MEDDELELSER OM GRØNLAND
UDGIVNE AF
KOMMISSIONEN FOR VIDENSKABELIGE UNDERSØGELSER I GRØNLAND
BD. 176 · NR. 6

OBSERVATIONS ON THE RELATION OF VEGETATION TO MASS-WASTING PROCESSES

IN THE MESTERS VIG DISTRICT, NORTHEAST GREENLAND

BY

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WITH 75 FIGURES AND 10 TABLES IN THE TEXT,
AND 1 PLATE

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1969

Abstract

This paper is a botanical companion piece to Dr. A. L. WASHBURN's publication on his instrumental observations of mass-wasting. It contains botanical analyses of the experimental sites reported in that publication: nos. 6, 7 and 8, 15, 16, and 17. For each experimental site there are descriptions of topography and soils, the moisture supply, frost heaving, downslope movement of targets by gelifluction and frost creep, and disturbance by erosion or other processes found to be active in the sites. The flora and distribution of vegetation types are described for each site, and the differing types of vegetation are analyzed in terms of the occurrence and behavior of their species on gradients of ground coverage, moisture, and physical disturbance of the soil. The study is summarized in terms of habitats rather than experimental sites, using analysis by species tolerance ratings on the gradients mentioned above. The paper contains suggestions for at least a partial rationalization of the open vegetation of the fjaeld-mark, proposing that external limiting factors should be assessed in light of the inherent capacities of the species to survive or utilize variations in the factor gradients. Second, the study is at least a partial test of the methods of analysis used, to see whether the basic information gathered from observations on species' tolerance in the whole Mesters Vig district could be applied to specific sites at large map scales.

CONTENTS

INTRODUCTION

Geomorphic processes concerned primarily with mass-wasting phenomena were described and analyzed by Washburn (1967). The basis for his analyses was in instrumental observations at experimental sites 6, 7, 8, 15, 16 and 17. The present paper deals with the vegetation of these sites, and attempts to relate their flora and its local distribution to the habitat complexes defined by Washburn's studies. His measurements over a five-year period have produced figures for amounts of heaving of targets and the quantities of downhill movement by creep and gelifluction. He has also presented data derived from moisture and particle size analyses in the soils, as well as data on local topography and temperature regimes.

The interpretation of the geomorphological data in terms meaningful to the life of the plants can be only approximated in view of our limited knowledge of the intimate physiological and structural relationships between plants and soils in the Arctic. To reach even an approximation it is necessary to find values in the vegetation which, though less precise than those available for the target behavior, are comparable in scale.

Botanical data to be used for comparison with physical data from the sites and geomorphic processes will be derived from six areas of analysis which are not all mutually exclusive: 1. distribution of types or "forms" of vegetation; 2. distribution of density in vegetative coverage of the ground; 3. distribution of the species of vascular plants based upon presence or absence; 4. local distribution of the frequency of occurrence of species; 5. distribution of tolerance ratings of species on gradients of coverage, moisture, and physical disturbance of the soil; 6. distribution of the various types of roots and underground stem systems. The way in which the botanical information basic to these analyses was accumulated in the Mesters Vig district has been described in earlier papers of the present series (Raup, 1965, p. 5–10; 1968, p. 34–38).

The order of treatment among the experimental sites differs from that used by Washburn. Sites 7 and 8 were closely related, and are discussed together. Moreover they were the largest and most complex of the sites, and the ones most intensively studied. They are therefore treated first and in somewhat more detail than the others. Site 6 is treated next because it was most closely related to ES 7 and 8. Sites 15 and 17 were both well defined gelifluction lobes, differing notably from ES 6–8. Site 17, being the larger and having the more complex flora, is dealt with before ES 15. Site 16, discussed last, differs from all the others because it is dry and illustrates processes absent or weakly defined in the other five sites.

METHOD OF ANALYSIS BY TOLERANCE RATINGS

An important element in the following studies is the use of tolerance ratings for interpretations of the distributional behavior of species at the various experimental sites. These ratings summarize many hundreds of observations on the local distribution of species along gradients in the environmental factors selected for study (see RAUP, 1968, Table 1). These data were gathered during several field seasons and at many places in the Mesters Vig district. Also they were supplemented by records published for the same general region by earlier students. The experimental sites described in the present paper contributed a considerable portion of the notes on tolerance ratings, though the information gathered at all other sites served to modify them materially.

