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THE RELATION OF THE VASCULAR FLORA TO SOME FACTORS OF SITE IN THE MESTERS VIG DISTRICT NORTHEAST GREENLAND

BY

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WITH 15 FIGURES AND 3 TABLES IN THE TEXT
AND 1 PLATE

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Abstract

A method of analysis is presented for botanical data gathered in the Mesters Vig district, Kong Oscars Fjord, Northeast Greenland, in the summer seasons of 1956, '57, '58, '60, and '64. The work was done in collaboration with Dr. A. L. Washburn who was at the same time making detailed studies of geomorphic processes. The basic information used in the present paper was published in 1965 (Raup, 1965 A), where it was dispersed throughout a floristic treatment of the Mesters Vig vegetation. Here it is collated in terms of the species' behavior with respect to their tolerance of variation on gradients of ground cover, moisture, and physical disturbance of the soils. Information on frequency and on the nature of roots and underground stem systems is also brought together. The flora is then analyzed in terms of the behavior of the species on the various gradients, using a 3-fold division in the rating of their tolerance to variation in the gradients. "Wide tolerance" indicates that a species was found growing successfully in 2/3's or more of the possible variations in a given gradient. "Narrow tolerance" means that a species was found in sites with only 1/3 of the possible variations or less. "Intermediate tolerance" indicates that a species was found in sites having between 1/3 and 2/3's of the possible variations. Lists of species for each of these tolerance categories are given for each of the gradients used. Data on coverage of the ground were obtained by estimating the percentage of the ground surface in a given site which was covered by living vascular plants when viewed from above. Moisture categories used were high, medium, and low. These were based upon ocular evaluations in the field and upon moisture analyses of soil collections. Two gradients were used in the analyses of the species' reactions to physical disturbance. The first was for disturbances induced by frost action, primarily frost heaving: the "frost disturbance gradient". The second, called the "nonfrost disturbance gradient", involved disturbances due to all other geomorphic processes that appeared to be limiting to the growth of plants. Most of the judgments made on the intensities of disturbances came from detailed studies being made concurrently by Dr. Washburn.

Assuming that the success with which a species could become established and persist was closely related to its reactions to external factors of the habitat, the species included in the major frequency classes were analyzed in terms of percentages that fell into widely and narrowly tolerant groups on each of the gradients. Widely tolerant species made up the bulk of the vegetation (common to abundant species), while narrowly tolerant ones were mainly the rare to occasional species. The paper contains a general review of previous research that has been pertinent and useful to the Mesters Vig studies.

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INTRODUCTION

Information on site preferences, life-forms and local distribution of the species of vascular plants was given in "The flowering plants and ferns of Mesters Vig, etc." (Raup, 1965 A). The purpose of the present paper is to assemble those data in such a way that they can be used for comparison among themselves, and also for correlation with data being derived concurrently from studies of physical factors of site (Washburn, 1965).

The inspiration for much that follows came from a series of rather elementary field observations in the Mesters Vig district. The flora, though small in number of species, is obviously well adapted to conditions of life in the Arctic. Working in collaboration with a geomorphologist whose major interest was an intensive study of processes of change in the soils, involving temperature and moisture regimes as well as physical disturbances, I was in an advantageous position to see relationships between these processes and species behavior. It was at once apparent that a large proportion of the species exhibited extraordinarily wide tolerances on the moisture and disturbance gradients. In spite of the apparent capacity of the plants to survive, there were large areas of the landscape that were nearly barren of plants or with sparse coverages of vegetation. These were mingled with areas of dense cover in complex interdigitated patterns. Lack of snow cover in winter, commonly used to account for such areas, could not be applied because the pattern would not allow it; and more important, nearly all of the Mesters Vig district was known to be under deep snow throughout the winter.

Attempts to describe repetitive communities of plants proved unavailing. Observations on the behavior of species with respect to coverage of the ground suggested the same wide tolerances that were evident on other gradients, indicating that the species which make up most of the vegetation are relatively independent of "association" with other species.

These observations were not new. Gelting (1934, p. 235) made the following remarks in describing a group of 44 species in the area of Northeast Greenland that he studied. They were the most abundant and widespread plants in his flora: "Nearly all the herbaceous dicotyledons of Group AI show an unaltered frequency in all three districts [outer coastal, outer fjord, inner fjord], which is closely connected with the fact that they are almost exclusively represented by extremely hardy species with a wide range in almost all ecological scales. On the whole, Group A I represents the hardiest species of the area." Something of the same range of tolerance can be gained also from perusal of Table II in SØRENSEN's "Remarks on the flora and vegetation of Northeast Greenland, etc." (in SEIDENFADEN & SØRENSEN, 1937, pp. 112–115). With regard to snow cover GELTING had this to say (1934, p. 237): "By far the majority of the species occurring in my area have been found on snow-free as well as on snow-covered ground." He looked upon snow cover as merely favoring certain species, giving rise to differences in frequency.

Recently developing knowledge of arctic soils and especially of the geomorphic processes affecting them, has emphasized a site factor complex which has not previously played a major role in the consideration of these Greenland problems. A pioneer paper by SEIDENFADEN in 1931 drew attention to the process, but not enough data were available fully to demonstrate its significance. In recent years a great deal has accumulated, and Dr. A. L. WASHBURN's intensive studies of geomorphic processes at Mesters Vig form the basis for much of the interpretation of this factor complex in the present paper (WASHBURN, 1965, 1967).

In the absence of clearly defined community structures in the vegetation at Mesters Vig, it seemed that a study of the relations of plant cover to site would best be concentrated upon the behavior of individual species. Not only would this afford more precise units of study, it would also be more likely to provide data useful at the large map scales required by the site investigations. Most students of plant communities look for ways to identify and bound these communities in terms of species. In most of the Northeast Greenland tundra, where a large percentage of the species are ubiquitous, those reliable for definition, if found at all, are almost certain to be of occasional or rare occurrence, or at most locally common. For such purposes the "ubiquists" are of little interest unless they happen to figure as "dominants". But in a study the avowed purpose of which is an understanding of vegetation-site relationships, a selection of this kind tends to eliminate at the outset, as irrelevant, the larger part of the material that is actually available for observation and study. This material is in the plants with the wide ranges on the "ecological scales". Not only are there many of them, but they bulk much larger in the total vegetation than the more "exacting" species, and they offer a greater range of variation within which to observe and compare differences. With these things in view I have ventured to begin all studies of species behavior with those having the widest tolerances.

Solutions for many basic problems in the plant-site relations of the tundra will require detailed field investigations of the living plants in situ, over periods of time. Such studies should be accompanied by comparative anatomical, physiological and cytological investigations, as well as by studies of the site processes that are affecting the life of the plants. In past years logistic limitations have made this kind of research difficult in the Arctic, but modern systems of transportation and supply are now making it much easier and less expensive. Meanwhile we use whatever observations we have on the plants and the sites, arranging them in systems of fact that can be compared and searched for suggestive coincidences. It is well to keep in mind, however, that our real knowledge of the life of these plants is still extremely limited.

I venture upon the following discussion with much diffidence and humility. My personal knowledge of the Greenland flora and its behavior is restricted to my Mesters Vig experience, and is therefore in great danger of bias. I consider it useful, however, to report what I have seen, and what I have thought while seeing it. I have no solutions for the problems of the Mesters Vig flora, but some of my notes may lead others to find new and fresh approaches to these problems.

The Greenland work would not have been possible without the generous assistance of many persons and institutions. I have already expressed my indebtedness to them (Raup, 1965 A & B), and will not repeat it here. I am especially grateful to the editors of the Meddelelser om Grønland for patient and critical care with which they have seen this and earlier papers into print.

REVIEW OF LITERATURE

The following review of literature will be concerned mainly with previous efforts to rationalize the behavior and localized distribution of vascular plants in northeastern Greenland. References to research outside this region will be used as they appear to serve this purpose. The review is not to be regarded as in any sense complete.

There is no intention of burdening the present paper with a general discussion of ecological theory. However, it is desirable to examine some of the earlier studies of Greenland vegetation and the assumptions on which they rested. It is suggested that by this means basic problems dealt with in the literature can be made to emerge more clearly.

The significance of scale in vegetation-site research

Organized ideas on the vegetation of the whole of Greenland began with WARMING. He published an account of this vegetation in 1888, and an English version appeared in 1928. When his general ideas on arctic vegetation (1909) were applied to the fjord region of Northeast Greenland most of the landscape came under the type he called "fjaeld-mark", or "fell-field". Lesser areas, particularly in the southern districts, were covered by "dwarf-shrub heath", "mat-herbage", "mat-grassland", "tundra bushland", and a form of "low moor". It is also possible that something resembling what he described as "moss-tundra" is found there. Because so much of the landscape is characterized by his "fell-field", this and the relations it bears to the other types have given rise to most of the vegetational problems of the region.

WARMING (1909, p. 256) characterized "fell-fields" mainly by the small stature of their plants, and by the fact that the *soil is never completely* covered by plants. He said that: "The cause for the poverty in individuals does not lie in the soil itself, for this indubitably contains a sufficiency of nutritive substances and water, and could certainly produce luxuriant vegetation *were sufficient heat* supplied. Between climate and vegetation there evidently must be a certain constant relation of such a kind that no more seeds or other propagative organs germinate or develop into plants than just suffice to maintain the vegetation at the standard once established." Further to the controlling influence of the heat factor he stated that "On *high mountains in Europe* and in *arctic countries* fell-fields prevail where the mean temperature of the warmest month is below 6° C." He thought that at somewhat lower latitudes fell-field was "confined to unfavourable localities, while plants on more favourable sites produce a closed formation." Presumably the reverse would also be true, and at higher latitudes, within the fell-field region, "closed formations" should be found on the "more favourable" sites. WARMING rationalized the occurrence and distribution of these "favourable" and "unfavourable" sites on the basis of local water supply, snow cover, soil, slope and exposure.

The mean temperature of the warmest month at Mesters Vig is approximately 6° C (6.2°, Av. for 1953–1961; *cf.* WASHBURN, 1965). Although there is considerable local variation, and a regional gradient from the outer coasts to the inner fjords, it is probable that most of the fjord region would satisfy WARMING's temperature requirement for fell-field.

In this description of fell-field as vegetation in which the ground was not completely covered by plants, WARMING did not define precisely what he meant by "covered". The most densely vegetated "heaths", herb-heaths and "low moors" in the Mesters Vig district, when studied carefully, did not show more than 90 % coverage. It can be assumed that this amount is well within the range of variation allowed by WARMING (1928) for "complete" coverage by vascular plants. The coverage proportion at which the vegetation becomes fell-field by his definition must also be assumed for application in the Mesters Vig district. If about 60 % (again vascular plants) is chosen, between 60 % and 70 % of the land surface probably would be in fell-field, and the remainder under denser vegetation.

Another element of uncertainty is in the thin organic crusts which are prevalent at Mesters Vig. Much of their content is dead, but there are blue-green algae in them, occasional lichens, and a few living fronds of mosses and hepatics. Whether they should be included in the plant "cover", in the sense of WARMING, is unknown. Because of their thin populations of living plants they have been included in "fell-field" for purposes of the present discussion. Vegetation of somewhat similar nature was described by BÖCHER (1933, pp. 90–91) in Southeast Greenland as of "snow-patch" origin. However it was observed at Mesters Vig emerging from the snow in early summer, simultaneously with "heaths", "low moors", and the bare soil of the "fell-field".

WARMING generalized the vegetation in terms of form and communal structures. His basic units of study and mapping were not so much taxonomically defined species as physiognomic or biologically interpreted life-forms, or formations and communities made up of these forms. He generalized site factors into units that would be roughly commensurate with his major units of vegetation.

Our investigations in the Mesters Vig district have dealt with a small geographic area (about 110 sq. km). Within this space our actual detailed studies have covered much smaller areas (ranging from a fraction of one hectare to 2–3 hectares). These operations have required maps of large scale, and have entailed great difficulty with definitions of, and boundaries for, types of vegetation and sites. They have placed a premium upon knowledge of behavior patterns, not only of the poorly defined vegetation types but also of the better defined taxonomic species. They have also required measurements of site factors at commensurate scales.

A major difference between the Mesters Vig studies and those begun many years ago by Warming is one of *scale*. In general, the last 60 years have seen increasing refinement in our knowledge of Greenlandic species, types of vegetation, and sites, with mapping possible at increasing scales. In the same period there has occurred a parallel increase in the specialization of the students carrying on the research. Warming appears to have kept his site and vegetation scales commensurate, but later students, with a few exceptions, have lost this habit. A search of the literature for material useful to the Mesters Vig studies is therefore much concerned with matters of scale. Research that has brought investigations of either vegetation or site to relatively small areas, using large map scales, is more desirable than that for large areas using small scales. Such research at large scales is likely to have used, also, the more clearly definable and precisely measurable units of vegetation and site. Most useful is research in which *both* clearly definable vegetational units and environmental variables have been measured and compared *in the same areas on commensurate scales.*

By far the most immediately useful papers in the literature reviewed below were published between 1931 and 1945 by the Danish botanists who worked in Northeast Greenland in the 1930's. These papers contain the basic taxonomic and geographic information on the flora, and the local arrangement of the flora to form the plant cover. Although their descriptions of sites are not entirely adequate for present needs, their voluminous and precise notes on the vegetation and its behavior are nearly all at the species level. Therefore the majority of them are usable for analyses of site relations at large scales.

Second in order of significance to the Mesters Vig problems, useful for methodology rather than directly, are a few recent papers on the vegetation of northern and western Alaska. These studies correlate the behavior of species with site in small areas at large commensurate scales.

Next is a series of studies in Greenland and other parts of the Arctic in which the scales used for vegetational analyses are at variance with those used for the attendant sites. In some cases detailed morphological and physiological studies of individual species were made, but the authors described the sites in such general terms that it is now impossible to place their plants in realistic habitats. Contrasting cases are mainly those in which a "community concept" of vegetation was used for analysis where the sites were described in great detail. Here the basic vegetational units were usable only at relatively small scales while the sites were being studied at large scales.

Finally, least useful for the Mesters Vig studies are papers that remain essentially in the WARMING tradition or refinements of it, dealing with vegetation-site relations in more generalized terms.

Danish publications on Northeast Greenland vegetation, 1931—1945

The principal botanists of the Danish Three-Year Expedition of 1931–1934 were THORVALD SØRENSEN, GUNNAR SEIDENFADEN, and PAUL GELTING. For their more intensive research and publication they divided the fjord region into three latitudinal divisions. SØRENSEN worked in the southern area, he and SEIDENFADEN covered the northernmost division, and GELTING took the central district. Later (1937) SEIDENFADEN and SØRENSEN published jointly a floristic review of the whole fjord region, and SØRENSEN published a local and regional geographic analysis of its vegetation.

The first major publication in this sequence was by SØRENSEN (1933) on the region between latitudes 71° and 73°30′. It was devoted primarily to a catalogue of the vascular plants known to occur there, but it also contained many notes on plant form and habitat, altitudinal limits, and geographic distribution. In concluding remarks SØRENSEN summarized information given throughout the text on general distribution within his region, and on the apparent preferences of the plants with respect to calcareous soils. A map, published as his Fig. 2, shows all collection localities, areas of more intensive study, and the geographic divisions of outer coasts, outer fjords, and inner fjords.

GELTING (1934) published a floristic and phytogeographic study of the middle part of the fjord region (lat. 73°15′ to lat. 76°20′). He spent an entire year (1931–32) in the region, wintering at Clavering Ø, and later spent the summer of 1933. Although he attempted no general organization of vegetation as did SØRENSEN (1937) with his "ecosystems", or as suggested by SEIDENFADEN in 1931 on the basis of solifluction disturbance, his paper of 1934 is filled with cogent observations on the relations of individual species to their habitats. He was thoroughly aware of the theory of the "community", and despaired of applying it to the arctic tundra; but he also knew the Greenland species in the field, and could watch their behavior with respect to each other and to their physical habitats. He not only noted their behavior on factor gradients, and their regional and local frequencies, but he studied their general morphology, with excavations to discover their root and underground stem systems.

His voluminous notes are all published in appropriate places, either in his 1934 paper, or in a later one on a special study of the food of the ptarmigan (1937). They constitute a mine of information that was found to be extremely useful in the Mesters Vig studies where most of it could be checked and utilized.

SEIDENFADEN and SØRENSEN produced, in 1937, a paper in two main parts, of which the first was a catalogue of the vascular flora of the northern division of the fjord region (lat. 74°30′ to 79°00′). Thus they completed the detailed treatment of the collections made during the Three-Year Expedition and brought up to date all previous floristic studies of the region. The second part of their joint paper was a summary of the entire vascular flora of East Greenland so far as it was known at that time. As would be expected, this required critical reviews of numerous taxonomic problems in various species complexes. They proposed seven phytogeographic areas on the East Greenland coastal strip and presented a table showing the distribution of species not only on the eastern coast but also by northern and southern limits on the west coast. They also designated those that were circumgreenlandic. Finally they discussed what they considered to be major groups of East Greenland plants with respect to their general affinities outside Greenland, and their probable routes and times of migration into Greenland.

Embedded in this paper, as item "III" in the first part, is a section under the sole authorship of SØRENSEN: "Remarks on the flora and vegetation of Northeast Greenland 74°30′–79° N. lat." SØRENSEN called it a "preliminary attempt" to arrange the vegetation of the fjord region primarily in terms of site. He recognized that many arctic plant "communities" are not definable as such, and therefore considered that site must be the basic feature of any organization of the vegetation. His work was firmly founded upon the collections, field observations and taxonomic studies of SEIDENFADEN, GELTING, himself and associates in the Danish expeditions of the early 1930's. Although the title of section III mentioned only the northern division of the region, the text extended the coverage so that it was effective for the region between latitudes 71° and 79°.

Twenty-two units of vegetation were defined, and called "ecosystems". Their basic organization was in terms of moisture supply: "Dry", "Moderately moist", and "Moist to wet". These were in turn modified variously by one or another (or both) of two other major factors: snow cover in winter, and "solifluction". The latter was defined in its broadest sense, as any soil disturbance due to frost action or the flow of saturated soils downslope over permafrost.

Much of the emphasis on solifluction found in Sørensen's paper derived from the cogent and far-seeing earlier work of Seidenfaden (1931) on the relations of vegetation to geomorphic processes in Northeast Greenland. These relationships had already been noted elsewhere in the Arctic by, among others, Wulff in northern Greenland (*cf.* Ostenfeld, 1923), by Summerhayes and Elton (1923, 1928) in Spitzbergen, and by Frödin (1918) in Swedish Lapland. Seidenfaden had been attached to the Danish East Greenland Expedition of 1930, and visited many points in the fjord region between lats. 72°54′ and 74°18′. General knowledge of the geomorphic processes at work in the landscape was limited, but he appears to have known the pervasive significance of moisture and soil texture for determining the intensity of physical disturbance of the soil due to gelifluction and frost action. He had no definitive measures for intensity of disturbance, nor did he distinguish clearly between disturbances of the soil due to frost heaving and gelifluction. All seem to have been grouped in a single category which he called "solifluction soil" or "moving soil". He mentioned "vertical movement" of the soil repeatedly, but did not elaborate on what he meant by it.

Seidenfaden described a series of situations to illustrate varying intensities of solifluction, ranging from soil that was moving so rapidly that no plants could live in it, to stable soils capable of supporting various groupings of species depending upon local conditions. Slowing down or stoppage of the movement could be caused by an undrained depression which would pond the water at the foot of a solifluction slope to form a stable swamp; or the flowing soil might be checked by large boulders anchored in permafrost; or it might be checked merely by loss of water due to evaporation or drainage. He quoted the work of Gripp (1927) in Spitzbergen to show that such "movements can only take place if an equilibrium exists between the water and the particles of solid material". He described situations in which the conditions of this "equilibrium" were met immediately after snow-melt, but in which the soils were so desiccated in late summer as to "reduce the vegetation". In other places the water supply and movement were continuous.

Seidenfaden made preliminary lists of species, first for sites with "slowly moving soil"; second, "swamps", which he considered to be stable sites; and third, well drained upland soils "where solifluction and formation of polygon soil do not take place". In each case he gave first a list of the commonest plants, and then a list of secondary species. This appears to have been a pioneer effort to give tolerance ratings to species on a physical disturbance gradient.

SØRENSEN, like SEIDENFADEN and GELTING, was acutely aware of differences in behavior among species with respect to moisture, coverage and (to some extent) disturbance gradients. This appears especially in his table of species showing their distribution among the various ecosystems. When his table is elaborated with his descriptions of the ecosystems the variation of tolerance among the species is striking. Some reinterpretation of his "solifluction" is necessary at several points, but this is possible in most cases because of the completeness of his descriptions. However, he had little more specific information on the rates and kinds of soil disturbance than had SEIDENFADEN in 1931, although he had, himself, done some careful research on the formation of structured soils (1935). Thus he was unable to go much further than SEIDENFADEN did with the refinement of relationships between plant behavior and the disturbance factors.

An attempt to enlarge the scales of vegetation and (to some extent) site "mapping" to make them useful in localized areas is found in a later paper by SØRENSEN (1941) on the phenology of Northeast Greenland plants. This paper was based mainly on SØRENSEN's own observations during the Danish Three-Year Expedition of 1931–34, another expedition in 1934–35, and a summer trip in 1937. In all he spent six summers and two winters in Northeast Greenland, giving him ample opportunity to observe the seasonal behavior of the plants. His paper contains a critical discussion of previous research in the subject, and extensive citations of literature.

In establishing the significance and parameters of his study, SØRENSEN made the following significant points: (1) that the arctic plants appear to be uninjured by winter cold of any intensity; (2) that their relation to temperature climate is limited to the thaw season when growth is possible; (3) that the temperature climate at the ground surface is more significant, particularly in spring, than that of the ambient air so far as plants are concerned; (4) that the vegetative and reproductive adaptations of plants to the varying lengths and conditions of their growing seasons are therefore of great importance to their survival in the Arctic. In general he conceived that the arctic flowering plants are admirably adjusted to their environment.

