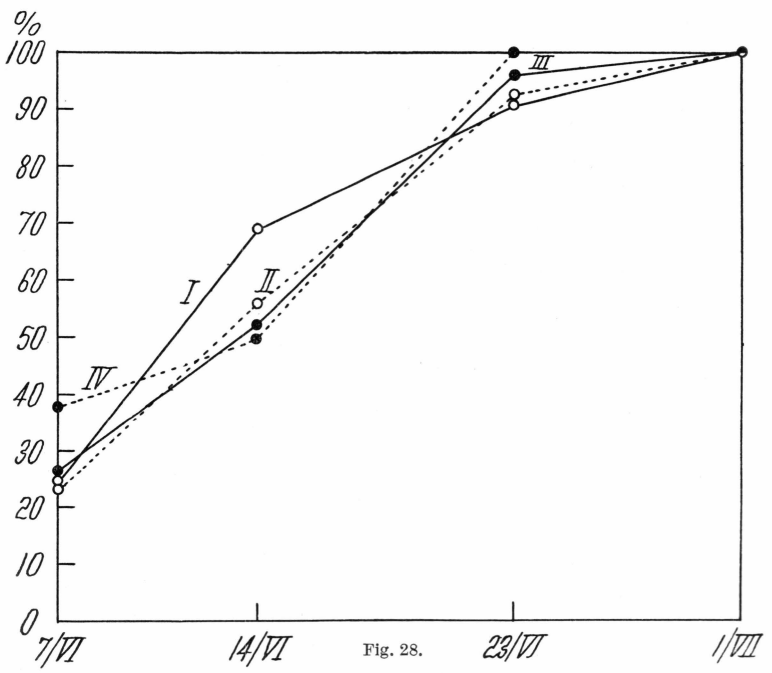



Fig. 28.

Figs. 27—28. Graphic representation of the germination frequency within the individual thawing groups. (For explanation, cf. Figs. 25—26, p. 231). The germination percentage shown in Fig. 27 is computed on the basis of the total number of species comprised by the experiment; in Fig. 28 on the basis of the number of species within the respective groups which germinated during the experiment (before July 1st).

minated poorly but this does not at any rate apply to the M and NS groups. The correlation between distribution and germination need not of course be taken to mean that difficulties in germinating are a hindrance to the distribution of the species altogether. It is perhaps more probable that species with a limited distribution have more special requirements for the maintenance of life in general than the widely distributed species, and that this property manifests itself already in the germinating seed (or more precisely: the seed that has not yet germinated). Conditions in a paper capsule on soil affected by solifluction cannot, of course, be ideal to all the plant species of the area. The deficient germination of the southern species may thus simply be due to too low temperatures. Slopes of solifluction soil—apart from their steep fronts—represent cool localities even with a southern exposure, and generally they harbour very few southern species. Fig. 26, like Fig. 25, illustrates the germination in relation to the distributional groups, but indicates the percentage of germinated species in relation to the total number of germinated species at the end of the experiment. The less steep increase of the S curve strongly suggests that on a continuation of the experiment under further increasing temperatures an even greater number of the species would have been found to germinate.

The germination percentage of the species in relation to their thawing group is illustrated in Figs. 27 and 28, in a similar way as for the distributional groups. Thawing group II, which shows a higher degree of correlative association with southern species than the other thawing groups (see Table 10, p. 189), exhibits a comparatively poor and slow germination, while the snow-patch plants (Group IV), which of course require diminutive amounts of heat, show the highest germination percentage and in addition as a rule the most rapid germination (see Fig. 28).

For the absolute temperatures at which the seeds germinated the reader is referred to the succeeding chapter (see p. 243 et seq., and Pls. 14—15).

# VII. THE SEASONAL MANIFESTATIONS OF PLANT LIFE IN RELATION TO THE TEMPERATURE CONDITIONS

## The importance of the temperature factor for plant distribution.

The correlation between climate and vegetation is diverse. RAUNKIÆR's life-form spectrum and its variation in relation to the hydrotherm graphs perhaps supplies the most striking example of such a correlation that can be pointed out at present. It is probable, however, that other biological or morphological characters also would exhibit a similar law-regulated behaviour in relation to the climatic belts of the earth. Attention may here be called to a character so generally disregarded as the colour of the flower. It is remarkable, for instance, that white and yellow flowers are relatively more abundantly represented in the Arctic than in Denmark, while red and blue flowers are more frequent in this country.

The reaction of the vegetation to the climate is only accessible to direct observations in its broadest features. Even in a more accurate computation of the different climatic factors our instruments for observation leave us at a loss, as the vegetation does not react to the individual meteorological factors separately, but to the total effect of all climatic factors, the climate character. Viewed in this light it may seem an absurdity to subject a single climatic factor, a single aspect of the climate, the temperature climate, to a special consideration, as done here. The fact alone that the seasons of the year, as marked by the rhythmic alternation of the vegetation between activity and rest in the temperate and more especially in the arctic regions, are closely correlated with the temperature climate, renders it justifiable to assume that the temperature factor is of decisive importance for the differentiation of the vegetation in northern tracts. Furthermore, that the manifestation of the biological type at present, like the type differentiation during the ages within the arctic vegetation, is closely correlated

with the thermic conditions and their seasonal sequence, that is to say, to the temperature climate. It must likewise be assumed that the occurrence or non-occurrence of the species will in a high degree be determined by the degree of adaptation to the extreme temperature climate possessed by the species.

In a country like Northeast Greenland, where the life functions of the plants are subject to such a marked seasonal periodicity, the temperature factor itself and its effects must, of course, principally be viewed in relation to the seasons of the year. If a plant species is to hold its own in the long run, it must in equal degree be adapted to the temperature climate prevalent in its habitat at all seasons of the year and varying with the seasons. The unequal distribution of the species within the different eco-systems in relation to exposure and snow-covering gives one the direct impression that the thermic local climate is of such great importance for the distribution of the plants in the Arctic that it may be paralleled with the factor of water supply, which even in the temperate zone seems to play a predominant role in that respect. Thus there may be reason to point out that the local temperature conditions play an increasingly great role as a plant-distributional factor in the direction from the tropics towards the Arctic, while reversely, the importance of the water supply conditions in the same respect increases from the Arctic towards the tropics. (Cf. also DRUDE 1932).

### Winter plant-climate of Northeast Greenland.

The influence of exposure and snow-covering on the differentiation of the local temperature climate is mainly, though not exclusively, limited to the summer. This must be immediately evident as regards the exposure; and as regards the influence of the snow-covering on the elementary climate of the winter, the temperature observations from Ella Ø (Pl. 12) will give some idea. The snowfall is capricious and often does not set in—as was the case in the autumn of 1931—till the temperature at the surface of the ground has fallen to very low values, thus on Ella Ø to more than 20° C. below zero, even in a locality which was constantly snow-covered later in the winter. It appears from the temperature observations below a cover of snow (Pl. 12) that the surface of the ground beneath 50 cm of snow in the month of April might fall to about 15° C. below zero, and likewise a snow-covering of 100 cm at the same date did not prevent the temperature from falling to about 12° C. below zero. Thus a snow-cover in winter protects the plants against the cold to a limited extent only, even though it is capable of essentially modifying the most violent temperature fluctuations, the extremely low temperatures.

The great importance of the snow-covering to the vegetation, especially to certain dwarf-bush formations, as a protection against the desiccating effects of the wind, more especially of the dry foehn wind, is indisputable (cf. HARTZ 1895).

Even the low winter temperatures have apparently no unfavourable influence on the vegetation, and the importance of the winter to the existing vegetation is chiefly restricted to the indirect one that it practically suspends the life functions of the plants, by which their active period is reduced to comprise only a small part of the year. However, that does not mean that the low winter temperatures do not set their mark on the floristic composition of the vegetation as a whole within the area.

Both the low degree of the winter temperature as a whole and the range of variation of the extreme temperatures are so little divergent within the part of Northeast Greenland treated here and are in such close agreement with the conditions in Scoresby Sund, situated south of it, that no sorting influence by these factors is exerted here. The sorting out of the species not capable of surviving the winter in Northeast Greenland has already taken place in more southern latitudes (cf. SHREVE 1914). However, a failing capability of surviving the winter need not necessarily be associated with such demands on the temperature conditions of the growth period as the summer of Northeast Greenland cannot fulfil. The influence of the winter temperature on the vegetation and flora of Northeast Greenland must accordingly be regarded with a view to the uniformity with which the low temperatures exert their influence on the vegetation of all the ecosystems within the area, from north to south, from the coast to the inland ice. However, the influence of the winter frosts on the vegetation of Northeast Greenland, on its floristic composition as well as on its content of life-forms, the nature of the wintering buds, etc., escapes analytic treatment on the basis of investigations made within this area alone. A detailed comparison of its climate and vegetation with an oceanic area in the Arctic might possibly lead to a well-founded estimate of the plant-geographical importance of the winter temperature.

## Summer plant-climate of Northeast-Greenland. The temperature conditions within the different ecosystems.

The most important plant-distributional factors in Northeast Greenland—besides the passage of water in connection with solifluction (cf. SØRENSEN 1935)—are, as stated above, exposure and snow-covering. The different combinations of these factors in connection

with the vegetation belonging to each combination form the basis of the division into ecosystems enumerated on pp. 56—58 of the present paper. Within the period with favourable temperatures the ecosystems will no doubt each of them be characterised by a local temperature climate differing from the meteorological one.

The temperature observations at the surface of the ground dealt with in Chapter III may contribute to illustrate such local climates. For both physical and biological reasons it seems to me that the temperatures at the surface of the ground are of special interest. Referring to the explanation of the measuring methods (p. 42) it should be pointed out here that the surface whose temperature was measured cannot be defined mathematic-physically, but probably biologically: The temperatures observed will no doubt approximately coincide with the actual temperatures of buds and stem axes in the greater number of the hemicryptophytes and the mesocorm and cushion chamaephytes. Separate temperature observations within each of the ecosystems of the area would have been desirable. However, since observations to such an extent were far beyond the limits of possibility, I must be satisfied to refer the reader to the two detailed observation series, representing two different ecosystems, and with them as a basis for comparison try to estimate the temperature conditions of the other ecosystems. In spite of the insufficiency of the observation material, it may contribute towards our knowledge of the temperature conditions under which the plants actually live, in short, of the plant-temperature-climate as compared with the purely meteorological temperature climate (DRUDE 1918, 1932).

Pls. 12 and 13 illustrate the daily mean temperatures for the air and the surface of the ground. Biologically, however, the fluctuations from the mean temperature are of no less interest than the mean temperatures themselves. For these fluctuations the reader is referred to Tables 40 and 41 (pp. 293—302). Besides, the hours with positive temperatures for each twenty-four hours, indicated for temperature intervals of 5°, are illustrated in Pls. 14 and 15.

The observation series made on Ella Ø (Pls. 12 and 14) illustrates the course of the temperature within Ecosystem I (cf. Table 6, p. 56): Fronts of Solifluction Tongues, Vegetation Type: Grass Brinks.

The observation series made at Eskimonæs (Pls. 13 and 15) illustrates the course of temperature within Ecosystem N: The Body of Solifluction Tongues, Vegetation Type: Grass Meadows.

It may be pointed out at once (cf. pp. 41 and 47) that the Ella Ø series comprises an early snow-free, warm ecosystem occurring in the summer-warm inner fjord area in a hot summer. The Eskimonæs series likewise

comprises an early snow free, but cool (damp solifluction ground) ecosystem within the cooler outer fjord area in a cold summer. This, in the first place, causes the difference in the air temperature for the two series to be greater than normal between the inner fjord and the outer fjord areas, and in the second place the temperatures of the soil surface to show greater differences between the two ecosystems than their "systematic" difference would justify. Actually, however, the two observation series show the same relation between the meteorological temperature climate and the "plant" temperature climate.

The chief results of the observations in a biological respect are as follows:

1) The diurnal mean temperature of the soil surface intersects the 0°-line in the spring 3—4 weeks before the mean temperature of the air.

2) In the autumn, as far as can be judged from the rather deficient observations from that season, there is only an inconsiderable or no corresponding increased extension of the positive soil surface temperatures as compared with the air temperature. That is to say, the diurnal mean temperatures for the surface of the soil and the air intersect the 0°-line at about the same date.

3) During an essential part of the vegetation period the mean values of the soil surface temperature lie 5—7° C. above the mean values of the air temperature.

4) The daily temperature amplitude for the surface of the soil is up to 4—5 times as great as for the air (cf. Tables 39—41, p. 292 et seq). The amplitude of the air temperature is greatest in the spring, while that of the surface of the soil at that time is fairly limited, the abundant moisture from the melting of the snow having a levelling effect on the temperature; in particular it should be mentioned that in this period, unlike later in the summer, the nocturnal minima at the surface of the soil do not fall below the minima of the air temperature.

5) The more "favourably" the locality is situated as regards exposure, and the drier it is, the greater is the amplitude of day and night. Thus in the Ella Ø observations (Table 40, p. 293 et seq.) the twenty-four hour amplitude not rarely attained 35—40° C. or more, in a single case it even amounted to no less than 46°, at a maximum temperature of 49°. In the Eskimonæs observations (Table 41, p. 298 et seq.) the amplitude did not exceed 25° C., and the maximum temperature not 27°.

6) The hourly distribution of the soil surface temperatures (cf. Pls. 14 and 15) within both series of observations show that a relatively large part of the twenty-four hours is occupied by the low temperature intervals. For the Ella Ø series the temperature in about one-half of

the twenty-four hours during a great part of the summer ranges between 0° and 15° C.; only later in the summer do a greater number of the twenty-four hours show temperatures of 35—40° or more. In the Eskimonæs series about half the number of the twenty-four hours show temperatures ranging between 0° and 5°, and only in periods do a greater number of the hours show temperatures above 15°. During a period of about two months the minimum temperature does not, or but rarely, fall below zero.

7) The Eskimonæs observations show that at the time the mean temperature of the air definitely passes the 0°-line in the spring, the soil has thawed to a depth of c. $^1/_2$ m (cfr. Pl. 13).

As will be seen, the temperature conditions under which the plants actually live are far more favourable—at any rate within the two ecosystems to which the observations have reference—than might be expected, judging from the purely meteorological data. That the effect of the direct insolation is relatively violent, has no doubt some connection with the slight humidity of the air which seems to be characteristic of the climate of Northeast Greenland (cf. also IVANOF 1929). HARTZ (1895) has previously called attention to the great biological importance of the insolation in the area of Scoresby Sound.

On the basis of the exact observations on the temperature conditions for the two ecosystems, I shall attempt to give—comparatively—a brief summary of the temperature conditions within the other ecosystems (cf. Table 6, pp. 56—59) during the summer months.

The observations on Ella Ø, Ecosystem: Fronts of Solifluction Tongues, may be regarded as the "type" of the conditions prevailing within the ecosystems belonging to Thawing Group I. Eight ecosystems are referred to this group. Of these, E: Dry sunny Slopes, and G: Sheltered Precipices, are probably more favourably situated than the "type", as the water supply is inconsiderable, while the exposure is always favourable. Ecosystems B: Loess Fields, C: Disintegrating Summits, and D: Dry Bird Places, are likewise dry, but on the other hand the exposure is not always favourable, these ecosystems spreading to level ground also. Ecosystem A: Barren Ground, is actually fairly heterogeneous; as a rule it will be colder than our "type". Ecosystem F: Dry clayey Flats, has decidedly a colder plant climate than the "type", being chiefly associated with level ground. Moreover the soil is subject to slight solifluction in the spring, which will have a cold effect especially during the first part of the growth period.

It will appear from Table 6 that the dry ecosystems within Thawing Group I have an early flowering. On the other hand they are exposed to intense desiccation at the height of the summer and in the late

summer; the vegetation period is actually limited to spring and summer. The damper ecosystems have a later flowering and a longer prefloration period, which is no doubt to a less extent due to the cooling by the thaw-water in the spring than to the circumstance that the water supply favours a more "exacting" vegetation comprising species with a more prolonged vegetative development and a later flowering. However, the spring plants need not be entirely absent on that account; thus Fronts of Solifluction Tongues and Terraces, in particular, show tendencies towards a vernal aspect, chiefly of the *Draba* and *Carex* species.

The Eskimonæs observation series, Ecosystem: Body of Solifluction Tongues, may be taken as a "type" of Thawing Group II. The series, however, is not quite typical of the solifluction tongues, since this ecosystem, in accordance with its placing in that thawing group, is as a rule associated with localities covered with snow in the winter. As the solifluction tongue used for the observations had an especially open situation, the snow easily drifted away from it. However, the essential factor determining the temperature conditions is the damp soil exposed to solifluction. Apart from the deviation in the early spring caused by the complete absence of snow, the observation series may be regarded as normal to the particular ecosystem. As regards the actual summer temperature most ecosystems of Thawing Type II are generally more favoured than the earth tongues. Thus Ecosystem H: Moist sheltered Sunny Slopes, represents the most favourable conditions at all for the vegetation within the group. Apart from the somewhat later date for the melting of the snow, the temperature conditions are no doubt similar to those illustrated by the Ella Ø series. The prolonged supply of temperate surface water, however, no doubt contributes to modify the extreme temperatures. This ecosystem includes a number of southern species, and the prefloration time is of a relatively long duration. Ecosystem J: Well-drained Fields (Ericaceous Heaths), and K: Seasonally overflowed Ground (Alluvial Meadows) are well off as regards temperature because the upper layers of the soil are of such a nature that solifluction does not take place. Ecosystem Q: Knolly Bogs, is distinguished by the early flowering of the species. The swampy moss tufts forming the substratum of the phanerogamous vegetation are probably fairly much heated on account of their being elevated above the level of the "ground water surface". The tufts dry out fairly much later in the summer, and the vegetation ends its activity at an early date.

The ecosystems of Thawing Groups III and IV not only have a shorter period with favourable temperatures than the preceding ecosystems, but also generally a lower temperature—perhaps with the exception of Ecosystems M and T, Moist sheltered Sunny Slopes and

River-deltas respectively. On account of the considerable water content of the growth substrate, particularly high temperatures will hardly be reached. Yet small pools and moss swamps may sometimes be heated to an astonishing degree. Furthermore it should be mentioned that since the melting of the snow takes place at a time when the insolation is most intense, the temperature rises very suddenly. Thus WEGENER (1911) states that on June 25, 1907 (Danmarks Havn) he registered up to 16° C. in pools only some few metres from the thawing snow-fan.

A more detailed discussion of the individual ecosystems will only be of little interest here, as the content of species cannot be dealt with.[1]) The chief purpose of the considerations set forth above is to show that the series of temperature observations published here do not illustrate exceptional cases, but that they are an approximate measure of the temperature conditions under which a number of the East Greenland plant communities actually live.

The maximum depth of thawing at the observation spot at Eskimonæs was c. 1 m, as stated above. In the dry ecosystems of Thawing Group I the depth of thawing was at any rate up to c. 2 m. The great intensity of the thawing here is principally due to the inconsiderable water content of the soil, and secondly to the lack of a closer cover of vegetation (cf. e. g. ÅNGSTRÖM 1937). For the wet ecosystems (Thawing Groups III and IV) the maximal depth of thawing often seems to amount to about 50—75 cm. On north-facing slopes with no particular snow-covering, whose vegetation was entirely dominated by mosses and whose phanerogamous species rarely contrive to produce ripe fruits, the maximal depth of thawing did not exceed 15 cm. A number of temperature observations in such moss vegetations showed that the temperature there entirely kept pace with the air temperature. On slopes with a less marked northern exposure the moss vegetation may pass into a poor snow-patch vegetation, which must accordingly be assumed to have a smaller twenty-four hour amplitude than similar types of vegetation on level ground or in localities with a slight southern exposure where the snow-covering is thicker in the winter and melts late.

Attention should here be called to the striking degree in which the hourly distribution of the solar energy on ground exposed to the south and north respectively (see Fig. 5, p. 33) is paralleled in the twenty-four-hour course of the temperature on ground with a corresponding exposure (cf. Pls. 14 and 15)[2]). Gramme calories and degrees of centigrade are of course incommensurable units, but their agreement shows to what a great extent the local temperature climate of the surface of

[1]) For the content of species of the different ecosystems, cf. SEIDENFADEN & SØRENSEN, 1937, Table II, p. 112 et seq. and pp. 137—138.

[2]) For the detailed course of the temperature, cf. SØRENSEN 1935, Tafel 1.

the soil depends on the direct insolation. If we imagine the theoretical case that the vegetation of Northeast Greenland were to live in the temperature climate directly indicated by the air temperature, hardly very much would be left after a number of years except the poorest vegetation of moss and the most easily satisfied snow-patch plants, resembling that now found on slopes with a northern exposure. The generative rejuvenescence within the existing phanerogamous vegetation on the north-facing slopes is no doubt chiefly effected by seed dispersal from localities more favoured as to temperature.

## The ecological significance of geographical latitude within Northeast Greenland.

The observations recorded above are derived from the central part (c. 73°—74° N. lat.) of the area of Northeast Greenland dealt with here. The question now arises with what approximation these observations may be assumed to be true of more northern or more southern latitudes of Northeast Greenland. In view of the diminutive difference in the air temperature curves for Scoresby Sund and Danmarks Havn it is indeed immediately surprising that such a large number of the species, more than one-fourth of the number of species of the area, have their northern limit between these extreme points.

*Saxifraga oppositifolia* flowers about a fortnight later at Danmarks Havn than at Scoresby Sund, which difference in time indicates the approximate retardation of the vernal aspect as a whole (cf. p. 63). The retardation of the later phenological seasons is much greater. The twenty-four hour irradiation energy at midsummer is roughly the same for all latitudes within the Arctic zone (see p. 31), but the local effectivity of this insolation will decrease northward in localities with a southern exposure, an increasingly large part of the insolation energy being withdrawn from the south-facing localities in favour of the north-facing ones. Only on level ground will the effectiveness of the insolation and its influence on the local temperature conditions remain the same for all latitudes. It is obvious that the twenty-four hour amplitude of the local temperature will be influenced by the distribution of the irradiation over the individual hours of day and night, and that the fluctuations will be less—the amount of insolation being otherwise equal—under conditions with midnight sun than when day and night alternate.

Let us consider the theoretical case that the mean temperature of twenty-four hours at the surface of level ground in the spring at Danmarks Havn and at Scoresby Sund is for instance 2° C. Where the

midnight sun shines (Danmarks Havn), the fluctuations will be inconsiderable, that is to say that during the greater part of the twenty-four hours the temperature will be about the mean; in localities where day and night alternate (Scoresby Sund) the fluctuations will be great, that is to say, only during a small part of the twenty-four hours will mean temperatures prevail, while during the greater part of the twenty-four hours the temperature will be either comparatively far above or far below the mean. If, quite arbitrarily, we reckon the lowest temperature for the life activity of *Saxifraga oppositifolia* (manifested in the expansion of the flowers) at 1°, it will be evident that at Danmarks Havn (on level ground) *Saxifraga* will have a greater number of effective working hours during the day and night than it will have at Scoresby Sund at the same daily mean temperature. As the temperature limit to growth of the arctic spring plants is indeed very low, and as the optimum temperature is probably likewise low (see LUNDEGÅRDH 1925, pp. 381—82), we may here have a plausible explanation of the fact that the vernal aspect, in relation to the total insolation, sets in relatively early the farther north we go. The spring flora on level ground, or in other words the flora of the snow-free hill-tops, will be relatively favoured northward, while the summer flora of the slopes with a southern exposure will be relatively more poorly situated the farther north we go, viewed in relation to the total insolation. There can then hardly be any doubt that the soil surface temperatures of the summer will be increasingly lower northward as compared with those of more southern regions, the more favoured (exposed to the south) the ecosystem is to which the observations have reference. This will have the conspicuous plant-geographical consequences that 1) the later aspects to the northward will be retarded to a constantly increasing extent as compared with the first vernal aspect, and that 2) the possibilities for existence of the southern species, which are associated precisely with ecosystems whose temperature conditions are especially favourable on account of the exposure, will decrease northward at an even more rapid rate than the normal deficit of the total amount of insolation energy in itself would suggest.

## The awaking of the vegetation in the spring in relation to temperature and thawing time.

As stated above, the mean temperature of the surface of snow-free ground reaches zero 3—4 weeks before the temperature of the air. This explains, on the one hand, the assumption of earlier times of an almost instantaneous expansion of the arctic spring flora, as it was taken for granted that the plants remained in their winter dormance

as long as the mean (meteorological) temperature was still below zero (cf. e. g. OSTENFELD 1923, p. 246, LUNDEGÅRDH 1925, p. 98). On the other hand it is not a matter of course that the awaking of the plants takes place at the same time as the mean temperature of the surface of the soil passes zero, all the more so since plants in no case react to mean temperatures. Theoretically, however, there is nothing to prevent that the growth may start even earlier. From the curve showing the hour values for the Eskimonæs observations (Pl. 15) it will be seen that already the days of April 30th and May 1st had four hours of positive temperatures. On gravelly south-facing slopes the soil had thawed to a depth of about 10 cm as early as April 30th, and *Bombyx* larvae were seen to move about on snow-free *Dryas*. The observation that for instance some *Cyperaceae* and *Gramineae* (cf. p. 81 and p. 87) were in distinct growth, and for instance *Melandryum affine*, *Sedum roseum*, and several species of *Draba* were in pollen formation as early as May 25—30th, shows that plants are capable of utilising the positive local day temperatures even though the night temperatures are still below zero. In the germination experiments mentioned in Chapter VI several species had germinated on June 7th, and the life-functions preparatory to the germination may probably be assumed to have started at least eight days previously. Germination had taken place though the paper capsules enclosing the seeds were constantly frozen during the experiments for almost half of the twenty-four hours. Several species, however, especially the southern ones, did not germinate till a later date, after the greater number of or all the twenty-four hours had positive temperatures (cf. Fig. 25 and Fig. 26, p. 231).

The snow-patch plants, it is reported, may begin their growth beneath the snow. That this takes place in the Alps (CHRIST 1879, BRAUN 1913) and in northern Norway (HOLMBOE 1912) is evidently accounted for by the fact that the soil beneath the snow-covering is not frozen in the winter (RÜBEL 1925). The conditions are, however, different in the Arctic, where the soil is always frozen below the snow (cf. p. 45). KIHLMAN (1890), it is true, reports from Lappland that the snow melts from below and that the temperature may rise to a certain height in the cavity. The same may be observed in Northeast Greenland on level ground with a fairly scanty snow-covering. The phenomenon occurs where the layer of snow has a crust of ice. The effects of the insolation make themselves felt through a layer of snow of c. 20—30 cm (WEGENER 1911, p. 300, RICHTER 1926), and the snow may then melt from below beneath the crust, which remains like the windows of a hotbed. If the delicate pane work, on being trod on, is broken in a single place, the whole construction will collapse like a house of cards in a greater and greater circle, spreading like the waves from a stone

thrown into the water. Even though the temperature may rise beneath the icy roof, the phenomenon is doubtless of diminutive ecological importance; for the snow always melts very quickly when its thickness does not exceed that with which we are concerned here. Owing to the insolation the melting of the snow here chiefly takes place at the surface of the soil, irrespective of whether or not a pane work of ice is formed (cf. RICHTER l. c.). In the actual snow-patches, where the snow has been blown hard and it is of greater thickness, the snow melts relatively more slowly, and the melting takes place from above. On account of the cementing effect of the oozing thaw-water a regular crust of ice is formed prior to the actual melting, in which crust the above-ground portions of the vegetation are embedded. Thus as regards Northeast Greenland it must be maintained that the plants do not, or only quite exceptionally, start their growth beneath the snow; *Saxifraga oppositifolia*, for instance, is apparently entirely shrunk when it thaws out of the snow, and the leaves do not become turgid till after about a week. Even the snow-patch plants do not commence growth till a number of days after the melting of the snow, which can be readily ascertained, the dust from the melting snow forming like a film on the plants. At first, after the melting of the snow the grey coating of dust lends to the vegetation an appearance as if it were dead.

In general the life activity of the plants seems to commence at about the same time as the mean temperature of twenty-four hours at the surface of the soil passes zero. It should be pointed out here, however, that this can only take place on account of the wide twenty-four hour amplitude, owing to which the actual temperatures at this time rise considerably above zero during several of the twenty-four hours. The negative night temperatures accordingly do not seem to have any essentially hampering influence on the growth as a whole, but of course it means a shortening of the "working day". However, this furnishes no evidence that the temperature threshold for the visible activities of life (growth) occurs precisely at zero. A constant temperature about zero would hardly result in the germination even of the seeds most easily satisfied as regards temperature, or in a continued growth of seedlings or adult plants.

However. the plants do not awake equally early, for instance it may be mentioned that *Carex rupestris* awakes before *Carex rigida* under the same external conditions. *Pedicularis hirsuta* and *Pedicularis lapponica* awake before *Pedicularis flammea* when the three species grow in company, which is occasionally the case. Furthermore it has been ascertained that *Eutrema Edwardsii* commences growth sooner after the melting of the snow than all the other species in company with which it usually occurs.

## The nature of the resting period viewed in relation to the sequence of organic development of the plants and to their habitats.

While the time for the awaking of the plants may thus with a certain approximation be said to be directly correlated with the rise of the temperature in the spring or after the melting of the snow, a corresponding universal rule for the end of the vegetation period can hardly be given. In fact, it is impossible in most cases to say at what time a plant is "ready" to pass into its winter dormance. The circumstance that at a relatively early date (August) the buds of many species have developed to the same degree as in the wintering state, in connection with the fact that a number of species actually wither long before the winter frost sets in, shows that the growth is often interrupted before the temperature conditions put an obstacle to its continuation. As regards the winter-green species, however, it is impossible to say anything definite about the time of the end of the growth. The end of the growth need not, of course, mean the seasonal suspension of the life functions. In the course of the last month before the winter sets in there seems generally to be a lively storing of reserve substances, and when the winter sets in, all the wintering organs are as a rule abundantly filled with starch. Thus winter-green leaves also function extensively as reservoirs of nourishment (cf. KERNER 1869, p. 36, above-ground bulbs).