The first purpose to be achieved by the use of the tolerance ratings in vegetation-site analyses is to test the validity of the ratings for application to specific, localized situations mapped at large scales. A second and related purpose is to find the extent to which the use of the ratings can be refined for comparative studies within site complexes.

There is a group of species in the Mesters Vig district that are widespread in the area, common to abundant, and present in a wide range of habitats. They are widely tolerant of variation in the coverage, moisture and physical disturbance gradients. They grow in both wet and dry sites, and in the most disturbed sites as well as in the most stable. At the other extreme of tolerance is a group that are narrowly tolerant on all gradients, sensitive to variations in coverage, moisture and disturbance. These species are occasional or rare in the district. Among the 154 species of vascular plants in the flora, 22 (14.3 %) make up the first group, of widely tolerant species. The second group, of narrowly tolerant plants, contains 17 species (11.0 %).

The number of species having universally wide or narrow tolerance on the gradients varies from one experimental site to another, and from one type of vegetation to another within the experimental sites. There is a general tendency for the percentages of them to vary inversely with the total numbers of species in the floras concerned. Their presence appears to be less indicative of environmental variations than of the sizes of the floras and of the areas occupied.

One of the principal purposes in using the tolerance ratings is for comparative studies among sites and vegetations. Because the above species have wide or narrow tolerance on all the gradients they have little or no value for comparative purposes, and are therefore considered to be non-definitive. They are significant for the analyses, however, for by subtracting their number in any given vegetation from the total number of species found there, a remainder consisting of definitive species is obtained. This number shows differences of tolerance rating among the vegetations compared and becomes the base number for computing percentages of definitive species with wide, intermediate and narrow tolerance in the given vegetations.

The above method for determining definitive species and the base numbers for percentages in the vegetations to be compared has been followed throughout the following analyses, with one exception. This was in experimental site 15, where the numbers involved became too small to be significant.

Species rated as intermediately tolerant are not emphasized in the comparative studies although their numbers are not subtracted from the totals. Their percentages are shown on the graphs because, though usually they have minor roles in the floras, they are sometimes present in numbers large enough to suggest intermediate qualities for the whole floras in which they are found.

The writer is deeply indebted to many persons and institutions for assistance in the Greenland field work and in the preparation of the present paper. Most of them have been mentioned in the first two numbers in the current series of publications and will not be named here (RAUP, 1965 A & B). Special thanks are due in the present instance to three individuals who gave valuable help in efforts to determine the nature of the organic crusts found at Mesters Vig: Dr. HOWARD A. CRUM of the University of Michigan, Dr. WILLIAM A. WEBER of the University of Colorado, and Dr. RUDOLPH M. SCHUSTER of the University of Massachusetts. Dr. ERNEST M. GOULD, Jr., and Dr. ARTHUR WESTING were most generous with suggestions and assistance in the presentation of data.

THE VEGETATION OF EXPERIMENTAL SITES 7 AND 8

Introduction

Experimental sites 7 and 8 were located on a southerly-facing slope in the Nyhavn hills. They were described by WASHBURN in paper No. 4 of the present series (1967, p. 33–72), and a map of the vegetation of the area covering them was published as his Figure 10. This map is reproduced here as Figure 1. WASHBURN demonstrated by instrumental measurements that the soils of the slope eastward of the trap cliffs were slowly moving downhill. The rates of movement varied from as little as 2.8 cm in a five-year period to as much as 29.7 cm in the same period. In addition to the slow general movement there were small gelifluction lobes forming at a more rapid rate in the surficial materials.

The rates of general movement and the relative intensities of frost heaving, frost creep and other surficial disturbances, were not distributed in a uniform pattern over the slope. Their distribution appeared most closely related to the seasonal regimes of moisture and frost, particularly as the moisture supply was related to the melting of large snowdrifts in the vicinity. A search for possible relationships between these regimes and geomorphic processes on one hand, and the tundra vegetation of the map area on the other, will be the subject of the following discussion.

Most of the significant data on soils and geomorphic processes came from the parts of the map area underlain by diamicton, east of the trap cliffs and talus. Therefore most of the studies of relationships between the geomorphic processes and the vegetation will be confined to the diamicton slope.