The paper is replete with specific phenological data on most of the vascular species. SØRENSEN used the Danish taxonomic and geographic studies of the preceding decade to build on (SØRENSEN, 1933; SEIDENFADEN and SØRENSEN, 1937; GELTING, 1934). On pp. 54–59 he related the phenological data to the 22 ecosystems which he had described in 1937 (in SEIDENFADEN and SØRENSEN, pp. 108–140). He also related them to geographic latitude (pp. 62–63; 164–183), and to distance from the open sea (pp. 61–62).

Whether or not SØRENSEN's findings, as set forth in this paper, can be applied to the Mesters Vig problems is uncertain. His most cogent applications of them appear to have been to larger geographic areas. Among his ecosystems there was some overlapping, particularly in the details of the floras of these systems. He noted this situation as follows (pp. 67–68): "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". SØRENSEN carries this idea even further by saying that because the individual species frequently are not limited to a single ecosystem, it is to a certain extent impossible to fix perfloration periods for each species. He concludes that:

"It will be evident . . . 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".

The above quotations point to basic difficulties in applying these data at Mesters Vig. Much of SØRENSEN's arrangement of ecosystems rested upon the behavior of the snow—its differing depths and times of departure in spring. Thus far the patterns of vegetation in the Mesters Vig district seem to bear little relationship to snow behavior except in cases of extreme snow-bed conditions. Some of the Mesters Vig vegetation that SØRENSEN would have placed in his wetter ecosystems, which should emerge late from the snow (in his "Thawing Group IV"), actually emerges from the snow simultaneously or even earlier than some that he would have placed in his dry ecosystems emerging early (in his "Thawing Group I"). The "ubiquists" which he mentions as standing in the way of "a natural division of the vegetation according to the content of species" are the species widely tolerant of variation on environmental gradients. Wide flexibility with respect to phenological adjustment might also be looked for in many of these species. The uncertainty of local differentiation of "thawing groups" in the Mesters Vig district, together with the extensive capacity of species to spread widely on environmental gradients, suggest that SØRENSEN's data in the form presented by him may not be applicable in so small an area. Nonetheless the large quantity of phenological information on individual species may be applicable when used directly in specific cases.

In 1945 SØRENSEN published a general summary of the botanical research carried out on the Danish expeditions to East Greenland in the years 1926–1939. On pp. 27–34 are excellent reviews of GELTING's work on the life-forms of the Northeast Greenland vascular plants, and of his own and GELTING's observations on the phenology of the species. On pp. 36–42 he reviewed his own and SEIDENFADEN's studies of solifluction and patterned ground, and on pp. 42–45 he reported GELTING's paper on ptarmigan foods. Pages 4–27 are devoted to floristics, taxonomic problems, and the geographic distribution of species.

These investigations vastly enlarged the scale of refinement in our knowledge of Northeast Greenland vegetation. From the few simple divisions that WARMING saw in fell-field, SØRENSEN had recognized 22 units that he could define with varying precision. But it was realized that the definition of these units was inherently weak, and that the species were more reliable for comparative study. The species, in turn, had become relatively well-known taxonomically and geographically. Further, their behavior on some of the more important environmental gradients had also become fairly well-known. But even though the vegetational scale was greatly enlarged, the site scale remained generalized by comparison. GELTING and SØRENSEN both sensed the variation among species in their spread on the moisture gradient, for example, but one looks in vain for a "case" where they *mapped* the behavior of the species and the moisture factor at the same scale and proved the coincidences. SEIDENFADEN may have reached greater refinement with his lists of plants capable of living on the moving soil of solifluction slopes. But his lack of values for rates and intensities of disturbance precluded his accomplishing much with it.

Viewing the botanical literature of Greenland in the 1930's as a whole, one gets the impression that the enlargement of scale in site studies fell far behind that in vegetation studies. Botanists were becoming more and more specialized—as taxonomists, or ecologists of various kinds, with limited attention to the earth sciences. The earth sciences, left in the Arctic almost entirely to geologists whose primary concern was with mineral deposits and bedrock stratigraphy, produced very little of immediate use for the rationalization of the vegetation-site relationship. Knowledge of Late-Glacial and Postglacial deposits, and the soils derived from them developed at snail's pace, while specialized knowledge of plants and plant cover was going forward much more rapidly. This process took the scales of reference in the studies of site and vegetation out of balance.

Vegetation-site studies on large commensurate scales

The varying adjustment capacities of the species themselves in the species-site relationship were given only cursory study for many years. Gelting (1934, 1937) was particularly conscious of wide ecological amplitudes of many tundra plants. Fernald (1925) had drawn attention to them in his concept of the persistence of plants in unglaciated areas, but he had no explanation for them other than "youth" and "senescence". In 1937 Hultén applied the idea to the entire arctic and boreal flora of the world, and by the late 1930's cytogenetic studies had accumulated enough data to give a reasonably sound genetic basis for differential adjustability among species in a flora (*cf.* Raup, 1941, for literature of the period).

A recent student of Greenland vegetation (Böcher, 1954) insists that the basic unit in the study of vegetation should be "ecologically and genetically . . . homogeneous, *i. e.*, it ought to be an ecotype or consist of related ecotypes". He believes that "communities are of little interest in themselves", and that the boundaries made to separate them are like the artificial lines of the geometrician, used to solve a particular (*ad hoc*) problem. Their only function is "a survey by which the ecology of the individual species can be illustrated and by which part of the vegetation of the earth can be described". Böcher's studies of western Greenland flora and vegetation (1938, 1952, 1954, 1963) utilize these points of view, and are opening new vistas to students of arctic plant geography (see also Drury, 1962, p. 76).

Wiggins (1951) drew up careful descriptions of the distribution of vascular plant species on polygonal patterned ground near Point Barrow, Alaska. The vegetational and ground features, including the soil profiles, were described and related at the same scale. The patterned ground here was of low relief (usually less than one meter), and with a few exceptions rather densely covered with vegetation. The exceptions were occasional pools of open water, and a few small areas of bare clayey soil apparently pushed to the surface by frost action. Even with this low relief, Wiggins described what he considered to be "some ecological sorting, with some species confined to the faintly drier tops of hummocks and ridges, while others occur only in the central pans or in the ditches separating the individual polygons. Still other plants are predominantly occupants of intermediate slopes". He stressed the extreme variability, within areas of "a few square meters", of the soils underlying this arctic vegetation, and proposed that "extensive investigations in this field are imperative before reliable conclusions can be drawn concerning the soil-vegetation relationships in the Alaskan arctic". Considerable progress has been made along this line by TEDROW and his associates since 1951 (see below).

WIGGINS made no extensive efforts to rationalize the behavior of individual species with respect to site factors, but on p. 47 of his paper are cogent remarks on *Oxyria digyna* and a few other species: "It may be significant that *Oxyria digyna* in the vicinity of Point Barrow commonly occurs most abundantly on rather pronounced slopes, particularly on ground that is subject to frequent movement. This movement is sometimes caused by caving as erosional effects from river currents or ocean waves cause undercutting, but more frequently by downhill 'creep' accompanying thawing in the spring and summer months". WIGGINS was struck by the fact that in his studies of polygonal ground this species was found only in "the bottoms of the ditches", between the polygons, "even though there is no appreciable 'creep' or erosion action present there". He proposed that only in these ditches were soil, moisture and aeration conditions suitable for *Oxyria* in the complex of sites presented by the polygons. However, in a footnote inserted at this point he discussed the problem further: "It is possible that *Oxyria* grows on the shifting slopes of hummocks, bluffs and lake shores, not so much because the moisture supply is particularly favorable but because its root system is able to adapt itself quickly to shifts in the surface and subsurface material. . . . Other perennials unable to establish themselves readily and quickly adjust to soil movements are left behind in competition with *Oxyria* and such other plants as *Potentilla*, *Equisetum*, *Taraxacum*, and a few others. If this be the case, the presence of *Oxyria* in the ditches . . . may be due to slumping and shifting of the soil following melting of the ice from the wedges underlying the ditches".

With these remarks WIGGINS was pointing the way to a wide field of observation and analysis of vegetation-site relationships that has progressed but slowly in the Arctic. His vegetational study, based on species, was commensurate in scale with the intricate complexity of the physical site. His close observation of the behavior of individual species with respect to the intricacies of the site brought some realistic problem statements closer than had been possible previously.

A notable contribution toward the rationalization of varying adjustability of species on local environmental gradients appears to have been made by JOHNSON and PACKER (1965; see also JOHNSON, PACKER and Reese, 1965). It is of particular interest to the present study because its scale is large enough to embrace the species level, and because the "map scales" used for both site factors and species characters are commensurate. Working in the Ogotoruk Creek valley, in the Cape Thompson district of northwestern Alaska, Johnson and Packer examined cytologically 234 species of vascular plants. They then arranged the plant habitats of the study area along gradients (on a scale of 1–6) of soil texture (fine to coarse), soil moisture (high to low), soil temperature (low to high), permafrost (shallow to deep), and intensity of disturbance (high to low). Sorting their cytological information about the species according to the distribution of the latter throughout this graded arrangement of habitats, they found clear evidence of high polyploidy in fine textured, wet, cold soils that were especially subject to physical disturbance. Conversely, the low percentages of polyploidy were in coarser textured, well-drained soils (sands and gravels) where the permafrost table was deep and disturbance was minimal. The authors propose that the plants with higher polyploidy have greater inherent capacity to withstand habitat variation. In the terms used in the present paper they would be regarded as some of the more widely tolerant species.

The physical aspects of the Northeast Greenland soils were described in general terms at many points in the literature, and their nutritive properties for plants noted in a few isolated places. But except for such special features as solifluction and polygon soils one gets the impression that none of the descriptions were actually "made in Greenland". Rather they were conceptions of mineral, textural and drainage categories made so broad and generalized that they could be used equally well in northwestern Europe. No pedological studies *per se* seem to have been made in the fjord region until Ugolini (1966A, B) first investigated the soils of the Mesters Vig district in 1961 and 1964. He correlated his work with concurrent botanical and geomorphological studies in that area, using the same scales, and also attempted to relate the development of soils in northern Greenland with that in arctic Alaska and Russia. His identification of an "Arctic Brown" profile in the Mesters Vig district, similar to that developed by pedogenic process in other parts of the Arctic (*cf.* Tedrow and Hill, 1955) established the existence of the process as well as the profile. Although the profile is not widespread in the landscape, and little is known about the rate of the process, the general state of profile development in a given soil, in relation to other edaphic factors and to vegetation, forms a valuable tool for vegetation-site rationalization.

Studies of vegetation and site on non-commensurate scales

Few students of Greenland vegetation have made direct attacks upon the problem of vegetation-site relations by investigating either the intimate details of the site or the structure, physiology and behavior of individual species.

One of the few to approach the problem thus directly was WAGER (1938). He spent a year (1932–33) on the southeast coast of Greenland in the vicinity of Watkins and Mikis Fjords making rather detailed studies of the success of reproduction around individual adult plants growing in open vegetation. He wrote a simple statement of his problem as follows: "Certain types of arctic and alpine climates tend to allow the development of open associations of plants, which have been called 'fjaeldmark' by WARMING. In these associations the adults live for a great length of time and appear to be healthy and grow to a large size, often producing abundant flowers and fertile seeds. It is clear that the climate is such that the plant species can flourish, so it is curious that in the course of time these areas should not have developed a closed association".

Interpretation of WAGER's results in terms currently useful depends largely upon how he selected the sites he used for study. In the areas selected he said there was "no preliminary growth of lichens and mosses before that of the flowering plants". He stated further that "In the district examined, the vegetation varies from a completely closed herb field association to barren land. These extremes are often found in close juxtaposition and appear to be fairly stable. In the writer's opinion a distinction must be made between areas which have suitable soil conditions for plants, *i. e.*, presence of moisture, soil stability, soil particle size, etc., and those which cannot be colonized because of unsuitable soil conditions. In the present account 'fjaeldmark' is only being used to describe the former type of areas". He used 12 quadrats, giving brief descriptions of each as to general situation, soil, and moisture. They varied from coarse-textured sandy gravels to silty loams, and from very dry to moderately moist. No precise values were presented. Although he took great pains with his study of seedlings he had much difficulty in recovering enough to make his results significant.

The paper closes with a discussion of factors limiting the growth of plants in "fjaeldmark". He found a high population of seedlings which showed a very slow growth rate and excessively high mortality. He agreed in part with WARMING that low summer temperature was a major factor, and in part with OSTENFELD that the short growing season was important. He recognized the significance of "solifluction soil" and "polygon fields", quoting SUMMERHAYES and ELTON (1923, 1928) on their importance to vegetation in Spitzbergen, but he could not see that they affected his quadrat areas. He reviewed the problem of nitrogen shortages but considering it in relative terms he did not think it significant to his immediate problem. Nor did he think that any shortage of mineral salts could affect relative growth materially. He also raised the question of water shortage, but considered this also to be of little consequence. He then looked for places where "good growth" was found—not fjaeldmark. These places, he said, were "sheltered", with a "southern aspect". On the other hand he said that fjaeldmark developed "in unsheltered places which are also damp and are often, as in the moraines investigated, subject to small local katabatic winds from some glacier or snow field above them".

He concluded further "that the 'weakness' of the 'fjaeldmark' plants is due to carbohydrate shortage brought about by the climate of the district". This meant merely that he thought the plants hadn't the time, at their low metabolic rates, to manufacture and use any more sugars than they did because of the cold short summers. But this did not explain why some plants managed to do it and others did not. Often they were of the same species, growing in close proximity, and having equal lengths of season.

This is an important paper because it deals with a fundamental problem at its core—the actual relations between individual species and sites. WAGER, at the beginning of his study however, instituted a basic source of error by assuming too much knowledge of site. He assumed that "suitable soil conditions" were known for plants in the Arctic with respect to moisture, texture and physical stability. He greatly enlarged the scale of his vegetation study, but left the site scale scarcely larger than WARMING's. Consequently it is impossible to relate the things he observed to the situation in which they actually existed except in terms hardly less general than those of WARMING. Further error came from his failure to insert a time factor involving changes in the temperature and moisture regimes.

Very few individual species have been given even a reasonable part of the intensive study suggested by BÖCHER (1954). One of these, familiar in the flora of Northeast Greenland, is *Oxyria digyna*, investigated in detail by MOONEY and BILLINGS (1961) (see also RUSSELL, 1940 B; WIGGINS, 1951). They collected material from much of the American and a little of the Greenland range of the species, grew it under controlled conditions, and described its genetic properties, structural and physiological variations, and its behavior under varying conditions. The most intensive aspect of the study was of necessity the reaction of the species to such phases of the environment as could be reproduced artificially. These could not include some of the more important processes that affect

Oxyria digyna in the Arctic such as the varied soil disturbances due to mass-wasting, the ubiquitous but extremely varied effects of frost heaving, and irregularly periodic changes in moisture supply. The authors secured as much data as they could on their collection sites—soil type and nutrients, plant associates, amount of plant cover, slope and exposure, and snow cover. Inferences of actual plant-site relationships from these data, to be used for comparative purposes, are hardly satisfactory. Further, the study is not as good for the Arctic as for the Cordillera, for the authors had only four thoroughly arctic collection stations. Three of these were on the north coast of Alaska and the other was at Thule, Greenland. A fifth station, essentially arctic, was on the Yukon Plateau in central Alaska. Even with these lacunae, MOONEY and BILLING's paper represents a new and highly promising innovation in the study of arctic-alpine phytogeography.

Specific information on species-site relations are often more apt to be found in taxonomic than in ecological literature. An example is the monograph of Greenland *Puccinellia* by SØRENSEN (1953), which contains abundant notes on the local behavior of the various species. Another is a recent study of variation in the genus *Dryas* by ELKINGTON (1965), who investigated the range of habitats occupied by *D. octopetala* and *D. integrifolia* in Greenland. He made a determined effort to find whatever relationships might exist between variants of these species and the sites on which they grew. Although his results in this search were negative, his published data demonstrate the wide tolerance of *Dryas* on the moisture and coverage gradients. Further, the soil analyses from his collection sites suggest that it also has a wide tolerance of variation in pH values.

A physiological approach to the vegetation-site relationship is illustrated by the research of the Oxford University Expedition of 1938 to Jan Mayen Island. RUSSELL and WELLINGTON (1940) described the vegetation of the island in the first of three papers from the expedition. Their general organization of sites and vegetation types was a simplified form of that used by SØRENSEN (1937) in Northeast Greenland. Jan Mayen is a volcanic island, apparently with a great deal of excessively drained soil. It also provides rookeries for great numbers of sea birds which have deposited nitrogenous fertilizer on many of the soils. The expedition visited the island only in the summer; nonetheless the authors could see the phenological behavior of many late-flowering species as the late-lying snowdrifts melted back. All of these things influenced their general conclusions that the "major factors which determine the distribution of the various types of vegetation" were: "the degree of exposure to the wind, nitrogen and water supply and the time of snow retreat".

The second paper (RUSSELL, 1940 A) gave the results of a more detailed study of the relationship of soil nitrogen to the vegetation types on Jan Mayen. Soil samples were collected from representative types and analyzed for moisture content, inorganic and total nitrogen, nitrifying bacteria and protozoa. As might have been expected, a close correlation was "found between the density of the vegetation, the soil micro-organisms and the nitrogen supply". Inorganic nitrogen was everywhere at a low level, and in soils under "sparse vegetation, nitrate nitrogen was nearly always absent". In his summary RUSSELL "concluded that in the island nitrogen deficiency is widespread and is a factor of foremost importance in determining the distribution and development of various types of communities". He suggested that the main cause of the nitrogen deficiency was the "slow rate of bacterial activity, due both to low temperature and to low nutrient supply . . .".

RUSSELL's work on soil nitrogen and micro-organisms in relation to the vegetation types as he defined them is no doubt good. But in arguing a case for the predominant importance of general nitrogen "deficiency" in the site he had, perforce, to draw a picture of a system of interlocking factors on only a few of which he had any specific information. On others he had some vague data extrapolated from a distance. He knew that still more factors existed but he had to disregard them because he had no data on them at all. Deficiency in any factor, as WAGER appears to have sensed, has to be assessed in terms relative to the demands made by plants growing in their native haunts, and also in terms of whole factoral systems that are more or less unique for different site complexes. RUSSELL's technical methods for study of soil and plant nitrogen and for micro-organisms were refined beyond the capacity of his site and vegetational scales to absorb them. His problem was leading him to species and micro-sites, but he dealt only with "communities" and a few samples of soil beneath them.

The third paper in this Jan Mayen series (RUSSELL, 1940 B) was on carbon assimilation, carbohydrate storage and stomatal movement in relation to the growth of a few species. Most of the work was done on *Oxyria digyna*, though *Polygonum viviparum* and *Taraxacum croceum* were also studied. Again, as might have been expected, the above processes proved to function sufficiently well to enable the plants to live where they were found.

Another physiological approach to the "problem of fell-field" somewhat similar to that of RUSSELL, and perhaps analogous to that of WAGER, was made by WILSON (1957), based on studies at Jan Mayen Island, and at Cornwallis Island in the Canadian Arctic. WILSON was impressed by the "poverty of the vegetation" and the "general impoverishment of growth". He expressed the view "that the immediate cause of this poverty is an exceptionally small amount of annual growth". He made clear he was not suggesting that low growth rates were the only cause for the open vegetation, for he said it "may result from solifluxion effects, and dwarfing of plants from genetic adaptation of arctic ecotypes". However, he made equally clear that he thought the poverty of the arctic vegetation resulted "primarily from an extremely low amount of annual growth, which in turn is due both to the shortness of the growing season and also to the slowness of plant growth even during the brief summer. These low growth rates result from the low temperatures—especially as aggravated by exposure of the plants to cooling winds—and, at least at Jan Mayen, from widespread deficiency of nitrogen, which arises through inhibition of soil microbiological activity by the low temperatures and the poor supply of organic material".

WILSON's study is a mixture of the specific and the general. He presented much firm information on a few species in the areas he visited, giving the results of careful observations and experiments on summer growth rates and plant temperatures, and on soil fertility. On the other hand he seems to have related none of these results to specific sites. Although we learn much about the plants' general position with respect to soil nutrients and air temperature, we have no clue to their positions on gradients of soil moisture, texture or disturbance.

It has already been noted that detailed local studies of site in the vegetation-site relationship have been less numerous and intensive in Northeast Greenland than those of vegetation. It was generally agreed that the soil was "suitable" for plants provided enough water was available, and enough heat. It was considered that nitrogen was in short supply, and mineral salts scanty, but that the plants seemed fairly well adjusted even though growth was extremely slow. SØRENSEN did what he could, with slender data, to reduce the earlier generalizations of the temperature climate (1941, pp. 28–47). But the shortage of data still prevails, and comparative local studies remain scanty.

There are several fields in the observation and analysis of site in northern Greenland which, judging by the literature, have been singularly neglected. Most of them involve the insertion of "process" into the investigation of climates, land forms and soils. Throughout the botanical literature there is little indication that students have considered the regional or local climates as anything other than "fixed"; or if changes have been considered they seem to have been thought of as "long-term" and not significant to present vegetation. In reality, rather clear evidence of climatic change on the Greenland coasts has accumulated (KOCH, 1945). The local effects of these changes have been found in archaeological sites, faunal migrations, and in the behavior of glaciers and sea ice. They have been brought down to effects upon the existing vegetation by studies in the Mesters Vig district (RAUP 1965 B). These local alterations involve less (or more) moisture in the soils, and therefore greatly affect the lives of plants directly, or indirectly through varying kinds and intensities of soil-forming and geomorphic processes.