As regards the alpine vegetation GRISCH (1907) has advanced the supposition that the resting period of species growing on snow-free soil is of an autonomous character, whereas this is hardly the case with the snow-patch plants. RÜBEL (1925) has demonstrated experimentally that the alpine snow-patch plants lack an autonomous rest, or that at any rate it is of very short duration. In Chapter V, above, attention has been called to features relative to the sequence of organic development of the Northeast Greenland species. The development of the species of the snow-free localities is to a greater extent than that of the snow-patch plants often subject to a pronounced periodicity in the initiation of the organs, and in such species the winter rest is probably of an "autonomous" character. It should be noted here, however, that at the same time as their growth ceases, the soil in the habitats of these species is as a rule subject to a high degree of desiccation, which is not rarely so violent that it would probably cause a general cessation of growth, apart from the autonomous tendency of the species. At any rate it has been ascertained with certainty that desiccation not rarely interrupts the development at a relatively early date, even in species which in more favourable habitats show an "autonomous" interruption of the

growth. As examples of such species I may mention *Arnica alpina* (cf. Pl. 9, Figs. 21—24) and *Melandryum triflorum*. All woody plants have an autonomous resting period or at any rate an autonomous interruption of the growth.

Species with an aperiodical initiation of the organs no doubt as a rule lack an autonomous resting period, the growth, at any rate of the vegetative organs, continuing steadily at the rate which the prevalent temperature conditions permit. The winter resting period of such species seems to be imposed by the low temperatures alone. In certain species, however, there seems to be an inhibition of the growth of the floral organs which does not coincide in time with the final temperature fall of the autumn (cf. also MÜLLER-THURGAU & SCHNEIDER-ORELLI 1912). Aperiodicity is closely correlated with a green state during the winter and is to a certain extent associated with species occurring within the higher degrees of snow-covering. Thus the arctic flora shows agreement with the alpine one in many respects. However, the correlation between snow-covering and developmental type is not complete. Thus one of the most typically aperiodical species, *Braya humilis*, always occurs on ground free of snow or but slightly snow-covered in the winter. The same is the case with *Campanula rotundifolia*, which behaves almost like an aperiodical species. However, as regards this species we cannot disregard the possibility that it is prepared by nature for a rhythmical alternation of growth and rest, but that its genotypical growth period is of such an extension that under the climatic conditions of East Greenland it is constantly interrupted every year by the frost before the tendency towards an autonomous rest contrives to make itself felt. In that case the developmental rhythm of the species is not in harmony with the rhythm of the climate (cf. SCHARFETTER 1922).

However, in the greater number of the species of Northeast Greenland a cessation of the growth may be demonstrated with greater or smaller certainty, at any rate as regards the floral organs, and this cessation is of an apparently autonomous character. But in many species the autonomous resting period seems to be of short duration. Thus it has turned out that a number of species, carried in a living state to Denmark to be planted there in the month of September, continued their growth and flowered in the same autumn. However, no too great conclusions should be drawn from this, as it is altogether doubtful whether an actual rest had set in before the plants, during the transport, were influenced by the higher temperatures.

Experiments on cultivation of the species of Northeast Greenland in the Danish climate for elucidation of the nature of the periodicity have not led to any great results so far, the majority of the species thriving poorly and having suffered extensively from attacks by omni-

vorous vermin. However, it has been possible to keep some few species under culture for several years. *Potentilla nivea*, which in the Arctic seems to end its growth at an early date, under culture continues its growth and flowering during a great part of the summer, though evidently with periodical interruptions of the flowering; it withers in the early autumn. *Potentilla rubella* retains its aperiodical growth. It winters in a green state, which is hardly the case in a corresponding degree in its native country. Species of *Draba* flower several times in the course of the summer. Finally it may be mentioned that *Salix arctica* sheds its foliage as early as the beginning of June, to start a new leafing after a short resting period. Accordingly the experiments seem to suggest that the interruptions of growth are of an autonomous character, and that the autonomous resting period is only of a short duration.

## Frost resistance of developing reproductive organs. Wintering of aperiodical species.

The question as to whether flowering and fructifying shoots are capable of surviving the winter frost as "naturlige Konserver" (naturally preserved objects) (HARTZ 1895, p. 184) and continue their development from one year to another does not seem to have found its final solution so far. The classical example is KJELLMAN'S *Cochlearia* plant from Pitlekaj, which, overtaken by the winter frost in the midst of its life's summer, continued its flowering next spring as if nothing had happened (KJELLMAN 1883, p. 480). However, KJELLMAN'S observation has been doubted. SIMMONS (1906) records from the North American archipelago that *Cochlearia* is often found to flower in the autumn, but that wintering of the inflorescences does not take place; and BRAUN (1913) on the basis of KJELLMAN'S records of time and place, is of opinion that a misrecollection must have taken place. According to my observations of the species in Greenland, the flowering main axis itself does not survive the winter, whereas lateral axes springing from its base may flower after wintering (see further p. 109). RESVOLL (1917), on the basis of observations on the Scandinavian snow-patch plants, has furnished other examples in support of the assumption that plant organs in an advanced stage of development continue their growth after wintering, and emphasises this as a means which the plants may employ to render themselves independent of the effects of a too short summer. In this respect, however, the examples are of a limited value, as they chiefly comprise viviparous species. In the three cases (l. c. Fig. 8, p. 80, viviparous grasses, and Fig. $9_1$, p. 82, *Saxifraga cernua*) we are distinctly concerned with a continued growth of bulbils which have not become detached from the withered mother axis, and in the fourth case (l. c.

Fig. $9_2$, p. 82, *Cardamine pratensis*) with young rooting rosettes developed, it is true, on the still fresh leaf rachis. As, however, the leaves of this species normally winter in a green state, the plant figured must be regarded as normal. In Northeast Greenland the root formation of such young plants springing from the leaf rachis takes place now in the first, now in the second year, according to the time of their formation. Finally *Salix herbacea* (l. c. p. 60) is mentioned as an example of a two years' fruit development, it having been ascertained that seed capsules open the year after their formation. In this example I can only see an evidence of a retarded seed dispersal.

It has been stated above (p. 202) that purely aperiodical species are fairly numerous within the flora of Northeast Greenland, and further, that the aperiodicity should possibly be regarded as an adaptation to a short period with favourable temperatures, the character being chiefly associated with the northern species occurring for the most part in localities thawing late. In a great number of the particular species the effectiveness of this adaptation is chiefly limited because the wintering of the floral organs which have developed beyond a certain stage cannot be completed. As suggested by RESVOLL (l. c.), the vegetative reproductive organs, bulbils and the like, are evidently especially resistant towards the low temperatures of the winter. Thus it has turned out (cf. p. 86) that the bulbil panicles of the viviparous *Poa alpina* seem to tolerate wintering at any stage of development, whereas this is not the case with the floral panicles of the normally fructifying *Poa alpina* (cf. Pl. 3, Figs. 28 and 31). Otherwise, however, there seems hardly to be any pronounced correlation between vivipary and aperiodicity, the viviparous species, like the seed-producing ones, comprising only a minority of aperiodical species. Of the viviparous species, in addition to the aforementioned *Poa alpina vivipara*, *Saxifraga stellaris comosa*, too, is aperiodical, and its heads of bulbils may winter in all stages of development. *Cardamine pratensis* is more or less aperiodical in its vegetative development; as regards the floral development a certain periodicity seems to be maintained. However, the material of flowering plants examined was too sparse to allow of a final decision of the question. (The cases of "vivipary" in *Caryophyllaceae* mentioned on p. 102 are likewise associated with species whose organic development is not strictly periodical). *Saxifraga cernua* and *Polygonum viviparum* are typically periodical with autonomous rest. The grasses *Festuca vivipara* and *Poa alpigena colpodea* behave like the majority of the *Gramineae*, the wintering stages being constant to a certain extent.

The maximal developmental phase for a successful wintering of the aperiodical species is altogether variable. Within the families *Saxifragaceae*, *Caryophyllaceae*, *Cruciferae*, and *Rosaceae* we find the most pro-

nounced power of resistance in floral organs in a fairly much advanced phase of development, associated with different degrees of aperiodicity. In accordance with this, the flowers of the early spring are essentially constituted by these families. The only species within these families—and within the flora of Northeast Greenland as a whole—in which floral and fructifying organs in any stage of development have been found to be capable of wintering without suffering any damage, and of continuing and completing the development after wintering, is *Braya humilis*. And it is not only capable of doing so, but the phenomenon occurs so frequently that it may be recorded as normal to the species. Fig. 11 (p. 108) shows a plant in the wintering state, in which an infructescence has started its development two summers previously, and finished its development in the summer just elapsed; another is developing, to complete its development the succeeding year in a similar way as the infructescense of the mother shoot generation. The power of the plant to resist the low temperatures of the winter in all growth phases is all the more impressive since it generally occurs in exposed localities but sparsely covered with snow in the winter. In consideration of this fact the strange impassibility of the plant to cold in the winter is—logically—entirely superfluous, and its paradoxical negligence of the climatic seasons cannot be regarded as an adaptation to a particularly short summer. In the habitats preferred by the species it has more than sufficient time to pass through all the stages of development within one and the same summer; this is also distinctly demonstrated by the fact that according to the more or less favourable external conditions it may produce altogether one, one and a half, or two shoot generations yearly. *Braya Thorild-Wulffii* and *Draba crassifolia* evidently possess a power of wintering in highly developed stages similar to that of *Braya humilis*; however, the material of these species available for examination was too sparse; yet certain developmental stages seem to be damaged by the frost.

Even though KJELLMAN's observation of the wintering of flowering *Cochlearia* has not been confirmed later, the case of *Braya humilis* shows with indisputable certainty that the type at any rate does exist and that the phenomenon is accordingly not beyond the limits of possibility.

### Annual duration of the growth period.

The period with favourable temperatures, that is to say the period in which the daily mean temperatures are actually above 0° C., for the most favoured ecosystems in central Northeast Greenland has a duration of about four months (HARTZ (1895) states 5—6 months for the interior of Scoresby Sund). The lower limit for the less favoured ecosystems,

apart from the actual snow-patches, must be fixed at about two months (the snow having melted about July 1st). Localities with an essentially shorter period with favourable temperatures than two months harbour a more or less marked snow-patch vegetation. The lower limit for the "summer" of the snow-patch vegetation cannot be stated. Such a limit must actually be said not to exist, considering the unequal thawing of the snow-fans in the individual years.

The question then arises how long the plants actually take to accomplish their yearly growth, flowering, and fructification. A normal, harmoniously ended growth season, even for the ecosystems harbouring the species which are the least exacting in regard to temperature, can hardly be accomplished in a shorter period than about two months. Such a quickly completed development may be found on the one hand in the snow-free dry ecosystems, whose active period ends by midsummer, and on the other hand in the ecosystems which are the last to melt, the snow-patches, whose active period begins at midsummer. It is not without interest to ascertain that a number of species which are especially modest as regards the length of the growth period, may exhibit a surprising power of adaptation as regards other growth conditions also. Thus certain species of the dry hillocks are often found to spread to the wet snow-patches, where, however, they are as a rule but sparsely represented. As examples of this the following species may be mentioned: *Saxifraga oppositifolia*, *Saxifraga cernua*, *Draba cinerea*, *Draba subcapitata*, *Minuartia rubella*. Furthermore *Saxifraga nivalis*, whose snow-patch form, *var. tenuis*, however, seems to be separated systematically from the main species.

The statement of two months as the minimum time for the development of a plant community as a whole does not mean that some few species do not complete their development in a shorter time. However, at any rate hardly any species will be able to accomplish a harmoniously ended seasonal development in less than one and a half months. It is especially the northern species, occurring chiefly in snow-free localities or in localities with a prolonged snow-covering (cf. Table 10, p. 189), which are content with so short a vegetation period. The greater number of the species of Northeast Greenland no doubt require a period of development of about three months, and to certain, especially southern, species this will not be sufficient in the long run; that is to say, fructification does not take place unless the vegetation period is about four months, and even in that case only under the most favourable temperature conditions realisable at all in these latitudes.

The period of development for the therophytes, *Koenigia* and *Euphrasia*, is estimated by GELTING (1934, p. 298) to be (at least ?) 4—5 weeks. If more strictly tested, this estimate will no doubt prove

to be too low; according to my observations 6 and 8 weeks for *Koenigia* and *Euphrasia* respectively seem to be the absolute minima under the temperature conditions of Northeast Greenland.

For a large number of the perennial species the period with favourable temperatures may, at any rate for occasional years, be much reduced without the plants evidently suffering other damage than a universal debilitation and the absence of flowering next year. In cold summers the snow-patch plants may undoubtedly now and then remain buried in the snow. THORE C. E. FRIES (1913) records from Lappland that *Salix reticulata* and *Salix herbacea* sometimes pass the summer beneath the snow without suffering any damage. In the cold summer of 1937 I dug out of the ice at the edge of a compact show-fan at Scoresby Sund at the end of August, when the melting of the snow was about to cease, the following fifteen species: *Carex Lachenalii*, *Festuca brachyphylla*, *Phippsia algida*, *Luzula confusa*, *Cerastium alpinum*, *Sagina intermedia*, *Silene acaulis*, *Draba lactea*, *Oxyria digyna*, *Polygonum viviparum*, *Ranunculus pygmaeus*, *Salix arctica*, *Saxifraga cernua*, *Saxifraga nivalis tenuis*, and *Saxifraga rivularis*. There is hardly any doubt that in case of a more effective melting of the snow in a subsequent year they would have been capable of continuing their growth after two or perhaps several years' dormance due to the cold.

## Microphenology in relation to nutrition conditions and to ecological temperature climate.

The pronounced correlation between the time for the incipient differentiation of the floral organs and the time of flowering (see Fig. 24, p. 214) suggests that the points of departure for the evident phenological manifestations of the plants, divergent as to time, lie buried far back in the ontogeny of the plant. In the majority of the Northeast Greenland plants the first morphologically recognisable preparations for the flowering antedate the flowering proper a whole year or an even longer time. Thus the flowering time is not only determined by the external conditions in the flowering year, but by an interaction between these conditions and the specific rate of growth of the species in connection with "das Saldo vom verflossenen Jahre" (MIDDENDORFF 1864, p. 660). This last-named concept is very comprehensive. The invigoration stage of the shoot, in many species extending over a more or less arbitrary number of years prior to the flowering, suggests that the state of nutrition of the plant as a whole must be of a certain importance for the transition of the shoot from the vegetative to the "floral" state. Some regulating power seems to prevent the formation

of flower buds as long as the shoot is too weak to accomplish the flowering and fructification. But how is the state of nutrition in general in the arctic plants? Opinions differ greatly in that respect. MÜLLER (1928) noted a satisfactory production of matter at low temperatures in plants on the island of Disko, West Greenland. According to KOSTUTSCHEV et al. (1930) the production of matter of the arctic plants is even startling. KOSTUTSCHEV summarises his results as follows (l. c. p. 168): "Die gleichmässige Produktion der organischen Stoffe während des ganzen Tages bedingt grosse Tagesausbeuten, die wahrscheinlich als die primäre Ursache der Kürzung der Vegetationsperiode verschiedener Pflanzen im arktischen Gebiet anzusehen ist."

However, in his investigations on "Growth and Survival of Plants in the Arctic" (Kangerdlugssuak, East Greenland, about 68° N. lat.) WAGER (1938) arrives at the result (l. c. p. 408) "that any plant growing in the Arctic is near to its subsistence level for carbohydrate production" on account of a too small amount of light and a too short period of assimilation. WAGER came to this surprising result because in an open "fjaeldmark" he noted a yearly death rate of 50 per cent among young plants younger than five years, for, as he says (l. c. p. 409), "It is unusual to have an association which is apparently stable and which depends on the maintenance of an unchanged average survival rate over long periods of time." And further: "Such a situation is essentially different from that in a closed association where the death rate of a species is controlled by the intensity of ecological competition."—I fail to see any reasons compelling us not to consider the death rate of a species in a "fjaeldmark" from the same point of view as in a closed association, all the more so since WAGER observed no injurious influence of external directly mechanically or physiologically acting factors. It seems to me, therefore—in contrast to the view held by WAGER—that the open vegetation of the fell-field, whose equilibrium is maintained by the constant death rate of the species, in itself strongly suggests that it is the competition of the root in connection with a limited access to water and accordingly to the mineral nutritive substances which is here the controlling factor of plant life. This needs not necessarily be in conflict with WAGER's view: that the high death rate among the young plants is correlated with a too great loss by respiration on account of a high root/top ratio as compared with adult plants. The access to light is the same for all plants within the open vegetation, disregarding size and age categories. However, the same does not apply to the access to water, for, as WAGER himself says (l. c. p. 408), "Any slight water shortage which there may be will be much more serious for small plants with a root system penetrating at the most about two inches into the soil, as it is the upper layer that will tend to dry up while the deeper layers

will remain damp." It will therefore be most natural to seek the primary cause of the weakened constitution of the young plants as compared with the adults in an insufficient access to water. Since (WAGER l. c. pp. 405—06) "the adults are large and healthy and not noticeably smaller than the plants of the same species growing in the neighbouring closed associations or in Iceland or in Great Britain," it seems to me that WAGER's investigations do not furnish a sufficient basis for the assumption that the arctic plants *en bloc* are near their subsistence level for carbohydrate production.

The fairly prolonged invigoration stage before the flowering of the arctic plants must be considered in view of the fact that their reduction in size as compared with the plants of the temperate regions is largely restricted to their vegetative parts, more precisely to organs serving in the assimilation of carbon dioxide, whereas the reproductive organs and the seed production per flower or per inflorescence are not subject to reduction to a similar extent. As is commonly known from early times, the arctic plants are, popularly speaking, large-flowered, that is to say, they have relatively large flowers or abundantly flowering inflorescences. Thus the accomplishment of the flowering of the shoot and the fructification of the arctic plants requires a comparatively large amount of concentrated energy.

While, as stated above, there are hardly any indications that the carbohydrate nutrition of the arctic plants is insufficient, there seems on the contrary to be every reason to assume that the nutrition of nitrogen is not of the same optimal character. The comparatively violent manifestation of the vigour of the plants as a reaction even to scanty supplies of nitrogen food would be impossible if the nitrogen nutrition were not under normal conditions very insufficient. In illustration of this phenomenon I shall quote here LUNDAGER's observation at Danmarks Havn, which is in full accord with my own observations: "Around skulls and other parts of skeletons, beautifully green oases in the surrounding desert are often to be seen, even from a distance; and in this relative luxuriance may grow vigorous tufts of *Melandrium triflorum* and *Hierochloe*, as also *Cerastium* and *Stellaria longipes* with elongated internodes, the thick-leaved *Saxifraga cernua*, and the inevitable *Polygonum viviparum*. A similar though less luxuriance is sometimes due to the manure around lemming-holes." (LUNDAGER 1912, p. 389).

WAGER (l. c.) does not believe that the nitrogen nutrition is essentially under-optimal: "On the other hand, it must be admitted that an increased supply of nitrogen to arctic plants does cause a more luxuriant growth in the course of time; but the same effect is observed in temperate regions. Further, Summerhayes & Elton (1928) state that in Spitzbergen this nitrophilous vegetation is not a mere development

of the normal "fjaeldmark" plants but is a special group of a more sub-arctic type of plant, and it is to be presumed that such plants can grow more strongly in favourable localities than the arctic types. ... Summing up it may be said that in the opinion of the writer nitrogen shortage is probably one of the factors contributing to the slow growth rate of the "fjaeldmark" plants, but it is believed not to be of major importance." (WAGER 1938, p. 406).

I quote this statement *in extenso*, considering that the observations made by the Spitzbergen investigators throw much light on the nitrogen problem in the Arctic and clearly show that it is precisely of major importance. The supply of nitrogen proves to be a plant-distributional factor of a high order, as it decides whether species of the higharctic or the subarctic type obtain the preference. "Der ökologisch massgebende Faktor ist als Regel entweder ein Faktor im Minimum oder in schädlichen Überfluss." (LUNDEGÅRDH 1925, p. 377). LUNDAGER'S observations as compared with those of SUMMERHAYES & ELTON do not indicate that the cause of the disappearance of the higharctic species from the manured localities is due to a surplus nitrogen nutrition, but more probably to the very common circumstance that where the physical conditions furnish possibilities of existence for the southern species, they will oust the higharctic species by their shadows owing to their tall growth (cf. also SCHMUCKER 1937). From what has been stated above we may conclude 1) that, growing under the same temperature conditions, the northern species are adapted to a lower nitrogen equilibrium than the southern ones, but that 2) the supply of nitrogen, even for the northern species, is normally under-optimal.

As regards the floral development of the shoot KLEBS (1918, p. 146 et seq.) distinguishes between three successive stages: 1) "Der blühreife Zustand", 2) "Die Blütenanlagen", and 3) "Die Bildung des Infloreszens". The relation between the passing of the shoot into the state "ripe" for flowering and its state of nutrition has not been finally settled. Intense illumination, low temperatures, and insufficient supplies of mineral food have long been known as agencies furthering the inclination of the plants to flower (e. g. SACHS 1863, 1865, KRAŠAN 1882, MÖBIUS 1897, LOEW 1905a, 1905b). KLEBS (1913) strongly emphasised the C/N ratio of the plant as decisive for the setting in of the state when the plant is ready for flowering. An abundant accumulation of assimilated matter in connection with a poor nitrogen nutrition is supposed to bring about a flowering. Thus all outer as well as inner conditions for flowering seem to be complied with in a special degree as regards the arctic plants. A closer study of the date for the first phases of the floral development would seem to support KLEBS's theory. In a great majority of the plants of Northeast Greenland the first signs of an approaching

flowering (the succeeding year!) appear immediately at the start of growth in the spring. Whether the state ready for flowering has been reached already in the autumn or it is not reached till the spring, cannot, of course, be decided. In some cases, however, the cone of growth is "floral" already in the autumn. In plants growing on dry soil—these plants are generally not winter-green—the C/N ratio must be supposed to be particularly high towards the end of the summer, when the assimilation is getting near its end at the same time as the water (and mineral food) intake diminishes on account of the desiccation of the soil. In winter-green species—which chiefly grow in damper soil—the C/N ratio must be assumed incidentally to reach a maximum in the early spring, since the green leaves must be assumed to be capable of commencing their assimilation immediately after the melting of the snow, while the frozen soil still prevents a normal intake of water (cf. GELTING 1937, p. 152 et seq.). Thus many of the arctic plants might at first sight seem to behave in accordance with KLEBS's theory. However, the theory has not been supported by experimental investigations in recent years (e. g. PURVIS 1934, POLSTER 1938), quite the contrary is the case (cf. also JOST 1912). According to these investigators, a high C/N ratio seems more probably to be a consequence of the transition of the plant to the floral stage than to cause this stage to set in.

In fact there is much to indicate that the arctic plants are constantly under the influence of a high C/N ratio. MÜLLER (1930) has shown for *Sinapis* plants that the mass of leaves is more reduced by nitrogen shortage than the mass of root and stem. The ratio: dry substance of root + stem divided by leaf area, is higher in the plants in want of nitrogen than in plants with a normal nutrition (cf. further SCHAFFNIT & VOLK 1928). A rather violent development of root and stem (mesocorm) as compared with the leaves is characteristic precisely of the arctic plants (cf. GELTING 1934, p. 298 et seq.). It is a fact long observed by gardeners and agriculturists that vegetative development and flowering are in some degree antagonistic to each other. This view has been maintained from scientific quarters also in recent times (ILLICHEVSKY 1929). Another view, namely that the vegetative growth and the flowering are two parallel phenomena, each of them following its own laws in relation to the external conditions, has in recent times found adherers, being supported by experimental investigations. Already DIELS (1906) in his inspiring work "Jugendformen und Blütenreife im Pflanzenreich" expresses himself in favour of a "weitgehende Selbständigkeit der generativen Reife dem vegetativen Wachstum gegenüber" (l. c. p. 21), and as regards the passing of the plant into the floral stage he says: "Jede günstige Constellation vermag sie (die Blütenreife) herbeizuführen, sollte auch die vegetative Entfaltung noch

geringfügig, das Alter noch jugendlich, sein" (l. c. p. 22). These views were strongly supported by GASSNER's pioneer work (1918) on the character of the life duration in summer and winter annuals, in which he claimed a sharp distinction between ecological cardinal points and physiological optima, a view which LUNDEGÅRDH (1925, pp. 139—140) expressed as follows: "Ganz allgemein scheint der Satz zu gelten, dass die [thermischen] Kardinalpunkte für die verschiedenen Wachstums- und Organbildungsvorgänge nicht zusammenfallen."

Our knowledge of the influence of the temperature and the temperature climate on the vegetation and, in the last instance, on the fundamental life functions of the individual plant species is still fairly limited. There is here a vast working field where physiology and ecology may meet. LUNDEGÅRDH even long ago recommended its cultivation.

The relations between the temperature climate and the yearly course of development of the vegetation is treated quite summarily by LUNDEGÅRDH and sketched out provisionally by a division of the temperature climate into four periods which almost coincide with the seasons of the year (l. c. p. 150): "1) Wachstums- (Frühlings-) Periode, 2) Assimilations- (Sommer- Herbst-) Periode, 3) Fruchtbildungs- (Herbst-) Periode, 4) Ausreifungs- (Winter-) Periode." On the background of well-founded conjectures as to the reality of the thermic cardinal points and of the assumption as to ecologically delimited periods of the temperature climate the developmental-morphological and phenological characteristics of the arctic plants stand out in a fresh, or at any rate a sharper light: Referring to the description given above (p. 219) of the contemporary development of the successive shoot generations in the higharctic plants, attention should be called to the fact that a special definition of the cardinal points characteristic of the different life functions is *a priori* impossible, as successive shoot generations are at the same time in different stages of development. The differentiation of the flower buds, the flowering, fructification, and assimilation are concurrent. In the aperiodical species, in particular, there is some confusion, all life functions taking place, all phases of development being completed, all courses of development being accomplished apparently irregularly throughout the whole growth period. Thus all LUNDEGÅRDH's temperature-climatic periods are united here into one single varied multifarious unit, the active period.

Whether this type of development of the shoot generations is of a genotypic or a phenotypic character, it seems to be closely correlated with a temperature climate like that of Northeast Greenland, that is to say, a climate of a continental character with a very short period with favourable temperatures. For comparison it may be mentioned here after WERTH (1906) for Kuergelen, which has a cold-oceanic climate

(mean temperature for the coldest month 0.4° and for the warmest 6.5° C.) that nearly all the species have a fairly prolonged development of leaves, either in the autumn after the flowering and fructification or in the spring before the flowering; that is to say, a more distinct separation between the vegetative and the floral phases than in the plants of Northeast Greenland. SKOTTSBERG's investigations (1909, 1912) on the vegetation of other oceanic regions in the Antarctic point in the same direction.

## Induced acceleration of the sequence of development. Thermoperiodic adaptation.

In this connection mention should finally be made of the modern Russian line of research concerning the relation between development and temperature, which is actually a direct pursuance of the investigations along the lines pointed out by GASSNER (l. c.). Under the guidance of LYSSENKO and more especially LJUBIMENKO surprising results have been arrived at. The theoretical starting point for the investigations is (WHYTE & HUDSON 1933, MAXIMOV 1935) that growth characterised by accumulation of matter and cell division on the one hand and development characterised by cell differentiation on the other, are two independent phenomena. "Reproduction is not to be regarded as a stage subsequent to vegetative development, but as a distinct process occurring independently of growth." (MAXIMOV 1935, p. 19).—"Owing to the nature of the changes occurring in development it is possible to accelerate or retard them long before the time of the actual morphological differentiation which they evoke, and this is why the phenomenon is referred to as "induction"" (MAXIMOV, l. c. p. 19). By subjecting germinating seeds or shoots in their first stages of development to the influence of low temperatures all the shaping processes of the plant are accelerated, causing flowering and fructification to take place earlier than in plants not influenced by the cold (jarovisation, vernalisation). "In almost all cases an acceleration in development is attained by a reduction in size or a simplification of the vegetative organs, i. e. by a curtailment of the generations of somatic cells" (MAXIMOV, l. c. p. 18).

According to LJUBIMENKO (1933) the wild-growing plants within the temperate zone and the Arctic are subject to vernalisation. "The influence of the cold distinctly hampers the growth, but it does not impede the shaping processes, which are completed secretly in the protoplasm. Since influence by cold and inhibition of growth take place with a fully regular periodicity, the result is an adaptation: By the natural selection a race is produced in which the shaping processes will proceed more rapidly at low temperatures. For this adaption to a

regular periodicity in the influence of the cold in the winter and the acceleration of the shaping processes produced by it, we propose the term "thermo-periodical adaptation"." (LJUBIMENKO 1933, p. 23).[1]) Thus according to LJUBIMENKO the time for the individual phases of development—the flowering included—is determined by "kryptonome Vorgänge" (GASSNER l. c. p. 473) and may not, accordingly, be directly correlated with the temperatures prevalent during the development of the organs.