Materials used in the study

Descriptions of terrain and vegetation, with detailed notes on the flora, were made around each target in experimental sites 7 and 8 between 13 July and 25 July, 1957. The vegetation at each target was again described on 20–23 July, 1964. As many other fixed (surveyed) points as possible were used for description. The sites of the thermocouple strings (TCS) were used in this way. When the contour map was made

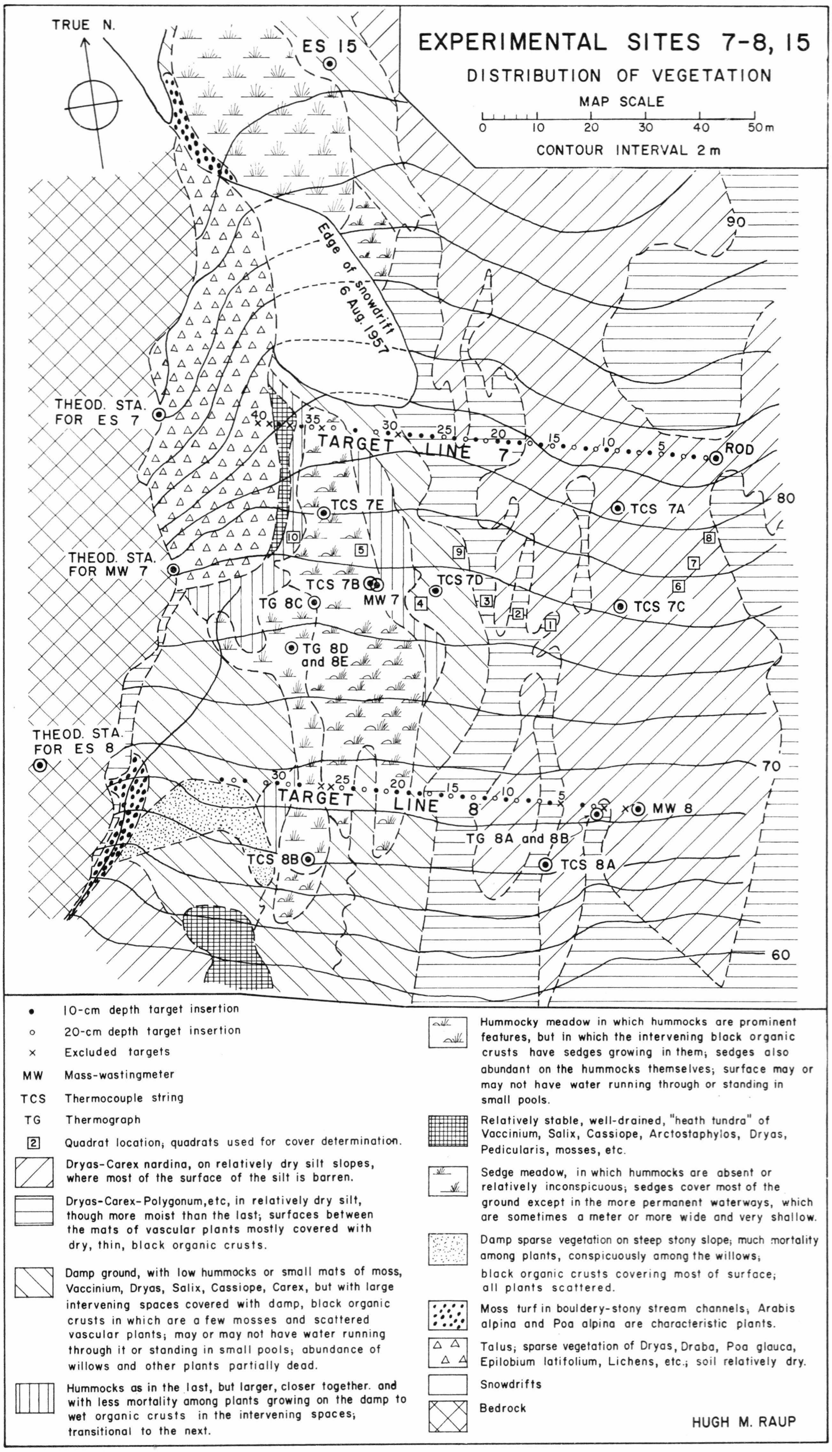

Fig. 1. Map of location, topography, and vegetation of Experimental Sites 7, 8 and 15. From WASHBURN, 1967, Fig. 10.

in 1957 the surveyors had a base line of four stakes across the slope more or less parallel to the contours, and an irregular transverse line of 18 stakes about the middle of the area. All of these stakes were used as reference points for mapping the vegetation. The extent of coverage of the ground by vegetation was noted in 10 quadrats scattered in the area between experimental sites 7 and 8. Five of these were mapped, all were photographed (Figs. 14, 15, 16, 18; also RAUP, 1968, figs. 2–7), and all were located on the map. Soil pits were dug at six points, and in each case the vegetation was described in considerable detail.