A great deal of attention has been given in the literature to the occurrence and vegetational effects of physical disturbance by frost action in structured soils (*cf.* TROLL, 1944; SØRENSEN, 1935; SEIDENFADEN, 1931; WASHBURN, 1956, 1965, 1967 for references). However, these features usually have been regarded as special conditions, occupying (where active) limited areas in the landscape, and of no great consequence to the vegetation as a whole. An important aspect of them is that they are conspicuous, and easily seen. A neglected phase of frost action has been frost heaving of non-structured soils. This process, though variable in intensity, is widespread in the "ordinary" soils of the landscape, no less important because it is for the most part invisible. It probably affects in some degree all kinds of vegetation. The formation of interstitial ice or ice lenses among soil particles causes volume changes in the soil. These changes are commonly great enough to injure roots or whole root systems, sometimes to such an extent that the plants are killed.

WARMING (1909, p. 73) was thoroughly aware of the effects of frost heaving. Discussing the general effects of snow cover he wrote: "Snow acts as a protection against those *changes of volume* in frozen soil, occasioned by hoar-frost, which cause plants to be ruptured and uprooted". On the other hand, nowhere in his discussion of soil water or soil temperature, or in his accounts of fell-fields and other arctic vegetation types, is the process mentioned. Nor have any discussions of it been found in the works of other students of Greenland vegetation. SUMMERHAYES and ELTON (1923, 1928) did not include it in the frost disturbances of soils on Spitzbergen, and it was not noticed by RUSSELL and WELLINGTON (1940) on Jan Mayen. Although WAGER (1938) was apparently unconscious of its existence, it probably accounted for much of the seedling "weakness" and mortality he found in his fell-field quadrats in Southeast Greenland. This process, together with, and interdigitated in the landscape with soils subject to extreme summer desiccation, and the whole system subject to secular change in moisture regimes at intervals short enough to be within the life-spans of the plants, probably would account for much of the openness of the fell-field vegetation.

In more recent years the significance of the process has been realized by a few students of Alaskan arctic vegetation, notably BENNINGHOFF (1952) and SIGAFOOS (1952). Knowledge of controlling factors, however, and adequate measurements of intensity have not been available there. A series of papers by GRADWELL (1954, 1955, 1957, 1960) based on his studies of soil frost at a high-country station in the South Island of New Zealand shows surficial soil structures closely resembling many seen in the Arctic. The formation of needle-ice described by GRADWELL, and exceptionally active in many parts of the north temperate regions, is present in Northeast Greenland but on a much smaller scale. Also the number of freeze-thaw cycles in spring and autumn is much less than in temperate climates. Nonetheless the annual cycle is a major one, violent in its effects, making up in total soil volume change for several lesser ones (*cf.* WASHBURN, 1967).

In contrast to that on northern Greenland, the literature on the physical properties of the surficial mantle in arctic America has grown to large proportions (*cf.* Proc. Internat. Conf. on Permafrost, 1966). The scales used in these studies are, in general, large and detailed, many of them far outstripping those in use by most of the botanists attached to the research projects involved. This literature is too extensive to be discussed in detail, but a few examples will suffice.

TEDROW and CANTLON (1958) discussed the correlation of soils and vegetation in the Alaskan arctic tundra. They had the advantage of many local studies of soil profiles and patterned ground, giving them information, at large scales, on drainage patterns, and on textural, organic and mineralogical variations in the profiles (*cf.* papers by TEDROW and HILL, 1955; TEDROW, DREW, HILL and DOUGLAS, 1958; DREW and TEDROW, 1962; TEDROW, 1962). On the other hand vegetational units used in the attempted correlations were "communities" of species, described in terms of form or species composition. These "communities" were ill-defined because of extensive overlapping, or lack of structure, or both (for evidence of the wide use of the community concept in the American Arctic see papers by POLUNIN, 1948; HANSON, 1953; CHURCHILL, 1955; BLISS, 1956; BLISS and CANTLON, 1957; BRITTON, 1957; SPETZMAN, 1959). Using such units, the authors could find reasonably good coincidences only where the site boundaries were relatively abrupt and clearly defined. These were in deep or shallow, well to excessively drained soils. Where such soils merged with those of more impeded drainage they met with increasing difficulties. They found that in these soils geomorphic processes had formed a great variety of micro-relief and profile variation within extremely small areas (*cf.* WIGGINS, 1951), and that therefore their map scales would have to be greatly enlarged. The arctic plant communities, at these large map scales, essentially disappeared. Consequently further correlations were halted for lack of vegetational map units amenable to the refinement achieved in the site studies.

Most attempts to enlarge the arctic vegetational map scales have been by species frequency analyses in the assumed plant communities or in biomass calculations (HANSON, 1950; CHURCHILL, 1955; BLISS, 1956; BLISS and CANTLON, 1957; BROWN and JOHNSON, 1965; LARSEN, 1965). These are of little value unless hedged by fairly complete and accurate knowledge of the floras of the study areas, by sampling systems adequate for the scales used on both vegetations and sites, and finally by some knowledge of the varying parameters of tolerance that are known to exist within and among the species. Examples of more successful enlargements of scale, based on the species level and leading to far more promising correlations with site, were in the studies of WIGGINS (1951) on the vegetation of polygonal patterned ground in northern Alaska (see above), in the work of JOHNSON and PACKER (1965) in northwestern Alaska (see above), in the geobotanical studies of HOPKINS and SIGAFOOS (1950) on the Seward Peninsula of Alaska, and of DRURY (1962) on Bylot Island. Approaches to them are also to be found in recent papers by DREW and SHANKS (1965) on the upper Firth River region of Alaska-Canada, and by SAVILE (1964) on the Lake Hazen area of Ellesmere Island.

It is probable that in only a few parts of the Arctic is the flora well enough known biologically to work with it at these scales without a great deal of preliminary study. Greenland is one of these areas due to the ground work laid during the past 60 years by the Danish botanists. Arctic Europe probably is another, and the beginnings of such knowledge are appearing in arctic Alaska. Translations from Russian sources (*cf.* TYRTIKOV, 1959) suggest that similar information will be forthcoming from arctic Russia.

Studies of vegetation and site on relatively small map scales

The difficulties in describing and analyzing the vegetation of Northeast Greenland in terms of plant "communities" were underlined by OOSTING (1948). He made botanical collections in the fjord region between lats. 72°09′ and 74°39′ in the summer of 1937, and published notes on the structure and development of the vegetation. He followed SØRENSEN (1937) in considering that moisture supply probably was the most significant factor affecting the distribution of plants. Second were snow cover and solifluction. He believed that "the developmental history of all the plant communities is at sometime affected by solifluction", and that "the species growing on moving soil must have some special adaptations which permit their survival, but the special features are not understood".

OOSTING's principal contribution was an attempt to arrange the "plant communities" into developmental sequences ("successions"). In doing this he was troubled immediately "by the appearance of the major species in almost every locality and under varying conditions. Frequently climax species may appear as pioneers and numerous pioneer species are always abundant in every climax community. Again, when the same species are found thriving under wide extremes of moisture, soil conditions, or exposure, a simple interpretation of successional relationships is not always possible". Thus he became aware of the effects of wide tolerance among the common species of the tundra, and of the difficulty of defining the communities which were to succeed one another. He had further trouble with the mechanism of succession, saying "that the vegetational development to be discussed as succession is often accomplished only through physiographic or edaphic changes which may be quite independent of plant influence". Because the geomorphic processes bringing about these "physiographic and edaphic" changes were so imperfectly known, and because the actual reactions of the plant species to the processes (mentioned above) had been so little studied, Oosting could only give "a general presentation of successional trends, without mention of the numerous variations".

Most of his "successional trends", therefore, were arrived at by inference. Some of his hydrarch successions, such as occur in sheet flow areas below snowdrifts, and at some types of pond margins, appear to have been correctly interpreted. Others, such as those on marine shores, many pond shores and delta deposits, are of exceedingly doubtful validity. He worked out some of the essentials of turf hummock development, but not the deterioration of hummocks. His xerarch successions rest very largely upon inference and are doubtful. Probably his most important contribution was his description of the development of vegetation in wet meadows below snowdrifts, and the subsequent growth of moss hummocks.

Two recent papers by Schwarzenbach (1960, 1961) describe the mountain vegetation of Northeast Greenland in broad terms using, for the most part, a community concept. Schwarzenbach was attached to the Danish geological expeditions to East Greenland in 1952 and 1956 under the leadership of Dr. Lauge Koch, and in addition used materials gathered by the expeditions of the 1930's and those collected by geologists in 1951, 1952, and 1958. He was fortunate in being able to visit several nunatak areas, and his 1961 paper described their flora and vegetation. He was much impressed by the extreme aridity of the nunatak sites, due to low precipitation and strong evaporation of moisture from the ground. He thought that the "moisture economy" of the plants was "determined to a large extent by the amount of the winter snowfall, by the progress of its melting and by the position of the permafrost table". The arid nature of the inner fjord region, emphasized by the Danish botanists in the early 1930's was further stressed by Schwarzenbach in 1960 when he characterized much of its vegetation as "arctic steppe". In both of these papers he emphasized the influence of calcareous vs. crystalline rocks upon the distribution of vegetation.

Is the Mesters Vig snow régime unique?

The significance of winter snow-cover (or lack of it) to the growth of plants in Northeast Greenland has been stressed by nearly all students of the vegetation of the region. The presence of heavy, continuous winter snow-cover in the Mesters Vig district (Washburn, 1965) has given rise to some problems of reinterpretation that need not be discussed in detail here (*cf.* Raup, 1965 B). There has been a question as to whether the Mesters Vig area is entirely unique in northern Greenland with respect to the winter snow regime, but there is now a suggestion that an area on the north coast resembles it.

Ostenfeld (1923) published a description of vegetation and plant habitats on the north coast based upon the collections and field notes of Dr. Thorild Wulff, naturalist to the Second Thule Expedition (1916–17). Wulff's voluminous journals were summarized under three main headings: External factors of importance to the plant life; Some biological features in the plants; Vegetation formations. Ostenfeld did not give a detailed expedition itinerary (see below). Unfortunately, Wulff did not survive the journey.

Wulff travelled the country while the winter snow was still present, and watched it disappear in spring. He emphasized the dryness of the air during the thaw season, and the rapidity with which much of the melt-water evaporated, thus suggesting a relatively dry, continental spring and summer climate not unlike that of the fjord region of Northeast Greenland. Judging by the diary excerpts given, his sense of fine differences in soil textures must have been well developed, though Ostenfeld seems to have made little of his observations on this. His descriptions of polygon fields and solifluction slopes were excellent.

Ostenfeld had some difficulty with his interpretation of Wulff's notes on snow-cover. He wrote (p. 255) that "Unfortunately no direct statement as to the extent of the snow-cover is given in Wulff's diaries, but indirectly some information is found". After reviewing this information he wrote the following: "Presumably we are allowed to draw the conclusion, that during winter and spring there is a coat of snow, covering everything, except in places most exposed to the wind". It was apparently the nearly continuous cover of snow, repeatedly suggested by Wulff in the diaries, that Ostenfeld found difficult to deal with, for his own rationalization of major differences in the arctic vegetation rested heavily upon there being areas relatively free of snow in winter, or with very light snow-cover.

This question became acute in his discussion of Wulff's notes on vegetation "Formations". Here he quoted Wulff as follows (pp. 262–3): "In these high-arctic regions the boundary lines, which Warming established regarding the plant formations in South Greenland, are rather vague. It is, in fact, 'Fjaeldmark' altogether, but with different facies, generally dependent on abundance of water, exposition, physical soil conditions and other ecological factors. Marshes, *Dryas*- and lichen-tundra, heath merely occupy smaller patches and always contain individuals belonging to all sorts of typical 'Fjaeldmark' plants . . .".

OSTENFELD criticized this statement on two counts. Using a strict definition of "fjaeldmark" he could not admit other kinds of vegetation to it as did WULFF when he suggested that the North Coast vegetation was fjaeldmark "altogether, but with different facies". More important than this, OSTENFELD appears to have questioned WULFF's actual observations. He wrote on p. 263 that "WULFF formed his opinion as early as in June and has not in his later notes attempted to distinguish the various formations . . ." and "WULFF's opinion is partly explained by the fact that in the early spring, when the snow merely is melted on a few patches, the areas free from snow are almost exclusively 'Fjaeldmark', this being the most hardy of all formations. The other formations do not become free from snow till later, being comparatively delicate, and these WULFF had hardly seen when he formed his opinion."

On the other hand, when WULFF wrote his opinion he not only mentioned some of the more "delicate" types of vegetation, but expressed the idea, without mention of snow-cover, that their distribution was related to local moisture supply, soil, and exposure. He would hardly have done this had they not been exposed to view along with the "hardy"-fjaeldmark vegetation. Furthermore, WULFF continued to write his diary throughout the months of June, July and into early August, with descriptions of vegetation. Some of these are quoted by OSTENFELD on pp. 264–7, for 10 June, 16 June, 2 July, 3 July, 10 July, 13 July, 14 July, 15 July, 7–8 August. During this time there is apparently no evidence that he changed his opinion.

From the narrative of the Second Thule Expedition (RASMUSSEN, 1927) WULFF's itinerary during May, June and July, 1917, can be stated with fair accuracy. From 16 to 30 May he and three Eskimos travelled along the coast from the vicinity of Kap May approximately to Kap Wohlgemuth. Other members of the exploring party were making surveys of the fjords, and WULFF's was primarily a hunting party. The group was again divided at the beginning of June, WULFF taking three Eskimos with the following plan of operation: to go (at once) "northward, over to DeLong Fjord, working over the ground north of here as far as Kap Morris Jesup in search of musk ox. Dr. WULFF accompanies this party, in order to see as much of the coast as possible". This party had their main camp at Low Point, a short distance west of Jewell Fjord, and hunted eastward as far as Kap Wijkander. It can be assumed that, hunting musk oxen, they ranged widely through the country back of the coast line. They rejoined KOCH, RASMUSSEN and the other Eskimo at Kap Neumayer on 16–17 June, only to leave them again for further hunting along the coast westward to Kap Salor during the next two weeks. The parties then travelled together back to the vicinity of Kap May (3–11 July) where they camped until 15 July. On this day they crossed Sherard Osborn Fjord to Dragon Point, from which they started home on 20 July. The remainder of July was spent on a difficult journey up St. George Fjord, and in early August they ascended the glaciers of the inland ice, which they crossed in the direction of Kap Agassiz. On the way they crossed a nunatak called Midgaardsormen where WULFF made notes on the scanty vegetation.

From this itinerary it is clear that most of WULFF's field data, and his opinions based on them, can be limited to a relatively small coastal area in North Greenland. For the most part it is bounded easterly by Kap Wijkander, and westerly by Dragon Point. The coast line is much broken by islands and fjords. WULFF's field work, both inland and on the coast, must have been modified constantly by the necessities of hunting, for the whole party was dependent upon this for survival. It can be assumed safely that in his hunting excursions he sampled all the kinds of terrain and vegetation which the landscape produced, many kilometers back from the coast. This was going on almost continuously, in WULFF's case, from 16 May to 29 June.

KOCH, who was a member of the same expedition, described the weather and snow conditions on the north coast (1928). He published two maps (pp. 356, 359) showing, respectively, the behavior of the two major wind systems (north and south) that affect the coastal and inland areas. On both of these maps the area in which WULFF operated was shown to be prevailingly calm. This did not mean that strong storm winds did not occur, with drifting snow. Rather it appears to have meant a relatively deep general cover of soft snow with deeper drifts. It is probable that exposed headlands were blown clear of snow as are many such places in the Arctic where strong winter winds prevail.

It is suggested here that WULFF was faithfully describing an actual situation, wherein a relatively heavy and continuous winter snow blanket was removed during June and early July, much of it by evaporation under a dry continental climate. Whether due to the shortness of the growing season or to the relative continuity of the snow-cover is uncertain, but local differences that occurred in the thickness of the snow-cover seemed to have little effect upon the distribution of vegetation. WULFF saw what OSTENFELD could credit as "fjaeldmark" but he also saw "marshes", "*Dryas*- and lichen-tundra", and "heath" all at the same time, coming out from the snow in June. He then made the pregnant remark that these vegetations always had species in them belonging to all the others. In short, he was faced with a patchwork distribution of species and vegetation patterns that was so kaleidoscopic that it defied analysis on any theoretical ground with which he was familiar. He was probably correct in looking to water supply and physical soil conditions for a rationalization. There appears to have been much in his experience of the structure and local distribution of species and plant cover that suggests the situation in the Mesters Vig district.

MATERIALS USED IN THE PRESENT PAPER

Most of the data used in the following analyses were published in "The Flowering Plants and Ferns of the Mesters Vig District, etc." (RAUP, 1965). Table 1 summarizes these data. Because only brief descriptions of the way in which the information was gathered were given, fuller accounts will appear in the ensuing pages.

The species of vascular plants listed in the flora of Mesters Vig prior to 1964 totaled 154. Addenda based on a few collections in 1964 brought the number to 157, and no doubt more will be added as exploration proceeds. Of this number, 7 are ferns and fern-allies, 55 are monocotyledons, and 95 are dicotyledons. The three species added in 1964 are not included in the following analyses.

THE RELATIVE ABUNDANCE OF VASCULAR PLANT SPECIES IN THE MESTERS VIG DISTRICT

Time available in the field seasons at Mesters Vig made it logistically impossible to accomplish a statistically adequate study of frequency in the complex of sites and vegetations that had to be examined. Nonetheless a quantity of data was gathered, and is presented in Table 1.

Sources of data

Actual counting of plants in specific units of area was done only on rare occasions. Rather, estimates of relative frequency were made on a gradient with four main divisions: abundant, common, occasional, and rare. In practice three intermediate levels were inserted. For example there are 78 species that were recorded at one or more times during the field operations as "common". However only 29 of them are generally common over the landscape. The remaining 49 were just as often, or perhaps more often, recorded as "occasional", but all of them were found to be locally common at one or more places. Hence the intermediate designations: rare and locally occasional, occasional and locally common, and common and locally abundant.

Notes of this kind were made on the plant lists for approximately half of some 300 sites that were studied in more or less detail. In a large percentage of these sites the vegetation consisted of very few plants, widely scattered over the ground surface. Estimates of frequency under these circumstances by the means outlined above are unsatisfactory. Consequently most of the sites for which estimates were made were among those with medium to dense vegetative coverages.

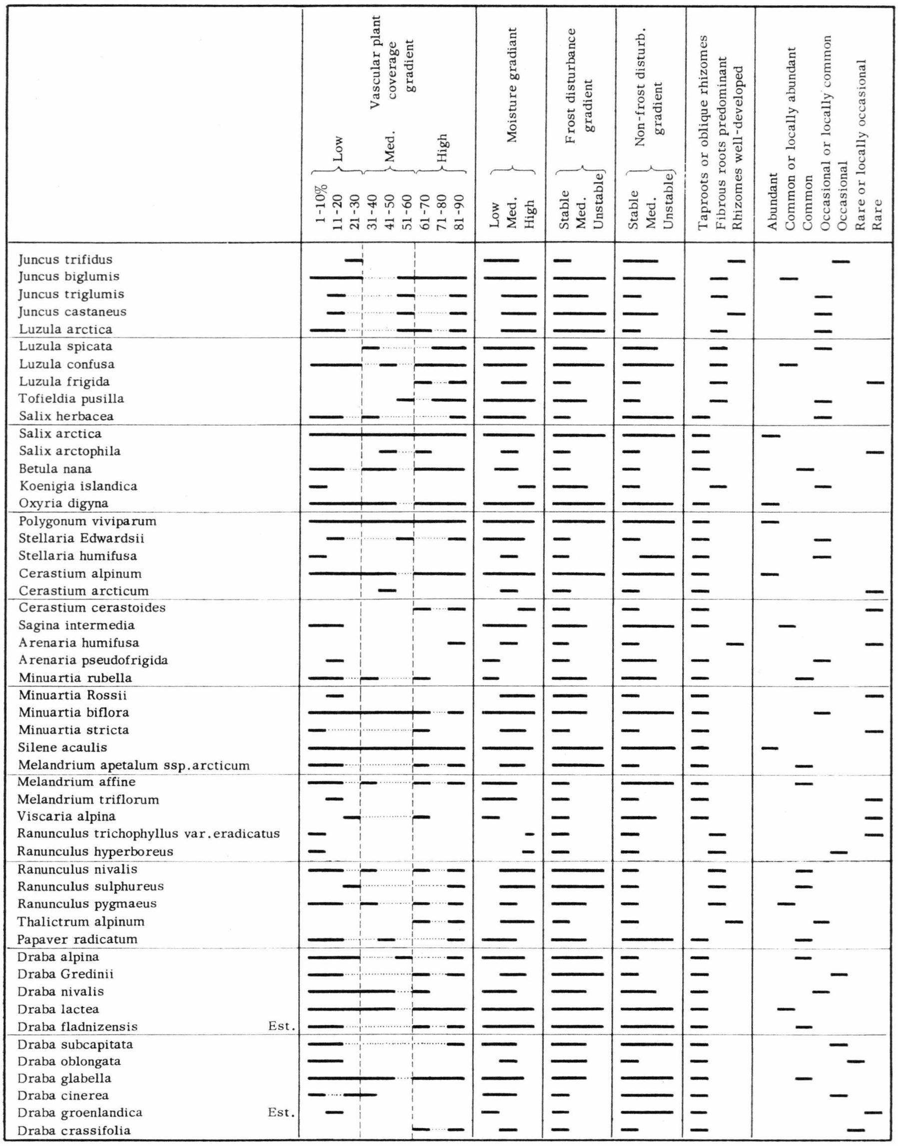
A second source of information is in a count of the number of times each species appeared in all 300 lists of plants made during the course of the study. From these data it is possible to arrange the species in a sequence of frequency groups, in a descending order, and arrive at a fair approximation of their relative general abundance in the landscape. However, these data have to be used with caution, and must be modified from other sources at many points. One example will suffice to illustrate this. The list of species, when drawn up in the order suggested above,