The contemporaneity of the shoot generations in the arctic plants which developmental-morphologically consist of an extensive anticipated shoot and flower development, is therefore in full accord with the conjecture as to an induced acceleration of the cellular differentiation, the development (cell differentiation) thus actually preceding the growth (accumulation of matter). The proleptic development of vegetative and floral shoots may accordingly be a consequence of a general vernalisation. Certain facts suggest that the thermoperiodical adaptation is a reality in many Northeast Greenland plants, viz. the fact that the Greenland plants under cultivation in our country flower relatively much later, taking into consideration the difference in temperature, than in their native country. That such a relative retardation of the flowering in (alpine and) arctic plants under culture in the Danish climate is of more or less general validity, seems to appear from a list of flowering times for (alpine and) arctic stone-hedge plants worked out by LÖYE & STEENBERG (CORREVON 1924). Thus according to this list a number of species flower at about the same date in Denmark and in Northeast Greenland; for instance the following species are recorded to flower in June, precisely as in Greenland (cf. Table 5, p. 51): *Campanula uniflora*, *Cerastium alpinum*, *Minuartia rubella*, *Potentilla nivea*, *Saxifraga nivalis*, and *Sedum roseum*. However, in Denmark certain species flower very early in the spring; it may probably be assumed that the anticipated development of the organs of such species is "hereditarily" established in the sense that it is independent of any external "induction". (Yet the time at which the flowering sets in may probably depend on the photo-periodic tendencies of the species (for literature, see e. g. MAXIMOV 1929c), and we cannot disregard, either, the possibility of an inductive interaction of the length of the day and the temperature (STEINBERG & GARNER 1936)).

## Some general rules for differentiation of species in the Arctic.

It seems to me that altogether there is a far-reaching analogous similarity between the arctic differentiation of perennial species with

[1]) Translated from the Russian.

an anticipated floral development on the one hand, and the season-dimorphic differentiation of species in therophytic *Scrophulariaceae* and *Gentianaceae* demonstrated by WETTSTEIN (1900) on the other hand. The early-flowering forms are here, like the arctic ones, reduced as regards their formation of vegetative organs. They have a more limited and a more special geographical distribution, and they are associated with more special, ecological conditions than the late-flowering forms. By a series of proofs based on probabilities WETTSTEIN thinks it possible to establish that the vernal forms are younger than, and developed from, the autumnal forms. Nobody will doubt that the greater part of the higharctic species are generally comparatively young—the majority belong to families which are usually considered young by systematists—and that they have developed from species growing under more temperate climates. The differentiation of the arctic perennials and the aforementioned therophytes flowering in the spring has thus proceeded according to the same laws; the development has tended towards an acceleration of the differentiation of organs at the expense of the vegetative equipment of the plant, in both cases as a means of completing the yearly life cycle within the shortest time.

# VIII. RESULTS AND CONCLUSIONS

By the aid of two years' series of meteorological and elementary climatic observations in Northeast Greenland (c. 73°—74° N. lat.) it is shown that the temperature climate of the elementary space differs essentially from the purely meteorological temperature climate.

To terrain with a slight or moderate southern exposure, which becomes free of snow early, it applies that

1) The mean temperature of the soil surface (as a plant-ecological concept) intersects the 0°-line 3—4 weeks earlier in the spring than the mean temperature of the air. In the autumn, when the frost sets in, the curves for the air temperature and the soil surface temperature intersect the 0°-line at about the same time.

2) During a great part of the period with favourable temperatures (mean temperature above zero) the surface of the soil shows temperatures whose mean value for twenty-four hours is 5—7 degrees of centigrade above the mean air temperature.

3) The average amplitude for twenty-four hours in the period with favourable temperatures is 4—5 times larger for the temperature of the soil surface than for the air temperature. The great temperature fluctuations for the soil surface as compared with those of the air are chiefly found in the diurnal maxima; the nocturnal minima, however, are but slightly lower for the soil surface temperature than for the air temperature.

4) When in the spring the mean temperature of the air passes the 0°-line, the soil is thawed to a depth of about half a metre.

A comparison of the twenty-four hour course of temperature of the soil surface with the twenty-four hour distribution of the absorbed solar energy shows that there exists a close direct correlation between the temperature of the soil surface and the insolation.

It has turned out that the temperature of the soil surface and the soil does not rise above zero as long as a snow-covering is still left.

Until the snow-covering has disappeared, the insolation only contributes to accelerate the melting of the snow, but not to a heating of the upper layers of the soil.

Thus exposure and snow-covering are of very essential importance for the differentiation of the thermic elementary climate of the soil surface.

Botanical studies in the field have shown that exposure and snow-covering (more correctly the time when the snow melts) are plant-distributional factors of a high rank. We may then conclude that the temperature climate of the soil surface is to a far greater extent than the meteorological temperature climate an expression of the actual "plant climate".

On the basis of the flowering times of a number of species and the flowering intensity of the vegetation of the area as a whole as well as some few other phenological data the following sequence of aspects has been proposed for Northeast Greenland: prevernal, vernal, æstival, serotinal, autumnal, and hiemal.

From 70° to 77° N. lat. the vernal aspect is retarded by about a fortnight. Within the area investigated the æstival and the serotinal aspects are subject to a greater calendar retardation with increasing geographical latitude than the vernal aspect. A similar retardation of the later aspects as compared with the vernal aspect can be observed in the direction from the fjord areas towards the outer coast.

While the relative retardation of the later aspects in the direction south-north is correlated with the deterioration of the thermic exposure-climate owing to the low position of the sun, the corresponding retardation in the coastal regions is a consequence of their greater humidity of the air and the cloud-covering, which exert a greater influence on the exposure-climate than on the meteorological climate.

As a whole the aspect sequence of the area is largely the total result of its elementary aspects. Each ecosystem (vegetation type), and in the last instance each individual ecotope (elementary community), has only one aspect in so far as the flowering is concerned. Accordingly the sequence of aspects becomes an aid in a characterisation of the vegetation and to an understanding of the ecology of the vegetation altogether. This is of special importance in an area like Northeast Greenland, where the number of species is comparatively small, and where the commonest species have often a very wide ecological amplitude.

A comparative study of the developmental morphology and periodical life manifestations of the Northeast Greenland plants on the one hand, and their geographical distribution within Greenland on the other hand, has shown that the northern limits of the species are in many

cases directly correlated with demonstrable peculiarities in the developmental morphology of the plant.

Of characters peculiar to the northern species and doubtless in great degree determining their northern occurrence, the following may be mentioned:

1) The distribution of the yearly leaf production over several successive shoots within the same sympode in connection with proleptic development of the innovation shoots.—Result: Simultaneous expansion of all the leaves of the sympode. Frequent flowering in spite of an inconsiderable yearly growth of the individual shoots.

2) Early prepared and highly advanced development of the floral organs during the growth year or years preceding the flowering.—Result: Early flowering.

3) Aperiodical initiation and development of organs.—Result: An effective utilisation of even a very short period with favourable temperatures for a continued development of the reproductive organs.

Other characters chiefly associated with the northern species groups are: chamaephytism, winter-greenness, lack of bud protection during the wintering.

In contrast to the northern species, the southern species-groups are distinguished by:

1) Concentration of the leaf production to a single shoot generation or to the flowering shoot proper.—Result: The plant "requires" a great total leaf production of each year's shoot, which must necessarily take place successively during the growth period, if flowering is to take place at all.

2) Slight development of the floral organs the year before the flowering.—Result: The plant "requires" a long prefloration period.

3) Periodical initiation and development of organs.—Result: The plant "requires" a certain minimum time for a harmonious accomplishment and termination of the yearly life cycle.

Other characters mainly associated with the southern species group are: Less tendency to chamaephytism; furthermore, summer-greenness and bud protection during the wintering.

While, thus, the northern occurrence, respectively the northern limits, of the species are in many cases clearly correlated with their developmental morphology on the one hand and with the short duration of the summer on the other hand, no developmental morphological foundation for the southern limit of the northern species can be ascertained. From this we must conclude that the northern and southern limits of the species in Northeast Greenland are not of the same value.

While the northern limits of the southern species are directly determined by the temperature climate in relation to the specific mode of development of the species, the southern limits of the northern species are determined by other causes. Evidently their inferiority in the competition, chiefly as regards light, with the taller and more rapidly growing southern species is of no unessential importance.

The awaking of the plants in the spring takes place at almost the same time as the daily mean temperature of the soil surface passes the 0°-line. However, this does not mean that the threshold value for the life functions of the plants (growth) lies actually at zero. Owing to the large twenty-four hour amplitude which characterises the temperatures of the soil surface, a number of hours about noon will show positive temperatures already at a twenty-four hour mean temperature of 0°, and similarly a fairly great part of the twenty-four hours may have negative temperatures even if the mean temperature of twenty-four hours is positive.

In germination experiments and from observations on the incipient growth of certain species in the spring it has been found that nocturnal degrees of frost do not prevent the plants from utilising the positive day temperatures.

As regards the central parts (73° N. lat.—74° N. lat.) of the area investigated it applies that the snow-free localities afford the plants a period with favourable temperatures (mean temperature above 0°) of about four months. In the snow-patches only two months or a shorter time have positive temperatures.

In dry localities which become free of snow early, the vegetation will end its development early; the active period of the plants, therefore, often does not exceed that of the snow-patch plants.

In damp and wet localities the plants utilise the whole, or the greater part of, the period with favourable temperatures.

The interruption of the growth of plants growing in dry localities seems generally to be of an autonomous character, even though it may be ascertained that a particularly early or a particularly intense desiccation further accelerates the termination of the growth.

Autonomous cessation of the growth and a succeeding autonomous resting period are characterised i. a. by a periodical initiation and development of the organs of the particular species and by the wintering of the floral organs at a well defined phase of development. These properties are especially characteristic of the summer-green species as well as of all woody plants, both evergreen and deciduous.

The lack of autonomous cessation of growth and of autonomous rest is manifested among other things by an aperiodical initiation and development of floral as well as vegetative organs in the particular species and

by the wintering of the floral organs at very different stages of development. These properties are especially characteristic of winter-green species and of a very few summer-green species whose leaves are not subject to a natural withering in the autumn, but are killed by the frost.

Early snow-free, dry localities have the greatest content of periodical species with an autonomous rest. However, aperiodical species are not entirely absent from such localities. Late snow-free, wet localities have the greatest content of aperiodical species without an autonomous interruption of the growth. Even in such localities, however, the periodical species dominate numerically.

Continuous growth of wintered, highly developed flower buds in more or less aperiodical species only takes place within the families *Cruciferae*, *Caryophyllaceae*, *Saxifragaceae*, and *Rosaceae*. The only species in which all the floral and fructificative stages have been found with certainty to continue their development entirely uninjured after the wintering is *Braya humilis*.

Within the periodical species we find representatives of every stage of development during the wintering, ranging from the first incipient differentiation of the floral organs to fully developed flower buds with fully developed pollen. Such buds are, of course, not injured by the frost.

Bulbils and similar vegetative propagation organs of viviparous species as a rule tolerate the winter frost in all, or at any rate in different, stages of development. However, there is no marked correlation between vivipary and aperiodicity.

There is no distinct limit between periodic and aperiodic species. Often the floral development seems to be subject to a stricter periodicity than the vegetative development. In a number of species (e. g. many *Cruciferae*, *Papaver*) the development of the flower buds stops at a certain stage, while in vigorous shoots the growth may continue in the development of a new (primordial) shoot generation. Even within the same growth season, this shoot generation may produce floral primordia, which may reach approximately the same stage of development as those of the mother shoot before the wintering ("regulation shoots").

The time for initiation of the floral organs in relation to the flowering time is closely connected with the rate of growth (rate of development), which seems to be constant for each species. In species with a very slow rate of growth the floral organs may on rare occasions be initiated two years before the flowering. In most cases, however, they are initiated in the spring one year before the flowering, though in a number of species not till later in the summer, and finally, in a minority with an especially rapid rate of growth, in the flowering year proper. Aperiodical species, in particular, as a rule show a very early initiation of the floral organs

and a slow rate of growth. The same applies to the northern species altogether, while the southern species are generally characterised by less prepared flowering in the wintering state in connection with a rapid rate of growth.

It would seem that as regards certain systematically old species groups (e. g. *Bicornes*, *Salix*) the two-year development of the floral organs, with initiation one year and expansion in the succeeding year, should be regarded as a case of "retarded" expansion of buds initiated "in time". This form of a retarded flowering is no specially arctic phenomenon. However, in the majority of the arctic plants the two-year floral development has no doubt arisen from an extensive anticipated shoot development, that is to say, from an initiation and development of the organs "before the time", which results in an expansion "in time". This mode of development seems to be a specially arctic phenomenon, an adaptation to a short period with favourable temperatures, and it is chiefly associated with systematically young families which are most abundantly represented in the Arctic.

The low, much branched growth form (the "cushion shape") of many arctic plants is closely associated with the proleptic shoot development and a prolonged development of the shoot generations. On this account the leaf production is distributed over several shoots within the same sympode, resulting in a simultaneous expansion of the whole mass of leaves. The "cushion shape" is accordingly a secondary adaptation to the short arctic summer.

Certain facts, the late flowering of a number of species kept in culture under the climatic conditions of the temperate zone, suggest that the anticipated formation of organs in the Arctic is in many cases induced by the low temperatures of the winter or early spring (thermoperiodical adaptation).

Thus the induced, phenotypic, mode of development and the genotypic differentiation of species within the Arctic seem to point towards the same goal: an acceleration of the developmental rate parallel with a corresponding reduction of the vegetative equipment of the plant.

## Postscript.

Unfortunately it was not till after the completion of the present paper that my attention was called to the investigations made by ZUBKOF at Russian Harbour, Novaya Zemlya (76°14′ N. lat.)[1]). As these investigations are on entirely the same line as my investigations in Greenland, I shall here give a brief summary of the most important of ZUBKOF's results.

It appears with all desirable distinctness from ZUBKOF's observations that the duration of the positive air temperatures is no reliable measure of the length of the vegetation period of arctic plants. Thus with a duration of the positive air temperatures of 78 days (June 19—September 12, 1933) a vegetation period of 107 days was ascertained for *Saxifraga oppositifolia.* Of the eleven species examined, *Saxifraga oppositifolia*, similarly as in Greenland, was the first to show signs of life, and its active period is accordingly relatively long. *Ranunculus sulphureus* had the shortest vegetation period, viz. 65 days. This and several other species in localities with a more prolonged snow-covering start their growth about one month later than *Saxifraga oppositifolia.*

ZUBKOF's temperature observations show a smaller difference between "soil surface" and air temperatures (c. 2° for the summer months) than do my observations in Greenland, probably largely because ZUBKOF's soil surface temperatures represent the air temperature c. 2 cm above the ground, while my soil surface temperatures represent the temperature of the upper layers of the soil. As regards the thawing of the upper layers of the soil in the spring before the mean twenty-four hour temperature reaches zero, ZUBKOF's and my observations show a satisfactory agreement. At the time the mean temperature of the air for twenty-four hours passes 0°, ZUBKOF found the soil to be thawed to a depth of c. 30 cm. The somewhat greater depth shown by my observations on Clavering Ø (c. 50 cm) at the corresponding time is probably due to the (slight) southern exposure (8°) at the observation spot. (As ZUBKOF states nothing about the nature of the observation spot, it must be assumed that the observations were made on horizontal

[1]) ZUBKOF 1935, see list of literature.

ground). Possibly a difference in the intensity of the direct insolation (in favour of Northeast Greenland) as a consequence of differences in the humidity of the air and the cloud-covering at the two observation spots is of some importance. However, nothing is known about this question.

Thus the two observation series from widely different places within the arctic area agree in showing the exceedingly great importance of direct insolation as a climatic factor exerting its influence on the vegetation of the far north.

# IX. LITERATURE


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# X. RÉSUMÉ

Det foreliggende Arbejde er et Resultat af en Aarrækkes botaniske Markundersøgelser i Nordøstgrønland (ca. 70°—ca. 78° n. Br.) væsentligt udførte under den 3-aarige Østgrønlandsundersøgelse 1931—34. Efter dennes Afslutning fortsattes mine Undersøgelser under et Ophold i de samme Egne 1934—35, samt under en Sommerekspedition 1937.

Treaars-Ekspeditionens botaniske Undersøgelser var væsentlig tilrettelagt med Løsningen af plantegeografiske og plantesociologiske Opgaver for Øje. Først i Løbet af Arbejdsaarene begyndte Konturerne for dette Arbejde lidt efter lidt at tegne sig paa Baggrund af Lovmæssigheden i Vegetationens Anordning set i Relation til lokalklimatiske Forhold. Ved Sommerens korte Udstrækning og dens lave Temperaturer bliver det termiske Lokalklima, betinget ved Variationen i Tidspunktet for Sneens Afsmeltning og ved Terrainets Eksposition, af relativt større Betydning for Plantefordelingen i Arktis end i de tempererede Egne. Det blev saaledes under Arbejdet i Marken indlysende, at Jordens Produktivitet, maalt ved Plantevækstens Udvikling, i ikke ringe Grad er bestemt af, hvad der i det hele taget kan naas indenfor det korte Tidsrum, hvor Temperaturforholdene giver Livsfunktionerne en Chance for at udfolde sig. Netop i Erkendelsen heraf er Rammerne for og Hensigten med nærværende Undersøgelse givet af sig selv. Formaalet har saaledes været at uddybe Kendskaben til Planternes tidsmæssige Livsmanifestation i Relation til det paa selve Voksestedet herskende termiske Lokalklima, som et Grundlag for en Bedømmelse af det paagældende Omraades plantegeografiske Forhold.

I Udgangsmaterialet for denne Undersøgelse kan man praktisk skelne mellem 3 forskellige Kategorier, nemlig 1) Temperaturmaalingerne, 2) de fænologiske Markiagttagelser og 3) Undersøgelsen over Planternes biologisk-morfologiske Karakterer under særlig Hensyntagen til deres Overvintringstilstand og saisonbestemte Udviklingsrytme. — Hertil kommer saa, ligeledes som et væsentligt Grundlag for Arbejdet, de vegetationsanalytiske Undersøgelser over Plantevækstens kvalitative og kvantitative Sammensætning inden-

for de forskellige Vegetationstyper. De detaillerede Resultater af Vegetationsanalyserne har dog nødvendigvis maattet henlægges til et senere Arbejde.

Temperaturmaalingerne repræsenterer to Aarsserier, hidrørende fra Ekspeditionens to Overvintringsstationer, Ella Ø (72°50′ n. Br.) for 1931—32 og Eskimonæs (74°08′ n. Br.) for 1934—35. Maalingerne omfatter Luft-, Jordflade- og Jordtemperaturer. Jordfladetemperaturmaalingerne er udført ved Hjælp af Termograf og er begrænset til sydexponeret Terrain, Hældningsvinkel for Ella Ø Maalingsstedet ca. 20°, for Eskimonæs Maalestedet ca. 8°. Resultaterne af Temperaturmaalingerne er grafisk fremstillet i Tavlerne 12—15. En Del af Talmaterialet, væsentlig for Sommermaanederne, er opført i Tabellerne 38—41 (Side 292—302).

Som de planteøkologisk vigtigste Resultater af Temperaturmaalingerne skal her fremhæves følgende angaaende Temperaturforholdene paa tidligt snefrit (svagt) sydeksponeret Terrain:

1) Jordfladens Døgnmiddeltemperatur passerer om Foraaret 0-Linien 3—4 Uger tidligere end Luftens Døgnmiddeltemperatur. Om Efteraaret passerer Jordoverfladens og Luftens Middeltemperaturer derimod omtrent samtidig 0-Linien.

2) Jordfladen er under store Dele af den temperaturgunstige Periode udsat for Temperaturer, hvis Døgnmiddelværdi ligger 5—7° C. over Lufttemperaturen.

3) Den gennemsnitlige Døgnamplitude andrager indenfor den temperaturgunstige Periode 4—5 Gange saa høje Værdier for Jordfladetemperaturen som for Lufttemperaturen. Jordfladens Temperaturudsving angaar i Sammenligning med Luftens væsentlig de daglige Maxima, medens de natlige Minima kun i betydeligt ringere Grad afviger fra Luftens.

4) Jordbunden er paa det Tidspunkt om Foraaret, da Luftens Middeltemperatur passerer 0-Linien, optøet til ca. $^1/_2$ Meters Dybde.

5) Saa længe Jorden er snedækket, hæver Jordoverfladens Temperatur sig overhovedet ikke over 0°. Indtil Snedækket er forsvundet bidrager Insolationen til at fremskynde Snesmeltningen, men ikke til Optøning af de øvre Jordlag.

Da de arktiske Planter har saavel den assimilerende Bladmasse som en stor Del af Rodnettet beliggende i den umiddelbare Nærhed af Jordoverfladen, maa man gaa ud fra, at Jordoverfladens Temperaturforhold med en vis Tilnærmelse kan betragtes som et Udtryk for selve "Plantetemperaturklimaet". Udstrækningen af Planternes temperatur-

gunstige Periode er indenfor visse Grænser bestemt ved Tidspunktet for Standpladsernes Afsmeltning. Selve "Plantetemperaturen", Jordfladetemperaturen paa Plantens Standplads er under Vækstperioden i væsentlig Grad afhængig af den direkte indstraalede Solenergi og viser store Afvigelser fra Lufttemperaturen. Om Vinteren adskiller Jordoverfladens Temperatur paa snefri Lokaliteter sig ikke væsentligt fra Lufttemperaturen. Et Snedække yder Beskyttelse mod de voldsomste Temperaturfald, men selv paa snedækket Bund er Jordoverfladen udsat for ret betydelige Kuldegrader.

De fænologiske Markundersøgelser omfatter, foruden Iagttagelser over Sneens Bortsmeltning indenfor de forskellige Kategorier af Standpladser, især en Konstatering af Arternes Blomstringstider samt af den saisonelle Blomstringsintensitet indenfor de forskellige Vegetationstyper. Paa Grundlag af disse Iagttagelser kan der for Nordøstgrønland paavises nedenstaaende Aspektfølge:

Prævernal Aspekt (Førforaar), fra Begyndelsen til Slutningen af Maj, karakteriseret ved Sneens begyndende Afsmeltning. Endnu ingen Arter i Blomst.

Vernal Aspekt (Foraar), fra Slutningen af Maj til Slutningen af Juni, kendetegnet ved Foraarsplanternes, ganske særlig Purpur-Stenbrækkens (*Saxifraga oppositifolia*'s) Blomstring og Dværgbuskenes Løvspring.

Æstival Aspekt (Sommer), fra Slutningen af Juni til Midten eller lidt over Midten af Juli, især kendetegnet ved Firkant-Lyngens (*Cassiope tetragona*'s) Blomstring.

Serotinal Aspekt (Sensommer), sidste Halvdel af Juli og første Halvdel af August; Elvdeltaerne farves her smukt røde af de store prangende Blomster af den arktiske Gederams (*Chamaenerium latifolium*).

Autumnal Aspekt (Efteraar), sidste Halvdel af August og Begyndelsen af September, kendetegnet ved, at Dværgbuskenes Løv antager stærke og karakteristiske gule og røde Efteraarsfarver.—Overgangen fra det autumnale til det

Hiemale Aspekt (Vinter) kan fastlægges til det Tidspunkt, da de øvre Jordlag fryser for stedse, d. v. s. omkring Midten af September.

Den angivne kalendariske Afgrænsning af Aspekterne gælder for Undersøgelsesomraadets centrale Del (ca. 73°—74° n. Br.). Med tiltagende geografisk Bredde lider det æstivale og det serotinale Aspekt en større kalendarisk Forsinkelse end det vernale. En lignende forholdsvis stærk Forsinkelse af de senere Aspekter i Forhold til det vernale gør sig gældende i Retning fra Fjordomraaderne ud imod Yderkysten.

Medens den Syd—Nord-gaaende Forsinkelse af de senere Aspekter staar i Relation til det termiske Expositionsklimas "Forværring" som Følge af den lavere Solhøjde, er Forsinkelsen for Kystegnene en Følge af disses større Luftfugtighed og stærkere Skydække, der paavirker Expositionsklimaet stærkt i ugunstig Retning og forsinker Snesmeltningen.

En Liste over de almindeligere Arters Blomstringstid paa Eskimonæs 1935 er givet i Tabel 5, Side 51—53. En Oversigt over den tidvise Blomstringsintensitet indenfor Nordøstgrønlands forskellige Vegetationstyper (Økosystemer) er givet i Tabel 6, Side 56—59. Her er tillige de omtrentlige Afsmeltningstider angivet. Det fremgaar af denne Tabel, at hver Vegetationstype i vid Udstrækning kun har een enkelt Blomstringstid. Først naar de tidligst snefri Vegetationer har afsluttet deres Blomstring, smelter Snelejevegetationerne frem i Lyset. Vegetationstyperne er saaledes ofte tydeligt fænologisk adskilte, undertiden ogsaa i saadanne Tilfælde, hvor den floristiske Adskillelse er mangelfuld. Aspektfølgen kan saaledes tjene som et Hjælpemiddel til en Karakteristik af økologisk forskellige, men floristisk vanskeligt definerbare Vegetationstyper.

Ved Undersøgelserne over Arternes Overvintringstilstand er der søgt tilvejebragt en Oversigt, dels over en Række biologisk-morfologiske Karakterer, saasom Livsform, Bladenes samt de vegetative og de florale Knoppers Overvintringstilstand, Skuddenes Udviklingstid og aarlige Bladproduktion, dels over Tidspunktet for den morfologiske Differentiation af Foryngelsesskud og Floralorganer. Resultaterne af disse Undersøgelser er opført i Tabel 7, Side 164—179.

Den indbyrdes Korrelation mellem de forskellige biologisk-morfologiske Karakterer samt Sammenhængen mellem disse Karakterer og Arternes grønlandske Udbredelse og deres Forekomst i Relation til Snedækning (Afsmeltningstidspunkt) er belyst ved en talmæssig Behandling af Undersøgelsesresultaterne (Tabel 8—35 og Fig. 20—24, Side 184—215).

Der er lagt ganske særlig Vægt paa at konstatere Blomsterknoppernes Udviklingsgrad under Overvintringen. Florale Overvintringsstadier for en større Del af Omraadets Arter er gengivet i Tavle 1—11. Medens Blomsterknopperne hos en stor Del af Arterne stadig overvintrer i tilnærmelsesvis samme Udviklingsfase, karakteristisk for hver enkelt Art, er en Række Arter i Modsætning hertil udmærkede ved en mere eller mindre fuldstændig Mangel paa Konstans i det florale Overvintringsstadium. Paa Grundlag af disse Iagttagelser er det godtgjort, at der kan skelnes mellem Arter med strengt periodisk Udviklingsrytme og saadanne med blot tilnærmet eller helt manglende Periodicitet i den fasiske Udvikling. Hos de fleste aperiodiske Arter taales Overvintringen kun af saadanne Blomsterknopper, hvis Udvikling ikke er naaet ud

over en bestemt maximal Grænse. Kun indenfor Nellikefamilien, de Korsblomstredes Familie og Stenbrækfamilien, samt i ganske enkelte Tilfælde indenfor Rosenfamilien har vi Eksempler paa, at særlig stærkt udviklede Blomsterknopper hos aperiodiske Arter er i Stand til at overvintre uskadt, idet dog de først udfoldede Blomster, der har overvintret som næsten fuldt udviklede Knopper, ikke sjældent er golde. Den eneste af de aperiodiske Arter, for hvilken det med absolut Sikkerhed er paavist, at alle florale og fruktifikative Organer i et hvilketsomhelst Udviklingsstadium fortsætter Udviklingen uskadt efter Overvintring, er *Braya humilis*, hørende til de Korsblomstredes Familie. Indenfor de periodiske Arter finder vi Repræsentanter for ethvert Udviklingsstadium under Overvintringen lige fra den første begyndende Uddifferentiation af Floralorganerne til fuldt uddannede Blomsterknopper med færdigdannet Pollen. Stærkt udviklede Blomsterknopper hos saadanne periodiske Arter skades naturligvis ikke af Vinterfrosten.

Medens streng Periodicitet i Organanlæggelse og -udvikling stadig synes at være forbundet med autonom Vækstafbrydelse inden Vinterfrostens Indtræden, er en manglende Periodicitet i Organanlæggelsen ofte, omend ikke altid, knyttet til en mere eller mindre regelløs fortsat Udvikling af Floralorganerne, lige indtil Væksten standses af Frosten. Hos en Del Arter, f. Eks. mange Korsblomstrede og den arktiske Valmue, synes Floralorganernes Udvikling at kunne standse paa et vist Stadium, medens Væksten fortsætter i Udviklingen af en ny (primordial) Skudgeneration. Denne kan indenfor samme Vækstsaison frembringe Blomsterknopper, der kan naa frem til tilnærmelsesvis samme Udviklingsstadium som Moderskuddets inden Overvintringen. Ved denne Anordning i Udviklingen synes de paagældende Arter at opnaa en Regulation i Blomstringsperiodiciteten i Overensstemmelse med Klimarytmen, samtidig med at der muliggøres en effektiv Udnyttelse af særlig favorable Vækstbetingelser.

Periodisk Organanlæggelse og -udvikling, stadig knyttet til en i det mindste tilsyneladende autonom Vækststandsning og Hvileperiode, er især karakteristisk for de sommergrønne (vintervisne) Arter, endvidere for alle Vedplanter, stedsegrønne saavel som løvfældende. De periodiske Arter er rigeligst repræsenterede paa tidligt snefri, tørre Standpladser, men langtfra alene knyttet til disse.

Aperiodisk Organdannelse og -udvikling, forbundet med manglende autonom Vækststandsning inden Vinterfrostens Indtræden, er især karakteristisk for vintergrønne Arter uden Knopbeskyttelse. Saadanne Arter er rigeligst repræsenterede paa sent snefri, vaade Standpladser.

Hos langt det overvejende Flertal af de sommergrønne Arter undergaar Bladene en naturlig Visnen inden Vinteren. Kun hos et Faatal,

og disse er da oftest aperiodiske uden autonom Hvile, visner Bladene ikke, men dræbes af Frosten.

Hos de vintergrønne Arter fortsættes de ikke fuldt udvoksede Blades Vækst efter Overvintring, uanset under hvilken Udviklingsfase Væksten er blevet afbrudt ved Vinterens Indtræden. Selv hos en Del sommergrønne Arter, især Star og Græsser, gør lignende Forhold sig gældende, idet Bladets distale Del funktionerer den første Sommer, og visner, medens den proximale Del først skyder sig frem over de gamle Bladskeder den følgende Sommer.