Thus there were 118 fixed points in the map area at which the vegetation was described. They served, however, as reference points for perhaps half as many more. Miscellaneous notes were made on the many occasions when the area was visited, and photographs were taken to illustrate seasonal changes and local differences in vegetation.

Topography and soils

The map shown in Fig. 1 covered a rectangular area about 120 × 185 m, comprising about 2.2 hectares. It was on a southerly-facing slope ranging, for the most part, between 10° and 14° (Fig. 2). The slope flattened out just above ES 15, and began dipping gently northward a short distance beyond this point. The top of the hill was in reality the summit of a low rounded ridge that extended east-southeast from the base of MS 112 m, gradually losing altitude in that direction. Its steepest slope was its southerly one, embodied in the map area.

The surface material was a diamicton, the uppermost few centimeters of which were a little coarser in texture than the deeper horizons. Boulders, cobbles, and pebbles were frequent, the boulders increasing in size (up to 1–2 m) toward the lower parts of the slope. On the west side of the area was a trap knob (MS 112 m). It rose abruptly from the lower part of the slope, but on the upper part it was skirted by a bank of gravelly debris noted on the map as "Talus".

Grain size analyses showed minor differences in the ratio of silt to clay sizes in the diamicton on the drier and wetter parts of the slope (WASHBURN, 1967). The percentages of silt were about the same in the "dry" and "wet" sectors (33 %), but the ratio of silt to clay was approximately 2:1 in the "dry" sector and 3:1 in the "wet" sector. Otherwise the diamicton was essentially uniform over the slope.