Table 1. *Analysis of the Mesters Vig vascular species in terms of their behavior on gradients of ground coverage, moisture and physical disturbance of the soil; also analyses in terms of their root and underground stem systems, and of their relative abundance.*

	Vascular plant coverage gradient: 1-10% , 11-20 (Low); 21-30, 31-40, 41-50 (Med.); 51-60, 61-70, 71-80, 81-90 (High)	Moisture gradient: Low, Med., High	Frost disturbance gradient: Stable, Med., Unstable	Non-frost disturb. gradient: Stable, Med., Unstable	Taproots or oblique rhizomes; Fibrous roots predominant; Rhizomes well-developed	Abundant; Common or locally abundant; Common; Occasional or locally common; Occasional; Rare or locally occasional; Rare
Equisetum arvense						
Equisetum variegatum						
Lycopodium Selago						
Lycopodium annotinum						
Botrychium Lunaria						
Woodsia glabella						
Cystopteris fragilis						
Triglochin palustris						
Festuca brachyphylla						
Festuca baffinensis						
Festuca vivipara						
Festuca rubra ssp. cryophila						
Colpodium Vahlianum						
Puccinellia angustata						
Puccinellia coarctata						
Puccinellia phryganodes						
Poa pratensis ssp. alpigena						
Poa arctica						
Poa alpina						
Poa glauca						
Poa Hartzii Est.						
Poa abbreviata						
Trisetum spicatum						
Arctagrostis latifolia						
Calamagrostis purpurascens						
Phippsia algida						
Hierochloe alpina						
Eriophorum Scheuchzeri						
Eriophorum callitrix						
Eriophorum triste						
Kobresia myosuroides						
Kobresia simpliciuscula						
Carex nardina						
Carex scirpoidea						
Carex parallela						
Carex rupestris						
Carex microglochin						
Carex ursina						
Carex maritima						
Carex Lachenalii						
Carex amblyorhyncha Est.						
Carex bicolor Est.						
Carex Bigelowii						
Carex subspathacea						
Carex norvegica ssp. inserrulata						
Carex supina ssp. spaniocarpa						
Carex glacialis						
Carex rariflora						
Carex atrofusca						
Carex misandra						
Carex capillaris						
Carex saxatilis						

ends with 35 species which appeared only once in the field plant lists. If accepted at face value this would be quite misleading. Review of all available information on the 35 species shows that only 12 of them were actually seen but once by our field group, and for most of these 12 there

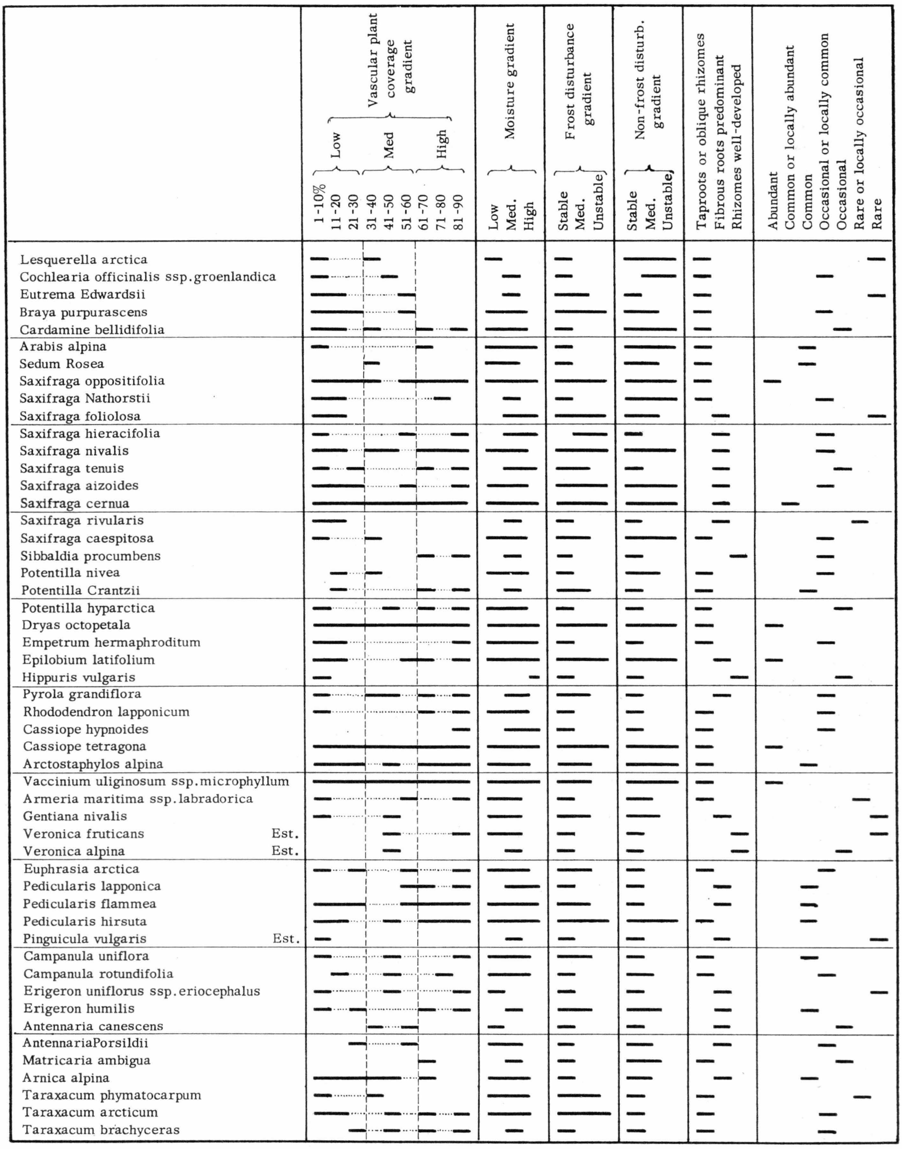
Table 1 (cont.).



is supplementary data from Sørensen (1933) that is apropos. Fifteen of the 35 were seen by us in the district two or three times during the various field seasons, and eight more were seen from several to many times. Their occurrence in the district, based on all data available, is summarized as follows: Rare, 18; rare or occasional, 3; occasional, 6; occasional or common, 6; common, 2.

Other data on relative abundance come from miscellaneous field

Table 1 (cont.).



notes. These are in the form of journal records of plants seen in areas not studied in detail, and scattered phenological notes. Such bits of information are individually of small consequence, but they often acquire large values when used in larger frames of reference.

Figure 1 shows the proportions of the vascular flora that fall into the various categories of abundance described above. Over 1/3 of the vascular flora (54 spp., 35.1 %) consists of species ranging from common

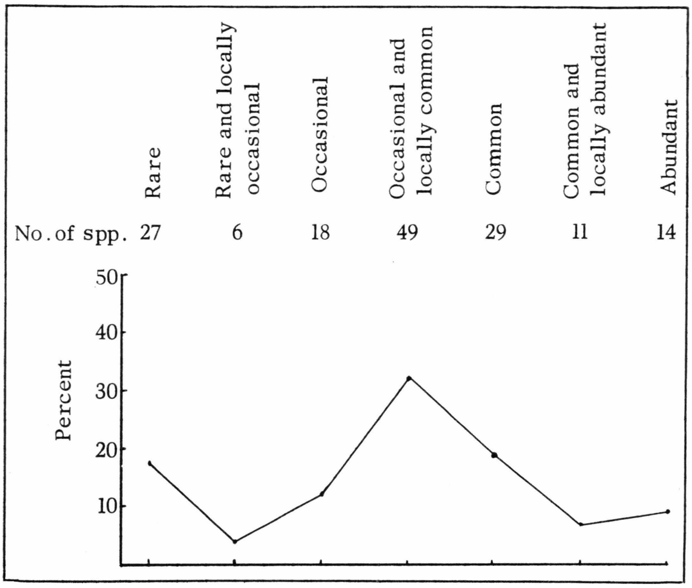


Fig. 1. Percentage distribution of the Mesters Vig vascular flora (154 spp.) among frequency classes.

to abundant in the tundra. Another 49 species were noted as locally common, bringing the total number that reach a frequency of common or greater in some or all parts of the tundra to 103 (66.9 %) of the flora). On the other hand 51 species (33.1 % of the flora) range from occasional to rare. If the overlapping 49 "occasional and locally common" species are added here also, there are 100 species (64.9 % of the flora) that are rare or occasional in some or all parts of the tundra.

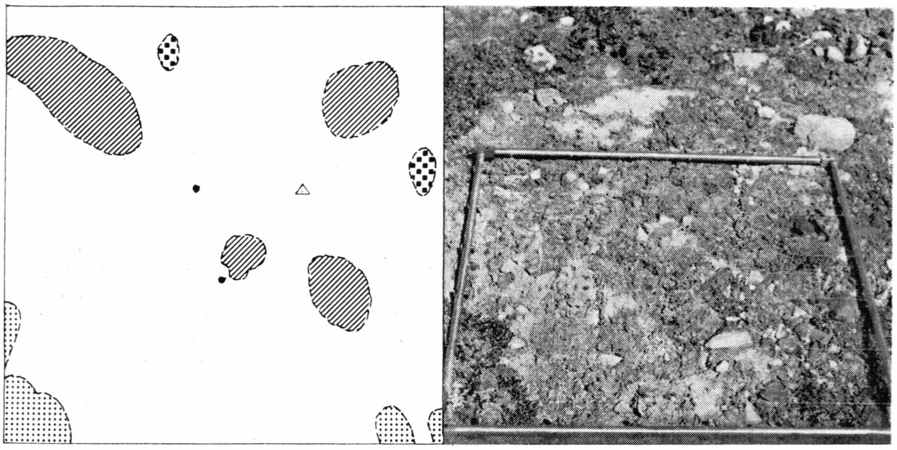
THE BEHAVIOR OF VASCULAR PLANTS IN THE MESTERS VIG DISTRICT WITH RELATION TO DENSITY OF VEGETATIVE COVERAGE OF THE GROUND

Casual observation in the Mesters Vig district, as in other parts of eastern Greenland, indicated that many species of vascular plants appeared to prosper equally well as isolated individuals on otherwise nearly bare ground, and in dense cover of vegetation (*cf.* Gelting, 1934; Sørensen, 1937; Wager, 1938, and others). It seemed desirable to achieve a measure by which the behavior of the species on a gradient of vegetative density could be compared. Further, the cause for large areas of nearly bare ground and thinly populated tundra in the district was a major problem. An analysis of the flora in terms of its behavior with respect to coverage density might suggest species that were critical for a study of these causal relations.

The data presented below are derived from an amalgam of detailed notes made at selected sites, ocular estimates at many more sites, and random field notes. Errors will undoubtedly be found as further work is done in the area. The detailed notes were made first, not only for the specific information they yielded, but also as "training" for ocular estimates. The latter were then made immediately, nearly all of them in the same field season.

A small grid was used in the field to assemble data for the estimation of cover density. This grid was square, 50×50 cm, and marked off in 10 cm squares. It was laid on the tundra, percentage estimates were made for each of the 10 cm squares, and then all of these were averaged to give a figure for the larger unit. The more precise figures for percent of coverage given in the accompanying text figures were obtained in this way.

The coverage of the ground was judged merely by looking straight down at the grid and estimating what percentage of one's vision of the ground surface was intercepted by living vascular plant parts. This estimate said nothing about what kinds of plants were present, or the numbers of plants, or what parts of them formed the cover. There were

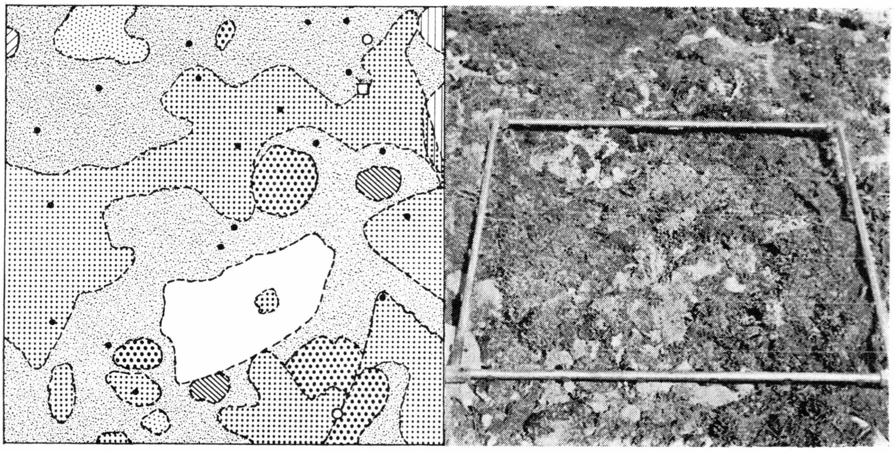


Bare soil. Lichens, mainly Stereocaulon. Dryas octopetala.

Saxifraga oppositifolia. △ Carex nardina (single plant). • Polygonum viviparum (single plants).

Coverage by vascular plants - 3.8%.

Fig. 2. Mapped quadrat no. 1 (in map area of experimental sites 7, 8 and 15), 9 July, 1958.



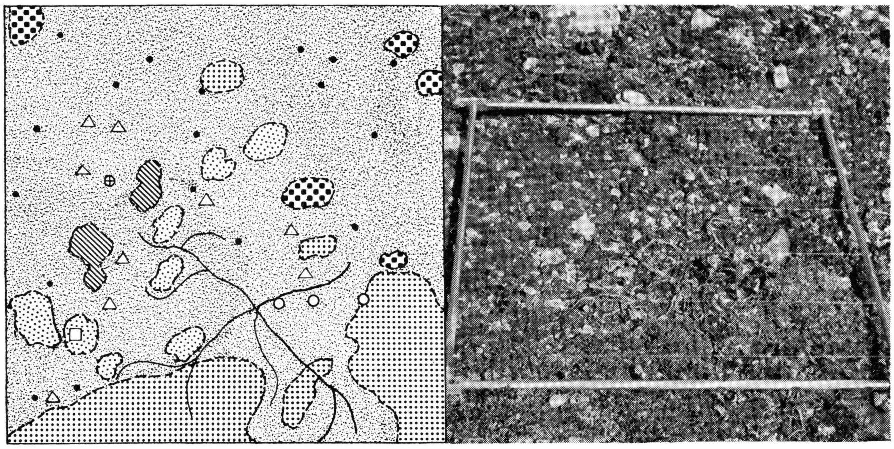
Living mats of Dryas octopetala. Dead mats of Dryas octopetala. Bare soil.

Thin mat of moss and black organic crust Salix arctica. Stereocaulon.

Cladonia pyxidata. Carex scirpoidea. • Polygonum viviparum.

□ Saxifraga oppositifolia. ○ Pedicularis hirsuta. Coverage by vascular plants - 39.4%.

Fig. 3. Mapped quadrat no. 2 (in map area of experimental sites 7, 8 and 15), 9 July, 1958.



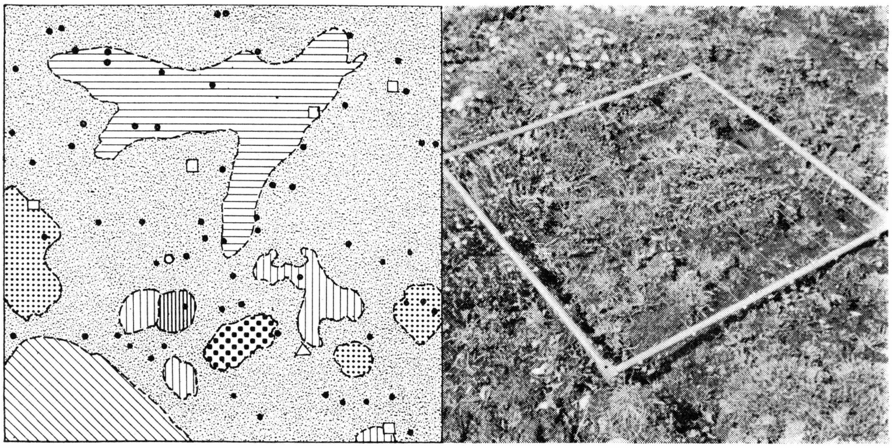
Thin, black organic crust, with a little living moss. Dryas octopetala.

Stereocaulon. Cladonia pyxidata. Saxifraga oppositifolia. △ Carex scirpoidea.

○ Pedicularis hirsuta. □ Saxifraga cernua. • Polygonum viviparum. Salix arctica.

⊕ Arenaria rubella. Coverage by vascular plants- 23.4%.

Fig. 4. Mapped quadrat no. 3 (in map area of experimental sites 7, 8 and 15), 9 July, 1958.



Vaccinium uliginosum (on low hummock). Thin mat of moss and black organic crust.

Cassiope tetragona (at margin of hummock). Silene acaulis.

Salix arctica. Saxifraga oppositifolia. Dryas octopetala (at margin of hummock).

• Carex scirpoidea. ○ Carex misandra. △ Pedicularis flammea.

□ Polygonum viviparum. Coverage by vascular plants-32.4%.

Fig. 5. Mapped quadrat no. 4 (in map area of experimental sites 7, 8 and 15), 9 July, 1958.

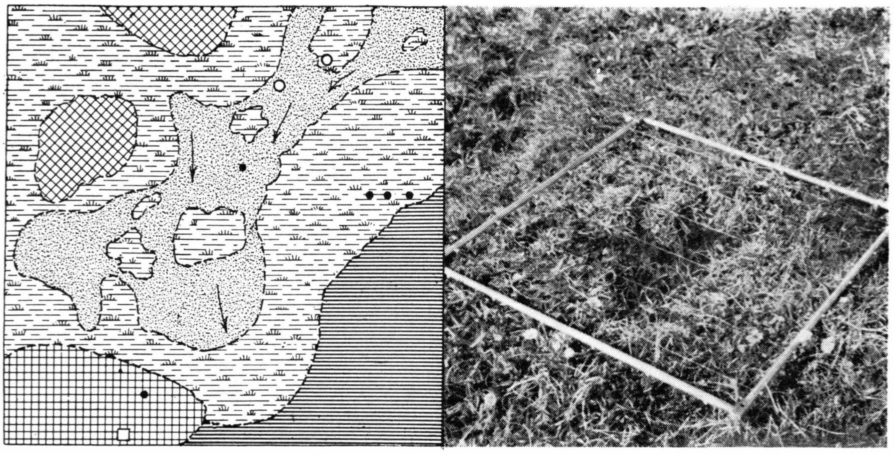


Fig. 6. Mapped quadrat no. 5 (in map area of experimental sites 7, 8 and 15), 9 July, 1958.

exceptions in places where mosses were prominent on the ground and some description was necessary. In a few cases separate coverage figures were made for mosses and lichens.

Twenty-six of these detailed quadrat studies were made, five of them with maps showing the disposition of species (Figs. 2–8). Areas were selected for them to represent as wide a range of cover densities, kinds of vegetation and sites as time permitted. Ocular estimates were then made by applying concepts gained from the detailed studies. They were made for nearly all of the sites at which detailed notes on vegetation were assembled. These ocular estimates are given in 10 $^0/_0$ units. Many of them, particularly those in the very high and very low percentages of cover, probably are fairly accurate to within 10 $^0/_0$. For those in intermediate densities the accuracy probably is more reliable within limits of 20 $^0/_0$.

No density was found to achieve more than about 90 $^0/_0$ cover of the ground surface. In the following discussion, therefore, it should be remembered that the total coverage gradient with which we are concerned extends from about 1 $^0/_0$ to only 90 $^0/_0$. Some estimates will be found at

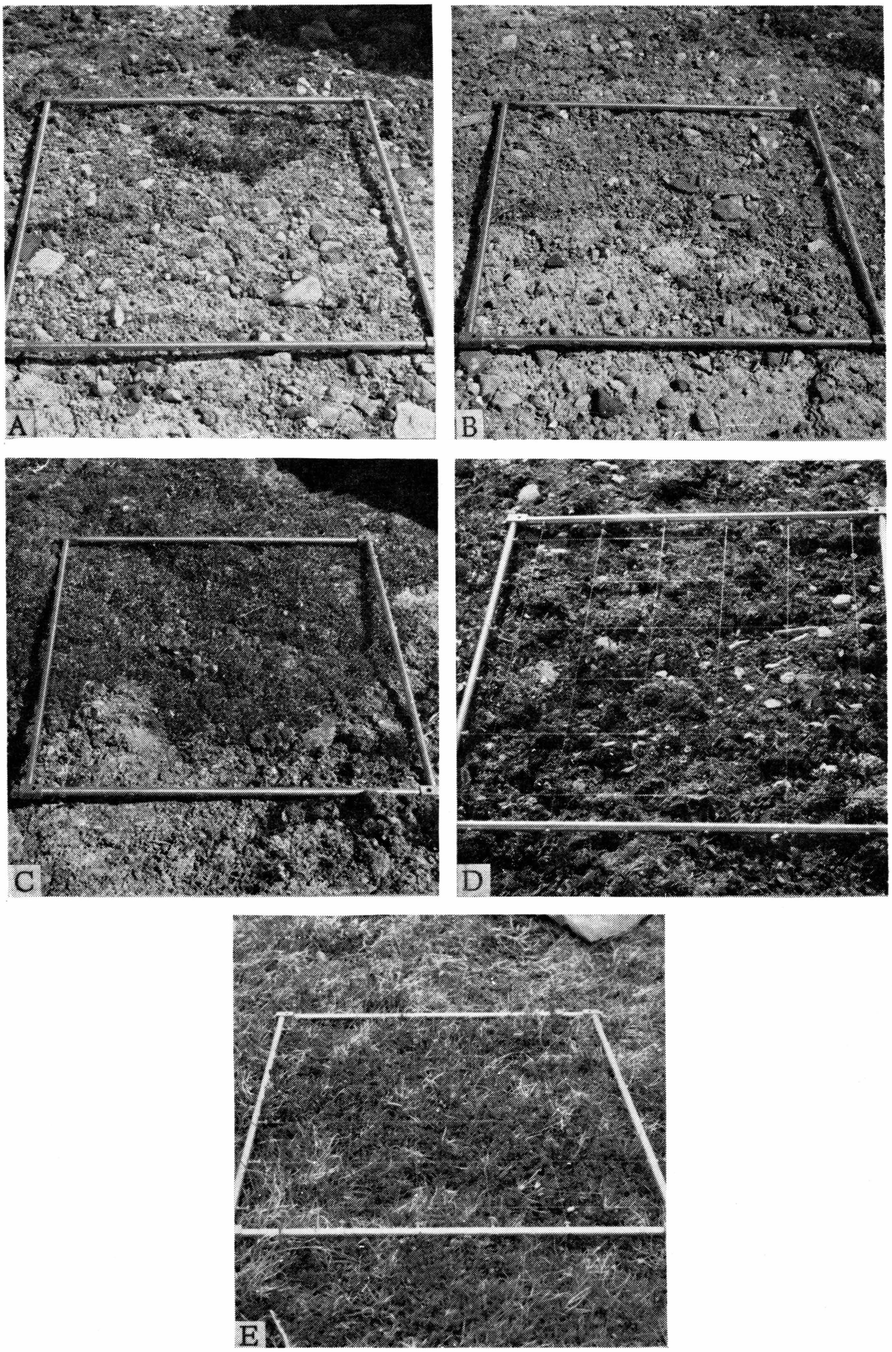


Fig. 7. Unmapped quadrats nos. 6–10 (in map area of experimental sites 7, 8 and 15). Coverages by living vascular plants: A — 5.5 %; B — 0.7 %; C — 46 %; D — 10.3 %; E — 68 %.