En Sammenligning af Arternes biologisk-morfologiske Karakterer, indbefattet deres Periodicitet eller Mangel paa Periodicitet i Organudviklingen paa den ene Side og deres Udbredelse indenfor Grønland paa den anden, har vist, at Arternes Nordgrænse i mange Tilfælde staar i direkte Relation til paaviselige Ejendommeligheder i deres Udviklingsmorfologi, d. v. s. til deres Fænologi i udvidet Forstand. Af Karakterer, der er særegne for de nordlige Arter, og som utvivlsomt i væsentlig Grad betinger disses nordlige Forekomst, kan fremhæves:

1) Fordelingen af den aarlige Bladproduktion paa flere efter hinanden følgende Skud indenfor samme Skudkæde i Forbindelse med proleptisk Udvikling af Fortsættelsesskuddene. — Følge: Samtidig Udfoldelse af alle Skudkædens Blade. Hyppig Blomstring paa Trods af ringe aarlig Tilvækst paa de enkelte Skud.

2) Tidligt forberedt og stærkt fremskredet Udvikling af Floralorganerne gennem Vækstaaret eller Vækstaarene gaaende forud for Blomstringen. — Følge: Tidlig Blomstring.

3) Aperiodisk Organanlæggelse og Udvikling. — Følge: En effektiv Udnyttelse af selv den korteste temperaturgunstige Periode til en fortsat Udvikling af de reproduktive Organer.

Andre Karakterer, der væsentlig er knyttet til de nordlige Artsgrupper, er: Chamæfytisme, Vintergrønhed, Mangel paa Knopbeskyttelse under Overvintringen.

I Modsætning til de nordlige er de sydlige Arter udmærket ved:

1) Koncentration af Bladproduktionen til en enkelt Skudgeneration eller til selve det blomstrende Skud. — Følge: Planten behøver, for i det hele taget at naa frem til Blomstring, en stor Bladproduktion paa det enkelte Aarsskud; Udviklingen af Skuddets Blade maa da nødvendigvis foregaa successivt gennem Vækstperioden.

2) Ringe Udvikling af Floralorganerne Aaret før Blomstringen. — Følge: Planten behøver en lang Præflorationstid.

3) Periodisk Organanlæggelse og -udvikling. — Følge: Planten behøver til en harmonisk Gennemførelse og Afslutning af den aarlige Livscyklus en bestemt minimal Tidsfrist.

De sydlige Arters „uheldige" Udviklingsmorfologi for nordlig Forekomst er dog til en vis Grad kompenseret ved et hurtigere Væksttempo, end det, der er Reglen for de nordlige Arter.

Andre Karakterer, der væsentlig er knyttet til de sydlige Artsgrupper, er: Ringere Tilbøjelighed til Chamæfytisme, endvidere Sommergrønhed og Knopbeskyttelse under Overvintringen.

Medens Arternes Nordgrænser saaledes i en Række Tilfælde staar i klar Relation til deres Udviklingsmorfologi paa den ene Side og til Sommerens korte Udstrækning paa den anden, kan der derimod ikke paavises noget udviklingsmorfologisk Grundlag for de nordlige Arters Sydgrænse. Man kan deraf slutte, at Arternes Nord- og Sydgrænser i Nordøstgrønland ikke er af samme Natur. Medens Nordgrænserne for de sydlige Arter er direkte bestemt af Standpladsens Elementarklima i Forhold til Artens specifike Udviklingsmodus, er Sydgrænserne for nordlige Arter øjensynlig bestemt ved disses Underlegenhed i Konkurrencen, væsentlig m. H. t. Lyset, med de mere højtvoksende og mere hurtigtvoksende sydlige Arter.

Planternes Opvaagnen om Foraaret sker paa det nærmeste samtidig med, at Jordfladetemperaturen passerer 0-Linien. Dette er dog ikke ensbetydende med, at Tærskelværdien for Planternes Livsfunktioner („Vækst") netop ligger ved 0°. Ved den store Døgnamplitude, der kendetegner Jordfladens Temperaturer, vil allerede ved et Døgnmiddel paa 0° et Antal Timer ved Middagstid have positive Temperaturer, ligesom en ikke uvæsentlig Del af Døgnet kan have negative Temperaturer, selv ved et positivt Døgnmiddel. — Ved Spiringsforsøg og ved Iagttagelser over visse Arters Begyndelse af Væksten om Foraaret, er det konstateret, at natlige Frostgrader ikke forhindrer Planterne i at nyttiggøre de positive Dagtemperaturer.

Undersøgelsesomraadets mellemste Dele (ca. 73—74° n. Br.) har mindre end 3 Maaneder med positiv Middelværdi for Lufttemperatur. For de selvsamme Omraader gælder imidlertid, at de snefri Lokaliteter yder Planterne en temperaturgunstig Periode (Middeltemperatur over 0°) paa mindst 4 Maaneder. Snelejerne (som Vegetationstype) har dog kun ca. 2 Maaneder eller derunder med positiv Temperatur. Paa tidligt snefri, tørre Lokaliteter afslutter Vegetationen imidlertid ofte sin Udvikling saa tidligt, at Planternes aktive Periode her ikke bliver af større Udstrækning end i de moderate Snelejer. Paa fugtige og vaade Lokaliteter udnytter Plantevæksten derimod i Reglen hele den temperaturgunstige Periode. Tidligt snefri, moderat fugtige Standpladser yder

saaledes, andre Forhold lige, Plantevæksten den længste Periode for aktiv Livsudfoldelse.

Den morfologiske Uddifferentiation af Floralorganerne tager for Flertallet af Nordøstgrønlands Arter sin Begyndelse om Foraaret et Aar før Blomstringen. Hos et Faatal af Arter, væsentlig aperiodiske, bliver Vækstpunktet tydeligt floralt allerede mod Slutningen af Vækstsaisonen ca. 2 Aar før Blomstringen. Ligeledes kun hos et ringere Antal Arter foregaar Vækstpunktets Overgang til den florale Tilstand først indenfor den selvsamme Sommer, hvor Blomstringen finder Sted. Der kan ikke paavises nogen udtalt Korrelation mellem Floralorganernes Udviklingsfase under sidste Overvintring og Tidspunktet for deres begyndende Anlæggelse. Saaledes er Udviklingen af Floralorganerne hos de Arter, hvis Blomsterknopper overvintrer med færdigt Pollen, oftest ikke tidligere forberedt end hos mange Arter, hvis Blomsterknopper overvintrer paa et mindre fremskredet Udviklingsstadium. Udviklingsstadiet af Floralorganerne under sidste Overvintring, set i Relation til Tidspunktet for deres Anlæggelse, staar imidlertid i nøje Forbindelse med Vækstempoet (Udviklingstempoet), der synes at være konstant for hver Art. I det store og hele gælder, at sydlige Arter har et hurtigere Vækstempo end nordlige.

Trods Arternes forskellige Vækstempo kan der konstateres en gennemgaaende Korrelation mellem Blomsterknoppernes Udviklingsgrad under Overvintringen og Blomstringstiden (se Fig. 24, Side 214). En stærkt fremskreden Floraludvikling og en tidlig Blomstring er karakteristisk for Chamæfyterne, medens Hydrofyterne har en yderst ringe Udvikling af Blomsterknopperne og sen Blomstring. Therofyterne, der ikke alene maa udvikle Blomsterknopperne, men endogsaa alle Plantens vegetative Organer indenfor selve Blomstringsaaret, har en relativ tidlig Blomstring (jvf. Fig. 21, Side 211). Dette godtgør, at Vækstempoet hos Therofyterne er hurtigere end hos de øvrige Livsformer.

De arktiske Planters Evne til at fuldende deres aarlige Livscyklus i Løbet af den korte Sommer synes saaledes i væsentlig Grad at være betinget enten ved en forudgaaende Forberedelse af Reproduktionsorganernes Udvikling eller ved et hurtigt Vækstempo. Muligvis kan visse Arter være underkastet begge disse Former for Tilpasning samtidig, men i det store og hele synes de to Tilpasningsformer at udelukke hinanden, idet de nordlige Arter gennemgaaende er karakteriseret ved en tidlig Forberedelse af Blomstringen i Forbindelse med et langsomt Vækstempo, de sydlige Arter ved en „mangelfuldt" forberedt Blomstring forbundet med et hurtigere Vækstempo.

Den 2-aarige Udvikling af Floralorganerne, med Anlæggelse det ene Aar og Udfoldelse det følgende, synes for visse fylogenetisk gamle Artsgruppers Vedkommende, f. Eks. Lyngplanterne og Pilene, at være at

opfatte som et Tilfælde af „forsinket" Udfoldelse af „rettidigt" anlagte Knopper. Denne Form for retarderet Blomstring er dog ikke et specielt arktisk Fænomen. Hos Flertallet af de arktiske Planter er den 2-aarige Floraludvikling imidlertid utvivlsomt fremkommet ved en vidtgaaende anticiperet Skududvikling, altsaa ved en „førtidig" Organanlæggelse, der resulterer i en „rettidig" Udfoldelse. Denne Udviklingsmodus synes at være et specielt arktisk Fænomen, og den er væsentlig knyttet til systematisk unge Familier, der er rigeligst repræsenteret i Arktis.

Den lave, stærkt grenede Vækstform („Pudeformen") hos mange arktiske Planter er nøje forbundet med den anticiperede Skududvikling og den langsomme, fleraarige Udvikling af Skudgenerationerne. Som Følge af denne Vækstmaade fordeles den aarlige Bladproduktion paa flere Skud indenfor samme Skudkæde, hvorved der sikres en samtidig Udfoldelse af hele Bladmassen. „Pudeformen" bliver saaledes rent sekundært en Tilpasning til den korte arktiske Sommer.

Visse Kendsgerninger, en Række Arters sene Blomstring ved Kultur under den tempererede Zones Klimaforhold, tyder paa, at den anticiperede Organdannelse i Arktis i mange Tilfælde er induceret ved Vinterens eller det tidligste Foraars lave Temperaturer (Termoperiodisk Adaptation). Den inducerede, fænotypiske, Fremskyndelse af Blomsterknoppernes Anlæggelse betegner kun et yderligere Skridt ad den Vej, den genotypiske Artsdifferentiation indenfor Arktis i Forvejen synes at følge. Maalet er tydeligt nok en Tilpasning til den korte Vækstperiode, tilkendegivet ved en Fremskyndelse af den ontogenetiske Udviklingsfølge (Organdifferentiation) jævnsides løbende med en Reduktion af Plantens vegetative Udstyr („Væksten").

# XI. TABLES SHOWING TEMPERATURE OBSERVATIONS

Table 38. Monthly means of air and soil surface temperatures for Ella Ø 1931—32 and Eskimonæs 1934—35, and the difference between the soil surface and the air temperatures.

| | Ella Ø 1931—1932 | | | Eskimonæs 1934—1935 | | |
|---|---|---|---|---|---|---|
| | Air | Surface of soil[1]) | Diff. | Air | Surface of soil[2]) | Diff. |
| | C° | C° | C° | C° | C° | C° |
| September | .. | .. | .. | 1.9 | 2.1 | 0.2 |
| October | — 9.8 | — 12.8 | — 3.0 | — 8.4 | — 4.4 | 4.0 |
| November | — 11.1 | — 11.1 | 0.0 | — 15.2 | — 11.0 | 4.2 |
| December | — 22.4 | — 14.0 | 8.4 | — 16.3 | — 17.6 | — 1.3 |
| January | — 19.2 | .. | .. | — 18.8 | — 14.6 | 4.2 |
| February | — 12.6 | — 12.6 | 0.0 | — 19.5 | — 20.8 | — 1.3 |
| March | — 13.0[3]) | — 13.7[3]) | — 0.7 | — 17.2 | — 17.5 | — 0.3 |
| April | — 17.9 | — 12.0 | 5.9 | — 17.2 | — 15.2 | 2.0 |
| May | — 0.8 | 5.3 | 6.1 | — 7.5 | — 1.8 | 5.7 |
| June | 6.2 | 13.0 | 6.8 | — 0.9 | 6.5 | 7.4 |
| July | 9.6 | 16.3 | 6.7 | 1.8 | 8.4 | 6.5 |
| August | 8.4[4]) | 13.4[4]) | 5.0 | 2.3[5]) | 6.6[5]) | 4.2 |

[1]) Oct.—March, level ground. April—August, S. exp. c. 20°. For snow-covering see Pl. 12.
[2]) S. Exp. 8°. For snow-covering see Pl. 13.
[3]) 1—24 March.
[4]) 1—26 August.
[5]) 1—14 August.

Table 39. Monthly mean values of the twenty-four hour amplitude for air and soil surface temperatures for Ella Ø 1931—32 and for the soil surface temperature at Eskimonæs 1934—35.

| | Ella Ø 1931—32 | | Eskimonæs 1934—35 |
|---|---|---|---|
| | Air | Surface of soil[1]) | Surface of soil[2]) |
| | C° | C° | C° |
| September | 7.2 | .. | 5.8 |
| October | 4.7 | 7.1 | 1.6 |
| November | 6.6 | 2.2 | 1.7 |
| December | 8.6 | 1.2 | 2.8 |
| January | 8.5 | .. | 1.6 |
| February | 12.1 | 4.2 | 3.5 |
| March | 8.0 | 3.8 | 4.5 |
| April | 10.4 | 14.4 | 9.4 |
| May | 9.3 | 19.3 | 9.9 |
| June | 8.9 | 27.8 | 14.0 |
| July | 6.3 | 32.3 | 16.1 |
| August | 6.9 | 33.2 | 13.6 |

[1]) October—March, level ground. April—August, S. exp. c. 20°. For snow-covering see Pl. 12.
[2]) S. exp. 8°. For snow-covering see Pl. 13.

Table 40. Mean temperatures, minimum and maximum temperatures, and amplitude for twenty-four hours for air and soil surface (S. exp. c. 20°) on Ella Ø in September, 1931, and April—August, 1932. (Temp. in C.°).

**September 1931**

| Date | Air | | | |
|---|---|---|---|---|
| | Mean | Min. | Max. | Ampl. |
| 1 | .. | .. | .. | .. |
| 2 | .. | .. | .. | .. |
| 3 | .. | .. | .. | .. |
| 4 | .. | .. | .. | .. |
| 5 | .. | .. | .. | .. |
| 6 | .. | .. | .. | .. |
| 7 | 1.1 | — 3.6 | 5.8 | 9.4 |
| 8 | 0.7 | — 3.3 | 4.7 | 8.0 |
| 9 | 1.6 | — 3.6 | 6.8 | 10.4 |
| 10 | 1.0 | — 4.0 | 6.0 | 10.0 |
| 11 | — 0.9 | — 4.5 | 3.7 | 8.2 |
| 12 | 1.6 | — 2.6 | 5.7 | 8.3 |
| 13 | — 0.2 | — 4.2 | 3.9 | 8.1 |
| 14 | 3.6 | — 3.4 | 10.6 | 14.0 |
| 15 | 2.9 | — 1.5 | 7.2 | 8.7 |

Table 40 (continued)

**September 1931**

| Date | Air | | | |
|---|---|---|---|---|
| | Mean | Min. | Max. | Ampl. |
| 16 | 1.8 | — 1.1 | 4.7 | 5.8 |
| 17 | — 2.0 | — 6.4 | 2.5 | 8.9 |
| 18 | 2.1 | — 2.3 | 6.4 | 8.7 |
| 19 | 2.4 | — 2.6 | 7.3 | 9.9 |
| 20 | 3.0 | 1.7 | 4.2 | 2.5 |
| 21 | 1.3 | — 0.2 | 2.7 | 2.9 |
| 22 | — 0.7 | — 5.7 | 4.3 | 10.0 |
| 23 | 0.9 | — 2.7 | 4.5 | 7.2 |
| 24 | 2.6 | 0.5 | 4.6 | 4.1 |
| 25 | 1.2 | — 2.4 | 4.8 | 7.2 |
| 26 | — 0.6 | — 4.2 | 3.0 | 7.2 |
| 27 | — 2.2 | — 4.5 | 0.1 | 4.6 |
| 28 | — 1.7 | — 3.3 | — 0.1 | 3.2 |
| 29 | — 1.9 | — 2.3 | — 1.5 | 0.8 |
| 30 | — 4.4 | — 6.5 | — 2.5 | 4.3 |

**April 1932**

| Date | Air | | | | Surface of soil | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | Min. | Max. | Ampl. | Mean | Min. | Max. | Ampl. |
| 1 | — 19.1 | — 27.1 | — 11.1 | 18.0 | — 12.1 | — 24.8 | 9.0 | 33.8 |
| 2 | — 21.3 | — 25.2 | — 17.3 | 7.9 | — 10.1 | — 22.8 | 10.1 | 32.9 |
| 3 | — 19.1 | — 24.9 | — 13.2 | 11.2 | — 9.3 | — 21.3 | 9.2 | 30.5 |
| 4 | — 17.7 | — 18.9 | — 16.4 | 2.5 | — 13.1 | — 17.1 | — 8.6 | 8.5 |
| 5 | — 21.7 | — 24.6 | — 18.7 | 5.9 | — 14.5 | — 13.6 | — 10.0 | 3.6 |
| 6 | — 23.8 | — 28.8 | — 18.7 | 10.1 | — 14.1 | — 18.2 | — 5.8 | 12.4 |
| 7 | — 22.8 | — 28.5 | — 17.2 | 11.3 | — 13.8 | — 17.7 | — 5.2 | 12.5 |
| 8 | — 17.4 | — 25.6 | — 9.1 | 14.5 | — 12.3 | — 16.8 | — 8.2 | 8.6 |
| 9 | — 14.8 | — 19.7 | — 9.8 | 9.9 | — 12.6 | — 17.2 | — 4.9 | 12.3 |
| 10 | — 18.1 | — 23.7 | — 13.4 | 10.3 | — 11.9 | — 20.3 | — 2.0 | 18.3 |
| 11 | — 20.2 | — 25.4 | — 14.9 | 10.5 | — 15.2 | — 25.1 | — 2.0 | 23.1 |
| 12 | — 20.4 | — 25.6 | — 15.1 | 10.5 | — 15.0 | — 24.9 | 1.3 | 26.2 |
| 13 | — 21.4 | — 27.6 | — 15.1 | 12.5 | — 12.2 | — 24.9 | 5.1 | 30.0 |
| 14 | — 19.3 | — 25.7 | — 12.8 | 12.9 | — 11.0 | — 16.1 | — 4.8 | 11.3 |
| 15 | — 13.1 | — 17.5 | — 8.6 | 8.9 | — 11.6 | — 16.0 | — 6.1 | 10.0 |
| 16 | — 12.5 | — 20.0 | — 5.0 | 15.0 | .. | .. | — 2.0 | .. |
| 17 | — 13.9 | — 18.0 | — 9.7 | 8.3 | .. | .. | .. | .. |
| 18 | — 11.9 | — 14.0 | — 9.8 | 4.2 | — 11.3 | — 12.0 | — 7.0 | 5.0 |
| 19 | — 16.2 | — 19.5 | — 12.9 | 6.6 | — 10.8 | — 16.5 | — 3.2 | 13.3 |
| 20 | — 9.1 | — 23.8 | — 14.4 | 9.4 | — 13.2 | — 16.0 | — 10.0 | 6.0 |
| 21 | — 17.9 | — 21.4 | — 14.4 | 7.0 | — 13.3 | — 17.8 | — 8.2 | 9.6 |
| 22 | — 21.5 | — 25.5 | — 17.5 | 8.0 | — 13.8 | — 17.8 | — 9.3 | 8.5 |

Table 40 (continued)

**April 1932**

| Date | Air | | | | Surface of soil | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | Min. | Max. | Ampl. | Mean | Min. | Max. | Ampl. |
| 23 | — 18.6 | — 23.8 | — 13.4 | 10.4 | — 12.6 | — 16.5 | — 7.1 | 9.4 |
| 24 | — 18.4 | — 22.5 | — 14.2 | 8.3 | — 12.2 | — 16.0 | — 6.6 | 9.4 |
| 25 | — 15.0 | — 20.7 | — 9.2 | 11.7 | — 11.3 | — 16.0 | — 4.7 | 11.3 |
| 26 | — 19.6 | — 26.6 | — 12.5 | 14.1 | — 11.3 | — 16.6 | — 4.3 | 12.3 |
| 27 | — 19.4 | — 26.1 | — 12.6 | 13.5 | — 11.2 | — 16.1 | — 4.2 | 11.9 |
| 28 | — 17.6 | — 23.4 | — 11.7 | 11.7 | — 10.0 | — 14.1 | — 3.0 | 11.1 |
| 29 | — 15.0 | — 22.0 | — 7.9 | 14.1 | — 9.0 | — 14.5 | — 3.0 | 11.5 |
| 30 | — 9.7 | — 16.5 | — 2.8 | 13.7 | — 6.6 | — 12.0 | — 0.2 | 11.8 |

**May 1932**

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 1 | — 10.6 | — 15.6 | — 5.6 | 10.0 | — 6.3 | — 11.9 | 0.0 | 11.9 |
| 2 | — 1.9 | — 13.8 | 10.1 | 23.9 | — 1.1 | — 10.1 | 12.6 | 22.7 |
| 3 | — 2.6 | — 10.0 | 4.9 | 14.9 | 5.0 | — 3.9 | 17.0 | 22.9 |
| 4 | — 1.9 | — 7.5 | 3.8 | 11.3 | 5.7 | — 3.9 | 17.6 | 21.5 |
| 5 | — 1.5 | — 6.0 | 3.1 | 9.1 | 5.0 | — 2.0 | 18.5 | 20.5 |
| 6 | 0.2 | — 2.7 | 3.1 | 5.8 | 6.0 | — 2.2 | 18.8 | 21.0 |
| 7 | — 1.9 | — 6.5 | 2.8 | 9.3 | 6.0 | — 3.0 | 19.5 | 22.5 |
| 8 | — 3.0 | — 7.5 | 1.6 | 9.1 | 6.0 | — 2.9 | 21.0 | 23.9 |
| 9 | — 1.9 | — 4.8 | 1.1 | 5.9 | 4.3 | — 1.4 | 19.0 | 20.4 |
| 10 | — 1.9 | — 3.0 | — 0.7 | 2.3 | 2.7 | — 0.6 | 8.1 | 8.7 |
| 11 | — 2.0 | — 3.5 | — 0.4 | 3.1 | 1.8 | — 1.1 | 12.6 | 13.7 |
| 12 | — 3.8 | — 4.6 | — 2.9 | 1.7 | 3.0 | — 3.5 | 12.0 | 15.5 |
| 13 | — 7.8 | — 12.0 | — 3.5 | 8.5 | 4.8 | — 4.7 | 18.6 | 23.3 |
| 14 | — 6.8 | — 12.3 | — 1.3 | 11.0 | 5.3 | — 4.0 | 19.5 | 23.5 |
| 15 | — 3.8 | — 9.8 | 2.2 | 12.0 | 6.5 | — 3.0 | 20.0 | 23.0 |
| 16 | 0.7 | — 5.0 | 6.3 | 11.3 | 7.0 | — 1.2 | 21.9 | 23.0 |
| 17 | — 0.2 | — 4.7 | 4.4 | 9.1 | 7.3 | — 1.0 | 22.0 | 23.0 |
| 18 | 0.4 | — 4.0 | 4.8 | 8.8 | 7.5 | — 1.5 | 22.0 | 23.5 |
| 19 | 2.9 | — 3.8 | 9.6 | 13.4 | 8.3 | — 1.0 | 24.5 | 25.5 |
| 20 | 1.3 | — 3.2 | 5.8 | 9.0 | 5.1 | — 0.8 | 18.0 | 18.8 |
| 21 | — 1.0 | — 2.4 | 0.4 | 2.8 | 5.5 | — 1.5 | 17.1 | 18.6 |
| 22 | — 2.7 | — 7.0 | 1.6 | 8.6 | 6.5 | — 1.3 | 16.0 | 17.3 |
| 23 | 1.1 | — 4.7 | 7.0 | 11.7 | 5.7 | 0.0 | 13.5 | 13.5 |
| 24 | 0.3 | — 2.5 | 3.1 | 5.6 | 5.9 | 0.5 | 12.1 | 12.6 |
| 25 | 2.5 | — 4.6 | 9.6 | 14.2 | 6.3 | 0.0 | 15.0 | 15.0 |
| 26 | 3.7 | — 3.2 | 11.8 | 15.0 | 6.4 | 0.0 | 12.0 | 12.0 |
| 27 | 7.0 | 3.8 | 10.2 | 14.0 | 7.4 | 0.0 | 16.0 | 16.0 |
| 28 | 3.2 | — 0.9 | 7.2 | 8.1 | 6.8 | 0.0 | 16.0 | 16.0 |
| 29 | 2.5 | — 0.7 | 5.7 | 6.4 | 9.2 | 0.0 | 24.9 | 24.9 |
| 30 | 2.4 | — 2.0 | 6.8 | 8.8 | 7.3 | 0.0 | 20.8 | 20.8 |
| 31 | 0.9 | — 1.7 | 3.5 | 5.2 | 10.7 | 0.0 | 24.0 | 24.0 |

Table 40 (continued)

**June 1932**

| Date | Air | | | | Surface of soil | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | Min. | Max. | Ampl. | Mean | Min. | Max. | Ampl. |
| 1 | 1.4 | — 1.4 | 4.2 | 5.6 | 10.4 | 0.1 | 24.0 | 23.9 |
| 2 | — 0.4 | — 2.4 | 1.6 | 4.0 | 7.8 | — 0.8 | 20.1 | 20.9 |
| 3 | — 0.8 | — 4.5 | 3.0 | 7.5 | 10.3 | 0.0 | 24.0 | 24.0 |
| 4 | 2.8 | — 1.0 | 6.5 | 7.5 | 12.3 | 1.0 | 24.5 | 23.5 |
| 5 | 3.0 | — 0.5 | 6.5 | 7.0 | 12.3 | 1.0 | 25.1 | 24.1 |
| 6 | 6.3 | — 2.5 | 15.0 | 17.0 | 10.8 | 1.0 | 25.0 | 24.0 |
| 7 | 8.8 | 6.0 | 11.5 | 5.5 | 15.2 | 1.0 | 35.0 | 34.0 |
| 8 | 5.8 | 2.0 | 9.5 | 7.5 | 10.3 | 1.0 | 24.5 | 23.5 |
| 9 | 1.5 | — 0.5 | 3.5 | 3.0 | 9.5 | 0.4 | 29.0 | 28.0 |
| 10 | 0.8 | — 1.5 | 3.0 | 4.5 | 11.8 | — 3.0 | 33.2 | 36.2 |
| 11 | 2.0 | — 3.0 | 7.0 | 10.0 | 9.8 | — 2.8 | 26.2 | 29.0 |
| 12 | 4.5 | — 2.5 | 11.5 | 14.0 | 14.6 | — 2.0 | 37.4 | 39.4 |
| 13 | 6.3 | — 0.5 | 13.0 | 13.5 | 10.4 | — 2.2 | 34.0 | 36.2 |
| 14 | 4.8 | 0.0 | 9.5 | 9.5 | 10.7 | — 2.2 | 32.1 | 34.3 |
| 15 | 3.3 | — 0.5 | 7.0 | 7.5 | 14.1 | — 1.0 | 34.3 | 25.3 |
| 16 | 8.0 | 1.5 | 14.5 | 13.0 | 14.3 | 1.0 | 24.9 | 23.9 |
| 17 | 13.8 | 10.5 | 17.0 | 6.5 | 16.6 | 6.0 | 32.5 | 26.5 |
| 18 | 12.0 | 3.5 | 20.5 | 17.0 | 22.4 | 8.2 | 40.6 | 32.4 |
| 19 | 13.5 | 7.0 | 20.0 | 13.0 | 18.0 | 10.8 | 30.5 | 19.7 |
| 20 | 13.0 | 7.5 | 18.5 | 11.0 | 20.9 | 3.9 | 42.0 | 38.1 |
| 21 | 9.3 | 5.0 | 13.5 | 8.5 | 19.8 | 5.2 | 40.9 | 35.7 |
| 22 | 6.0 | 2.0 | 10.0 | 8.0 | 11.4 | 3.0 | 23.1 | 20.1 |
| 23 | 4.0 | 0.5 | 7.5 | 7.0 | 13.2 | 3.0 | 31.1 | 28.1 |
| 24 | 9.8 | 3.0 | 16.5 | 13.5 | 16.3 | 4.7 | 36.8 | 31.1 |
| 25 | 12.0 | 6.0 | 16.0 | 10.0 | 14.9 | 4.9 | 43.2 | 38.3 |
| 26 | 7.3 | 3.0 | 11.5 | 8.5 | 15.0 | 2.2 | 40.6 | 38.4 |
| 27 | 6.3 | 3.0 | 9.5 | 6.5 | 7.6 | 2.0 | 15.2 | 13.2 |
| 28 | 5.8 | 2.0 | 9.5 | 7.5 | 7.9 | 2.2 | 16.1 | 13.9 |
| 29 | 6.3 | 3.0 | 9.5 | 6.5 | 11.4 | 5.6 | 27.5 | 21.9 |
| 30 | 7.8 | 5.0 | 10.5 | 5.5 | 9.8 | 3.4 | 18.1 | 14.7 |
| **July 1932** | | | | | | | | |
| 1 | 7.5 | 4.5 | 10.5 | 6.0 | 14.4 | 3.2 | 38.8 | 36.5 |
| 2 | 8.3 | 5.0 | 11.5 | 6.5 | 18.4 | 4.8 | 40.0 | 35.2 |
| 3 | (7.9) | .. | .. | .. | 16.3 | 5.8 | 30.0 | 24.2 |
| 4 | 7.5 | 5.0 | 10.0 | 5.0 | 14.0 | 1.0 | 29.8 | 28.8 |
| 5 | 7.3 | 4.0 | 10.5 | 6.5 | 16.8 | 2.0 | 40.8 | 38.8 |
| 6 | 7.8 | 3.5 | 12.0 | 8.5 | 18.4 | 4.0 | 42.2 | 38.2 |
| 7 | 8.0 | 4.5 | 11.5 | 7.5 | 17.6 | 5.9 | 40.9 | 35.0 |
| 8 | 7.1 | 4.7 | 9.4 | 4.7 | 7.3 | 4.9 | 10.8 | 5.9 |
| 9 | 6.8 | 4.1 | 9.6 | 5.1 | 13.0 | 5.9 | 30.0 | 24.1 |
| 10 | 6.5 | 4.5 | 8.5 | 4.0 | 11.0 | 6.2 | 18.6 | 12.4 |
| 11 | 7.0 | 5.5 | 8.5 | 3.0 | 12.8 | 6.3 | 29.5 | 23.3 |
| 12 | 7.0 | 5.0 | 9.0 | 4.0 | 14.0 | 6.1 | 29.8 | 23.7 |
| 13 | 8.3 | 6.0 | 10.5 | 4.5 | 16.8 | 4.8 | 32.9 | 28.1 |
| 14 | 8.0 | 5.5 | 10.5 | 5.0 | 15.1 | 4.9 | 37.0 | 32.1 |