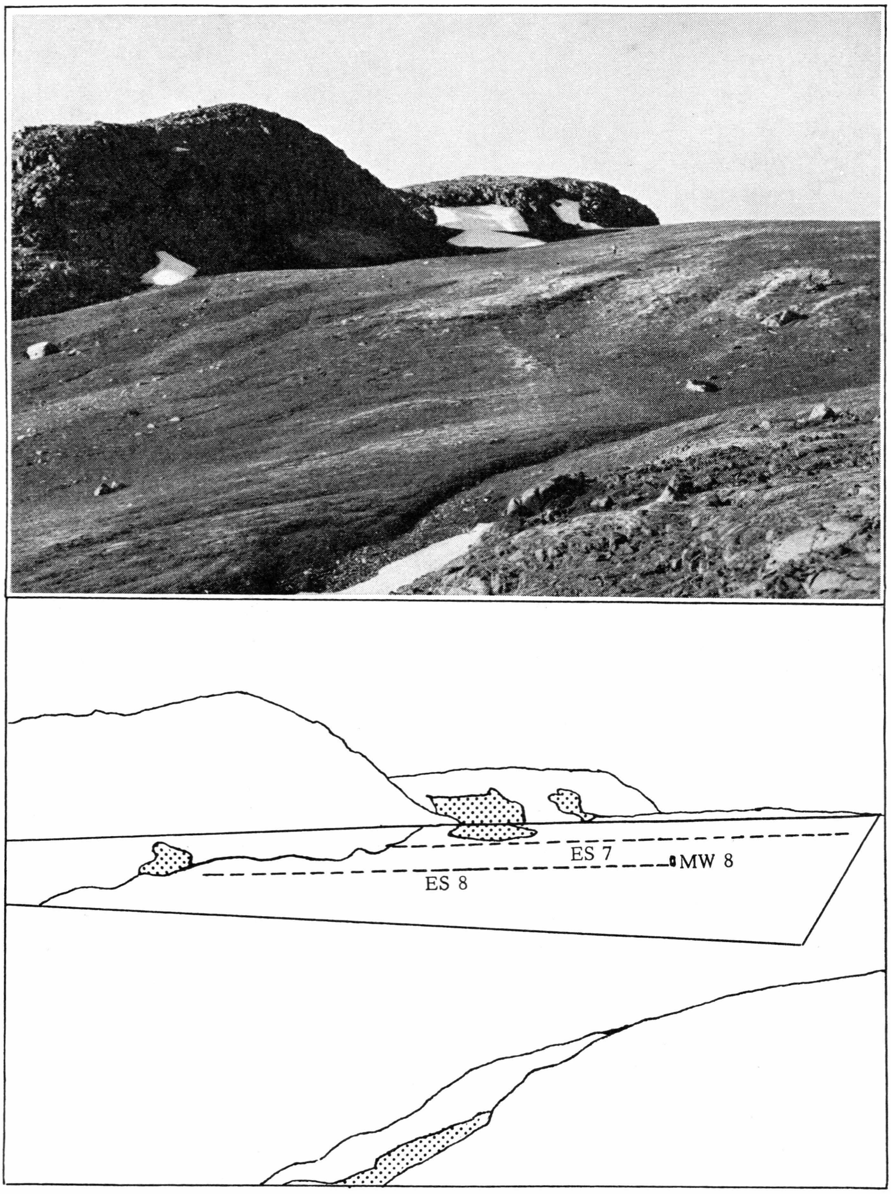

Fig. 2. View of ES 7 and 8 map area looking northwest.

The moisture supply

The principal source of moisture for plants during the growing season in the map area was from melting snow and ground ice, mainly the former. The contours of the trap knob on the western border of the area appeared to determine the positions of one large and one small snowdrift. The largest of these drifts accumulated each year at the base of the trap cliffs at the top of the slope in the northwest corner of the map area. This was a lee slope for the northwesterly winter winds from the fjord valley, and the position of the drift was determined by a shallow gap in the knob. The lesser drift (see Fig. 2) accumulated against the base of the cliff between the target line of ES 8 and the southern end of the gravel talus.

Small streams were seen near the northwest and southwest corners of the map area. They were intermittent, but never carried more than a small amount of water.

When the winter snow melted in spring the fine-textured clayey silt of the diamicton was saturated. Exposed to sun and wind, with no appreciable summer precipitation, it lost moisture rapidly, and dried to brittle hardness at the surface within a few days. Only where a moisture supply was continuous did it retain a degree of plasticity. Thus any transect across the slope in the map area, except one made immediately after the disappearance of the winter snow, showed a dry zone in the easterly part (beyond reach of water from the snowdrifts), and a wet zone in the westerly part (watered by the snowdrifts). Because the drifts melted back gradually each year, the border zones were watered for progressively longer times as the wet areas were approached.

The sizes of the snowdrifts varied from year to year, as did the rates at which they melted back. The target exposure data for ES 7 and 8 given by Washburn (1967) indicate some of these differences. When the map was made in 1957 (Aug. 6) the upper snowdrift extended down to within a few meters of the target line of ES 7. Again in 1958 all of the targets in this line were exposed by 16 July, but in 1960 only six targets in the line were exposed before 1 July, and three not until 7 August. In sharp contrast this drift had entirely disappeared by mid-July in 1964, and the entire slope was drier than our parties had seen it previously.

When these two drifts are projected across the map area, following the directions indicated by their forms, an area of greater snow depths is seen to extend from the general locality of the upper drift shown on the map southeastward to embrace all of ES 7 and perhaps a third of the area between ES 7 and 8. Another area of deeper snow was in the southwestern part of the surface between the target lines. It covered the western half or two-thirds of the targets of ES 8, and much of the slope below ES 8.

Evidence for this distribution of snow depths was seen in the spring of 1960 when the spring thaw was observed over a period of weeks. The first snow-free ground appeared in the hummocky meadow just east of the southern part of the gravel talus. This was in the interval between the two major drift accumulations. Although a few bare spots soon appeared on the talus itself, the largest expansion of bare ground was in a southeasterly direction. It continued in this direction, as rather a long "peninsula", until the eastern targets of ES 8 were exposed. At this time the western part of ES 8 and all of ES 7 were still under a meter or more of snow (see WASHBURN, 1967, Fig. 26). Another area of relatively shallow snow depths was on the top of the ridge above ES 7 but beyond the effects of the drifting snow.

The configuration of the map suggests the effects of past mass-wasting processes. As previously noted, the downslope movement of surficial materials has been thoroughly documented (WASHBURN, 1967). The small gelifluction lobes seen in the wetter parts of the diamicton slope and at ES 15 merged into inactive ones on the drier parts of the slope. Much of the dry easterly part of the slope, especially above the target lines, had a micro-relief of broad, faint, lobate structures marked by low ridges running up- and downhill, small steps that were sometimes turf-banked, and other features that indicated flow of the material.