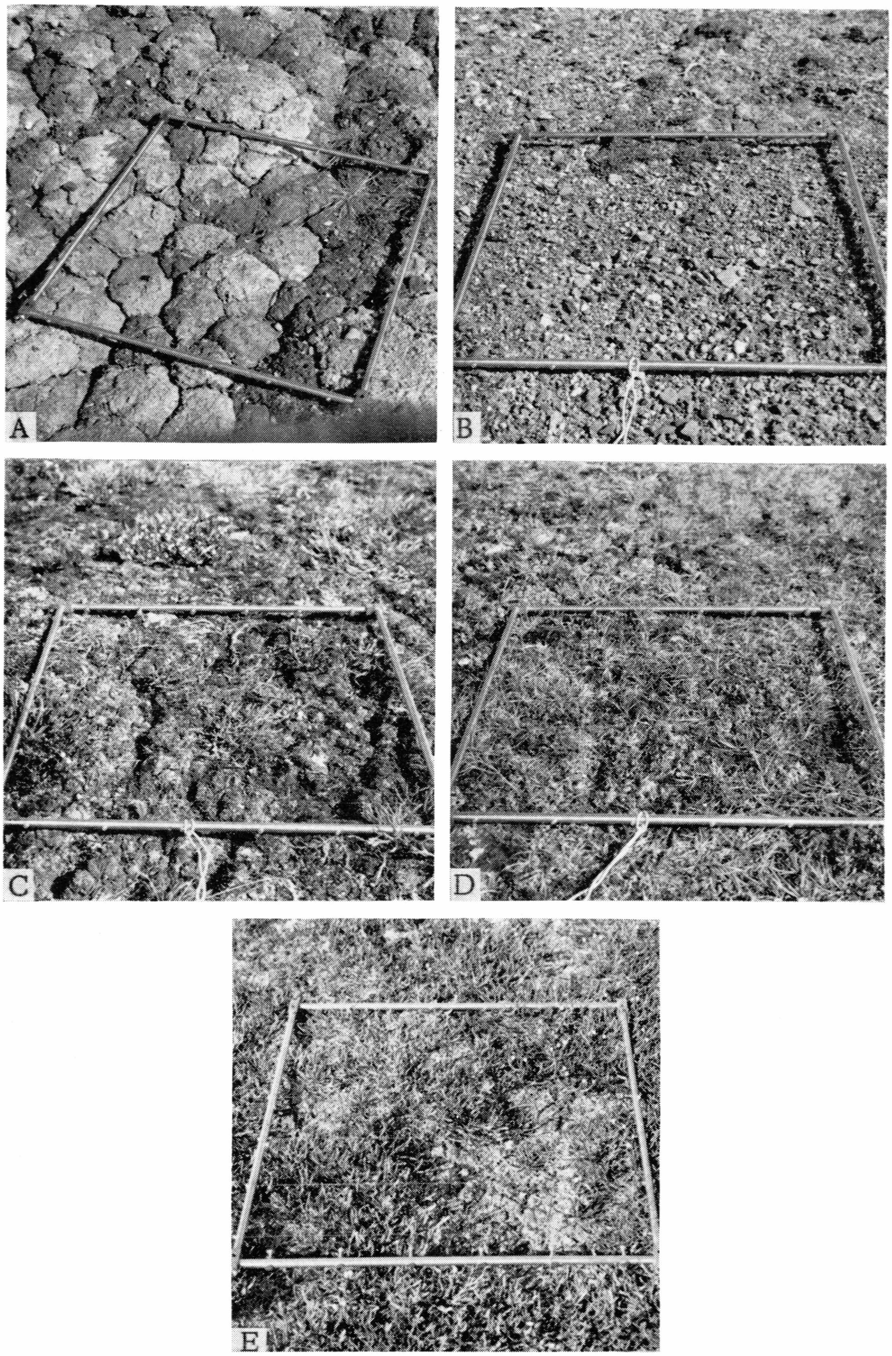


Fig. 8. Miscellaneous unmapped quadrats: A — on non-sorted circle, Labben peninsula, coverage 0.4 %; B — on ancient delta remnant ca 110 m alt., coverage 1.8 %; C — same locality, coverage 8 %; D — same locality, coverage 40 %; E — same locality, coverage 65 %.

the lower extreme, however, that extend to less than 1 %. These are included because it is thought useful to have a record of the species that can and do grow in the most nearly barren areas. In some cases also notes were made on the presence of dead plants, a common and conspicuous feature of much of the thinly vegetated tundra of the Mesters Vig district.

The occurrence of the species on the coverage gradient of 1 % to 90 % is given in Table 1. Most of the data for this table were taken from species lists, many of them supported by collections, made on about 150 study sites where the coverage estimates were also made. A few came from miscellaneous notes accumulated in random observations on the tundra, and a few more were derived from previously published studies of the vegetation of the region, notably those of Sørensen (1933, 1937). The solid black bar in the table indicates only that the species was present, alive, and apparently flourishing.

Examination of the table shows wide variation in the extent to which species occupy the gradient, and in the continuity with which they occupy segments of it. In the first instance at one extreme there is *Salix arctica*, probably the most nearly ubiquitous vascular plant in the Mesters Vig district. Not only was it found in all coverage densities, from less than 1 % to 90 %, but it was recorded as present in about 80 % of the sites for which lists were made. Nearest to it in number of recorded occurrences was *Polygonum viviparum*, which appeared in about 54 % of the sites. At the other extreme are 24 species that were noted in only a single 10 % interval of the gradient. Most of these had only one record each in the notes, though two of them had three each, and one had two. Some of them are rare or infrequent, while others are so narrowly restricted to certain habitats that their position in the coverage gradient is also narrowly restricted.

In drawing the table the solid bars, which indicate presence on the various parts of the gradient, are connected by means of dotted lines to suggest that the species probably are continuous but merely were not observed. This was done even though a species was recorded only in the 1–10 % and 81–90 % segments. The assumption seems reasonably valid in cases where at least one intervening segment of the gradient is occupied, and it is inserted hypothetically for the more extreme cases. It becomes less questionable as the total extent of the gradient occupied becomes less. Of the species that occupy 70 % or more of the gradient, 10 were noted only in the 1–10 % and 81–90 % segments. Of those occupying 60 %, one was found only at these extremes; of those occupying 50 %, five were found; and of those in the 40 % group, six were found only at the extremes.

There are nine species in the table for which no personal observations are available. For these published information about their habitats and

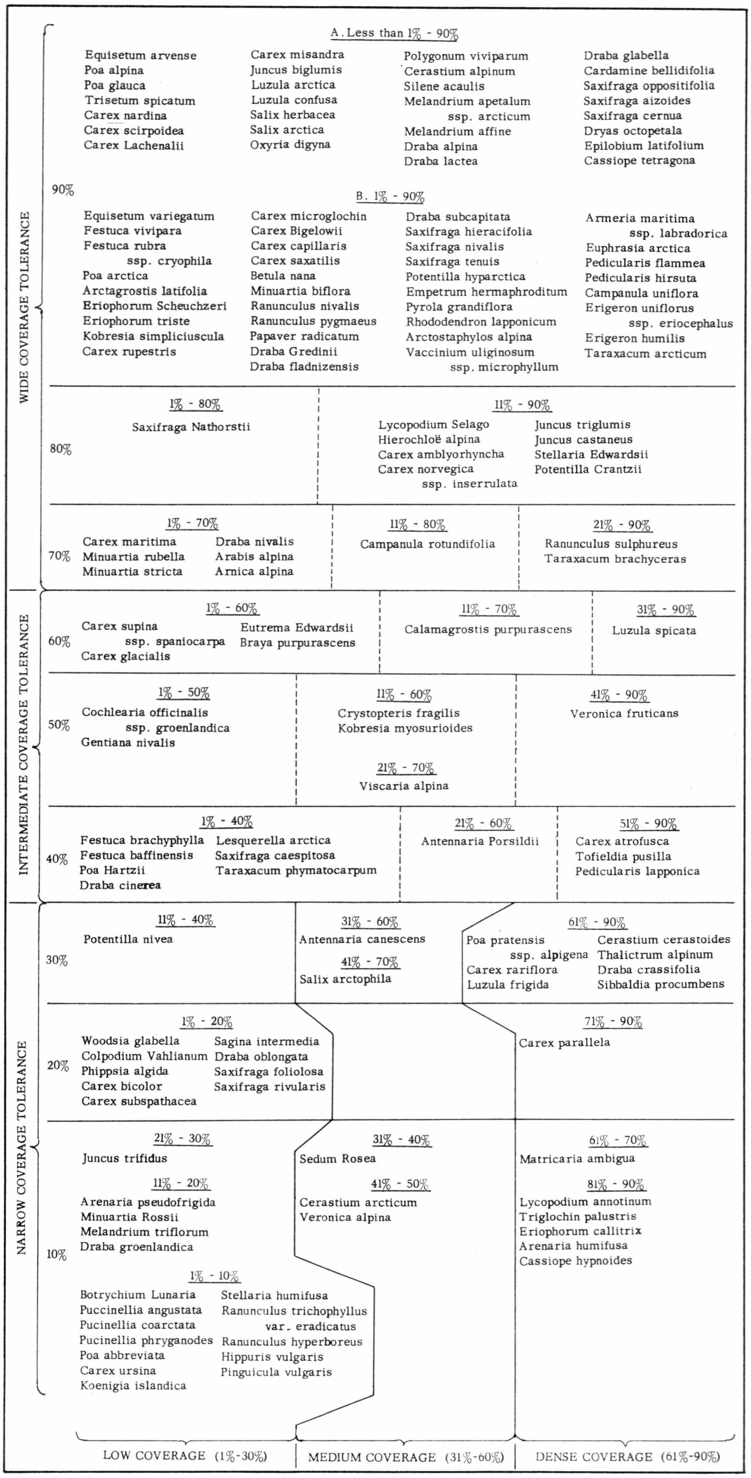


Fig. 9. Analysis of the Mesters Vig vascular flora with respect to the behavior of the species on the coverage gradient.

such field data as could be found on herbarium specimens were used. They are indicated by the symbol "Est".

Figure 9 presents an analysis of the vascular flora of the Mesters Vig district in terms of its observed behavior on the coverage gradient. The analysis has two major results, though others emerge from it. First it divides the flora among nine "levels of tolerance", each of which is exprcssed by the number of 10 % spans of vascular plant coverage that a species occupies or within which it appears to be limited. Second, it makes a three-fold division, where possible, between species more or less restricted to low, medium and high densities of ground cover.

It is apparent that the largest single group of species is at the highest level of tolerance. This group contains 67 species (43.5 % of the flora), all of them observed at both extremes of the 90 % span of the gradient, and nearly all of them at many intermediate points. They are subdivided into two subgroups: A and B. Subgroup A, of 29 species, consists of plants distinguished by having been found also in coverages of less than 1 %. This suggests that they may have slightly wider tolerances than the remaining 38 species in subgroup B, which were not found in coverages below 1 %.

Nine species were found occupying 80 % of the gradient. At this level a two-fold division of species on the gradient is suggested, but it is doubtfully justified. Eight of the species were missing only from the 1–10 % span, thus suggesting a very slight tendency toward preference for denser cover. The ninth species, *Saxifraga Nathorstii*, is known to be most common in more open vegetation. It was found in 1–20 % cover, but also occurred in the relatively dense cover of 71–80 %, with no intervening stations on the gradient.

At the tolerance level of 70 % a three-fold division on the gradient is suggested, ranging from low coverage density at the left to high at the right. The division is here a rough one, with much overlap. Species showing a slight preference for low coverage are missing in the 71–90 % span, while those with a slight preference for high coverage density are missing in the 1–20 % span. The single intermediate species is missing in the 10 % spans at both ends of the gradient. The division of species among low, intermediate and high coverage preferences continues to be poorly defined through the tolerance levels of 60 %, 50 % and 40 %, though the definition becomes increasingly sharp toward the lower of these levels. At the 30 % level there is very little overlap in the apparent preference groups, involving only two species; and in the 20 % and 10 % levels the preference divisions are clearly defined.

For use in subsequent analyses the species in the tolerance levels may be arranged in three groups, again on the basis of a three-fold division of the coverage gradient. In this case, however, the measure is designed merely for comparison of the breadth of tolerance of the species on the gradient, and says nothing about the position of each species on the gradient. First are the plants with limits extending to more than two thirds of the gradient (70%, 80% and 90% levels). There are 85 of these, or 55.2% of the flora. Second are 23 species, 14.9% of the flora, that have been observed growing within limits of not more than two thirds of the gradient nor less than one third (60%, 50% and 40% levels). Finally there are 46 species, 29.9% of the flora, which appear to be more or less confined to one third of the gradient (30% 20% and 10% levels).

A striking feature brought out by the above analysis is the large disparity in numbers of species between the groups showing preferences for low and high coverage densities. If all species showing tolerance levels from 10% to 70%, inclusive, are taken together the total is 78. Again, if the three-fold arrangement of the species as to coverage preference is used as given in Table 1, 46 species (59% of the 78) are found in or toward the low coverage densities, 11 species (14.1%) are intermediate, and 21 (26.9%) are found in or toward the high densities. As previously indicated, however, the preference division is progressively obscure above the 30% level of tolerance. If only the species in the lower third of the tolerance scale are considered, the numbers noted above are greatly reduced but the percentages are not much altered: low coverage preference, 27 species (58.7%); intermediate, 5 species (10.9%); high coverage preference, 14 species (30.4%).

The analysis suggests that over half the vascular flora (ca 55%) is essentially independent of obligate "communal" relationships and that over a third of this group is completely independent. These species appear to grow and flourish about equally well as isolated individuals on nearly bare ground, or in thinly populated tundra, or in tundra of medium density, or in dense heaths of various kinds. The six species in the 60% level of tolerance, although they are included in the intermediate group, could with propriety be included here, bringing the total to 91 species with wide tolerance (ca 59% of the flora).

In the lower tolerance levels there is a preponderance of species showing lower coverage preferences. These preferences are weak in the 70%, 60% and 50% levels, but even if they are included with the more pronounced ones below, only 21 species in the whole flora (13.6%) can be looked upon as possible "character" or "indicator" species for plant communities that cover more than 60–70% of the ground surface. Another 11 species (bringing the total percentage to 20.8 in the whole flora) might be added if the species with intermediate coverage preferences are included. Experience with these species, however, shows that they have no significance as indicator plants. Eleven of them are quite rare in the district, 19 are sometimes common locally but are only seen occasionally, and only two are fairly common. All of them are extremely scattered in occurrence. Although they may be highly restricted to certain kinds of sites, they may or may not appear in these sites. Wet mossy lake margins were examined in several places, for instance, but *Triglochin palustris* and *Carex rariflora* were found at only one or two places. *Lycopodium annotinum* grows only in damp, upland *Cassiope* heath, but in all the hundreds of hectares of this vegetation in the area, it was seen only two or three times. Each time it was abundant where it was found.

From these results comes the suggestion that about 85 % of the flora of the Mesters Vig district shows a distinct capacity for growing in relatively open ground, independent of association with other species. The openness of the ground may range from almost no plants at all to coverage of 30–40 %. It may be that much of the difficulty experienced by students of arctic vegetation in defining "communities" in the tundra has come in part from the inherently wide coverage tolerance of a large proportion of the species. It may have come also in part from the absence of reliable character species in those parts of the coverage gradient in which "communities" might be readily definable on physiognomic or other grounds.

THE BEHAVIOR OF MESTERS VIG VASCULAR PLANTS ON THE MOISTURE AND PHYSICAL DISTURBANCE GRADIENTS

An outline of the way in which data were gathered on the behavior of the vascular plants in the Mesters Vig district with respect to the moisture and physical disturbance gradients was presented in the Introduction to the recently published flora of the district (RAUP, 1965 A). It is enough to say here that the basic information given below came from the same sites that were studied in detail for coverage of the ground and other phenomena, including in many cases geomorphic processes. The data have been supplemented with my own miscellaneous observations elsewhere in the district and with whatever data gleaned from studies by earlier observers in the area appeared to be applicable.

The point is worth emphasizing that in most cases the general patterns of behavior of the species on the moisture gradient, and in a large proportion of the cases on the disturbance gradients, were already present in the published observations of SØRENSEN (1933, 1937), GELTING (1934) and OOSTING (1948). The work at Mesters Vig served to fill in details of many of the patterns and bring them into sharper focus. This has been possible because there was much less information available in the 1930's than there is at present on the nature and extent of moisture and physical disturbance in the soils. Consequently observations on the behavior of plants in relation to them could be extended and elaborated.

Behavior of species on the moisture gradient

For purposes of field observation and comparison the moisture gradient was divided into the following five categories. They apply to the uppermost 5–15 cm of the soil, which is the horizon in which most of the plant roots are found.

Low { Dry — No feeling of dampness to the fingers; soil runs freely through the fingers.

Medium Moist — wets the fingers when handled.

High	Wringing wet — water does not flow from the soil, but can be squeezed out by hand. Dripping wet — water drips out when the soil is handled but not squeezed. Free water standing or running over surface of the soil.

The five categories were then grouped to make a three-fold division of the gradient, ranging from soils with generally "low" moisture (dry), through those with "medium" moisture (moist), to those with "high" moisture content (wringing wet, dripping wet and in free water).

Generalization from the observed positions of any given species on this gradient to show its probable real relationship to moisture is not easy. GELTING seems to have had trouble with it also, as indicated by the following remark: "On the whole it is very difficult to characterise the species of the area on the basis of their demand of moisture . . .". (GELTING, 1934, p. 239). He thought that this was due to the fact that here, "as in all Arctic continental areas, the moisture fluctuates considerably from spring to autumn". It is possible that had he realized the extent of inherently wide tolerance of moisture variation among the species he might have added this as a major cause of the difficulty.

The same difficulty is reflected to some extent in SØRENSEN's arrangement of species in ecosystems (1937, pp. 112–115, Table II). He arranged these ecosystems in three groups: the first six in a "dry" series, the next three in a "moderately moist" series, and the remaining nine in a "moist to wet" series. He classified 130 species in the system. Only about one third of them (46 spp.) were limited to one ecosystem each. Another 38 species appeared in two ecosystems each, most of them separated from one another by at least one ecosystem in the moisture gradient. Sixteen species were in three ecosystems and 16 more in four ecosystems, etc. Using SØRENSEN's three-fold division cf the gradient, 96 of his 130 species are confined to one or another of his three main categories of moisture, 17 occur in two of them, and 17 occur in all three.

Both GELTING and SØRENSEN oriented their studies primarily toward a classification of habitats, rather than species tolerances to the habitat processes. It seems worthwhile, not only in the case of the moisture gradient, but also with others, to project what information is available on the behavior of the species against what we know of the habitats.

In Table 1 a much generalized "rating" is given for each species on the moisture gradient. The dry end of the gradient is at the left and the wet at the right. The division is three-fold, corresponding to the low, medium, and high groups of moisture categories used for field observation (see above). In the chart (Table 1) the three divisions are equal in length. The total length of the bar for a given species indicates its relative tolerance of variation in the moisture gradient, in three categories. If the length is more than two thirds of the possible bar length, the tolerance is "wide". If it is between one and two thirds of the possible length, the tolerance is "intermediate". If it is one third the possible length or less, the tolerance is "narrow". The position of a bar with respect to the right or left side of the chart shows the approximate limits in the gradient within which a species has been found. The data on each species indicate only presence, and give no indication of frequency. If reported at all, the species was found alive, growing, and apparently established well enough either to reproduce itself or to persist for a period of years.