Table 40 (continued)

**July 1932**

| Date | Air | | | | Surface of soil | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | Min. | Max. | Ampl. | Mean | Min. | Max. | Ampl. |
| 15 | 8.0 | 5.0 | 11.0 | 6.0 | 15.8 | 3.0 | 39.5 | 36.5 |
| 16 | 8.8 | 5.5 | 12.0 | 6.5 | 18.2 | 4.0 | 41.0 | 37.0 |
| 17 | 7.8 | 6.5 | 11.0 | 4.5 | 14.0 | 5.9 | 29.0 | 23.1 |
| 18 | 7.5 | 5.0 | 10.0 | 5.0 | 15.1 | 2.9 | 41.3 | 38.4 |
| 19 | 9.1 | 6.5 | 11.7 | 5.2 | 19.3 | 6.0 | 41.5 | 35.5 |
| 20 | 12.5 | 8.2 | 16.8 | 8.6 | 17.8 | 3.8 | 40.0 | 36.2 |
| 21 | 12.5 | 8.7 | 16.2 | 7.5 | 19.4 | 3.9 | 44.1 | 40.2 |
| 22 | 11.8 | 8.5 | 15.2 | 6.7 | 17.6 | 4.8 | 39.5 | 34.7 |
| 23 | 12.8 | 9.2 | 16.4 | 5.2 | 17.1 | 4.2 | 41.0 | 36.8 |
| 24 | 12.5 | 7.2 | 17.7 | 10.5 | 17.3 | 5.3 | 30.8 | 35.5 |
| 25 | 9.9 | 10.9 | 18.8 | 7.9 | 15.8 | 5.5 | 34.5 | 29.0 |
| 26 | 15.1 | 10.5 | 19.6 | 9.1 | 17.6 | 5.8 | 38.1 | 33.7 |
| 27 | 14.4 | 9.7 | 19.1 | 9.4 | 17.5 | 3.1 | 41.5 | 38.4 |
| 28 | (13.5) | .. | .. | .. | 17.9 | 3.8 | 40.1 | 36.3 |
| 29 | 12.6 | 8.0 | 17.2 | 9.2 | 17.8 | 3.0 | 41.5 | 38.5 |
| 30 | 11.3 | 8.0 | 14.5 | 6.5 | 20.3 | 3.1 | 46.0 | 42.9 |
| 31 | (11.5) | .. | .. | .. | 19.8 | 2.2 | 45.2 | 43.0 |
| **August 1932** | | | | | | | | |
| 1 | 11.8 | 8.0 | 15.5 | 7.5 | 16.8 | 3.0 | 49.0 | 46.0 |
| 2 | 6.8 | 5.0 | 8.5 | 3.5 | 8.9 | 4.6 | 15.8 | 11.2 |
| 3 | 6.8 | 5.0 | 8.5 | 3.5 | 8.6 | 4.0 | 15.1 | 11.1 |
| 4 | 9.3 | 6.5 | 12.0 | 5.5 | 16.3 | 0.0 | 39.0 | 39.0 |
| 5 | 10.3 | 5.0 | 15.5 | 10.5 | 16.5 | 0.5 | 42.9 | 42.4 |
| 6 | 10.8 | 7.0 | 14.5 | 7.5 | 17.7 | 0.5 | 44.8 | 44.3 |
| 7 | .. | .. | .. | .. | 17.0 | — 0.2 | 45.1 | 45.3 |
| 8 | .. | .. | .. | .. | 14.9 | 0.0 | 45.1 | 45.1 |
| 9 | 9.8 | 4.0 | 15.5 | 11.5 | 16.2 | 3.6 | 38.7 | 35.1 |
| 10 | 9.3 | 2.0 | 16.5 | 14.5 | 15.8 | 6.2 | 44.5 | 38.3 |
| 11 | 8.8 | 5.5 | 12.0 | 6.5 | 13.4 | 4.9 | 35.7 | 32.8 |
| 12 | 8.3 | 5.5 | 11.0 | 5.5 | 12.3 | 5.0 | 36.0 | 31.0 |
| 13 | 7.5 | 5.0 | 10.0 | 5.0 | 10.1 | 0.9 | 23.0 | 22.1 |
| 14 | 9.0 | 5.5 | 12.5 | 7.0 | 12.9 | 1.5 | 34.9 | 33.4 |
| 15 | 8.3 | 6.0 | 10.5 | 4.5 | 13.9 | 0.5 | 43.8 | 43.3 |
| 16 | 8.8 | 4.5 | 13.0 | 8.5 | 14.9 | 5.0 | 36.6 | 31.6 |
| 17 | 9.3 | 6.5 | 12.0 | 5.5 | 10.8 | 3.6 | 22.2 | 18.6 |
| 18 | 8.8 | 6.5 | 11.0 | 4.5 | 10.4 | 1.0 | 33.1 | 32.1 |
| 19 | .. | .. | .. | .. | 8.3 | 0.6 | 16.5 | 15.9 |
| 20 | .. | .. | .. | .. | 9.2 | — 4.1 | 30.3 | 34.4 |
| 21 | 9.3 | 2.3 | 16.2 | 13.9 | 13.1 | — 1.5 | 32.5 | 34.0 |
| 22 | 10.4 | 8.0 | 12.7 | 4.7 | 15.2 | 2.0 | 46.0 | 44.0 |
| 23 | 6.5 | 4.1 | 8.8 | 4.7 | .. | .. | .. | .. |
| 24 | (6.3) | .. | 8.6 | .. | .. | .. | .. | .. |
| 25 | 3.7 | 1.5 | 5.9 | 4.4 | .. | .. | .. | .. |
| 26 | 4.0 | 1.0 | 7.0 | 6.0 | .. | .. | .. | .. |

Table 41. Mean temperature of twenty-four hours for the air, and mean temperatures, minimum and maximum temperatures, and amplitude for the soil surface (S. exp. c. 8°) at Eskimonæs, September 1934, and April—August 1935. (Temp. in C.°).

**September 1934**

| Date | Air | Surface of soil | | | |
|---|---|---|---|---|---|
| | Mean | Mean | Min. | Max. | Ampl. |
| 1..... | 5.1 | 5.8 | 0.0 | 16.0 | 16.0 |
| 2..... | 4.4 | 6.4 | 0.0 | 16.8 | 16.8 |
| 3..... | 2.1 | 6.3 | 2.0 | 14.5 | 12.5 |
| 4..... | 3.2 | 3.7 | 2.5 | 5.6 | 3.1 |
| 5..... | 3.9 | 4.4 | 1.8 | 7.6 | 5.8 |
| 6..... | 3.3 | 4.7 | 2.5 | 7.5 | 5.0 |
| 7..... | .. | 4.2 | — 1.0 | 14.0 | 15.0 |
| 8..... | .. | 2.6 | — 1.6 | 11.6 | 13.2 |
| 9..... | 2.4 | 3.2 | — 1.5 | 10.5 | 12.0 |
| 10..... | 3.3 | 3.8 | 1.0 | 7.8 | 6.8 |
| 11..... | 2.6 | 3.7 | 0.0 | 10.0 | 10.0 |
| 12..... | 1.7 | 2.3 | — 1.9 | 6.0 | 7.9 |
| 13..... | .. | 1.1 | — 1.9 | 3.1 | 5.0 |
| 14..... | .. | 2.5 | — 0.4 | 7.0 | 7.4 |
| 15..... | .. | 1.0 | — 1.8 | 6.8 | 8.6 |
| 16..... | — 0.7 | 0.5 | — 2.0 | 7.6 | 9.6 |
| 17..... | — 1.5 | — 0.2 | — 1.7 | 2.9 | 4.6 |
| 18..... | — 1.4 | — 0.5 | — 0.2 | 0.1 | 0.3 |
| 19..... | 3.2 | 0.8 | — 1.0 | 1.8 | 2.8 |
| 20..... | 2.9 | 1.2 | 0.0 | 3.0 | 3.0 |
| 21..... | 1.7 | 0.5 | 0.0 | 1.2 | 1.2 |
| 22..... | .. | 1.3 | 1.0 | 2.0 | 1.0 |
| 23..... | 1.4 | 1.3 | 0.5 | 2.8 | 2.3 |
| 24..... | — 0.1 | 0.6 | 0.0 | 1.0 | 1.0 |
| 25..... | 0.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| 26..... | 0.3 | 0.0 | 0.0 | 0.1 | 0.1 |
| 27..... | 1.8 | 0.0 | 0.0 | 0.2 | 0.2 |
| 28..... | 2.2 | 0.0 | — 0.2 | 0.2 | 0.4 |
| 29..... | 1.8 | 0.0 | — 1.0 | 0.8 | 1.8 |
| 30..... | 1.1 | 0.7 | 0.0 | 1.0 | 1.0 |

**April 1935**

| | | | | | |
|---|---|---|---|---|---|
| 1..... | — 23.8 | — 20.0 | — 24.0 | — 15.2 | 8.8 |
| 2..... | — 24.1 | — 21.8 | — 24.3 | — 18.0 | 6.3 |
| 3..... | — 23.1 | — 21.3 | — 24.2 | — 16.1 | 8.1 |
| 4..... | — 19.9 | — 20.0 | — 24.0 | — 14.5 | 9.5 |
| 5..... | — 20.0 | — 18.8 | — 22.5 | — 14.2 | 8.3 |
| 6..... | — 16.3 | — 16.7 | — 21.0 | — 11.0 | 10.0 |

Table 41 (continued)

**April 1935**

| Date | Air | Surface of soil | | | |
|---|---|---|---|---|---|
| | Mean | Mean | Min. | Max. | Ampl. |
| 7 | — 20.8 | — 17.8 | — 21.4 | — 11.6 | 9.8 |
| 8 | — 24.4 | — 19.4 | — 21.6 | — 13.9 | 7.7 |
| 9 | — 22.8 | — 19.0 | — 23.0 | — 12.2 | 10.8 |
| 10 | — 21.2 | — 19.1 | — 23.0 | — 12.1 | 10.9 |
| 11 | — 21.3 | — 18.6 | — 22.5 | — 11.5 | 11.0 |
| 12 | — 20.9 | — 18.2 | — 22.8 | — 11.0 | 11.8 |
| 13 | — 19.4 | — 17.7 | — 22.4 | — 12.0 | 10.4 |
| 14 | — 20.1 | — 15.1 | — 21.0 | — 8.0 | 13.0 |
| 15 | — 19.1 | — 14.9 | — 20.0 | — 8.0 | 12.0 |
| 16 | — 21.1 | — 15.0 | — 20.6 | — 8.0 | 12.6 |
| 17 | — 18.4 | — 14.9 | — 20.8 | — 7.2 | 13.6 |
| 18 | — 18.8 | — 15.3 | — 19.4 | — 10.2 | 9.2 |
| 19 | — 15.3 | — 13.8 | — 18.0 | — 8.0 | 10.0 |
| 20 | — 15.1 | — 13.5 | — 18.0 | — 7.2 | 10.8 |
| 21 | — 17.0 | — 13.2 | — 18.0 | — 7.1 | 10.9 |
| 22 | — 12.7 | — 13.2 | — 18.0 | — 10.2 | 7.8 |
| 23 | — 11.0 | — 12.4 | — 15.5 | — 10.6 | 4.9 |
| 24 | — 13.7 | — 14.0 | — 15.5 | — 12.2 | 3.3 |
| 25 | — 9.2 | — 12.5 | — 15.0 | — 10.0 | 5.0 |
| 26 | — 10.0 | — 11.1 | — 14.0 | — 7.2 | 6.8 |
| 27 | — 11.5 | — 9.9 | — 12.9 | — 5.1 | 7.8 |
| 28 | — 8.5 | — 8.6 | — 12.9 | — 5.8 | 7.1 |
| 29 | — 8.4 | — 5.2 | — 10.0 | 0.9 | 10.9 |
| 30 | — 8.5 | — 5.0 | — 10.0 | 1.9 | 11.9 |

**May 1935**

| | | | | | |
|---|---|---|---|---|---|
| 1 | — 9.2 | — 4.6 | — 10.0 | 1.6 | 11.6 |
| 2 | — 9.0 | — 4.7 | — 9.8 | 0.4 | 10.2 |
| 3 | — 11.4 | — 7.0 | — 8.9 | — 4.2 | 4.7 |
| 4 | — 11.5 | — 5.4 | — 10.0 | 0.4 | 10.4 |
| 5 | — 10.9 | — 4.3 | — 10.0 | 2.8 | 12.8 |
| 6 | — 10.1 | — 3.9 | — 9.2 | 2.1 | 11.3 |
| 7 | — 9.6 | — 4.4 | — 8.8 | 0.5 | 9.3 |
| 8 | — 9.0 | — 4.0 | — 10.0 | 1.0 | 11.0 |
| 9 | — 10.4 | — 4.3 | — 10.0 | 2.0 | 12.0 |
| 10 | — 10.4 | — 3.0 | — 10.0 | 3.2 | 13.2 |
| 11 | — 9.7 | — 2.9 | — 9.0 | 3.6 | 12.6 |
| 12 | — 6.3 | — 1.3 | — 6.5 | 5.2 | 11.7 |
| 13 | — 5.2 | — 0.3 | — 7.0 | 6.6 | 13.6 |
| 14 | — 11.1 | — 2.1 | — 8.0 | 4.0 | 12.0 |
| 15 | — 9.5 | — 1.2 | — 8.0 | 6.9 | 14.9 |

Table 41 (continued)

**May 1935**

| Date | Air | Surface of soil | | | |
|---|---|---|---|---|---|
| | Mean | Mean | Min. | Max. | Ampl. |
| 16 | — 6.8 | — 2.2 | — 6.0 | 2.5 | 8.5 |
| 17 | — 4.0 | 0.2 | — 2.2 | 5.8 | 8.0 |
| 18 | — 6.4 | — 2.0 | — 4.9 | 2.2 | 7.1 |
| 19 | — 9.6 | — 3.6 | — 5.0 | — 2.0 | 3.0 |
| 20 | — 8.4 | — 3.0 | — 4.9 | — 0.9 | 4.0 |
| 21 | — 8.8 | — 4.1 | — 7.0 | — 2.1 | 4.9 |
| 22 | — 6.5 | — 2.1 | — 7.0 | 5.5 | 12.5 |
| 23 | — 6.1 | 0.8 | — 6.0 | 8.9 | 14.9 |
| 24 | — 7.6 | 0.5 | — 3.5 | 6.1 | 9.6 |
| 25 | — 5.5 | — 0.2 | — 3.0 | 4.9 | 7.9 |
| 26 | — 3.2 | 1.2 | — 2.4 | 5.2 | 7.6 |
| 27 | — 2.3 | 2.0 | — 2.4 | 8.0 | 10.4 |
| 28 | — 5.2 | 2.0 | — 1.5 | 8.0 | 9.5 |
| 29 | — 3.8 | 2.3 | — 1.4 | 8.0 | 9.4 |
| 30 | — 3.2 | 2.0 | — 1.0 | 6.1 | 7.1 |
| 31 | — 3.2 | 3.7 | — 0.1 | 9.5 | 9.6 |

**June 1935**

| | | | | | |
|---|---|---|---|---|---|
| 1 | — 4.1 | 4.3 | — 1.3 | 11.4 | 12.3 |
| 2 | — 3.6 | 2.2 | — 1.0 | 8.6 | 9.6 |
| 3 | — 2.0 | 5.3 | — 0.2 | 14.4 | 14.6 |
| 4 | — 3.1 | 5.7 | 0.0 | 14.5 | 14.5 |
| 5 | — 2.6 | 4.8 | 0.0 | 10.0 | 10.1 |
| 6 | — 4.9 | 2.9 | — 0.8 | 9.4 | 10.2 |
| 7 | — 4.3 | 2.0 | — 0.4 | 6.0 | 6.4 |
| 8 | — 0.4 | 5.3 | 0.0 | 12.0 | 12.0 |
| 9 | — 1.9 | 5.9 | — 0.6 | 15.1 | 15.7 |
| 10 | — 3.5 | 6.5 | 0.9 | 15.0 | 14.1 |
| 11 | — 3.3 | 6.0 | 0.0 | 14.5 | 14.5 |
| 12 | 0.6 | 6.7 | 0.0 | 16.1 | 16.1 |
| 13 | 2.0 | 7.5 | 0.2 | 16.8 | 16.6 |
| 14 | 1.0 | 6.7 | 0.6 | 15.0 | 14.4 |
| 15 | — 1.7 | 6.4 | 0.8 | 15.4 | 14.6 |
| 16 | — 3.8 | 6.7 | 0.7 | 14.1 | 13.4 |
| 17 | — 4.2 | 4.5 | 0.0 | 10.9 | 10.9 |
| 18 | — 3.5 | 5.7 | 0.0 | 14.2 | 14.2 |
| 19 | — 1.9 | 6.9 | 1.5 | 15.0 | 13.5 |
| 20 | 3.5 | 7.7 | 0.5 | 18.0 | 17.5 |
| 21 | — 0.6 | 5.8 | 1.0 | 11.8 | 10.8 |
| 22 | 1.5 | 7.2 | 2.5 | 13.0 | 10.5 |
| 23 | 1.5 | 9.8 | 3.8 | 17.8 | 14.0 |

Table 41 (continued).

**June 1935**

| Date | Air | Surface of soil | | | |
|---|---|---|---|---|---|
| | Mean | Mean | Min. | Max. | Ampl. |
| 24..... | —0.6 | 5.1 | 2.1 | 10.0 | 8.0 |
| 25..... | 1.2 | 7.5 | 0.5 | 16.6 | 16.1 |
| 26..... | —1.3 | 7.4 | 1.0 | 16.9 | 15.9 |
| 27..... | 0.3 | 9.1 | 0.5 | 18.8 | 18.3 |
| 28..... | 3.9 | 11.8 | 2.5 | 22.4 | 19.9 |
| 29..... | 5.6 | 13.2 | 2.4 | 24.0 | 21.6 |
| 30..... | 2.4 | 11.1 | 2.1 | 23.0 | 20.9 |

**July 1935**

| | | | | | |
|---|---|---|---|---|---|
| 1..... | —0.3 | 6.5 | 1.0 | 13.8 | 12.8 |
| 2..... | —0.1 | 7.3 | 2.0 | 20.8 | 18.8 |
| 3..... | 0.7 | 9.2 | 0.0 | 20.8 | 20.8 |
| 4..... | —0.9 | 6.7 | 1.1 | 13.5 | 12.4 |
| 5..... | 1.0 | 11.9 | 2.0 | 26.9 | 24.9 |
| 6..... | 3.7 | 12.7 | 4.4 | 27.0 | 22.6 |
| 7..... | 1.7 | 10.6 | 1.0 | 22.7 | 21.7 |
| 8..... | 0.0 | 9.0 | 2.0 | 20.0 | 18.0 |
| 9..... | —0.5 | 8.8 | 1.9 | 19.5 | 17.6 |
| 10..... | 0.8 | 4.5 | 2.1 | 6.3 | 4.2 |
| 11..... | 2.1 | 9.0 | 0.2 | 19.1 | 18.9 |
| 12..... | 0.2 | 5.0 | 1.4 | 12.1 | 10.7 |
| 13..... | 2.6 | 7.3 | 3.1 | 14.1 | 11.0 |
| 14..... | 1.3 | 10.8 | 1.9 | 22.5 | 20.6 |
| 15..... | 0.6 | 8.4 | 1.8 | 19.8 | 18.0 |
| 16..... | 2.9 | 8.8 | 3.7 | 17.0 | 13.3 |
| 17..... | 1.9 | 7.5 | 1.8 | 15.0 | 13.2 |
| 18..... | 0.2 | 5.5 | 2.1 | 10.2 | 8.1 |
| 19..... | 1.5 | 6.4 | 2.5 | 14.0 | 11.5 |
| 20..... | —0.4 | 6.3 | 3.0 | 13.5 | 10.5 |
| 21..... | 3.0 | 5.7 | 3.1 | 11.5 | 8.4 |
| 22..... | 0.8 | 4.7 | 0.1 | 10.0 | 9.9 |
| 23..... | 0.5 | 8.2 | 0.8 | 18.8 | 18.0 |
| 24..... | 2.4 | 9.0 | 2.0 | 19.5 | 17.5 |
| 25..... | 2.7 | 8.4 | 3.0 | 15.9 | 12.9 |
| 26..... | 3.3 | 7.9 | 3.0 | 18.1 | 15.1 |
| 27..... | 3.3 | 10.0 | 0.5 | 23.1 | 22.6 |
| 28..... | 3.5 | 11.1 | 1.0 | 24.6 | 23.6 |
| 29..... | 5.1 | 10.8 | 1.3 | 25.6 | 24.3 |
| 30..... | 6.4 | 11.5 | 4.0 | 23.8 | 19.8 |
| 31..... | 5.1 | 10.3 | 4.1 | 23.0 | 18.9 |

Table 41 (continued)

**August 1935**

| Date | Air | Surface of soil | | | |
|---|---|---|---|---|---|
| | Mean | Mean | Min. | Max. | Ampl. |
| 1..... | 1.9 | 5.5 | 2.2 | 8.9 | 6.7 |
| 2..... | 2.2 | 4.7 | 2.5 | 7.8 | 5.3 |
| 3..... | 2.1 | 6.5 | 1.5 | 16.0 | 14.5 |
| 4..... | 2.1 | 7.4 | — 0.7 | 16.0 | 16.7 |
| 5..... | 1.5 | 7.3 | — 1.0 | 17.0 | 18.0 |
| 6..... | 0.4 | 6.8 | 1.8 | 14.6 | 12.8 |
| 7..... | 2.4 | 6.2 | 3.1 | 11.2 | 8.0 |
| 8..... | 2.1 | 6.1 | 2.9 | 10.9 | 8.0 |
| 9..... | 1.8 | 6.5 | 2.1 | 15.5 | 13.4 |
| 10..... | 2.9 | 6.0 | 2.1 | 11.0 | 8.9 |
| 11..... | 3.8 | 8.6 | 2.1 | 19.4 | 17.3 |
| 12..... | 3.9 | 7.1 | — 1.0 | 18.8 | 19.8 |
| 13..... | 2.7 | 7.1 | — 1.0 | 19.7 | 20.7 |
| 14..... | 2.0 | 7.0 | — 1.0 | 18.7 | 19.7 |

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Færdig fra Trykkeriet den 13. November 1941.

# PLATES

## Plate 1.

**Wintering stages of the flora of Northeast Greenland.**

Fig. 1. *Carex alpina.* Inflorescence × 10. Terminal spike with male flowers only at the base, side spikes female.

Fig. 2. *Carex alpina.* Apex of the terminal spike × 27. Secondary axes of the female flowers of a distinctly compound character, bearing rudimentary leaf primordia.

Fig. 3. *Carex alpina.* Secondary female axis, at the base of the ovary the utricle. × 33.

Fig. 4. *Carex alpina.* Male flower with its supporting scale × 27.

Fig. 5. *Carex aquatilis stans.* Inflorescence × 10. The female spikes at the base very small, the lowermost with a leafy bract.

Fig. 6. *Carex atrofusca.* Male flower with scale × 27. The anthers only in incipient differentiation; filaments not developed.

Fig. 7. *Carex atrofusca.* Two female secondary axes with their supporting scales × 27. Secondary axes distinctly compound with rudimentary leaf primordia and axillary growing points. At the base the utricle, visible as a leafy process.

Fig. 8. *Carex capillaris.* Inflorescence × 10. Terminal spike male, side spikes female, the lowermost with a leafy bract.

Fig. 9. *Carex capillaris.* Female spike × 27. The two first stigmas of the pistil and the utricles visible.

Fig. 10. *Carex capillaris.* Male flower with its scale × 27.

Fig. 11. *Carex Lachenalii.* Inflorescence × 10. The stalk is unusually much stretched. The side spikes, appressed to the terminal one, hardly visible.

Fig. 12. *Carex Lachenalii.* Fragment of the terminal spike at the transition from the male to the female part, × 27. One male and two female flowers are seen. Pistils with long stigmas, utricles already urn-shaped, reaching to the base of the stigmas.

Fig. 13. *Carex microglochin.* Spike × 27. Female at the base, male at the apex.

Fig. 14. *Carex microglochin.* Female flower × 33. The secondary axis recognisable by its breath and two lateral protuberances, a nodus, is seen protruding from the inside of the utricle, in front of the two stigmas.

Fig. 15. *Carex misandra.* Inflorescence × 10. The terminal spike male at the base, female at the apex. Side spikes female.

Fig. 16. *Carex misandra.* Fragment of the terminal spike at the transition from the male to the female part × 27. A male and a female flower with their scales are seen. Within the utricle of the female flower the short blunt secondary axis is seen, and above this the ovule.

Fig. 17. *Carex nardina.* Spike × 10. Female at the base, male at the apex.

Fig. 18. *Carex nardina.* Female flower × 33. Within the utricle the very short secondary axis is seen, and within the pistil the ovule.

Fig. 19. *Carex nardina.* Growing point at the transition to the "floral" stage × 33.— The shoot is in the last wintering but one before flowering.

Fig 20. *Carex parallela.* Female spike × 10.

Fig. 21. *Carex parallela.* Female flower × 27. The utricle reaches halfway up the stigmas.

Fig. 22. *Carex pedata.* Inflorescence × 10. Terminal spike male, side spike female.

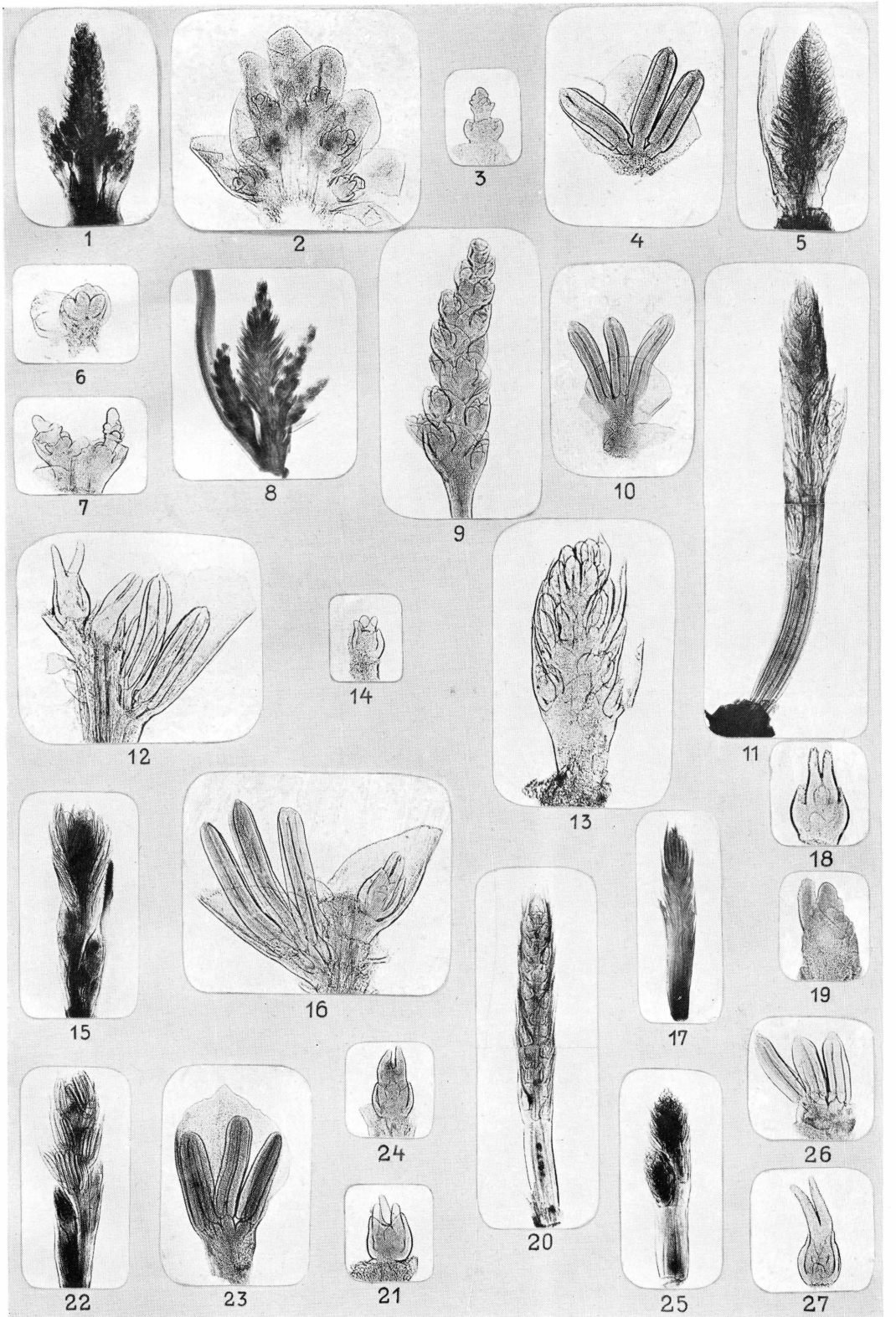
Fig. 23. *Carex pedata.* Male flower with its scale × 27.