Also on these dry slopes were occasionally found "perched" willows (*Salix arctica*) similar to those found on the Labben slopes (RAUP, 1965). The bases of the stems of these willows were sometimes several centimeters above the surface of the ground, indicating that they germinated and grew in a substratum of wet moss at that level. These things suggest that the "dry" part of the map area was formerly "wet", possibly made so by a much larger snowdrift than now develops on the upper part of the slope. The willows, still living, suggest further that this may have occurred within the last 60–75 years.

Distribution of soil moisture on the diamicton slope, ES 7 and 8

Quantitative data on soil moisture at several points on the diamicton slope were gathered in the years 1957 to 1961, incl., and have been published by WASHBURN (1967, Appendix F). The data afford usable information for only five of the seven vegetation map units intercepted by the ES 7 and 8 target lines, and in only four of these are the data fully comparable. For these four the samples were collected on 15 Aug., 1961. The fifth site, at a point 5 m downslope from target 37 in ES 7, was in the densely vegetated heath tundra, and was sampled on 15 Aug., 1958. These data are used because samples collected on the same day at the sites utilized in 1961 yielded information comparable to that gathered in the latter year. Furthermore the background meteorological data published by WASHBURN (1965, p. 22, Fig. 3) indicate that the July and August (1–15) precipitation for Mesters Vig in 1958 and 1961 were nearly identical.

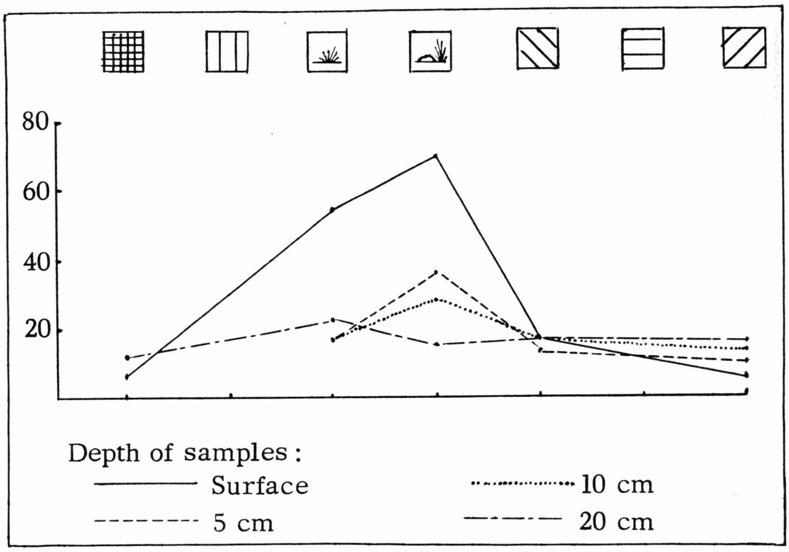

Fig. 3. Distribution of moisture, expressed as dry weight of solids, in soils of vegetation types on diamicton slope, ES 7 and 8, 15 Aug., 1961 (Heath tundra, 15 Aug., 1958).

Figure 3 is a graph comparing these scanty data. For each of two of the vegetation types, *Dryas* — *Carex nardina* and hummocky meadow, two sets of samples were available, and the charted values are averages.

This graph leaves much to be desired but it indicates major divisions and supports field observations. The latter observations were, of course, dominated by surface conditions, and the desiccated surface soils in the eastern parts of the diamicton slope are clearly shown by the low surface moisture percentage there. The sampling site in the damp organic crust type was described as "5 m downslope [from] T 27–30". This placed it near the eastern border of the type, which was the least moist portion. Thus, although its surface soil had three times as much moisture as the preceding type, a sample 10–15 m farther west along the target line would have yielded considerably more. Field observations showed repeatedly that the surface soils in the organic crust remained wet or moist throughout the summer, whereas in the two types east of it they became dry. A truer curve would show higher average surface moisture in the organic crust areas, perhaps at some intermediate level such as 30–40 $^0/_0$. Levels for the "dry" types would remain low in late summer, ca. 5 $^0/_0$. No usable moisture data are available for the soils under the turf hummock vegetation. It may be assumed from their position, however, and from many field notes on the general moisture conditions encountered in their vegetation, that their moisture was intermediate between those of the sedge meadow and heath tundra.