In the total vascular flora of 154 species 61 (39.6 %) were found growing in more than two thirds of the moisture gradient, and are therefore considered to have wide tolerances of moisture variation in their habitats (Fig. 10). There are two suggested levels of tolerance among them depending upon their presence or absence at the extremely dry or wet ends of the gradient. Thirty-two of them (20.8 %) were observed throughout the gradient, including these extremes. Twenty-eight (18.2 %), however, were not seen on the wettest ground (sites with free water). One species (0.6 %) was found on the latter but not on the driest sites. Observations on this single species (*Carex norvegica* ssp. *inserrulata*) are of questionable significance because it is rare in the district. It was also noted as rare by both SØRENSEN (1933, p. 108) and GELTING (1934, p. 158), but when their habitat notes are put together with the scanty information from Mesters Vig the species appears to have a wide range of tolerance.

Forty-eight species (31.2 %) were found in sites representing between one third and two thirds of the moisture gradient, and are regarded as intermediate in moisture tolerance. It is possible to suggest two levels in this group. The first is composed of 40 (26.0 %) species that span fully two thirds of the gradient, while the remaining eight species (5.2 %) occupy approximately half of it.

The division of the widely tolerant species into two groups involved a suggested avoidance in 28 species of slightly more wet habitats, and in one species of slightly more dry sites. This tendency toward avoidance (or preference) appears more strongly in the intermediate level of tolerance. Seventeen (11.0 %) occupy their two thirds of the gradient toward the dry end, while 23 (14.0 %) have their two thirds toward the wet end. All of the eight species that occupy about half the gradient lie in the medium and a part of the high moisture segments.

There are 45 species (29.2 % of the flora) which were seen in only one third of the gradient or less, and are regarded as having narrow tolerances. Although, as in the preceding levels, there are undoubtedly many gradations of tolerance among the species, the only subdivision of

WIDE TOLERANCE

Widest tolerance

Festuca vivipara
Festuca brachyphylla
Festuca baffinensis
Colpodium Vahlianum
Poa arctica
Poa alpina
Phippsia algida
Carex scirpoidea
Carex Bigelowii
Carex misandra
Carex capillaris
Juncus biglumis
Luzula spicata
Tofieldia pusilla
Salix arctica
Polygonum viviparum
Oxyria digyna
Cerastium alpinum
Minuartia biflora
Silene acaulis
Draba lactea
Draba fladnizensis
Arabis alpina
Saxifraga oppositifolia
Saxifraga cernua
Dryas octopetala
Epilobium latifolium
Empetrum hermaphroditum
Cassiope tetragona
Vaccinium uliginosum ssp. microphyllum
Pedicularis flammea
Pedicularis hirsuta

Not in wettest sites

Festuca rubra ssp. cryophila
Puccinellia angustata
Poa glauca
Trisetum spicatum
Carex nardina
Carex rupestris
Carex glacialis
Luzula confusa
Salix herbacea
Stellaria Edwardsii
Sagina intermedia
Draba glabella
Draba alpina
Braya purpurascens
Cardamine bellidifolia
Saxifraga nivalis
Saxifraga aizoides
Saxifraga caespitosa
Potentilla nivea
Potentilla hyparctica
Arctostaphylos alpina
Rhododendron lapponicum
Euphrasia arctica
Campanula uniflora
Campanula rotundifolia
Arnica alpina
Taraxacum phymatocarpum
Taraxacum arcticum

Not in driest sites

Carex norvegica ssp. inserrulata

INTERMEDIATE TOLERANCE

Low and medium moisture

Botrychium Lunaria
Cystopteris fragilis
Woodsia glabella
Hierochloë alpina
Kobresia myosuroides
Juncus trifidus
Melandrium affine
Melandrium triflorum
Papaver radicatum
Draba nivalis
Draba subcapitata
Draba cinerea
Sedum Rosea
Armeria maritima ssp. labradorica
Gentiana nivalis
Veronica fruticans
Antennaria Porsildii

Medium and high moisture

Equisetum arvense
Equisetum variegatum
Lycopodium Selago
Eriophorum triste
Carex parallela
Carex Lachenalii
Carex amblyorhyncha
Carex subspathacea
Carex bicolor
Carex microglochin
Carex atrofusca
Carex saxatilis
Juncus triglumis
Juncus castaneus
Luzula arctica
Ranunculus nivalis
Ranunculus sulphureus
Thalictrum alpinum
Saxifraga foliolosa
Saxifraga tenuis
Saxifraga hieracifolia
Cassiope hypnoides
Pedicularis lapponica

Puccinellia coarctata
Poa pratensis ssp. alpigena
Luzula frigida
Minuartia Rossii
Minuartia stricta
Melandrium apetalum ssp. arcticum
Draba Gredinii
Pyrola grandiflora

NARROW TOLERANCE

LOW MOISTURE

Minuartia rubella
Viscaria alpina
Draba groenlandica
Lesquerella arctica
Erigeron uniflorus ssp. eriocephalus
Antennaria canescens
Poa abbreviata
Poa Hartzii
Calamagrostis purpurascens
Carex supina ssp. spaniocarpa
Arenaria pseudofrigida

MEDIUM MOISTURE

Lycopodium annotinum
Puccinellia phryganodes
Carex ursina
Carex maritima
Salix arctophila
Betula nana
Ranunculus pygmaeus
Stellaria humifusa
Cerastium arcticum
Arenaria humifusa
Draba oblongata
Draba crassifolia
Cochlearia officinalis ssp. groenlandica
Eutrema Edwardsii
Saxifraga Nathorstii
Saxifraga rivularis
Potentilla Crantzii
Sibbaldia procumbens
Veronica alpina
Pinguicula vulgaris
Erigeron humilis
Matricaria ambigua
Taraxacum brachyceras

HIGH MOISTURE

Triglochin palustris
Arctagrostis latifolia
Eriophorum Scheuchzeri
Eriophorum callitrix
Kobresia simpliciuscula
Carex rariflora
Koenigia islandica
Ranunculus trichophyllus var. eradicatus
Ranunculus hyperboreus
Cerastium cerastoides
Hippuris vulgaris

LOW MOISTURE — MEDIUM MOISTURE — HIGH MOISTURE

Fig. 10. Analysis of the Mesters Vig vascular flora with respect to the behavior of the species on the moisture gradient.

this group that is readily discernible is in aquatic sites. Of the 45 species found only in one third of the gradient, six occupy something less than one third, and were seen only in standing or slowly moving water. It is probable that they are the most narrowly tolerant on the moisture gradient of any species in the flora. They are as follows: *Triglochin palustris*, *Carex rariflora*, *Koenigia islandica*, *Ranunculus trichophyllus* var. *eradicatus*, *Ranunculus hyperboreus*, *Hippuris vulgaris*.

At this level of tolerance the apparent preferences of the species for the various segments of the gradient are rather clearly defined, and there is very little overlap. Eleven species (7.1 %) appear to be essentially confined to the low moisture segment, 23 species (14.9 %) to that of medium moisture, and 11 species (7.1 %) to the segment with high moisture.

Probably the most striking result from the preceding figures is the large proportion of the vascular flora that shows a relatively wide tolerance of variation in the moisture regimes of its habitats. One can only speculate, in the present state of knowledge, on the means by which the plants accomplish their tolerances. They may do it by timing of their seasonal growth and reproductive processes so as to bring these into adjustment with moisture regimes. Or there may be minor ecotypic variations within the species, extremely local and unrecognizable taxonomically, that are sufficient to account for the tolerance ranges seen. Whatever the means, fully 70 % of the flora can and do live, at one place or another in the region, in at least two thirds of the total moisture gradient. Of these species (109) well over half (61) span more than two thirds. Although there is a certain amount of preferential segregation within the gradient at the level of intermediate tolerance in 48 of the species, there is overlap in all of them at this level. Therefore none of these 109 species having wide or intermediate tolerance can be very useful, on a presence or absence basis, to characterize the moisture regimes of sites.

This leaves 45 species that show fairly good preferential segregation within the moisture gradient. Fifteen of these are recorded in our field notes as rare, and another nine as occurring only occasionally. Although each of these species is consistent in always having been found in its preferred segment of the gradient, its rarity consists in its appearing only infrequently in that segment though representative habitats for it are common or abundant. Thus these plants appear to be so randomly scattered that they are not good indicators even of their preferred places in the moisture gradient. Sørensen, in 1933, regarded 13 of them as either rare or localized in occurrence, six as plants highly localized in seashore, lake shore or aquatic sites, and one somewhat restricted as a calciphile. Four of them did not appear in his list.

Of the remaining 21 species only eight can be regarded as thoroughly common in the Mesters Vig district. They are: in the dry segment of the gradient *Carex supina* ssp. *spaniocarpa* and *Minuartia rubella*; in the median segment *Puccinellia phryganodes*, *Betula nana*, *Ranunculus pygmaeus*, *Potentilla Crantzii*, and *Erigeron humilis*; and in the wet segment *Eriophorum Scheuchzeri.* All of the other species, though they are sometimes common locally, are not widely enough distributed to characterize their respective moisture regimes. In this they resemble the rare or locally occasional species noted above. Examples are such species as *Calamagrostis purpurascens*, *Lycopodium annotinum*, *Taraxacum brachyceras* and *Arctagrostis latifolia.* The *Calamagrostis* is locally conspicuous in loose stony grus on the tops of trap knobs and ridges, and on dry stony till knolls; but there are many sites in the district that give every indication of similarity though the *Calamagrostis* is absent. The case of the *Lycopodium* has already been mentioned in connection with the coverage gradient analysis. Though locally common in *Cassiope* and *Cassiope—Vaccinium* heath, it occurs only sporadically in the many areas of this vegetation. *Taraxacum brachyceras* is sometimes found growing in profusion on turfy banks such as occur on river bluffs, or on the fronts of large gelifluction lobes, or on the fronts of debris slides from earth flow. But there are scores of similar sites in the landscape in which this species could not be found. *Arctagrostis latifolia* grows in wet moss-sedge meadows or hummocky wet meadows, of which there are a great number in the landscape. Some of them have this species as a common constituent, in others it is rare, and in still others it occurs not at all. If there are site differences to account for this they are subtle, and were not detectable by the means at our disposal in the field.

The net result of the preceding analysis is that we are left with the eight species listed above as the only ones sufficiently common and widespread to be used as fair "indicators" of the three main segments of the moisture gradient. It is of interest that five of them are in the median segment where the soils are "moist" and where subdivisions of the sites on the basis of moisture are at a minimum. Only one species is available to represent the more complex series of moisture categories in the wet segment of the gradient, and only two for series in the drier segment. It appears entirely understandable that Gelting should have found it "very difficult to characterize the species of the area on the basis of their demand of moisture". An inverse statement of this seems equally clear: that it is extremely difficult to characterize the moisture regimes in terms of species requirements.

The behavior of species on the physical disturbance gradients

A central theme of our joint research program in the Mesters Vig district was a quantitative study of geomorphic processes, particularly those in which the arctic frost climate is a major conditioning factor. This led to a constant focus of attention upon evidence of physical disturbance in the active layer of the soils (above the permafrost). Because the arctic climate and the permafrost are pervasive, all geomorphic processes are in some measure affected by them, directly or indirectly. Therefore all of the processes that were discernible in the district were given a certain amount of study, though only a few were investigated in detail (WASHBURN, 1965, 1967).

The following is a list of geomorphic processes that were found to be active in the Mesters Vig district, and at the same time limiting to vegetation. Their segregation as separate processes usually is not clearly defined, for they are often closely interrelated in their action upon soil materials, landforms and vegetation.

- Frost cracking
- Frost heaving and thrusting
- Frost creep
- Gelifluction
- Earthflow
- Rock fall
- Debris slide
- Non-frost creep
- Slushflow
- Fluvial erosion and deposition
- Sheet wash and rillwork
- Eluviation
- Rainsplash
- Lacustrine erosion and deposition
- Marine erosion and deposition
- Wind deflation and deposition
- Wind abrasion

The processes that were studied most intensively were frost heaving and thrusting, gelifluction, frost creep, and non-frost creep. Others that received a great deal of attention were slushflow and earthflow. The evidence of movement and soil instability due to these processes, accumulated in the past few years, is striking and conclusive (WASHBURN, 1965, 1967). In the landscape as a whole, however, there is an almost kaleidoscopic patchwork of disturbance intensities ranging from essential stability to activity in the soil so intense that no plants can survive it. Further, this patchwork pattern changes with time, at rates that differ with slope, exposure, length of season, water supply, and soil textures. The species with the widest tolerances appear to be the ones most capable of adjusting to this variable and shifting habitat base.

For all processes a system was devised whereby rough evaluations could be made of the extent to which they disturbed the soils and the vegetation at specific places and times. The action of a process depends upon the grain size and structure of the soil, the water supply, the slope, and the temperature regime. Further, different combinations of the variables among these basic conditions appear in different parts of the open season, and their total effect depends upon the length of the open season. By setting up for each disturbing process a relatively small number of standardized categories of intensity (more or less arbitrarily determined, and three to six in number), it was possible to summarize for any site the relative intensity of physical disturbance to which its soils were subjected. Sites could then be compared in terms of the intensity of disturbance. It was also possible to estimate what kind of disturbance probably was most effective in any site thus analyzed, and in what part of the vegetative season it probably occurred.

An additional disturbing process in the region is due to the advent of man. Its effects are closely similar to many of those that come from the geomorphic processes mentioned above. We found no adventive "weeds" in the Mesters Vig flora, but a great many of the native plants behave like weeds along roadsides and in the disturbed soils around habitations, mining installations and shore facilities. These plants behave on artificially disturbed sites as they do on gelifluction terraces, river gravels and other soils disturbed by non-human processes.

Among notes on the behavior of species with respect to physical disturbance in the soils, recently published in the flora of the district (Raup, 1965 A), a distinction usually was made between two main kinds of disturbance: one due primarily to frost action, and the other to one or another of the processes in which frost action is not directly involved. The two are closely related at many points, and the division is to some extent arbitrary. In the first category are included frost heaving, frost creep, frost cracking, while in the second are all the remaining processes listed above. It is difficult to segregate these two kinds of processes without much careful instrumentation (Washburn, 1967), but a number of plants indicate by their habitat preferences that they are able to do it.

Gelifluction (solifluction associated with frozen ground; see Washburn, 1967, p. 11–12) usually is considered a frost-related process, but the plants appear to react to it differently than they do to such frost action as frost heaving and thrusting. Their behavior with respect to gelifluction is more nearly like their reaction to the nonfrost processes, or they are indifferent to it. Therefore, in the tolerance ratings of species used here, and in vegetational analyses based on them, gelifluction is treated as though it were a nonfrost process.

The chart in Table 1 shows an evaluation of the behavior of each species on gradients of physical disturbance due primarily to frost action and to nonfrost induced processes. Each gradient has a three-fold division indicating three degrees of tolerance on the part of the species. These degrees of tolerance are subjective judgments. They are based on summaries of the notes pertaining to each species presented in the flora, projected against the analysis of specific sites outlined in the preceding paragraphs. Fifty-seven representative sites were analyzed in detail, and the results from these were extrapolated to about 150 more. The ratings of the species can be refined in some cases with refinement of the analyses of the sites.

The tolerance ratings on the physical disturbance gradients are similar to those used on the one for moisture. A bar that covers more than two thirds of the possible space indicates that the species has a wide tolerance of physical disturbance on that gradient. If the bar extends to more than one third but not more than two thirds of the possible space, the species is rated as having intermediate tolerance. Bars extending to one third of the possible space or less indicate species with narrow tolerances.

On the gradient itself the most stable soils are indicated on the left and the least stable at the right. The value of having an intermediate group of habitats segregated serves to emphasize the two extremes, and at the same time it demonstrates, in part, the existence of progressive stages in the capacity of plants to survive the rigors of disturbance.

The term "stable" as used here is applied to the "root zone" of the soil. In nearly all of the Mesters Vig district this is the uppermost 15 cm, and in many places the uppermost 10 cm. A few roots penetrate to greater depths than 15 cm, but they are not common; and if they do occur they are nearly always in relatively dry, coarse-textured soils in which there is very little frost action and almost no disturbance of any other kind. Motion in the surficial deposits does not, in itself, indicate disturbance in the root zone of the soil. On many gelifluction slopes the annually thawed materials are moving downhill *en masse*, though many areas of their surface soils, in which the plant roots are growing, remain essentially stable. Movement of this kind commonly has little effect upon the plants. Surficial gelifluction on the other hand, occurring in the upper 10–20 cm of the mineral soil, usually is to some extent injurious to plants.

The frost disturbance gradient

On the basis of the criteria described above, 43 species in the Mesters Vig flora (27.9 %) have wide tolerance of frost-induced physical disturbance in their soils (Fig. 11). They are found on stable soils, in habitats where frost heaving is only moderate in intensity, and in the intensely heaved soils of some of the more active patterned ground. At the other extreme are 76 species (49.4 % of the flora) that appear to have a narrow range of tolerance on this gradient. Nearly all of them were seen growing only on soils relatively free of frost disturbance. Throughout the study a search was made for species that seemed to be confined to disturbed

SPECIES WITH WIDE TOLERANCE ON THE FROST DISTURBANCE GRADIENT

Equisetum arvense	Carex Bigelowii	Silene acaulis	Saxifraga foliolosa
Equisetum variegatum	Carex misandra	Melandrium apetalum	Saxifraga hieracifolia
Woodsia glabella	Carex capillaris	ssp. arcticum	Saxifraga nivalis
Festuca brachyphylla	Juncus biglumis	Ranunculus nivalis	Saxifraga aizoides
Festuca baffinensis	Juncus castaneus	Ranunculus sulphureus	Saxifraga cernua
Colpodium Vahlianum	Luzula arctica	Draba alpina	Dryas octopetala
Poa arctica	Luzula confusa	Draba Gredinii	Epilobium latifolium
Poa alpina	Salix arctica	Draba lactea	Cassiope tetragona
Arctagrostis latifolia	Oxyria digyna	Draba fladnizensis	Pedicularis hirsuta
Carex nardina	Polygonum viviparum	Braya purpurascens	Taraxacum arcticum
Carex scirpoidea	Cerastium alpinum	Saxifraga oppositifolia	Taraxacum phymatocarpum

SPECIES WITH INTERMEDIATE TOLERANCE ON THE FROST DISTURBANCE GRADIENT

Poa pratensis	Carex supina	Ranunculus pygmaeus	Potentilla Crantzii
ssp. alpigena	spp. spaniocarpa	Papaver radicatum	Pyrola grandiflora
Poa glauca	Juncus triglumis	Draba nivalis	Arctostaphylos alpina
Poa abbreviata	Luzula spicata	Draba subcapitata	Vaccinium uliginosum
Trisetum spicatum	Tofieldia pusilla	Draba oblongata	ssp. microphyllum
Eriophorum Scheuchzeri	Koenigia islandica	Draba glabella	Gentiana nivalis
Eriophorum triste	Sagina intermedia	Eutrema Edwardsii	Euphrasia arctica
Carex maritima	Minuartia rubella	Saxifraga tenuis	Pedicularis flammea
Carex Lachenalii	Minuartia Rossii	Saxifraga caespitosa	Campanula uniflora
	Minuartia biflora		Erigeron humilis

SPECIES WITH NARROW TOLERANCE ON THE FROST DISTURBANCE GRADIENT

Lycopodium Selago	Carex ursina	Arenaria pseudofrigida	Potentilla nivea
Lycopodium annotinum	Carex amblyorhyncha	Minuartia stricta	Potentilla hyparctica
Botrychium Lunaria	Carex bicolor	Melandrium affine	Empetrum hermaphroditum
Cystopteris fragilis	Carex subspathacea	Melandrium triflorum	Hippuris vulgaris
Triglochin palustris	Carex norvegica	Viscaria alpina	Rhododendron lapponicum
Festuca vivipara	spp. inserrulata	Ranunculus trichophyllus	Cassiope hypnoides
Festuca rubra	Carex glacialis	var. eradicatus	Armeria maritima
ssp. cryophila	Carex rariflora	Ranunculus hyperboreus	ssp. labradorica
Puccinellia angustata	Carex atrofusca	Thalictrum alpinum	Veronica fruticans
Puccinellia coarctata	Carex saxatilis	Draba cinerea	Veronica alpina
Puccinellia phryganodes	Juncus trifidus	Draba groenlandica	Pedicularis lapponica
Poa Hartzii	Luzula frigida	Draba crassifolia	Pinguicula vulgaris
Calamagrostis purpurascens	Salix herbacea	Lesquerella arctica	Campanula rotundifolia
Phippsia algida	Salix arctophila	Cochlearia officinalis	Antennaria canescens
Hierochloe alpina	Betula nana	ssp. groenlandica	Antennaria Porsildii
Eriophorum callitrix	Stellaria Edwardsii	Cardamine bellidifolia	Erigeron uniflorus
Kobresia myosuroides	Stellaria humifusa	Arabis alpina	ssp. eriocephalus
Kobresia simpliciuscula	Cerastium arcticum	Sedum Rosea	Matricaria ambigua
Carex parallela	Cerastium cerastoides	Saxifraga Nathorstii	Arnica alpina
Carex rupestris	Arenaria humifusa	Saxifraga rivularis	Taraxacum brachyceras
Carex microglochin		Sibbaldia procumbens	

Fig. 11. Analysis of the Mesters Vig vascular flora with respect to the behavior of the species on the frost disturbance gradient.

soils but no clear cases of this could be found with the possible exception of the scanty sea strand flora. Among the species with narrow tolerances on the frost disturbance gradient are *Puccinellia coarctata*, *P. phryganodes*, and *Phippsia algida*, all of them occurring at or near high tide level on sea beaches. These species have been placed in the median segment of the frost disturbance gradient. It is possible that this is not entirely proper for *Phippsia*, for it also occurs on the fairly stable soils of clayey slopes. Between the two extremes of tolerance on this gradient are 35 species (22.7 %) of the flora) that have been called "intermediate". All of them grow in relatively stable soils and also in soils with a medium intensity of frost disturbance.