Fig. 24. *Carex pedata.* Female flower × 27. Within the pistil the ovule can be seen.

Fig. 25. *Carex pseudolagopina.* Inflorescence × 10. Terminal spike male at the base, female in the upper part. Side spike female with one male flower at the base.

Fig. 26. *Carex pseudolagopina.* Male flower × 27.

Fig. 27. *Carex pseudolagopina.* Female flower × 27. The utricle is seen to be very deeply split. Within the utricle the short, blunt secondary axis is seen at the base of the pistil.


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## Plate 2.

**Wintering stages of the flora of Northeast Greenland.**

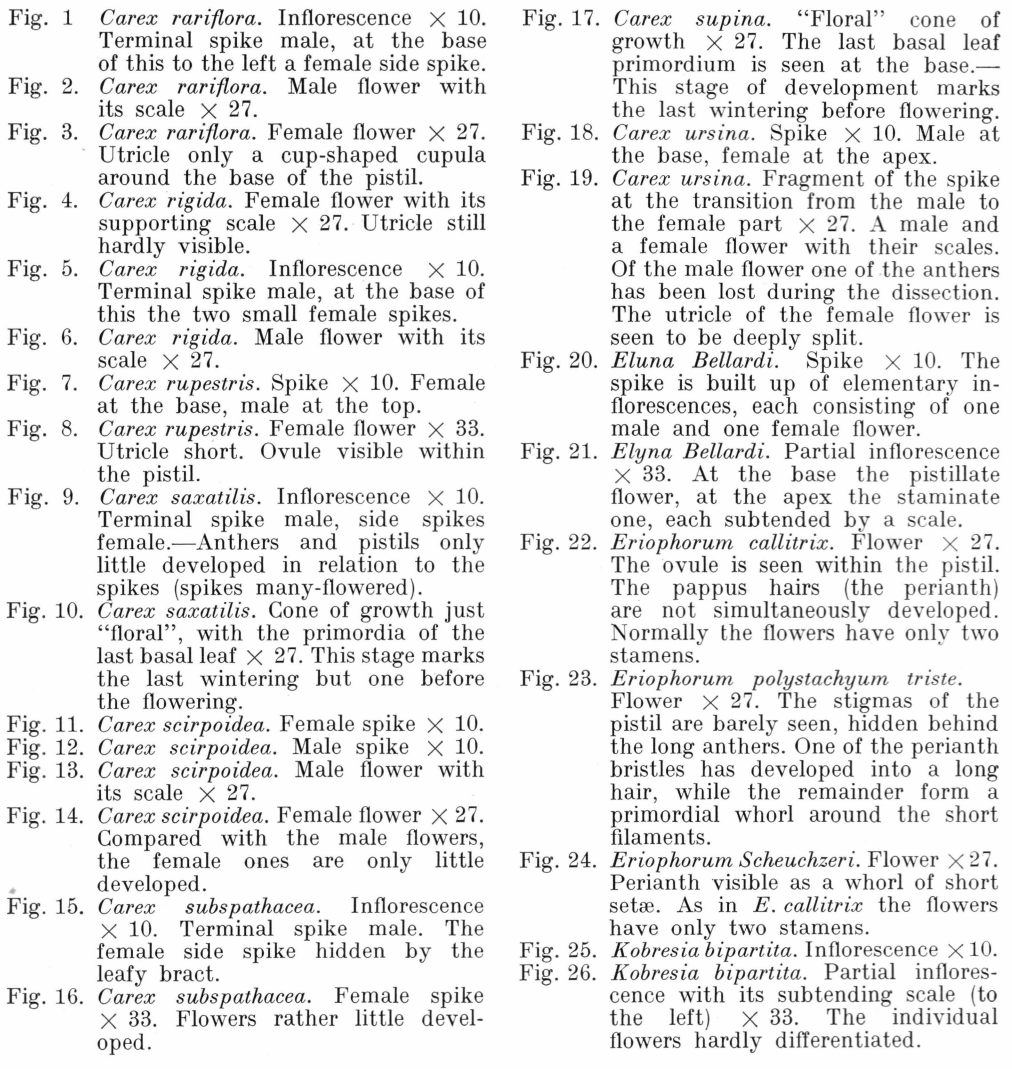
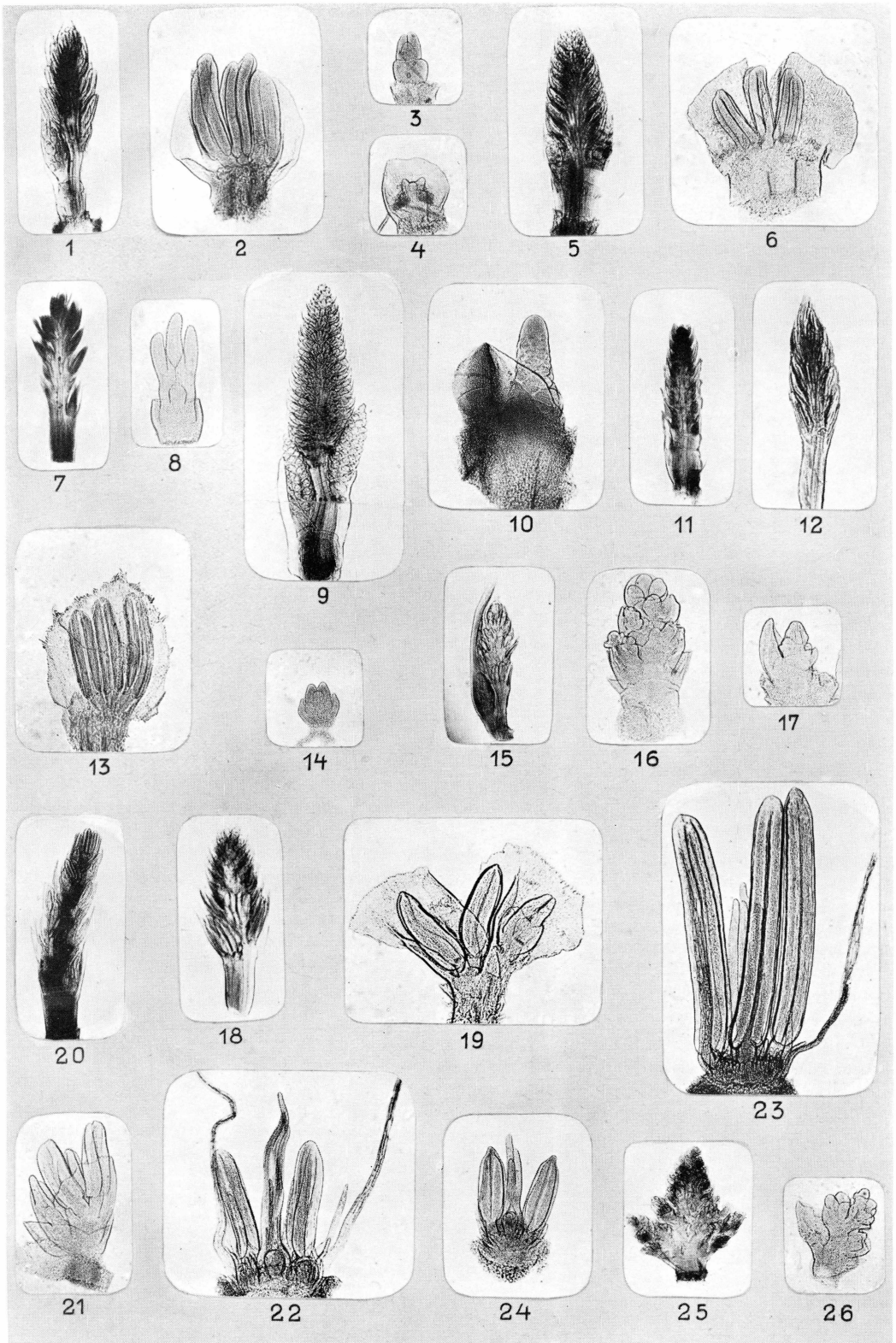


Fig. 1 *Carex rariflora.* Inflorescence × 10. Terminal spike male, at the base of this to the left a female side spike.
Fig. 2. *Carex rariflora.* Male flower with its scale × 27.
Fig. 3. *Carex rariflora.* Female flower × 27. Utricle only a cup-shaped cupula around the base of the pistil.
Fig. 4. *Carex rigida.* Female flower with its supporting scale × 27. Utricle still hardly visible.
Fig. 5. *Carex rigida.* Inflorescence × 10. Terminal spike male, at the base of this the two small female spikes.
Fig. 6. *Carex rigida.* Male flower with its scale × 27.
Fig. 7. *Carex rupestris.* Spike × 10. Female at the base, male at the top.
Fig. 8. *Carex rupestris.* Female flower × 33. Utricle short. Ovule visible within the pistil.
Fig. 9. *Carex saxatilis.* Inflorescence × 10. Terminal spike male, side spikes female.—Anthers and pistils only little developed in relation to the spikes (spikes many-flowered).
Fig. 10. *Carex saxatilis.* Cone of growth just "floral", with the primordia of the last basal leaf × 27. This stage marks the last wintering but one before the flowering.
Fig. 11. *Carex scirpoidea.* Female spike × 10.
Fig. 12. *Carex scirpoidea.* Male spike × 10.
Fig. 13. *Carex scirpoidea.* Male flower with its scale × 27.
Fig. 14. *Carex scirpoidea.* Female flower × 27. Compared with the male flowers, the female ones are only little developed.
Fig. 15. *Carex subspathacea.* Inflorescence × 10. Terminal spike male. The female side spike hidden by the leafy bract.
Fig. 16. *Carex subspathacea.* Female spike × 33. Flowers rather little developed.
Fig. 17. *Carex supina.* "Floral" cone of growth × 27. The last basal leaf primordium is seen at the base.—This stage of development marks the last wintering before flowering.
Fig. 18. *Carex ursina.* Spike × 10. Male at the base, female at the apex.
Fig. 19. *Carex ursina.* Fragment of the spike at the transition from the male to the female part × 27. A male and a female flower with their scales. Of the male flower one of the anthers has been lost during the dissection. The utricle of the female flower is seen to be deeply split.
Fig. 20. *Eluna Bellardi.* Spike × 10. The spike is built up of elementary inflorescences, each consisting of one male and one female flower.
Fig. 21. *Elyna Bellardi.* Partial inflorescence × 33. At the base the pistillate flower, at the apex the staminate one, each subtended by a scale.
Fig. 22. *Eriophorum callitrix.* Flower × 27. The ovule is seen within the pistil. The pappus hairs (the perianth) are not simultaneously developed. Normally the flowers have only two stamens.
Fig. 23. *Eriophorum polystachyum triste.* Flower × 27. The stigmas of the pistil are barely seen, hidden behind the long anthers. One of the perianth bristles has developed into a long hair, while the remainder form a primordial whorl around the short filaments.
Fig. 24. *Eriophorum Scheuchzeri.* Flower × 27. Perianth visible as a whorl of short setæ. As in *E. callitrix* the flowers have only two stamens.
Fig. 25. *Kobresia bipartita.* Inflorescence × 10.
Fig. 26. *Kobresia bipartita.* Partial inflorescence with its subtending scale (to the left) × 33. The individual flowers hardly differentiated.


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## Plate 3.

**Wintering stages of the flora of Northeast Greenland.**

Fig. 1. *Agropyrum violaceum* Inflorescence (spike) and the last basal leaf primordium × 10. Spikelets barely differentiated (normal stage of development).

Fig. 2. *Agropyrum violaceum.* Retarded "floral" cone of growth × 33.

Fig. 3. *Agropyrum violaceum.* Vegetative growing point with the two latest differentiated leaf primordia × 33.

Fig. 4. *Alopecurus alpinus.* Inflorescence (panicle) × 10. (Normal stage of development).

Fig. 5. *Alopecurus alpinus.* Retarded panicle primordium × 10. The branches of the panicle recognisable as rows of protuberances.

Fig. 6. *Alopecurus alpinus.* Two spikelets × 33. (Normal stage of development, cfr. Fig. 4). Carpels and stamens differentiating from the torus. Glumes and pales barely recognisable as rounded protuberances.

Fig. 7. *Arctagrostis latifolia.* Inflorescence (panicle) in its last wintering ×10. (Phasic development as *Alopecurus alpinus*).

Fig. 8. *Arctagrostis latifolia.* Panicle primordium in the last but one wintering × 10. Panicle branches scarcely differentiated.

Fig. 9. *Calamagrostis arundinacea purpurascens.* Inflorescence (panicle × 10. Spikelets not yet differentiated.

Fig. 10. *Deschampsia brevifolia.* Inflorescence (panicle) × 10. Most advanced developmental stage for successful wintering. Spikelets recognisable. Anthers and carpels differentiating.

Fig. 11. *Deschampsia brevifolia.* "Floral" growing cone × 33. Basal part hidden by the last ground leaf primordium. Panicle primordia wintering at this stage of development will pass one more wintering at a stage like that seen in Fig. 10, before flowering.

Fig. 12. *Dupontia Fisheri.* Inflorescence (panicle) × 10.

Fig. 13. Detail of the preceding × 33 showing the one-flowered spikelets. Anthers differentiated, surrounding the urn-shaped pistil.

Fig. 14. *Dupontia Fisheri.* Cone of growth just "floral", in the last wintering but one before the flowering × 10.

Fig. 15. *Festuca brachyphylla "brevifolia".*[1]) Inflorescence (panicle) × 10. Spikelets formed. The awns of the pales considerably longer than the spikelet.

Fig. 16. *Festuca brachyphylla "supina".*[1]) Upper part of a shoot with an inflorence (panicle) × 10. Leaf primordia removed. At the base of the inflorescence the proleptically developing rejuvenating buds are seen.

Fig. 17. *Festuca rubra.* "Floral" cone of growth × 10. At the base to the right the last basal leaf primordium is seen, to the left a rejuvenating bud.

Fig. 18. *Hierochloe alpina.* Vegetative growing point surrounded by the two latest differentiated leaf primordia × 33.

Fig. 19. *Hierochloe alpina.* Panicle branch with three spikelets × 10. The long-awned pales and the glumes are seen. Stamens with short filaments. Pistils closed and two-horned at the apex.

Fig. 20. *Hierochloe alpina.* Cone of growth just "floral" in the last wintering but one before flowering × 33.

Fig. 21. *Phippsia algida.* Inflorescence (panicle) × 10. Spikelets and floral organs differentiated. Common wintering stage.

Fig. 22. *Phippsia algida.* Younger panicle primordium × 10. Primordia in this stage of development normally require one more wintering before flowering.

Fig. 23. *Pleuropogon Sabinei.* Inflorescence (panicle) × 10. Panicle composed by seven many-flowered spikelets, dominated by the large anthers. Glumes and pales very slightly developed.

Fig. 24. *Poa abbreviata.* Inflorescence (panicle) × 10. The 4—6-flowered spikelets differentiated.

Fig. 25. *Poa abbreviata.* Spikelet × 10. Only the lowermost flowers with distinctly differentiated anthers. Glumes distinct. Pales in their first primordial stage.

Fig. 26. *Poa alpigena colpodea.* Panicle × 10. Common wintering stage. Viviparous spikelets hardly differentiated.

Fig. 27. *Poa alpina* (Type 2). Inflorescence (panicle) × 10. Common wintering stage. Spikelets hardly differentiated.

Fig. 28. *Poa alpina* (Type 2). Upper part of panicle killed by the frost during the preceding winter × 10. Glumes and pales distinctly formed. The figure illustrates a developmental stage too advanced for a succesful wintering.

Fig. 29. *Poa alpina* (Type 2). Young panicle primordium ×10.—Primordia wintering at this stage presumably require a whole growth season and one more wintering before flowering, or, under favourable growth conditions, they will develop late flowering panicles already the following summer.

Fig. 30. *Poa alpina* (Type 1). Shoot apex with cone of growth just "floral" × 10. Leaf primordia removed except the last ones. To the right and left rejuvenating buds, giving rise to proleptic shoots at the time of flowering of the mother shoot, are seen.—This wintering stage is commonly met with in *Poa alpina*, type 1, in dry sunny localities.

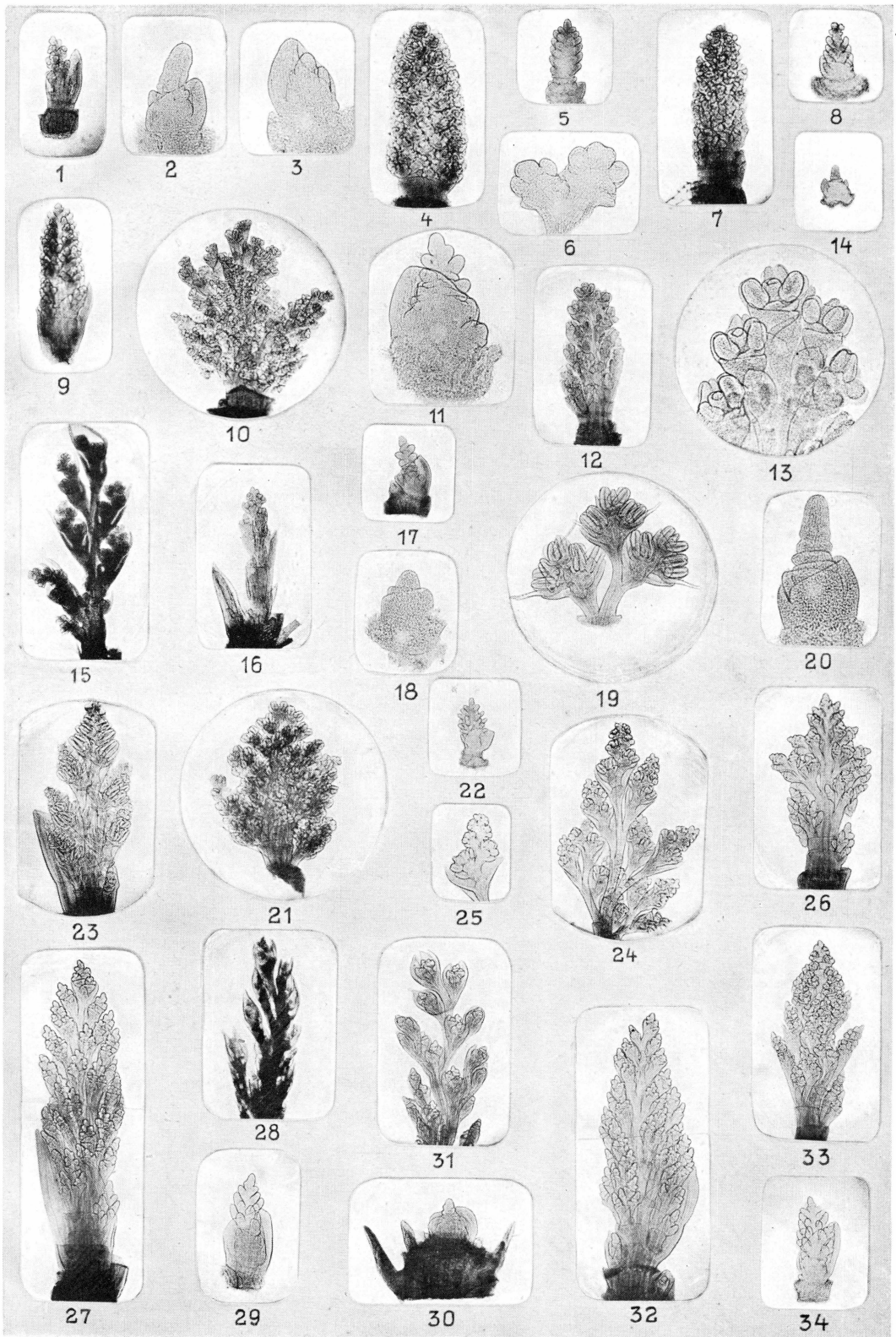
Fig. 31. *Poa alpina vivipara.* Upper part of panicle × 10. Developmental stage the same as that shown in Fig. 28. The panicle primordium of the viviparous plant will survive the winter frost and continue its development after wintering.

Fig. 32. *Poa alpina vivipara.* Panicle × 10. Common wintering stage.—Morphologically not yet distinguishable from the non-viviparous panicle shown in Fig. 27.

Fig. 33. *Poa arctica.* Inflorescence (panicle) × 10. Spikelets hardly differentiated. —Panicle primordia at a younger developmental stage are often found.

Fig. 34. *Poa glauca.* Inflorescence (panicle) × 10. Panicle branches only in incipient differentiation.

[1]) Cf. pag. 74.


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## Plate 4.

**Wintering stages of the flora of Northeast Greenland.**



Fig. 1. *Poa Hartzii.* Inflorescence (panicle) × 10. Spikelets not yet differentiated.

Fig. 2. *Poa pratensis.* Inflorescence exceptionally well advanced in development × 10. Panicle-branches differentiating.

Fig. 3. *Poa pratensis.* Cone of growth just "floral" × 33.—Seems to be the "normal" wintering stage of the species.

Fig. 4. *Puccinellia angustata.* Inflorescence (panicle) × 10. Spikelets and anthers just discernible.—Seems to be the commonest wintering stage.

Fig. 5. *Puccinellia angustata.* Younger panicle primordium × 10. Spikelets not yet distinct. Rejuvenating buds are seen at the base of the panicle.

Fig. 6. *Puccinellia angustata.* "Floral" cone of growth × 33. Panicle branches differentiating. Such a primordium will not normally flower till two summers later.

Fig. 7. *Puccinellia phryganodes.* Inflorescence (panicle) × 10. Spikelets not yet differentiated. At the base: young rejuvenating buds.

Fig. 8. *Puccinellia Vahliana.* Inflorescence (panicle) × 10. Relatively much advanced developmental stage.

Fig. 9. *Puccinellia Vahliana.* Upper spikelets of the same panicle × 33. Anthers of the lowermost flowers of the spikelets distinct. Glumes and pales very short.

Fig. 10. *Puccinellia Vahliana.* Younger panicle × 10. Spikelets just discernible. Rejuvenating buds at the base.

Fig. 11. *Puccinellia Vahliana.* Young "floral" cone of growth × 33. Panicle branches differentiating.—Flowering not till two summers after wintering.

Fig. 12. *Trisetum spicatum.* Inflorescence (panicle) × 10. Exceptionally much advanced wintering stage, no doubt second wintering. Spikelets distinct. Awns of the pales often developed.

Fig. 13. *Trisetum spicatum.* Panicle in "normal" wintering stage × 10. Spikelets hardly discernible.

Fig. 14. *Trisetum spicatum.* Younger panicle primordium × 10. Panicle branches differentiating.—Gives rise to a retarded flowering the following summer, or winters once more in an advanced stage of development.

Fig. 15. *Trisetum spicatum.* Cone of growth just "floral" × 33.—Flowering not till two summers later.

Fig. 16. *Juncus arcticus.* Inflorescence exceptionally advanced in development, × 10. The stem-like involucral leaf removed. The outermost bract of the inflorescence is seen to the left. Inflorescence 3-partite. Floral organs not differentiated.

Fig. 17. *Juncus biglumis.* Inflorescence with erect involucral leaf × 10.

Fig. 18. *Juncus biglumis.* The two-flowered inflorescence after removal of the involucral leaf × 33. Perianth, anthers, and ovary formed. Style and stigmas not yet developed.

Fig. 19. *Juncus castaneus.* Highly advanced "floral" growing point × 33. The growing point is seen in front of a ground leaf primordium.

Fig. 20. *Juncus castaneus.* Vegetative growing point situated nearly laterally at the base of the latest leaf primordium × 33.

Fig. 21. *Juncus triglumis.* "Floral" growing point at the base of the subtending involucral leaf × 33.

Fig. 22. *Juncus triglumis.* "Floral" growing point and the first bract primordium after removal of the involucral leaf × 33.

Fig. 23. *Luzula confusa.* Inflorescence × 10. To the right a bract-like stem leaf.

Fig. 24. *Luzula confusa.* Partial inflorescence × 27. The fringes of the bractlets are early developed, enveloping the primordial clusters.

Fig. 25. *Luzula confusa.* Elementary cluster primordium × 33. Floral organs of the apical flower in incipient differentiation.

Fig. 26. *Luzula nivalis.* Inflorescence × 10. Wintering stage commonly met with. Primordia of the bracts subtending the partial inflorescences project above the apex of the inflorescence.

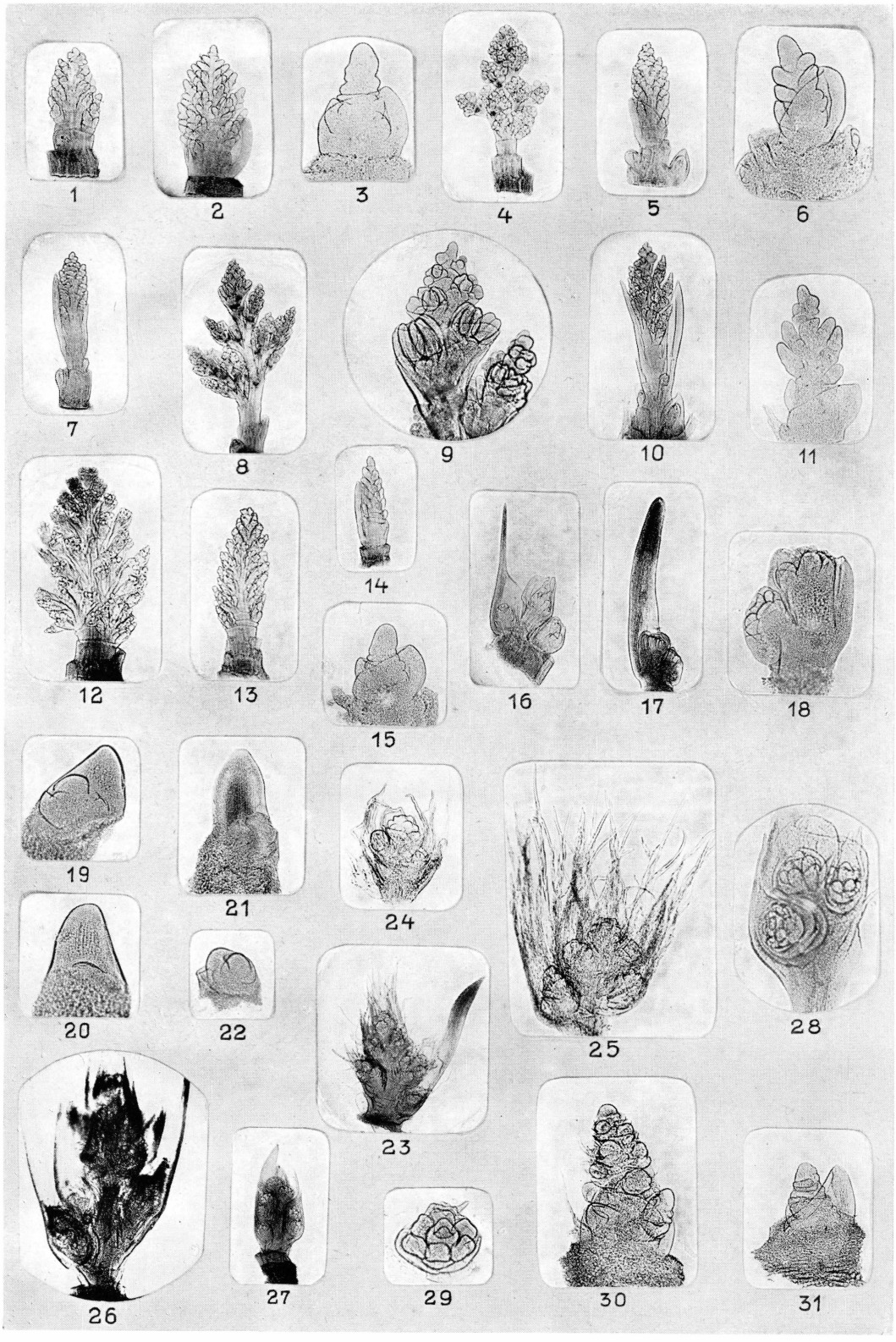
Fig. 27. *Luzula nivalis.* Smaller, less compound inflorescence × 10. Nearly at the same developmental stage as that shown in the preceding figure.

Fig. 28. *Luzula nivalis.* Partial inflorescence with three flower buds × 33.

Fig. 29. *Luzula nivalis.* Flower bud × 33. Anthers and the trigonal-urnshaped pistil, not yet covered by the perianth, distinctly visible.

Fig. 30. *Luzula spicata.* Exceedingly advanced "floral" cone × 27. The axes of the partial inflorescences differentiating.

Fig. 31. *Luzula spicata.* Normal "floral" cone × 33. Secondary axes not yet differentiated. At the base a ground leaf primordium is seen.


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## Plate 5.

**Wintering stages of the flora of Northeast Greenland.**

Fig. 1. *Triglochin palustre.* Upper part of a floral shoot × 27. The last leaf primordium subtending the rejuvenating bud is inserted at the base of the raceme. Flower primordia with disk-like torus. Anthers and pistils not yet differentiated.

Fig. 2. *Tofieldia coccinea.* Flower bud after removal of the perianth × 27. Stamens well differentiated. The ovules are seen within the pistil.