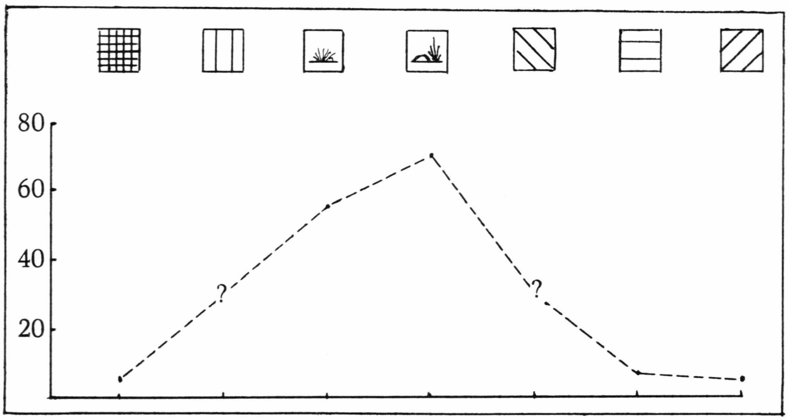

Fig. 4. Probable distribution of moisture in surface soils of vegetation types on diamicton slope, ES 7 and 8, based on quantitative data coll. 15 Aug., 1961, and 15 Aug., 1958 (See Fig. 3). Supplemented by field observations.

Figure 4 shows the probable distribution of moisture in the surface soils, embodying the alterations suggested in the preceding paragraph.

The major differences for 15 Aug., 1961, were in the uppermost five cm of the soil, and these differences gradually disappeared with depth. Essential uniformity over most of the slope for this date was reached at about 20 cm (14–22 $^0/_0$). At 50 cm (not shown on the graph) the moisture was between 13 and 15 $^0/_0$.

Experimental site 8 was examined on July 20 in the dry summer of 1964. Along the line of the targets damp surface soil was first encountered at target 14. It was found again at target 17, and from that point on was increasingly moist to targets 27–28. Along the line of ES 7 three days later a little living moss was found in the dry organic crust near targets 23 and 24, but there was little evidence of moisture in the soil until target 29 was reached. These observations suggest that there was surface moisture available to plants in the "dry" sector of ES 8 somewhat later in the season than in that of ES 7.

A few data from soil moisture analyses also indicate that the drier sector of ES 8 was slightly more moist throughout the season than the driest part of ES 7. They are abstracted from WASHBURN, 1967, Appendix F. The per cent water used is that expressed in terms of "dry weight", *i. e.*, $W = \frac{\text{wt of water}}{\text{wt of solids}}$. Two spots were selected for comparison because samples were collected from them on the same days (July 12 and 31, Aug. 7 and 15) in the summer of 1961. Also both were in the same vegetation type, in the driest parts of ES 7 and 8. Table 1 presents the figures so that they can be compared in the two sites at the ground

Table 1. *Comparison of soil moisture in two spots in the ES 7 and 8 map area (see Fig. 1), one in the vicinity of ES 7 and the other near ES 8.*

Dates	Depths of samples	Vicinity of TCS 7A % W	Vicinity of TCS 7A Av.	About 5m below targets 4-5 ES 8 % W	About 5m below targets 4-5 ES 8 Av.
July 12, 1961	Surface	3	8.8	7	10.0
	5 cm	11		10	
	10 "	10		11	
	20 "	11		12	
	50 "	12		19	
July 31, 1961	Surface	1	7.3	1	10.8
	5 cm	9		8	
	10 "	9		23	
	20 "	10		11	
	50 "	13		9	
Aug. 7, 1961	Surface	7	8.5	6	13.3
	5 cm	5		8	
	10 "	12		17	
	20 "	10		22	
	50 "	10		13	
Aug. 15, 1961	Surface	7	11.7	3	11.0
	5 cm	-		11	
	10 "	14		14	
	20 "	14		16	
	50 "	15		14	

surface and at depths of 5, 10, 20 and 50 cm. The sites can be located readily by reference to the map (Fig. 1).

These differences are not large, but they appear to be fairly consistent. The most significant moisture for the growth of the plants was in the uppermost 10–15 cm of the soil. Therefore the percentages in each profile from the surface down are averaged to include the 20 cm sample. These all showed higher values in ES 8 except those made from samples collected in mid-August. Another way of summarizing the data given in Table 1 is to average the percentages for each horizon for each of the sites, as shown in Table 2.

Here again averages indicate that somewhat more moisture carried through the drier part of the growing season in ES 8 than in ES 7, and helps to account for the slightly more hygrophilous nature of the flora.