SPECIES WITH WIDE TOLERANCE ON THE NON-FROST DISTURBANCE GRADIENT

Poa arctica	Luzula confusa	Draba lactea	Saxifraga nivalis
Poa alpina	Salix herbacea	Draba fladnizensis	Saxifraga aizoides
Poa glauca	Salix arctica	Draba subcapitata	Saxifraga cernua
Poa Hartzii	Oxyria digyna	Draba glabella	Saxifraga caespitosa
Trisetum spicatum	Polygonum viviparum	Draba cinerea	Dryas octopetala
Carex nardina	Cerastium alpinum	Draba groenlandica	Epilobium latifolium
Carex scirpoidea	Sagina intermedia	Lesquerella arctica	Cassiope tetragona
Carex Bigelowii	Minuartia biflora	Cardamine bellidifolia	Arctostaphylos alpina
Carex supina	Silene acaulis	Arabis alpina	Vaccinium uliginosum
ssp. spaniocarpa	Melandrium affine	Saxifraga oppositifolia	ssp. microphyllum
Juncus biglumis	Papaver radicatum	Saxifraga Nathorstii	Pedicularis hirsuta

SPECIES WITH INTERMEDIATE TOLERANCE ON THE NON-FROST DISTURBANCE GRADIENT

Equisetum arvense	Hierochloë alpina	Juncus trifidus	Cochlearia officinalis
Botrychium Lunaria	Kobresia myosuroides	Juncus castaneus	ssp. groenlandica
Woodsia glabella	Carex rupestris	Luzula spicata	Braya purpurascens
Cystopteris fragilis	Carex ursina	Stellaria humifusa	Sedum Rosea
Festuca brachyphylla	Carex maritima	Arenaria pseudofrigida	Saxifraga foliolosa
Festuca baffinensis	Carex amblyorhyncha	Minuartia rubella	Saxifraga hieracifolia
Poa abbreviata	Carex subspathacea	Viscaria alpina	Potentilla nivea
Puccinellia coarctata	Carex misandra	Draba nivalis	Erigeron humilis
Puccinellia phryganodes			Matricaria ambigua
Phippsia algida			Arnica alpina

SPECIES WITH NARROW TOLERANCE ON THE NON-FROST DISTURBANCE GRADIENT

Equisetum variegatum	Carex norvegica	Melandrium apetalum	Pyrola grandiflora
Lycopodium Selago	ssp. inserrulata	ssp. arcticum	Rhododendron lapponicum
Lycopodium annotinum	Carex glacialis	Ranunculus trichophyllus	Cassiope hypnoides
Triglochin palustris	Carex rariflora	var. eradicatus	Armeria maritima
Festuca vivipara	Carex atrofusca	Ranunculus hyperboreus	ssp. labradorica
Festuca rubra	Carex capillaris	Ranunculus nivalis	Gentiana nivalis
ssp. cryophila	Carex saxatilis	Ranunculus sulphureus	Veronica fruticans
Colpodium Vahlianum	Juncus triglumis	Ranunculus pygmaeus	Veronica alpina
Puccinellia angustata	Luzula arctica	Thalictrum alpinum	Euphrasia arctica
Poa pratensis	Luzula frigida	Draba alpina	Pedicularis lapponica
ssp. alpigena	Tofieldia pusilla	Draba Gredinii	Pedicularis flammea
Arctagrostis latifolia	Salix arctophila	Draba oblongata	Pinguicula vulgaris
Calamagrostis purpurascens	Betula nana	Draba crassifolia	Campanula uniflora
Eriophorum Scheuchzeri	Koenigia islandica	Eutrema Edwardsii	Campanula rotundifolia
Eriophorum callitrix	Stellaria Edwardsii	Saxifraga tenuis	Erigeron uniflorus
Eriophorum triste	Cerastium arcticum	Saxifraga rivularis	ssp. eriocephalus
Kobresia simpliciuscula	Cerastium cerastoides	Sibbaldia procumbens	Antennaria canescens
Carex parallela	Arenaria humifusa	Potentilla Crantzii	Antennaria Porsildii
Carex microglochin	Minuartia Rossii	Potentilla hyparctica	Taraxacum arcticum
Carex Lachenalii	Minuartia stricta	Empetrum hermaphroditum	Taraxacum phymatocarpum
Carex bicolor	Melandrium triflorum	Hippuris vulgaris	Taraxacum brachyceras

Fig. 12. Analysis of the Mesters Vig vascular flora with respect to the behavior of the species on the nonfrost disturbance gradient.

The nonfrost disturbance gradient

The disturbance factors affecting plants in this gradient are extremely varied. They range from the slow creep of dry grus and sandy loams on steep slopes, to fluvial erosion by glacial streams, or to ice scour on sea beaches. Some are highly localized in the landscape (rockfall, debris slide, lake- and sea-shore processes, fluvial erosion and deposition, wind deflation and deposition). Others are widely distributed (gelifluction, slushflow, earthflow, sheetwash, eluviation). In the aggregate these processes, together with frost creep, have formed the surficial soils and microrelief of most of the plant habitats in the Mesters Vig district. Among them gelifluction, earthflow (and possibly slushflow) are by far the most significant.

Forty-two species (27.3 %) of the flora) are considered as widely tolerant in the nonfrost disturbance gradient (Fig. 12). Periodic inundation and abrasion by floods, gelifluction movement of their soils, deflation of their substratum by wind or partial burial by blowing sand, dry creep of their soils down slope, and sundry other vicissitudes of equal violence seem not to destroy these plants. At the same time, of course, they thrive in stable soils nearby, and in soils of all degrees of stability. The other extreme shows 77 species (50.0 % of the flora) that have narrow tolerances. These have all been found in soils relatively free of nonfrost disturbance. There are 35 species in the intermediate tolerance range (22.7 % of the flora). All but seven of them appear to be plants of stable soils capable of growing also under conditions of moderate nonfrost disturbance. The seven possible exceptions are plants found mainly on sea shores within reach of high tides. It might be said that the exceptional habitat for these species is one with a stable substratum.

Comparison of frost and nonfrost disturbance gradients

Although the distribution of percentages of the flora among the three levels of tolerance is nearly identical in these two gradients, the species compositions at equivalent levels show notable differences. Fully half (22) of the 43 species showing wide tolerance on the frost disturbance gradient are also widely tolerant on the nonfrost gradient. Of the remainder, however, nine are intermediate and 12 have narrow tolerances on the latter gradient. More than half (47) of the 76 species with narrow tolerance on the frost disturbance gradient are also narrowly tolerant of nonfrost disturbance. Of the remaining 29, 20 are intermediate while only nine are widely tolerant on the nonfrost gradient. Among the 35 species that have intermediate tolerance on the frost disturbance gradient, nine have wide, 20 have intermediate, and 18 have narrow tolerance on the nonfrost disturbance gradient.

It was evident from field observations that some species seemed able to survive any kind of disturbance in their substrata, no matter what the cause. Others appeared to be selective. Some were found on ground disturbed by frost heaving while others were on ground stirred by nonfrost processes such as gelifluction, periodic flooding, or deflation by wind. A rough measure of this selectivity is seen in the figures given in the preceding paragraph. It is possible that further refinement could be made, though none is apparent in the data at hand.

Thus 22 species can be named as the most tolerant of disturbance in the entire vascular flora. These species have wide tolerance not only on the disturbance gradients, but also on the moisture and coverage gradients. All of them are common or abundant in the district. In contrast there is a group of nine species that have wide tolerance in the nonfrost disturbance gradient, but narrow tolerance in that of frost disturbance:

Poa Hartzii
Salix herbacea
Melandrium affine
Lesquerella arctica
Cardamine bellidifolia
Arabis alpina
Draba groenlandica
Draba cinerea
Saxifraga Nathorstii

To draw the contrast still further, 12 species have wide tolerance in the frost disturbance gradient, but narrow tolerance in that of nonfrost disturbance:

Equisetum variegatum
Colpodium Vahlianum
Arctagrostis latifolia
Carex capillaris
Luzula arctica
Ranunculus nivalis
Ranunculus sulphureus
Melandrium apetalum ssp. *arcticum*
Draba alpina
Draba Gredinii
Taraxacum phymatocarpum
Taraxacum arcticum

These are among the more extreme cases of selectivity that have appeared. It could be illustrated further by means of species with intermediate tolerances, but the above will suffice.

A rating of species tolerance on a general disturbance gradient

It is desirable to attempt a rating of the Mesters Vig species in terms of their capacity to survive physical disturbance in a broad sense, combining the results of observations on their reactions to both frost- and nonfrost-induced disturbances. It probably is impossible to do this without using one or the other of the above analyses as the basic structure. But the use of one of them for this purpose carries the assumption that the disturbing processes involved in it are more significant to the plants of the district than those in the other.

Most of the species that are found in habitats much affected by nonfrost disturbances are also widely distributed in tundra sites that are disturbed by frost action. In the latter sites they are variously tolerant of frost-induced disturbance. The principal exceptions to this are in the seashore plants, of which there are only about half a dozen. Partial exceptions are also in the group of nine species listed above as having narrow tolerance in the frost disturbance gradient, but wide tolerance in the non-frost gradient.

It is probable that the areal extent of sites disturbed by nonfrost processes, particularly at any one time, is always much less than that affected by frost disturbance. This is due in part to the localized nature of most of the nonfrost processes. Those that are more widespread in the landscape have their effects reduced in part by sporadic occurrence (slushflow, earthflow). Much of the gelifluction movement that occurs is massive, leaving the surface soils essentially intact for long periods of years. Surficial gelifluction of sufficient violence to preclude plant life is localized.

Consequently it is probable that relatively lesser fractions of the total populations of the species found in the Mesters Vig district are affected by nonfrost disturbances than by frost disturbance. The latter, represented mainly by frost heaving and frost creep, is nearly universal in soils of medium texture.

If we are dealing here, as suspected, with inherent adjustability to disturbance (or lack of it) on the part of the plants, a long time period for selection is of the essence. There is geographic evidence of considerable age for the Greenland flora. It probably has had its present general structure since early Pleistocene time. Geomorphological studies indicate that the major processes now forming microrelief features in the Arctic are those involved in mass wasting, frost heaving and frost creep. Subaerial erosion and deposition, deflation and deposit by wind, and other processes more familiar in temperate regions are of minimal significance. It is entirely probable that this situation has also existed in much of arctic Greenland throughout the Pleistocene.

The destruction of a living plant by heavy flooding in a stream channel is just as final as its death from being heaved out of the ground by frost action. In the frame of reference with which we are working, however, this effect upon the individual plant is far less significant than the relative effects of the different kinds of disturbance upon total plant populations over time. Considering the predominance of frost heaving in the Mesters Vig landscape, and the wide distribution of most species populations over many kinds of sites, there is strong indication that the behavior of species in the frost disturbance gradient carries more significance than their behavior in the nonfrost gradient. The former can therefore be used as the basic structure for a general disturbance gradient.

A general rating of species tolerance to physical disturbance, in a descending order, is suggested in Fig. 13. It begins with the 22 species previously mentioned as having the widest ranges of tolerance on both gradients. Next to these come 21 species that have wide tolerance in the frost disturbance gradient, but intermediate or narrow ranges on the nonfrost gradient. In Fig. 13 the nine species accompanied by the symbol (I) are intermediate on the latter gradient, while the remaining 12 have narrow tolerances on it.

WIDE TOLERANCE

Species with wide tolerance on both frost and non-frost disturbance gradients

Poa arctica	Luzula confusa	Silene acaulis	Saxifraga cernua
Poa alpina	Salix arctica	Draba lactea	Dryas octopetala
Carex nardina	Polygonum viviparum	Draba fladnizensis	Epilobium latifolium
Carex scirpoidea	Oxyria digyna	Saxifraga oppositifolia	Cassiope tetragona
Carex Bigelowii	Cerastium alpinum	Saxifraga nivalis	Pedicularis hirsuta
Juncus biglumis		Saxifraga aizoides	

Species with wide tolerance on the frost disturbance gradient, but intermediate or narrow tolerances on the non-frost gradient

Equisetum arvense (I)	Arctagrostis latifolia	Melandrium apetalum	Braya purpurascens (I)
Equisetum variegatum	Carex misandra (I)	ssp. arcticum	Saxifraga hieracifolia (I)
Woodsia glabella (I)	Carex capillaris	Ranunculus nivalis	Saxifraga foliolosa (I)
Festuca brachyphylla (I)	Juncus castaneus (I)	Ranunculus sulphureus	Taraxacum arcticum
Festuca baffinensis (I)	Luzula arctica	Draba alpina	Taraxacum phymatocarpum
Colpodium Vahlianum		Draba Gredinii	

Wide tolerance on non-frost disturbance gradient; intermediate tolerance on frost disturbance gradient

Poa glauca	Minuartia biflora	Papaver radicatum	Arctostaphylos alpina
Trisetum spicatum	Sagina intermedia	Draba subcapitata	Vaccinium uliginosum
Carex supina		Draba glabella	ssp. microphyllum
ssp. spaniocarpa		Saxifraga caespitosa	

INTERMEDIATE TOLERANCE

Wide tolerance on non-frost disturbance gradient; narrow tolerance on frost disturbance gradient

Poa Hartzii	Lesquerella arctica	Draba groenlandica
Salix herbacea	Cardamine bellidifolia	Draba cinerea
Melandrium affine	Arabis alpina	Saxifraga Nathorstii

Intermediate tolerance on frost disturbance gradient; intermediate or narrow on the non-frost gradient

Poa pratensis	Carex Lachenalii	Ranunculus pygmaeus	Pyrola grandiflora
ssp. alpigena	Juncus triglumis	Draba nivalis (I)	Gentiana nivalis
Poa abbreviata (I)	Luzula spicata (I)	Draba oblongata	Euphrasia arctica
Eriophorum Scheuchzeri	Tofieldia pusilla	Eutrema Edwardsii	Pedicularis flammea
Eriophorum triste	Koenigia islandica	Saxifraga tenuis	Campanula uniflora
Carex maritima (I)	Minuartia rubella (I)	Potentilla Crantzii	Erigeron humilis (I)
	Minuartia Rossii		

NARROW TOLERANCE

Narrow tolerance on the frost disturbance gradient; intermediate tolerance on the non-frost gradient

Botrychium Lunaria	Kobresia myosuroides	Juncus trifidus	Sedum Rosea
Cystopteris fragilis	Carex rupestris	Stellaria humifusa	Potentilla nivea
Puccinellia coarctata	Carex ursina	Arenaria pseudofrigida	Arnica alpina
Puccinellia phryganodes	Carex amblyorhyncha	Viscaria alpina	Matricaria ambigua
Phippsia algida	Carex subspathacea	Cochlearia officinalis	
Hierochloë alpina		ssp. groenlandica	

Species with narrow tolerance on both frost and non-frost disturbance gradients

Lycopodium Selago	Carex norvegica	Minuartia stricta	Cassiope hypnoides
Lycopodium annotinum	ssp. inserrulata	Melandrium triflorum	Armeria maritima
Triglochin palustris	Carex bicolor	Ranunculus trichophyllus	ssp. labradorica
Festuca vivipara	Carex rariflora	var. eradicatus	Pedicularis lapponica
Festuca rubra	Carex atrofusca	Ranunculus hyperboreus	Veronica alpina
ssp. cryophylla	Carex saxatilis	Thalictrum alpinum	Veronica fruticans
Puccinellia angustata	Luzula frigida	Draba crassifolia	Pinguicula vulgaris
Calamagrostis purpurascens	Salix arctophila	Saxifraga rivularis	Campanula rotundifolia
Eriophorum callitrix	Betula nana	Potentilla hyparctica	Erigeron uniflorus
Kobresia simpliciuscula	Stellaria Edwardsii	Sibbaldia procumbens	ssp. eriocephalus
Carex parallela	Cerastium arcticum	Empetrum hermaphroditum	Antennaria canescens
Carex glacialis	Cerastium cerastoides	Hippuris vulgaris	Antennaria Porsildii
Carex microglochin	Arenaria humifusa	Rhododendron lapponicum	Taraxacum brachyceras

Fig. 13. Analysis of the Mesters Vig vascular flora with respect to the behavior of the species on a gradient combining frost and nonfrost induced disturbances in the soil.

If the reasons given above are valid for considering wide tolerance of frost disturbance more significant than that of nonfrost disturbance, the next 20 species in Fig. 13 probably are transitional between those having some wide tolerance and those having nothing but intermediate. All of them show wide tolerance on the nonfrost disturbance gradient. Eleven of them have ratings of intermediate tolerance on the frost disturbance gradient, and these are included among the species with generally wide tolerances. The other nine have narrow tolerances on the frost gradient, and are therefore placed lower in the general scale, among the intermediates.

Following these is a group of 24 species among which there is no wide tolerance, and in which all show intermediate tolerance on the frost disturbance gradient. Six of them are also intermediate on the nonfrost gradient, accompanied by the symbol (I) in Fig. 13, while the remaining 18 have narrow tolerances on this gradient.

Again assuming the validity of the preeminence in significance of tolerance to frost disturbance (or lack of it), the next 20 species are grouped with the narrowly tolerant on the combined gradient. This is done in spite of the fact that they show intermediate tolerance on the nonfrost gradient. However, they are listed first and separately among the narrowly tolerant plants, suggesting a slightly higher level in the general scale.

There remain the 47 species which were recorded in the field notes as having narrow tolerances on both kinds of disturbance gradients. With the exception of a few strand plants placed in median positions on the gradients they were all found growing in relatively stable soils. The group contains more than half (55.6 %) of the plants noted as rare in the district, and also a high proportion (45.8 %) of those that were seen only occasionally. It might be argued that the small number of observations on these plants makes ratings of them on the gradients unrealistic. Counter to this is the argument of consistent observation of their *absence*, and also their own consistently narrow tolerance where they were found. There are certainly minor levels of tolerance within the group, but with the present degree of refinement in our knowledge of the plants and of their habitats it is impossible to make a reasonable subdivision.

Continuing to maintain three main levels of tolerance, there are now 54 species (35.1 % of the flora) that show wide tolerance on a general disturbance gradient, 33 species (21.4 %) that show intermediate tolerance, and 67 species (43.5 %) that show narrow tolerance.

THE ROOT AND UNDERGROUND STEM SYSTEMS OF THE MESTERS VIG PLANTS

Continued observations of soils and geomorphic processes in the Mesters Vig district involved frequent attention to the roots of the plants growing in the soils. It was considered axiomatic that with few exceptions whatever limiting effects the active processes might have upon the life of the plants would function through the underground parts of the latter. There was no opportunity to investigate fully the detailed absorptive and storage structures of roots and rhizomes, nor was it possible to look into the physiological processes involved. Nevertheless it was thought worthwhile to see whether there might be a relationship between the gross morphology of the root and underground stem systems on one hand, and on the other the varying success of survival among the plants.

To this end numerous observations of the plant structures were made in field excavations and on plant collections. In order to achieve a degree of uniformity of treatment, these observations were checked against, and merged with the larger and much more complete series published by GELTING (1934). The latter described the general structure of stem and root for each species in his catalogue of the flora. Then he summarized most of the same information in his classification of the flora of his area according to the Raunkiaer system of life-forms (*l. c.*, pp. 289–298). Because the Mesters Vig district is some distance south of the region in which GELTING worked, a number of species were found there which GELTING did not include. Our notes on most of these were supplemented with those published by BÖCHER (1938). All of these data for the various species are given briefly in the published flora of the Mesters Vig district (RAUP, 1965 A). The present treatment merely summarizes them (see Table 1).

It is possible to sort the underground parts of most of the plants of the district into categories of fibrous roots, taproots and rhizomes without much difficulty. There are a few, however, that from the viewpoint of survival in disturbed soil may be intermediate, or they may have supplementary structures or growth habits.

Most of the species in the first group mentioned above are relatively simple in general structure and in their reproductive mechanisms. They are single plants with stem and root systems, reproducing by seeds, spores, bulblets or other asexual reproductive bodies. But eight of them produce slender stolons or runners which are capable of rooting at the tips and producing new plants. In three of these species the runners are above the surface of the soil: *Puccinellia phryganodes*, *Antennaria Porsildii*, *Antennaria canescens*. In the other five they are beneath the surface: *Festuca rubra* ssp. *cryophila*, *Saxifraga rivularis*, *Epilobium latifolium*, *Pyrola grandiflora*, *Pedicularis lapponica*. If any of these eight species should be growing in disturbed soil, its chances of survival should be better than those of most of the species without this kind of regenerative system. The destruction of the parent could be expected to leave one or more of those started from runners intact. It is probable that those with above-ground runners would have an advantage over those with runners below ground, for the runners themselves would be less subject to injury. In either case new plants, with their own root systems, would be started at distances ranging from a few centimeters to more than a meter from their parents. Many forms of disturbance, particularly those involving frost action, occur in micro-patterns the scales of which are commensurate with the sizes of these vegetative reproductive systems in the plants.

A few other plants in the group accomplish vegetative propagation. *Lycopodium Selago* sometimes roots at the nodes of its stems. Two species that are aquatic or at least semi-aquatic regularly reproduce vegetatively by the same means: *Ranunculus trichophyllus* var. *eradicatus* and *Ranunculus hyperboreus*.

A few species are added to this group although on structural grounds they do not belong here. *Carex scirpoidea* and *Hierochloë alpina* are rhizomatous species. However, they both have rather short rhizomes, and although they sometimes have simple aerial stems, it is more usual to find them densely caespitose, with many fibrous roots at the base of a mat of stems. As such the "plants" function more like single units with many fibrous roots than like spreading rhizomatous species. Another rhizomatous plant that might possibly be placed here, though with more question, is *Carex Bigelowii* which often has the same habit of growth. For the present, however, it is left among the species with well-developed underground rhizomes.