Fig. 3. *Tofieldia palustris.* Flower bud after removal of the perianth × 27. Seen obliquely from beneath. Pistil hidden by the anthers and the torus of the flower.

Fig. 4. *Potamogeton filiformis.* Spike × 33. To the right the uppermost stem leaf. Torus of the flowers disk-like, flattened. Anthers just at the beginning of differentiation.

Fig. 5. *Betula nana.* Male flower (stamens) × 10.

Fig. 6. *Betula nana.* Female catkin × 10. Foliage leaf primordia of the stalk removed.

Fig. 7. *Betula nana.* Female flower with its supporting tripartite scale × 27. Pistil disk- or cup-shaped (very often each tripartite scale supports only one female flower).

Fig. 8. *Arenaria ciliata pseudofrigida.* Advanced flower primordium seen from above × 27. Sepals and anthers recognisable. Female organs not differentiated.

Fig. 9. *Cerastium alpinum.* Highly advanced two-flowered inflorescence × 10. Stamens and pistil formed.

Fig. 10. *Cerastium alpinum.* "Normal" two-flowered inflorescence × 10. Stamens differentiated. Axial placenta arching, carpels not developed.

Fig. 11. *Cerastium alpinum.* Slightly retarded two-flowered inflorescence with prefolia × 27. Terminal flower with the anthers differentiating.

Fig. 12. *Cerastium alpinum.* More retarded inflorescence with prefolia × 27. Terminal flower crown-shaped owing to the incipiently differentiating sepals and anthers.

Fig. 13. *Cerastium Regelii.* Flower after removal of the sepals and some of the anthers × 27. The axial globular placenta is seen. By zonal growth the whorl of carpels is developing from the torus covering the placenta.

Fig. 14. *Honckenya peploides.* "Floral" shoot tip with flower- and leaf primordia × 27. Terminal flower crown-shaped from the incipient differentiation of sepals and anthers.

Fig. 15. *Melandryum apetalum.* Floral shoot apex with the terminal and a lateral flower bud × 10. Leaf primordia removed. Although the stem is constantly one-flowered, primordia of one or two lateral flowers are always to be found.

Fig. 16. *Melandryum apetalum.* The same after removal of the calyx of the terminal flower bud, × 10. The two staminal whorls are seen. The petals are discernible as small scale-like bodies on the dorsal side of the stamens of the latest developed whorl. Pistil high, cylindrical, open at the apex.

Fig. 17. *Melandryum triflorum.* Inflorescence × 10. Calyx of the terminal flower partly removed. Lateral flower buds much retarded in development compared with the terminal one. To the right, a rejuvenating bud.

Fig. 18. *Minuartia biflora.* Three-flowered inflorescence × 27. Calyx of the terminal flower removed.

Fig. 19. *Minuartia biflora.* Pistil and one stamen × 27. The ovules are seen within the pistil. The three styles in incipient differentiation.

Fig. 20. *Minuartia rubella.* Flower bud × 27. Sepals removed. The second whorl of stamens hardly differentiated. The pistil, open at the apex, is seen within the staminate whorls.

Fig. 21. *Minuartia stricta.* Flower bud with prefolia × 27.

Fig. 22. *Sagina caespitosa.* Flower bud with its prefolia × 27. The young flower bud crown-shaped, anthers in incipient differentiation.

Fig. 23. *Sagina caespitosa.* Less advanced "floral" shoot apex, × 27. Sepals of the terminal flower in incipient differentiation.

Fig. 24. *Sagina intermedia.* Upper part of floral shoot with terminal and lateral flower buds × 10.

Fig. 25. *Sagina intermedia.* Floral shoot apex after removal of the calyx of the terminal flower × 27. Within the pistil the central placenta and the ovules are seen. To the left a lateral flower bud hidden by its foliaceous prefolia.

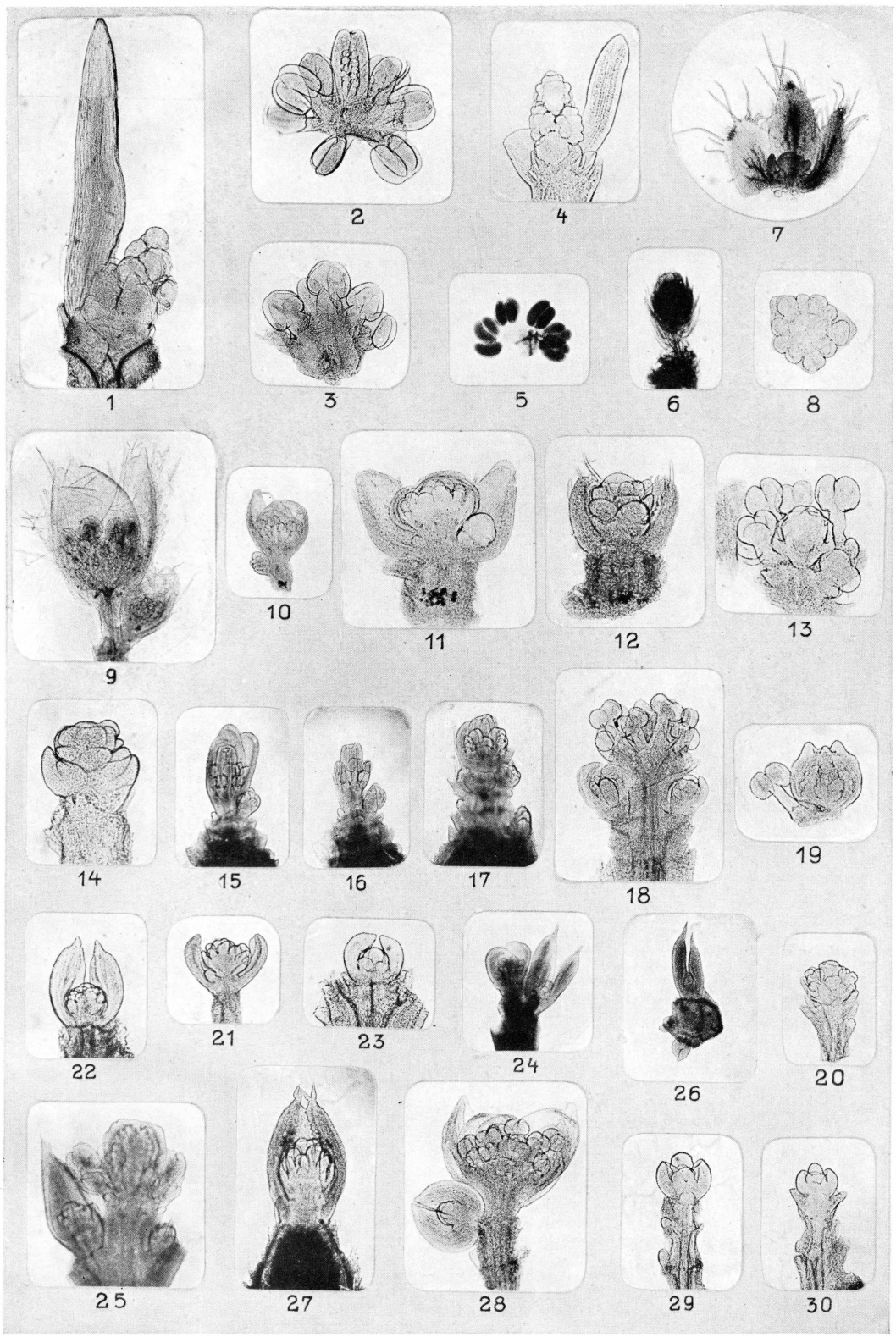
Fig. 26. *Sagina intermedia.* Apex of a vegetative monopodial axis after removal of the leaf primordia, seen from above, × 10, to show the continuous development of floral side shoots from the leaf axils. Three young side shoots with their first pair of leaves are distinctly seen.

Fig. 27. *Silene acaulis.* Flower bud × 10. The stem leaf primordia removed, except the last pair, which quite enclose the flower bud. Appearance and developmental stage as in the *Melandrya.*

Fig. 28. *Stellaria humifusa.* Flower bud in advanced development × 27. To the left a young floral primordium enclosed into its prefolia.

Fig. 29. *Stellaria humifusa.* Shoot apex transitional from the pure vegetative to the flowering stage × 27. The "floral" character of the shoot is indicated by the broad, blunt growing point (compare the next figure).

Fig. 30. *Stellaria humifusa.* Apex of a purely vegetative shoot × 27.


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## Plate 6.

**Wintering stages of the flora of Northeast Greenland.**

Fig. 1. *Stellaria longipes.* Inflorescence in an advanced stage of development × 27. Leaf primordia of the main axis removed.

Fig. 2. *Stellaria longipes.* Inflorescence in a "normal" stage of development × 27.—At the place of the dome-shaped protuberance from the centre of the disk-like torus of the flower, the axial placenta will be formed later.

Fig. 3. *Viscaria alpina.* Vegetative shoot apex × 27. Four pairs of leaf primordia are seen.

Fig. 4. *Viscaria alpina.* Shoot apex transitional to the "floral" stage, × 27.

Fig. 5. *Sedum roseum.* Partial inflorescence (three-flowered cyme) × 10.

Fig. 6. *Sedum roseum.* Male flower bud × 27. The anthers are seen through the sepals. Pistils small, situated at the centre of the cup-shaped torus, hidden by the anthers (male and female flowers planned in the same manner as bisexual).

Fig. 7. *Arabis alpina.* Flower bud × 27. Anthers and pistil are seen within the calyx. Also the petals may be distinguished as small obovate scale-like primordia.

Fig. 8. *Braya humilis.* Medium-sized inflorescence × 10.

Fig. 9. *Braya humilis.* Flower bud after removal of the sepals × 10. Pistil containing ovules; stamens and petals are seen.

Fig. 10. *Braya humilis.* Young inflorescence × 27.

Fig. 11. *Braya linearis.* Inflorescence seen from above × 27. Within the flower buds: the anthers in incipient differentiation, partly hidden by the sepals.

Fig. 12. *Braya purpurascens.* Inflorescence × 10.

Fig. 13. *Braya purpurascens.* Flower bud after removal of the sepals, × 10. Stamens and pistil are seen.

Fig. 14. *Braya Thorild-Wulffii.* Medium sized flower bud × 10. All floral organs formed, pistil containing ovules.

Fig. 15. *Cardamine bellidifolia.* Floral shoot apex × 10. Inflorescence and three foliage leaf primordia. At the base of the leaves the stipulary squamae are seen.

Fig. 16. *Cardamine bellidifolia.* Detail of the same shoot apex × 27. Inflorescence and the uppermost leaf supporting the rejuvenating bud are seen. The sepals have been removed from the flower bud to the left.

Fig. 17. *Cardamine pratensis.* Floral shoot apex × 10. Inflorescence hidden by the upper stem leaf primordia.

Fig. 18. *Cardamine pratensis.* Flower bud × 27. Anthers in incipient differentiation.

Fig. 19. *Cochlearia officinalis.* Flower bud × 10. Sepals very large compared with the sexual organs of the flower.

Fig. 20. *Cochlearia officinalis.* Flower bud after removal of the sepals × 10. Anthers and pistil, containing ovules in incipient differentiation, are visible.

Fig. 21. *Draba Bellii.* Flower bud × 10.

Fig. 22. *Draba Bellii.* Flower bud after removal of the sepals × 10. All organs of the flower, even the petals, are formed.

Fig. 23. *Draba daurica.* Inflorescence × 10. To the left a stem leaf is seen. At the base of the scape a small shoot primordium is seen.

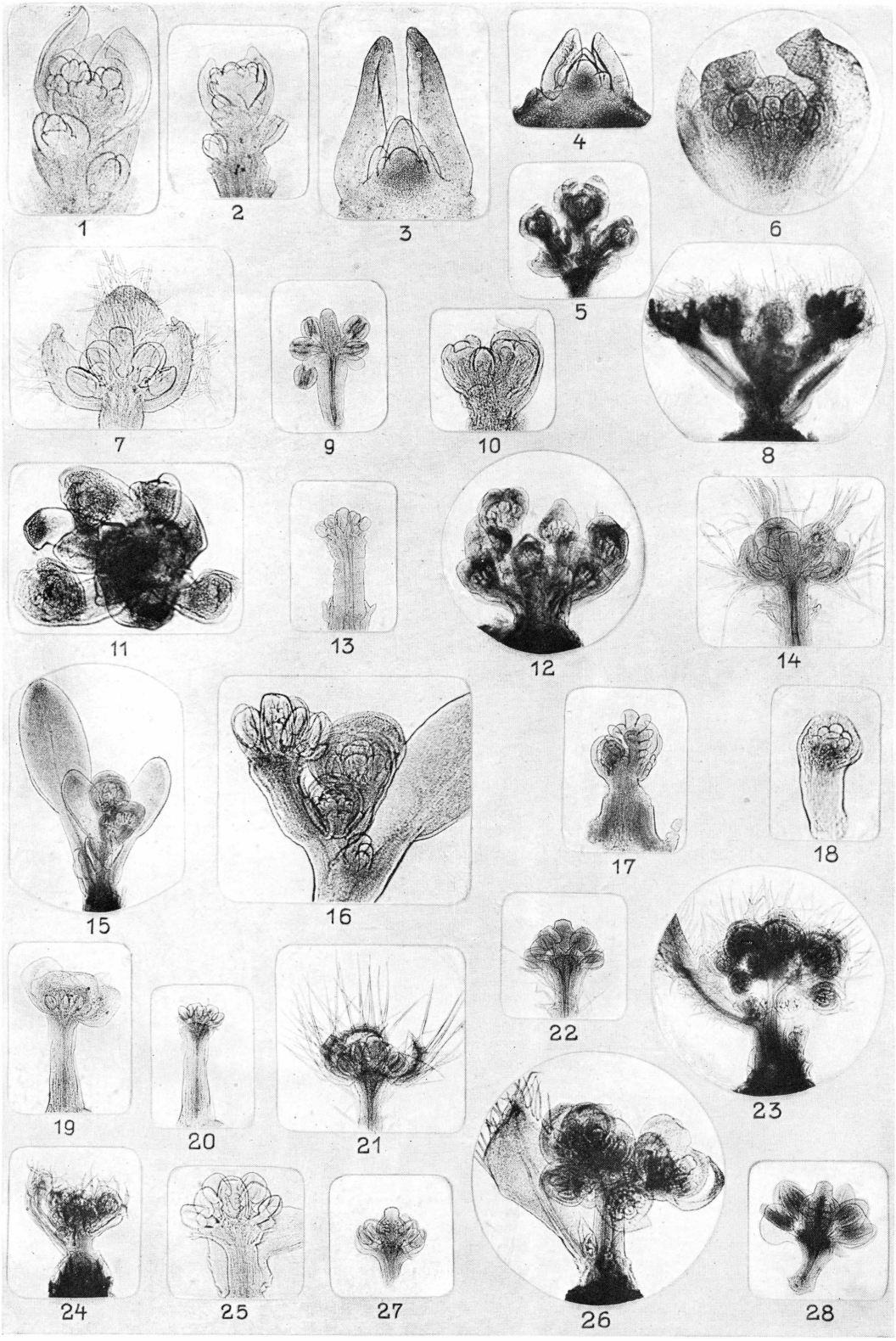
Fig. 24. *Draba fladnizensis.* Inflorescence × 10. At the base (left) of the scape a leaf primordium supports a small floral regulation shoot primordium.

Fig. 25. *Draba fladnizensis.* Flower bud after removal of the sepals × 27. Petals and ovules hardly differentiated. Subtending stem-leaf (bract) visible.

Fig. 26. *Draba lactea.* Inflorescence × 10.

Fig. 27. *Draba lactea.* Flower bud after removal of the sepals × 10. All the floral organs, even the papillous stigma, are distinctly formed.

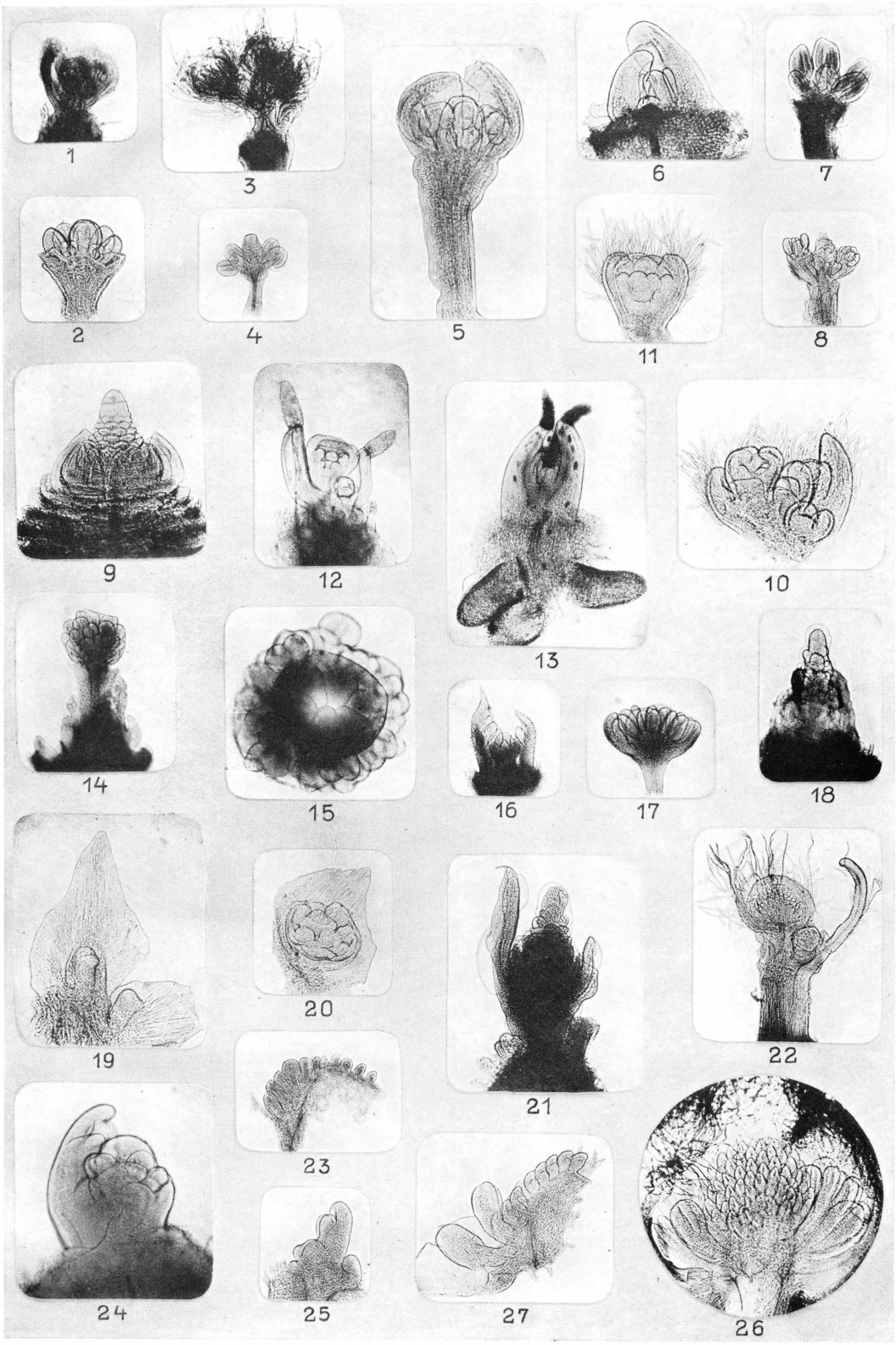
Fig. 28. *Draba micropetala.* Flower bud after removal of the sepals × 10. The flower ready to expand. The anthers contain pollen grains.


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## Plate 7.

**Wintering stages of the flora of Northeast Greenland.**

Fig. 1. *Draba nivalis.* Inflorescence × 10.
Fig. 2. *Draba nivalis.* Flower bud after removal of the sepals × 27. Ovules not differentiated. Pistil not fully closed at the apex.
Fig. 3. *Draba subcapitata.* Inflorescence × 10. At the base of the scape to the right, the rejuvenating bud is seen.
Fig. 4. *Draba subcapitata.* Flower bud after removal of the sepals × 10. All parts of the flower are formed, petals, however, small.
Fig. 5. *Eutrema Edwardsii.* Flower bud × 27.
Fig. 6. *Eutrema Edwardsii.* The second order rejuvenation bud, situated at the base of the shoot in the flower bud stage, × 27. Three leaf primordia with their stipulary squamae and the growing point of the shoot are readily seen.
Fig. 7. *Lesquerella arctica.* Most advanced flower bud, sepals removed, × 10. Pistil containing ovules and the style developed.
Fig. 8. *Lesquerella arctica.* Most retarded inflorescence × 10. The sepals are removed from the two lowermost flower buds. Pistils not yet closed at the apex.
Fig. 9. *Hippuris vulgaris.* Shoot apex after removal of the outer leaf primordia enveloping the cone of growth × 27.
Fig. 10. *Chamaenerium latifolium.* Inflorescence × 27.
Fig. 11. *Chamaenerium latifolium.* Flower bud, split and spread out, × 27. The four anthers in incipient differentiation on the rim of the cup-shaped torus.
Fig. 12. *Epilobium arcticum.* Floral shoot apex × 27. The most advanced flower bud with anthers differentiated. To the right a younger flower bud (normally only one bud develops into a flower, the others degenerate). Note the curious leaf tips in this and the following figure.
Fig. 13. *Epilobium arcticum.* Second order rejuvenating bud issuing from the base of the shoot in the flower bud stage × 27. Incipient root formation.
Fig. 14. *Papaver radicatum.* Flower bud, whose sepals have been removed, × 10.
Fig. 15. *Papaver radicatum.* The same flower bud seen from above × 27. In the pistil the placentae are growing from the outer walls towards the centre; pistil still open at the apex.
Fig. 16. *Papaver radicatum.* Regulation shoot primordium with a young flower bud, × 10. Anthers hardly visible.
Fig. 17. *Oxyria digyna.* Advanced flower bud × 27. Mainly only the anthers are seen.
Fig. 18. *Oxyria digyna.* Young "floral" growing cone × 27. Flowering stage not reached till two summers later.
Fig. 19. *Polygonum viviparum.* Two bulbil primordia with their subtending scales × 27.
Fig. 20. *Polygonum viviparum.* Flower bud × 27. The cyclically situated anthers surround the open pistil at the centre of the flower.
Fig. 21. *Rumex Acetosella.* Female "floral" shoot apex × 27. Secondary inflorescence axes in incipient differentiation. To the left and right: stem leaf primordia.
Fig. 22. *Ranunculus affinis.* Stem- and inflorescence-primordium × 10. Lower stem leaf removed.
Fig. 23. *Ranunculus glacialis.* Longitudinal section through the torus of a normal flower bud. To the left the stamens, to the right the apocarpous carpels × 10. Carpels not yet closed.
Fig. 24. *Ranunculus glacialis.* Young floral primordium × 27. To the left a ground leaf primordium. The sepals of the flower in incipient differentiation.—This stage of development indicates the last but one wintering before the flowering.
Fig. 25. *Ranunculus hyperboreus.* Advanced, just "floral", growing point × 27. To the right the last leaf primordium, to the left the flattened "floral" growing point. (Last wintering before the flowering).
Fig. 26. *Ranunculus nivalis.* Flower bud × 10. Anthers and carpels are seen to be surrounded by the hairy sepals.
Fig. 27. *Ranunculus nivalis.* Longitudinal section through the torus × 10. From left to right: petal, stamens, and carpels.


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## Plate 8.

**Wintering stages of the flora of Northeast Greenland.**

Fig. 1. *Ranunculus pygmaeus*. The sexual organs of a flower bud × 27. Six stamens and numerous apocarpous carpels are seen. Carpels not yet closed.

Fig. 2. *Ranunculus pygmaeus*. Growing point transitional from the vegetative to the floral stage × 27. Two sheathing leaf bases surround the growing point proper. (Same morphological stage as *R. hyperboreus*, Pl. 7, Fig. 25, where it indicates the last wintering; in *R. pygmaeus*, however, the last wintering but one).

Fig. 3. *Ranunculus sulphureus*. Longitudinal section through the torus of flower bud × 10. To the left stamens, to the right carpels.

Fig. 4. *Thalictrum alpinum*. Inflorescence primordium × 27. Individual flowers not yet distinctly differentiated.

Fig. 5. *Dryas octopetala*. Calyx tube seen from within × 27. Anthers, petals, and sepals are seen.

Fig. 6. *Dryas octopetala*. Longitudinal section through the receptacle with the apocarpous carpels × 27. Carpels not yet closed.

Fig. 7. *Potentilla Crantzii*. Inflorescence × 10.

Fig. 8. *Potentilla Crantzii*. Receptacle with the apocarpous carpels × 27. At the apex of the carpels the channelled style differentiating.

Fig. 9. *Potentilla emarginata*. Carpel of a flower bud, wintering in the pollen stage × 27.—Flowers wintering in the pollen stage seem to be able to expand; fruits, however, are not developed.

Fig. 10. *Potentilla emarginata*. Receptacle with apocarpous carpels, of a medium-sized flower bud × 27. Ovules in incipient development. Styles still channelled.

Fig. 11. *Potentilla emarginata*. Calyx tube of the same flower seen from within × 10. Anthers distinctly seen. Petals may be discerned as scale-like primordia, projecting only a little above the anthers.

Fig. 12. *Potentilla emarginata*. Receptacle with carpels of a younger flower bud × 27.

Fig. 13. *Potentilla nivea*. Inflorescence × 10.

Fig. 14. *Potentilla nivea*. Receptacle and the apocarpous carpels from the apical flower of fig. 13, × 27.

Fig. 15. *Potentilla pulchella*. Inflorescence × 27. Receptacle with very inconspicuous papilla-like carpels.

Fig. 16. *Sibbaldia procumbens*. Inflorescence × 27. Sexual organs hardly differentiating.

Fig. 17. *Salix arctica*. Male flower with its supporting scale × 10. The anthers discernible as a dark spot at the base of the hairy scale.

Fig. 18. *Salix arctica*. Male flower (stamens) × 27.

Fig. 19. *Salix arctica*. Female flower (pistil) × 27. Styles in incipient differentiation. Ovules are seen in the pistil.

Fig. 20. *Salix arctica*. Axillary bud of second order, from the axil of a foliage leaf primordium of a vegetative winter bud × 27. Prefolia and growing point are seen. The prefolia will constitute the protecting scale of the bud in the following winter.

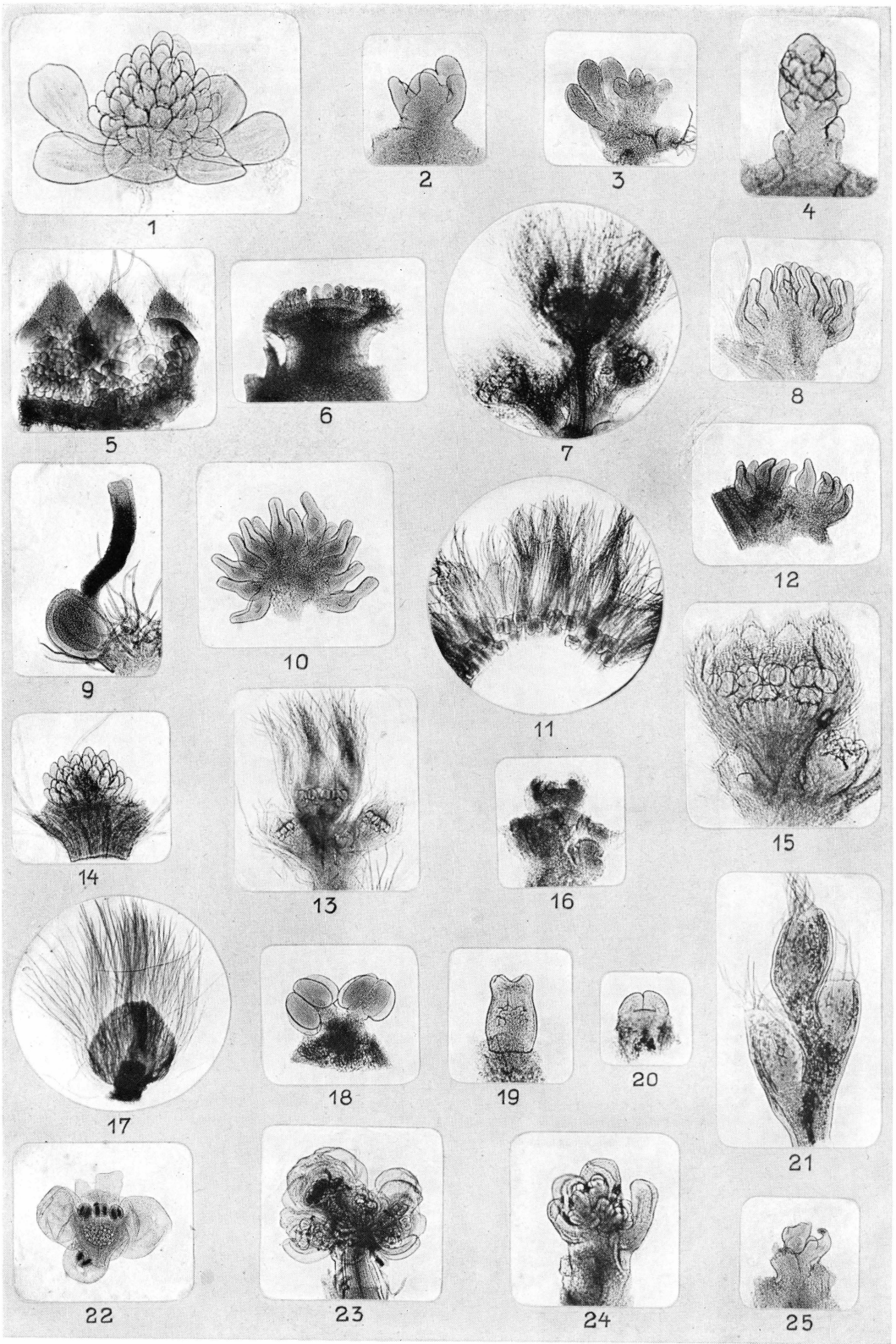
Fig. 21. *Salix herbacea*. Three-flowered female catkin × 27. Pistils partly hidden by their supporting sparsely haired scales.