Among plants with taproots the occurrence of runners is less common, for it has been noted in only three species in the Mesters Vig district: *Stellaria Edwardsii*, *Salix herbacea*, and *Vaccinium uliginosum* ssp. *microphyllum*. In all of these the runners are underground. On the other hand most of the woody taprooted plants have the habit of rooting at the nodes of their prostrate branches: *Salix arctica*, *Salix herbacea*, *Salix arctophila*, *Empetrum hermaphroditum*, *Arctostaphylos alpina*, *Cassiope tetragona*, *Cassiope hypnoides*, *Vaccinium uliginosum* ssp. *microphyllum*, and possibly *Dryas octopetala.* Our observations of *Dryas octopetala* agree with those of GELTING (1934, p. 99), who noted that although this species produced an abundance of adventitious roots from its trailing stems, these roots were rarely found to penetrate the soil and become functional. A few other taprooted species produce roots at the nodes of their aerial stems, and are thus sometimes able to spread vegetatively: *Stellaria humifusa*, *Arenaria pseudofrigida*, *Saxifraga oppositifolia.*

Three species which on structural grounds are rhizomatous are placed here. They are plants with very short, oblique underground stems: *Cystopteris fragilis*, *Woodsia glabella* and *Polygonum viviparum.* The last is the only stem-tuberous plant in the flora. All of these three have the general form of plants with only fibrous roots, though they have something of the underground storage capacity of taprooted plants.

Storage capacity in underground organs is no doubt significant as a hedge against disturbance or drought injury. It is to be expected that a plant capable of remaining alive for a time at the expense of stored moisture and photosynthates would have more chances of rehabilitation than one with less time in which to do it. If this is the case the species with relatively large taproots would have the advantage, and those with relatively heavy, well-developed rhizome systems might also have some advantage.

In theory, the capacity of plants with underground stems (rhizomes) to "travel" vegetatively, starting new plants as they go, should give them the same additional chances of survival that are acquired by plants with runners or rooting branches. On the other hand all such expanding growth that takes place beneath the surface is kept to a slow rate by low temperatures, and is subject to the same frost damage as roots. If the soil warms very much it also becomes exceedingly dry, which also slows the growth rate. Questions similar to that of *Carex Bigelowii* could be raised with respect to the classification of species such as the abundant *Poa arctica.* This plant is usually strongly rhizomatous, but occasionally a densely caespitose form appears (ssp. *caespitans*) which has the structure of plants with only fibrous root systems and no conspicuous rhizomes. But this is not the common form in the Mesters Vig district, and *Poa arctica* is therefore left among the plants with rhizomes. Other species that are usually strongly rhizomatous but sometimes caespitose are *Carex supina* ssp. *spaniocarpa* and *Poa pratensis* ssp. *alpigena.*

Arrangement of the Mesters Vig species in the three major groups produces a striking result in that by far the largest proportion of the plants have their underground parts in the form of fibrous roots or taproots. Between these two they are about equally divided. Using the criteria outlined above, with the exceptions noted, the numbers and percentages are as follows:

Species with fibrous roots predominent	64 (41.6 %)
Species with taproots or short oblique rhizomes ..	65 (42.2 %)
Species with well-developed underground rhizomes	25 (16.2 %)

It was suggested above that plants whose underground organs consist primarily of fibrous roots or taproots have more chances of surviving physical disturbance in the soil if they have means of vegetative propagation. Although in the flora as a whole the total number of species able to accomplish this kind of propagation is not great, they are of considerable importance in the sites they occupy because of their capacity to multiply against odds. The numbers of them may be summarized as follows:

Species with fibrous roots and aboveground vegetative propagation	6 (3.9 %)
Species with fibrous roots and underground vegetative propagation	7 (4.5 %)
Species with taproots and aboveground vegetative propagation	11 (7.1 %)
Species with taproots and underground vegetative propagation	3 (1.9 %)

ON THE RELATION OF SPECIES TOLERANCE RATINGS TO SOME ENVIRONMENTAL GRADIENTS IN THE MESTERS VIG DISTRICT

Comparison of the lists of widely tolerant species in the analyses of the Mesters Vig flora with respect to coverage of the ground (Fig. 9), moisture (Fig. 10), and physical disturbance of the soil (Fig. 11, 12, 13) shows a large number of species in common among the lists. Reference to Table 1 brings out the fact that most of these widely tolerant species are in the common, common and locally abundant, and abundant categories of occurrence. It hardly need be said that the obverse is also true: that the lists of narrowly tolerant species have much in common, and are made up mainly of occasional and rare plants.

The widely tolerant species represent the group of plants noted by Gelting in 1934 (p. 235) in his Group A 1: "... the hardiest species in the area ...", "... with a wide range in almost all ecological scales". Thus Gelting appears to have sensed the significance of capacities for adjustment to external conditions—capacities that varied from species to species, and seemed to be fixed for each species within the area he studied. He made the reasonable assumption that species with large capacities for adjustment (with "wide ranges on the ecological scales", or "wide tolerances") should be more successful at regenerating themselves, occupying space, or at mere survival in unusually difficult conditions, than those with small capacities.

There are 22 species (14.3 %) of the flora) that are widely tolerant on all gradients. The number 22 is derived by using the gradients of frost and nonfrost induced physical disturbance separately. When these are combined to form a general disturbance gradient, as in Fig. 13, the number of species widely tolerant on all gradients is increased to 32 (20.8 % of the flora). All but four of them were noted as common or abundant in the Mesters Vig district, and these four were noted as locally common. It will be well to list the 32 plants, for they form the "core" of the Mesters Vig flora and plant cover.

Poa arctica
Poa alpina
Poa glauca
Trisetum spicatum
Carex nardina
Carex scirpoidea
Carex Bigelowii
Carex misandra
Carex capillaris
Juncus biglumis
Luzula confusa
Salix arctica
Polygonum viviparum
Oxyria digyna
Cerastium alpinum
Minuartia biflora
Silene acaulis
Draba alpina
Draba lactea
Draba fladnizensis
Draba glabella
Saxifraga nivalis
Saxifraga oppositifolia
Saxifraga aizoides
Saxifraga cernua
Dryas octopetala
Epilobium latifolium
Arctostophylos alpina
Cassiope tetragona
Vaccinium uliginosum ssp. *microphyllum*
Pedicularis hirsuta
Taraxacum arcticum

At the other extreme are 17 species (11.0 % of the flora) that are narrowly tolerant on all gradients. Again if a general disturbance gradient is used, combining frost and nonfrost induced disturbance, the number is increased to 22 species (14.3 % of the flora). Sixteen of these were noted as rare or occasional in the Mesters Vig district, five as occasional and locally common, and only one, a seashore species, was regarded as common. The 22 narrowly tolerant species are as follows:

Lycopodium annotinum
Triglochin palustris
Puccinellia phryganodes
Eriophorum callitrix
Carex ursina
Carex rariflora
Salix arctophila
Stellaria humifusa
Cerastium arcticum
Cerastium cerastoides
Arenaria humifusa
Arenaria pseudofrigida
Ranunculus trichophyllus var. *eradicatus*
Ranunculus hyperboreus
Draba crassifolia
Saxifraga rivularis
Sibbaldia procumbens
Hippuris vulgaris
Pinguicula vulgaris
Veronica alpina
Antennaria canescens
Matricaria ambigua

Using the same assumption that GELTING appears to have made—that species with wide tolerances of variation on environmental gradients are the most successful in the region—then the gradient of relative abundance used in the present analysis can be considered as a measure

Table 2. *Analysis of the total Mesters Vig vascular flora (154 spp.), showing percentage distribution of common to abundant, occasional to locally common, and rare to locally occasional species on gradients of ground coverage, moisture and physical disturbance.*

	No. of spp.	Abundant; common and loc. abund; common %	No. of spp.	Occasional and locally common; occasional %	No. of spp.	Rare and loc. occasional; rare %
Coverage gradient						
Wide tolerance	49	90.7	30	44.8	5	15.2
Narrow tolerance	2	3.7	24	35.8	20	60.6
Moisture gradient						
Wide tolerance	35	64.8	23	34.3	3	9.1
Narrow tolerance	7	13.0	19	28.4	19	57.6
Frost disturbance gradient						
Wide tolerance	28	51.9	12	17.9	3	9.1
Narrow tolerance	9	16.7	42	62.7	25	75.8
Non-frost disturbance gradient						
Wide tolerance	30	55.6	9	13.4	3	9.1
Narrow tolerance	18	33.3	36	53.7	23	69.7
General disturbance gradient						
Wide tolerance	36	66.7	15	22.4	3	9.1
Narrow tolerance	7	13.0	38	56.7	22	66.7

of this "success". If this is true and the assumption is tenable, species with wide tolerances on the environmental gradients should be most heavily represented among the common and abundant plants, while those with narrow tolerances should show higher percentages among the occasional and rare species. Table 2 and the graphs in Fig. 14 contain an analysis of the Mesters Vig flora in these terms.

The gradient of relative abundance could be subdivided in various ways, but a simple three-fold division was chosen, with the common to abundant plants at one extreme, and the rare or only locally occasional species at the other. Intermediate plants are those that are occasional in the landscape, or only locally common. Intermediate tolerance percentages are not shown for they are usually small and not definitive.

It is apparent that the suspected ratios are present. On the coverage gradient there are 16 times as many widely tolerant species among the common to abundant plants as there are narrowly tolerant ones, and

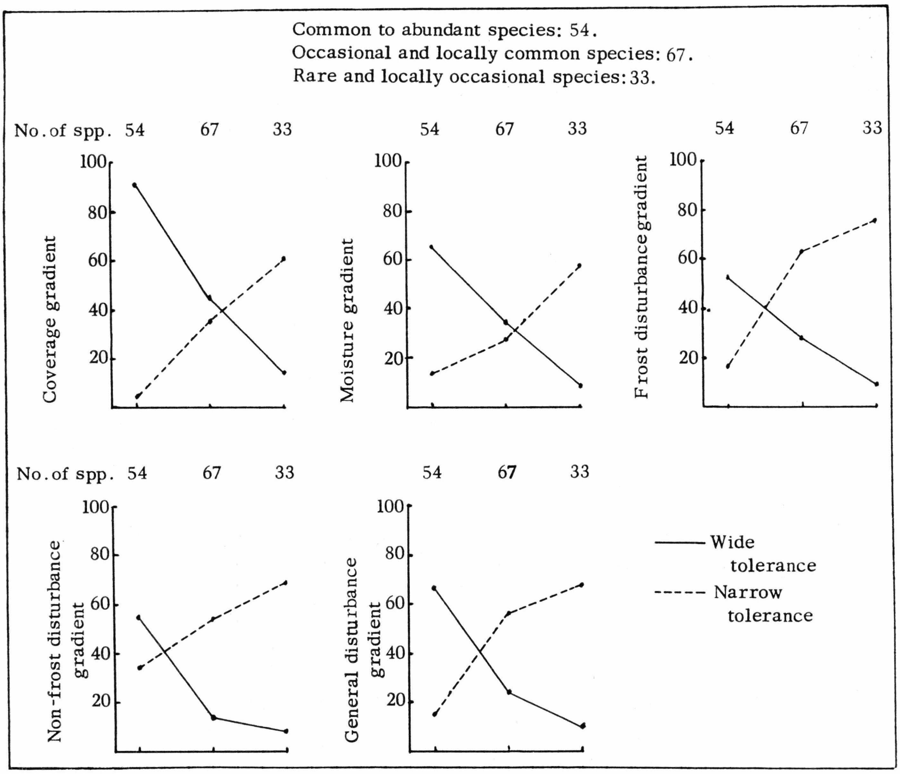


Fig. 14. Graph based on Table 2, showing percentage distribution of three frequency groups in the total Mesters Vig vascular flora on gradients of ground coverage, moisture, and physical disturbance.

about four times as many narrowly tolerant species among the rare and locally occasional plants as widely tolerant ones. In terms of probability this suggests that species found growing in vegetation coverage densities ranging over two-thirds or more of the total coverage gradient are 16 times more likely to be common or abundant in the district as a whole than are those whose ranges on the coverage gradient are restricted to one third of this gradient or less. In the case of rare or locally occasional plants the obverse is true by a factor of about four. The generally occasional or locally common plants form an intermediate group, though with a slightly higher percentage of widely tolerant than narrowly tolerant species.

Among the common to abundant species there are more than four times more widely tolerant than narrowly tolerant species in the moisture gradient. And on this gradient among the rare or locally occasional plants there are more than six times more narrowly tolerant than widely tolerant species. Again the occasional or locally common plants form an inter-

Table 3. *Analysis of species widely and narrowly tolerant (32 and 22 respectively) on gradients of ground coverage, moisture, and physical disturbance, showing percentage distribution of common to abundant, occasional to locally common. and rare to locally occasional species on the gradients.*

	No. of spp.	Common to abundant species %	No. of spp.	Occasional and locally common species %	No. of spp.	Rare to locally occasional species %
Coverage gradient						
Wide tolerance	28	100.0	4	26.7	0	0.0
Narrow tolerance	0	0.0	11	73.3	11	100.0
Moisture gradient						
Wide tolerance	28	100.0	4	26.7	0	0.0
Narrow tolerance	0	0.0	11	73.3	11	100.0
Frost disturbance gradient						
Wide tolerance	23	82.1	3	20.0	0	0.0
Narrow tolerance	0	0.0	11	73.3	11	100.0
Non-frost disturbance gradient						
Wide tolerance	25	89.3	3	20.0	0	0.0
Narrow tolerance	2	7.1	8	53.3	10	91.0
General disturbance gradient						
Wide tolerance	28	100.0	4	26.7	0	0.0
Narrow tolerance	2	0.0	11	73.3	11	100.0

mediate group among which there are slightly more widely than narrowly tolerant ones.

There are nearly three times as many widely as narrowly tolerant species in the common to abundant group on the frost disturbance gradient, and more than seven times as many narrowly as widely tolerant in the rare and locally occasional group. The intermediate frequency group shows a trend toward the latter of these ratios, with over twice as many narrowly as widely tolerant species. The ratios for the non-frost disturbance gradient show a somewhat similar pattern except that widely tolerant species exceed narrowly tolerant ones among the common to abundant plants by only about 50%.

The graph for the general disturbance gradient summarizes the preceding two. Among the common to abundant plants the factor is about 4.5, and among the rare or locally occasional species it is between 7 and 8.

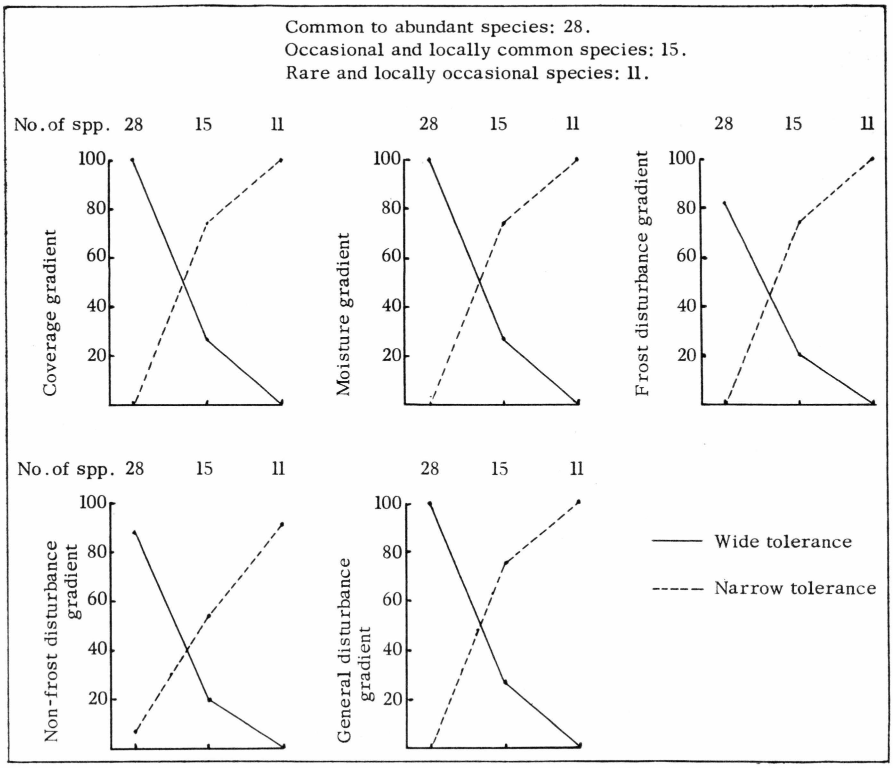


Fig. 15. Graph based on Table 3, showing percentage distribution of three frequency groups among species widely and narrowly tolerant on gradients of ground coverage, moisture, and physical disturbance.

The contrasting behavior of widely and narrowly tolerant species is most sharply defined among the 54 species that represent the extremes in these behavior patterns. As noted above, 32 of them are widely tolerant on the ground coverage, moisture and general disturbance gradients, while the other 22 are narrowly tolerant on all of these gradients. Table 3 and Fig. 15 show analyses of these groups in terms of the relative abundance or rarity of the species that compose them.

Among these 54 species (35 %) of the flora), most of those with wide tolerance are generally common to abundant in the Mesters Vig landscape, while none are rare or locally occasional. In contrast, all those having narrow tolerance ratings are rare, occasional, or common only locally, and none are generally common or abundant. The general pattern of contrast here resembles that shown for the general disturbance gradient rather than that for the coverage and moisture gradients. Again there are about 2.5 times as many narrowly tolerant as widely tolerant plants among the occasional or locally common species.

The above observations suggest that we are dealing here not only with factor gradients in the sites, but also ecotypic clines or variants within the species (*cf.* JOHNSON and PACKER, 1965; BÖCHER, 1954). The species variants appear to express selectivity in both extent and kind of tolerance to variation in site factors. It is probable that more detailed observation will refine this conception to some extent, but experiments with the plants in the field will no doubt be necessary to clarify the relationships.

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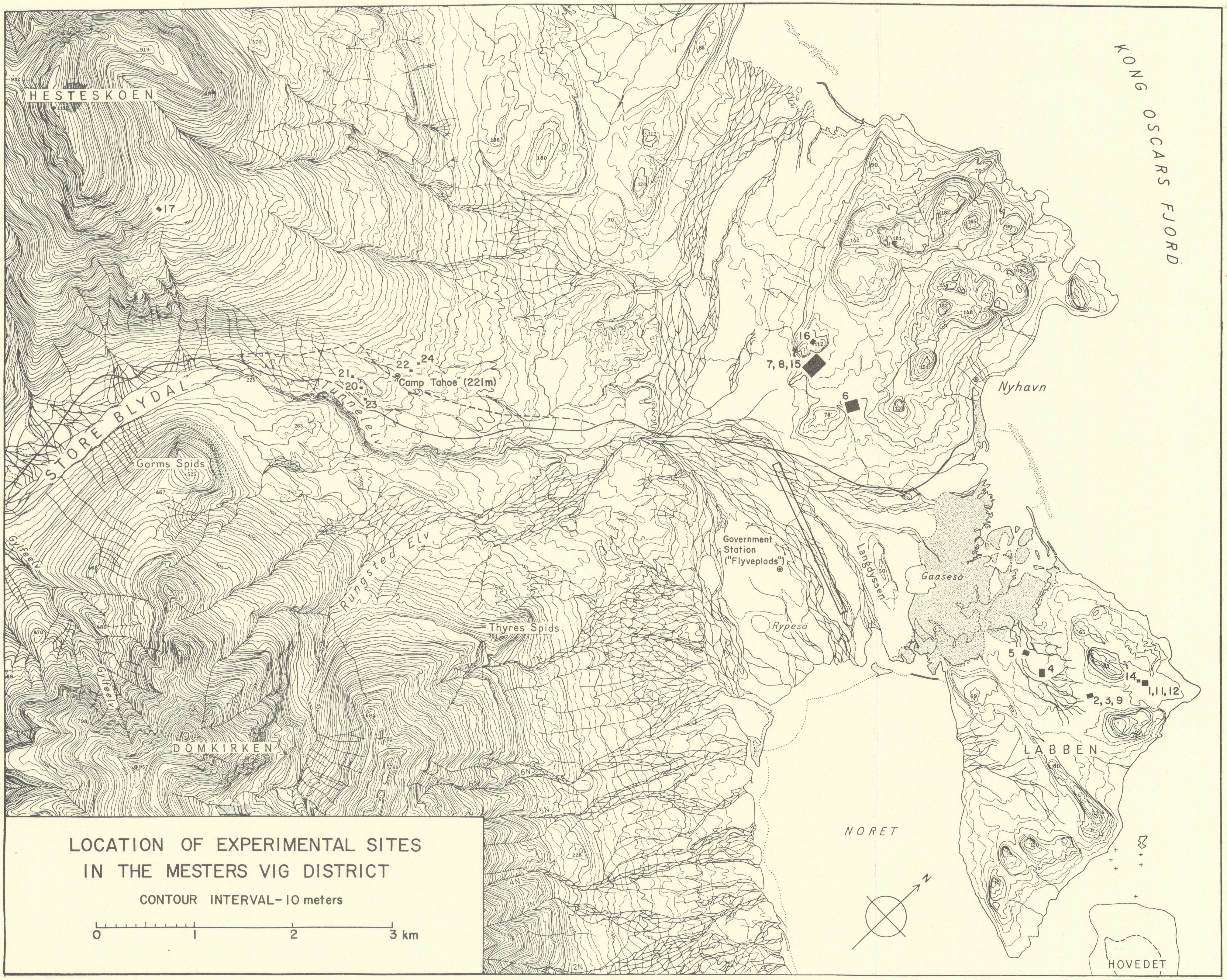

Map of Mesters Vig district, showing location of experimental sites.