Fig. 22. *Chrysosplenium tetrandrum*. "Normal" flower bud seen obliquely from above × 10. The four anthers, containing ripe pollen, and the ovules are distinctly seen.

Fig. 23. *Chrysosplenium tetrandrum*. Somewhat retarded inflorescence × 10.

Fig. 24. *Chrysosplenium tetrandrum*. Much retarded inflorescence × 27.

Fig. 25. *Chrysosplenium tetrandrum*. Shoot apex at the transition from vegetatative to floral stage × 27.—Such a wintering shoot presumably will not flower till two summers later.


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## Plate 9.

**Wintering stages of the flora of Northeast Greenland.**

Fig. 1. *Saxifraga aizoides.* Exceedingly advanced flower bud × 27. Anthers developed.

Fig. 2. *Saxifraga aizoides.* Just "floral" shoot apex × 27. Growing point distinctly flattened.—Would seem to be the commonest wintering stage of shoots flowering the following summer.

Fig. 3. *Saxifraga caespitosa.* Slightly developed "floral" shoot apex × 27. Growing point disk-like flattened.—Such wintering shoots will normally winter once more before flowering.

Fig. 4. *Saxifraga caespitosa.* Inflorescence × 10. The rejuvenating buds are seen to the left at the base of the stem.—Wintering stage commonly met with.

Fig. 5. *Saxifraga caespitosa.* Terminal flower of the inflorescence shown in fig. 4, seen from above. × 10.

Fig. 6. *Saxifraga caespitosa.* Central part of the flower shown in fig. 5, × 27. The antipetalous anthers larger than the antisepalous ones. The petal-primordia are seen immediately at the dorsal side of the first-named ones. Pistil closed, at the apex two-horned owing to the developing styles.

Fig. 7. *Saxifraga cernua.* Upper part of a stem. × 10. The solitary flower bud is seen at the apex of the stem. The lateral buds are bulbil-primordia, whose supporting stem leaves have been removed.

Fig. 8. *Saxifraga flagellaris.* Upper part of a floral shoot × 10. Leaves removed. Besides the terminal flower bud a smaller lateral one. At the base of the stem a stalked rejuvenating bud. The following summer the bud stalk will develop into the leafless flagellum.—The stage of development figured seems to be commonly met with in wintering rosettes.

Fig. 9. *Saxifraga flagellaris.* A rejuvenating bud × 27.

Fig. 10. *Saxifraga Hirculus.* Upper part of a "floral" shoot × 10. Leaf primordia removed. Only one terminal flower bud.

Fig. 11. *Saxifraga Hirculus.* Flower bud, seen from above, × 27. The sepals and the hardly developed anthers are seen.

Fig. 12. *Saxifraga oppositifolia.* Flower bud, deprived of the calyx, × 10.

Fig. 13. *Saxifraga oppositifolia.* Fragment of the short perianth tube, seen from within, × 10. Stamens and petals are seen. Sepals have been removed.

Fig. 14. *Saxifraga oppositifolia.* Pistil containing the ovules × 10.

Fig. 15. *Saxifraga rivularis.* Advanced flower bud seen from above × 10.

Fig. 16. *Saxifraga stellaris comosa.* Medium-sized bulbil seen from above × 27.

Fig. 17. *Campanula rotundifolia.* Still vegetative growing point of lateral (floral) shoot × 27.

Fig. 18. *Campanula uniflora.* Flower bud × 27. Anthers and the conical apex of the closed pistil distinguishable within the calyx.

Fig. 19. *Antennaria alpina.* Growing point transitional from the vegetative to the floral stage × 27. Shoots in this wintering stage will presumably not flower till two summers later.

Fig. 20. *Antennaria alpina.* Inflorescence in a wintering stage commonly met with × 27. Florets of the capitulum seen as rather undifferentiated papillæ.

Fig. 21. *Arnica alpina.* "Normal" flower head × 10. Stem with one pair of leaf primordia.

Fig. 22. *Arnica alpina.* Longitudinal section through the flower head × 27. To the right an involucral bract. Corolla and the anthers of the florets developed. The pistillary cavity not yet limited above.

Fig. 23. *Arnica alpina.* Retarded flower head × 27. Florets in incipient differentiation.

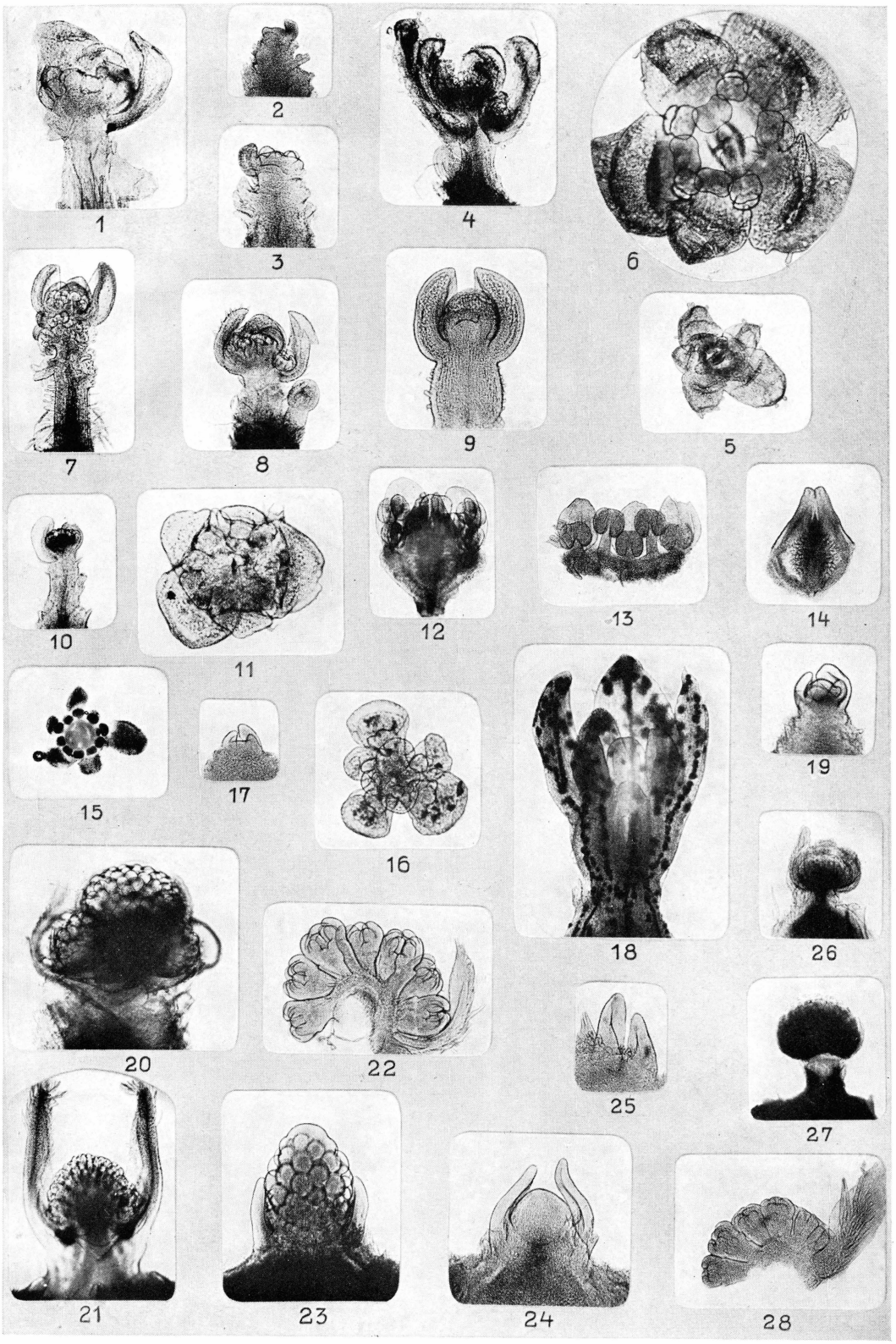
Fig. 24. *Arnica alpina.* Much retarded "floral" growing cone, from a plant growing in a very dry locality × 27. Florets not yet differentiated upon the receptacle.

Fig. 25. *Arnica alpina.* Vegetative growing point surrounded by the two latest leaf primordia × 27. Primordial axillary hairs are seen.

Fig. 26. *Erigeron compositus.* "Normal" flower head × 10.

Fig. 27. *Erigeron unalaschkensis.* Flower head deprived of its involucre × 10.

Fig. 28. *Erigeron unalaschkensis.* Longitudinal section through a flower head × 27. From right to left: bract, one female ray-flower primordium, one female tube-flower primordium, and four bisexual disk-flower primordia. In the last ones the corolla and anthers are developing.


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## Plate 10.

**Wintering stages of the flora of Northeast Greenland.**

Fig. 1. *Matricaria inodora.* Most advanced (successfully) wintering flower head × 10.

Fig. 2. *Matricaria inodora.* Longitudinal section through the flower head shown in fig. 1, × 27. To the left an involucral bract. The florets only formed as cup-shaped papillæ upen the receptacle.

Fig. 3. *Matricaria inodora.* Younger flower head primordium × 27. Florets not yet differentiated.

Fig. 4. *Matricaria inodora.* Growing cone transitional to the "floral" stage, surrounded by leaf primordia × 27.

Fig. 5. *Taraxacum arcticum.* "Normal" flower head × 10. The rejuvenating bud is seen to the left at the base of the scape.

Fig. 6. *Taraxacum arcticum.* Longitudinal section through the "normal" flower head × 27. To the left an involucral bract. Corolla and anthers of the florets formed. Pistillary cavity discernible.

Fig. 7. *Taraxacum arcticum.* Retarded flower head surrounded by basal leaf primordia × 10.

Fig. 8. *Taraxacum arcticum.* Vegetative growing point × 27. In the figure the growing point proper is hidden by the dome-shaped youngest leaf primordium between the second and the third youngest primordia, to the left and right respectively.

Fig. 9. *Taraxacum phymatocarpum.* Flower head × 10.

Fig. 10. *Taraxacum phymatocarpum.* Longitudinal section through the flower head × 27. To the left an involucral bract. Corolla and anthers of the florets recently differentiated. Pistillary cavity not yet recognisable.

Fig. 11. *Taraxacum pumilum.* Flower head × 10. The rejuvenating bud is seen to the left at the base of the scape.

Fig. 12. *Taraxacum pumilum.* Longitudinal section through the flower head × 27. To the left an involucral bract. Corolla and anthers of the florets developed. Pistillary cavity may be discerned.

Fig. 13. *Arctostaphylos alpina.* Flower bud × 27. All the organs of the flower developed. Pistil hourglass-shaped, the quinquepartite stigma discernible.

Fig. 14. *Cassiope hypnoides.* Flower bud, Calyx and corolla removed, × 27. Anthers containing pollen grains. Pistil with ovules and the head-shaped stigma are seen.

Fig. 15. *Cassiope tetragona.* Flower bud deprived of calyx and corolla × 27. Anthers with pollen. Style nearly cylindrical, furrowed.

Fig. 16. *Cassiope tetragona.* Axillary "floral" growing point during the winter one year before the stage illustrated in fig. 15, × 27. In the figure the vascular bundles (grey) are seen to contrast with the dark-coloured fundamental tissue of the stem. Prefolia in incipient differentiation.

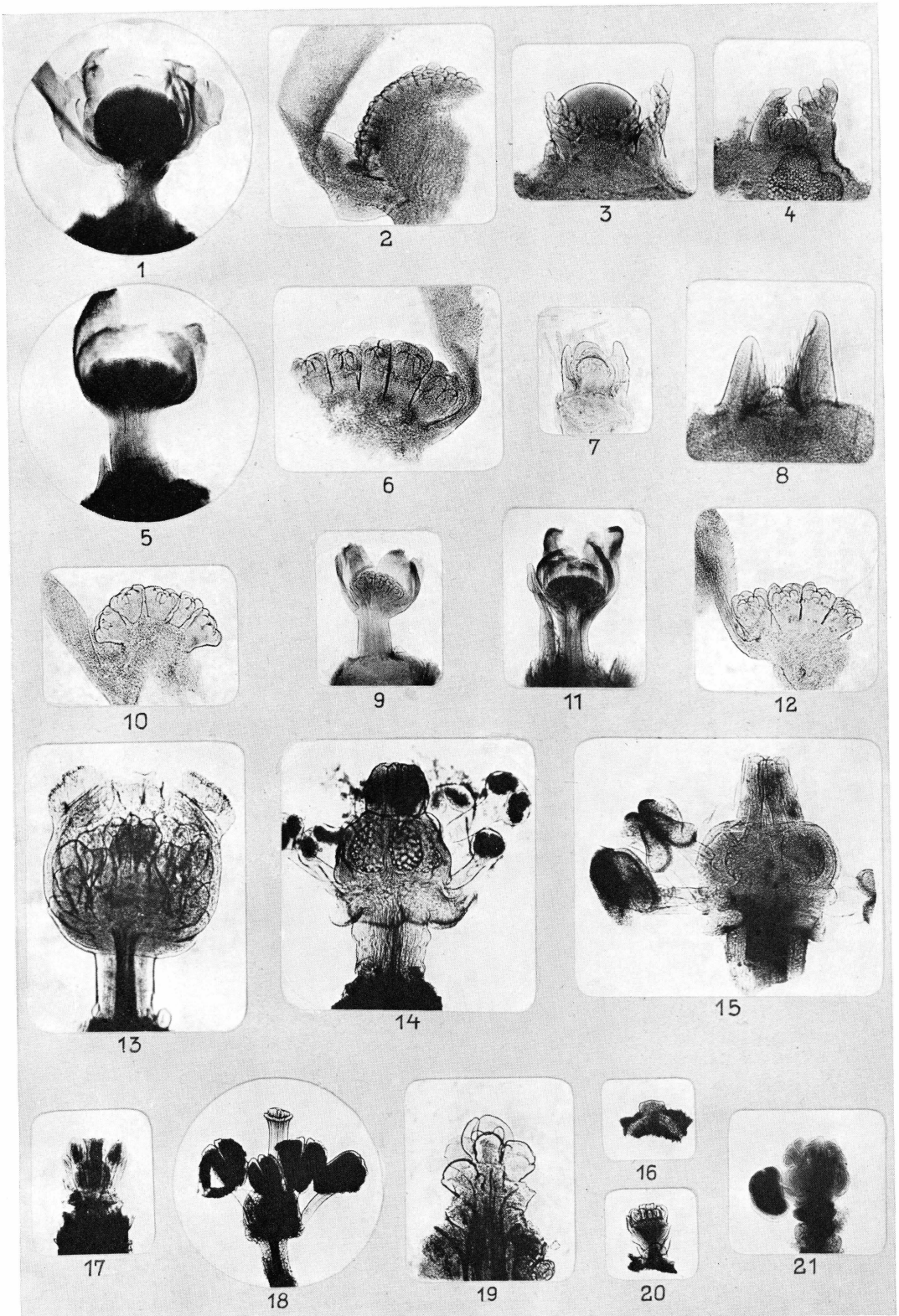
Fig. 17. *Phyllodoce coerulea.* Flower bud deprived of its calyx and corolla × 10. Anthers, pistil, and style are seen.

Fig. 18. *Rhododendron lapponicum.* Flower bud deprived of its calyx and corolla × 10. Anthers contain ripe pollen grains.

Fig. 19. *Rhododendron lapponicum.* Floral shoot apex in summer condition. × 27. The figure shows the condition of a new (wintering) inflorescence at the time when the plant is in full flower. It will be seen that the umbel is not originally terminal, as the shoot apex bears leaf primordia above the laterally inserted young flower buds.

Fig. 20. *Vaccinium uliginosum.* Flower bud, calyx removed, × 10. Anthers and stigma are seen.

Fig. 21. *Empetrum nigrum.* Monandrous bisexual flower after removal of the perianth leaves × 10. The anther contains pollen grains. The somewhat flattened pistil bears the multipartite crown-shaped stigma.


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## Plate 11.

**Wintering stages of the flora of Northeast Greenland.**

Fig. 1. *Pingvicula vulgaris.* Growing point × 27. Growing point dilated, tumid. To the left, the latest leaf primordium.

Fig. 2. *Armeria vulgaris.* Flower head × 10. Developmental stage commonly met with. The individual flowers in the involucre have hardly differentiated.

Fig. 3. *Armeria vulgaris.* Young "floral" shoot apex × 10. Cone of growth surrounded by the latest basal leaf primordia. On the growing cone, the whorls of involucral leaves in incipient differentiation.

Fig. 4. *Armeria vulgaris.* Purely vegetative growing point surrounded by ground leaf primordia. × 10.

Fig. 5. *Polemonium boreale.* Medium-sized inflorescence. To the left an incurved leaf primordium.

Fig. 6. *Primula stricta.* Inflorescence × 10. At the base of the scape the last ground leaf primordium supporting the rejuvenating bud.

Fig. 7. *Primula stricta.* Flower bud × 10. Calyx densely clothed with club-shaped hairs. Ovary, filled by the globular central placenta, closed at the apex. Style still rather short, cylindrical. Corolla with the stamens inserted above the base, shorter than the calyx, corolla and anthers of the same height.

Fig. 8. *Pyrola grandiflora.* Inflorescence somewhat advanced in development × 10. The bracts supporting the three lowermost flowers have been removed.

Fig. 9. *Pyrola grandiflora.* Advanced flower bud × 27. The petals and the anthers within the calyx only in incipient differentiation. Pistil not yet developed

Fig. 10. *Pyrola grandiflora.* Flower bud × 27, in a developmental stage commonly met with. Torus disk-like, dilated. Calyx in incipient differentiation.

Fig. 11. *Pedicularis flammea.* Inflorescence × 10.

Fig. 12. *Pedicularis flammea.* Flower bud × 10. Anthers and pistil may be discerned in the calyx. Ovules not yet differentiated.

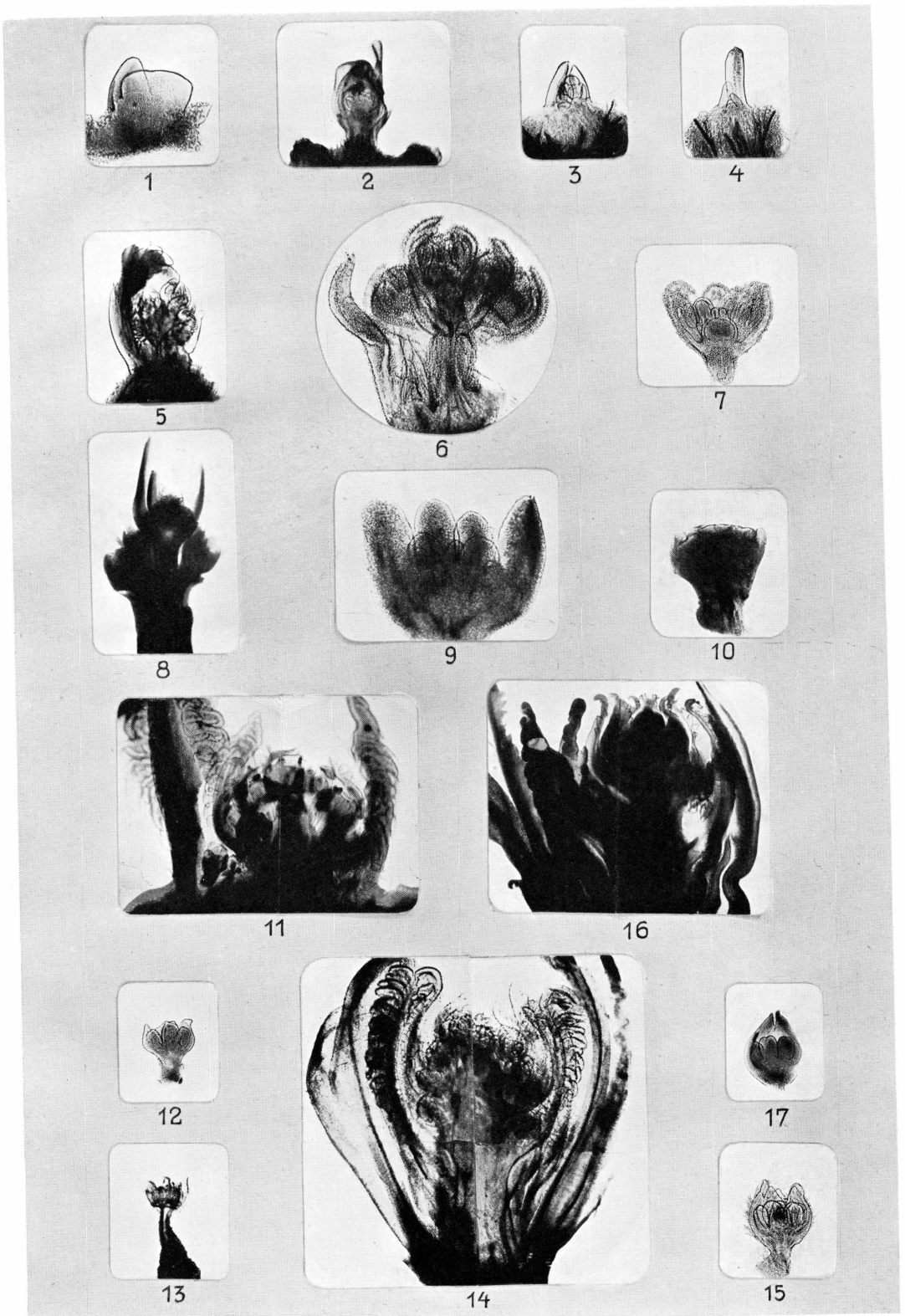
Fig. 13. *Pedicularis flammea.* Abortive flower bud from a lower leaf axil of a grown-up stem × 10.

Fig. 14. *Pedicularis hirsuta.* Inflorescence × 10.

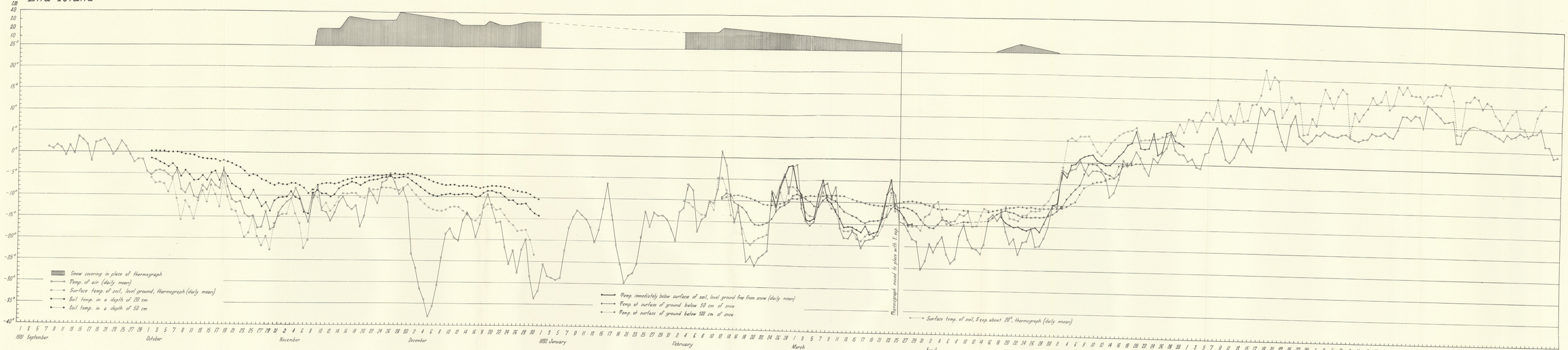
Fig. 15. *Pedicularis hirsuta.* Flower bud × 10. Developmental stage about the same as in *P. flammea.*

Fig. 16. *Pedicularis lapponica.* Inflorescence × 10.

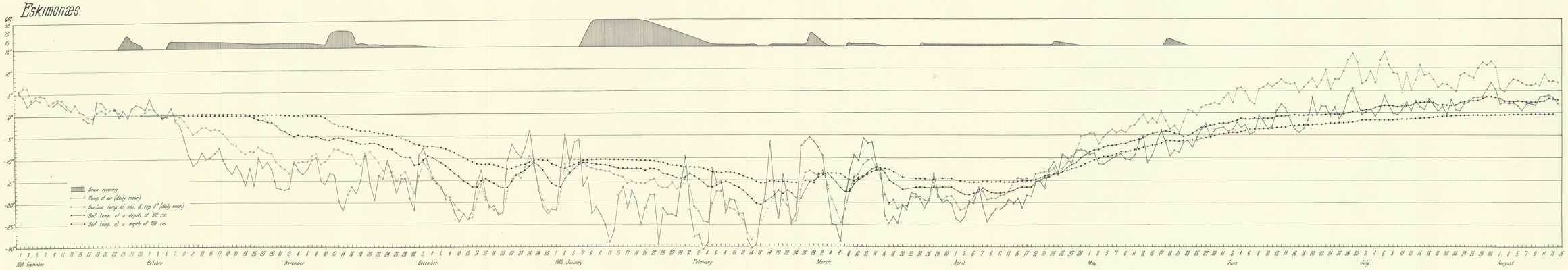
Fig. 17. *Pedicularis lapponica.* Flower bud × 10. The bilabiate calyx twice as long as the anthers.


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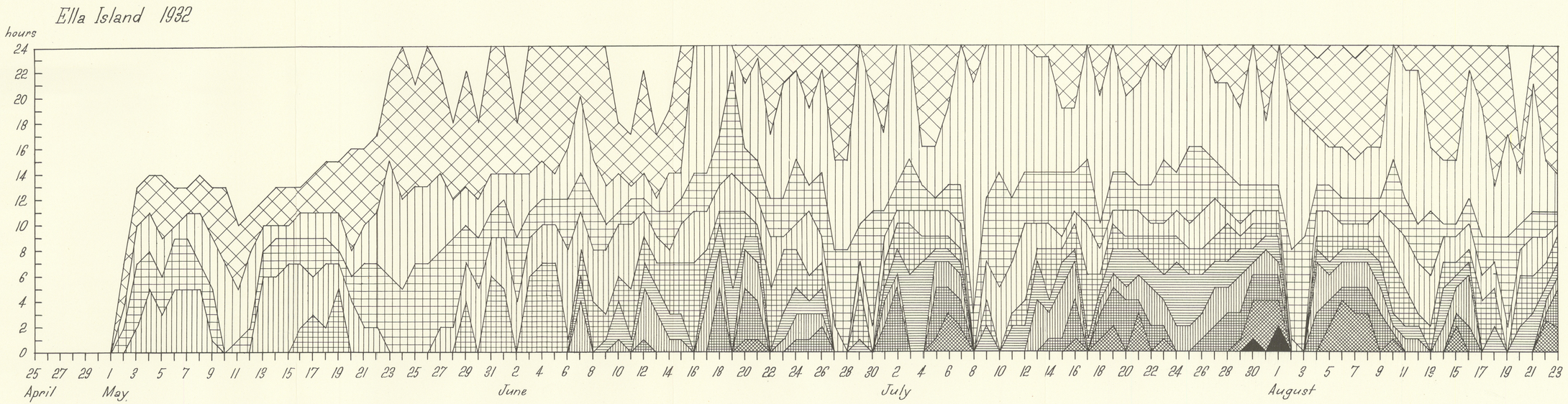
# Ella Island



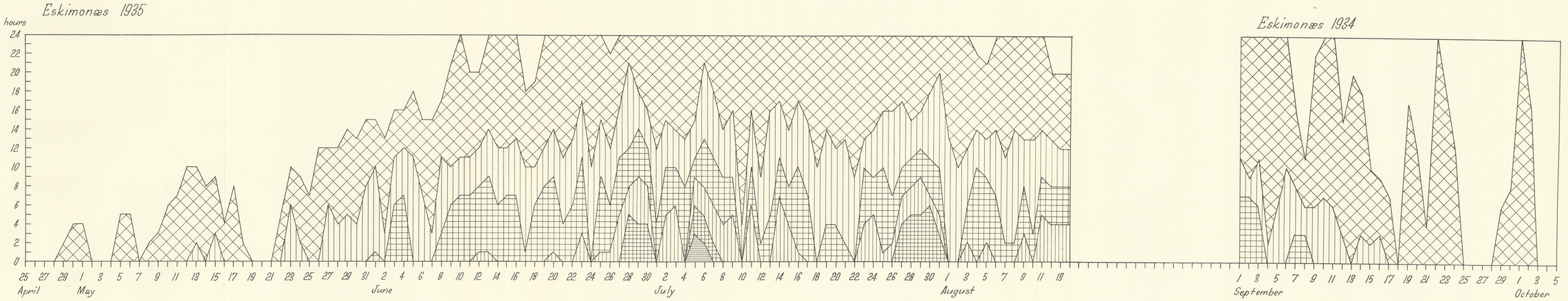

Graphic representation of the temperature series observed for air, soil surface, and soil on Ella Ø 1931-32.




Graphic representation of the temperature series observed for air, soil surface, and soil at Eskimonæs 1934-35.




Graph showing the hourly distribution of the positive temperatures of the soil surface on Ella Ø in the summer half-year of 1932. S. exposure c. 20°.




Graph showing the hourly distribution of the positive temperatures of the soil surface at Eskimonæs in the autumn of 1934 and the summer half-year of 1935. S. exposure c. 8°.