It is possible that the small observed differences in soil moisture between ES 7 and 8 during mid-summer, recorded in the "dry" eastern

Table 2. *Comparison of soil moisture in the two spots in the ES 7 and 8 map area compared in Tab. 1, in terms of averages for soil horizons.*

	Vicinity of TCS 7 A	About 5 m below targets 4–5, ES 8
	Av %	Av %
Surface	4.5	4.3
5 cm	8.3	9.3
10 cm	11.3	16.3
20 cm	11.3	15.3
50 cm	12.5	13.8

sector of the diamicton slope, reflect a much larger difference which appeared during the thaw season in spring. This seasonal aspect of moisture distribution on the slope has considerable significance for later discussions, and will be described here.

The general disposition of snow depths on the diamicton slope has already been described. The first targets exposed in either site when the snow melted in spring were in the "dry" eastern sector of ES 8. In this position they were below a low "ridge" of relatively deep snow which was in reality a long southeasterly extension from the snowdrift at the top of the slope. When seen in May and early June, 1960, this "ridge" was 1–2 m deep and covered all of ES 7 including the "dry" sector. North of it, however, on the rounded top of the hill, the snow was much thinner and soon disappeared.

Thus there was a period of 2–3 weeks during snow-melt when the diamicton in the "dry" sector on the lower part of the slope received abundant water. As soon as the remains of the drift extension were gone the soil quickly dried out. At some time during the 2–3 week period the eastern part of ES 7 was progressively exposed. But before this occurred the snow above it on the slopes, thin to begin with, had already disappeared. Consequently there was no large supply of melt-water for the eastern part of ES 7, and the diamicton there dried out within a few days after the snow disappeared.

The net result of these events was that although the general appearance of soil and vegetation on the upper and lower parts of the slope in the "dry" sector was much the same in late summer, the seasonal behavior of the moisture regimes was quite different. The "dry" diamicton on the upper slope, in the vicinity of ES 7, was exposed a little later in spring than that on the lower slope, and remained at or above its liquid limit with melt-water for a relatively short time in early summer (7–10 days). The "dry" diamicton on the lower slope, in the vicinity of ES 8, was exposed 1–3 weeks earlier than the above, and remained that much longer at or above its liquid limit.

Cone-target heaving in the ES 7 and 8 area

Although the intimate relations of roots and rhizomes to frost heave disturbance could not be seen, evidence of disturbance in the upper horizons of the soil was clear from the behavior of targets. Further, differences in the amount of disturbance were measureable, at least in relative terms.

The targets of ES 7 were placed on 13 Aug., 1956, and those of ES 8 on 22 Aug., 1956. Final measurements of heave were made and the targets excavated in ES 7 on 23–26 Aug., 1964; those in ES 8 on 20–23 Aug., 1964 (Figs. 5, 6, 7).

After summarizing observations on the heaving of targets in the experimental sites, WASHBURN proposed that the critical variables controlling it were the moisture content of the mineral soil, the depth of target insertion, and the vegetation. He regarded temperature conditions and grain size as sufficiently similar at most sites (including ES 7 and 8) to be considered constant. He believed that in general heaving increased with increasing moisture and with greater depth of penetration of the target pegs. On the other hand, he thought that heavy vegetation in wet areas had a tendency to reduce heaving. He thought that most of the heaving probably occurred in the autumn with the annual freeze-thaw cycle, in soils that remained moist throughout the summer or received autumn moisture from rain or melting snow.

In the areas of the diamicton slope that became dry in late summer the heave was small and exhibited relatively minor differences. In ES 7, 26 of the 28 targets representing it were measured for heave. The average was 0.9 cm, and the range 0 to 2 cm. In ES 8 there were 15 "dry" site targets. Targets 32, 33 and 34 were mapped as on "damp ground", but the actual site of these targets on a knoll was a localized dry area within otherwise generally damp soils. The average heave of all these targets was about 1.1 cm, 2 mm more than the average for targets in the same category in ES 7. There was also a little greater range: from zero to 3.5 cm.

There were only slight differences in heave in the "dry" sectors of ES 7 and 8 that might be related to presence of ground cover, or to the kind of cover. In ES 7 nine targets were on essentially bare soil, and averaged 1 cm of heave. Nine were on organic crusts and averaged 1.1 cm. The eight targets sitting on flat mats of *Dryas* and *Salix* averaged about half as much heave (0.56 cm). In ES 8, three targets on bare soil averaged 1.7 cm of heave, four on organic crust averaged 1.3 cm, and again those on mats of vegetation averaged a little less (0.9 cm).

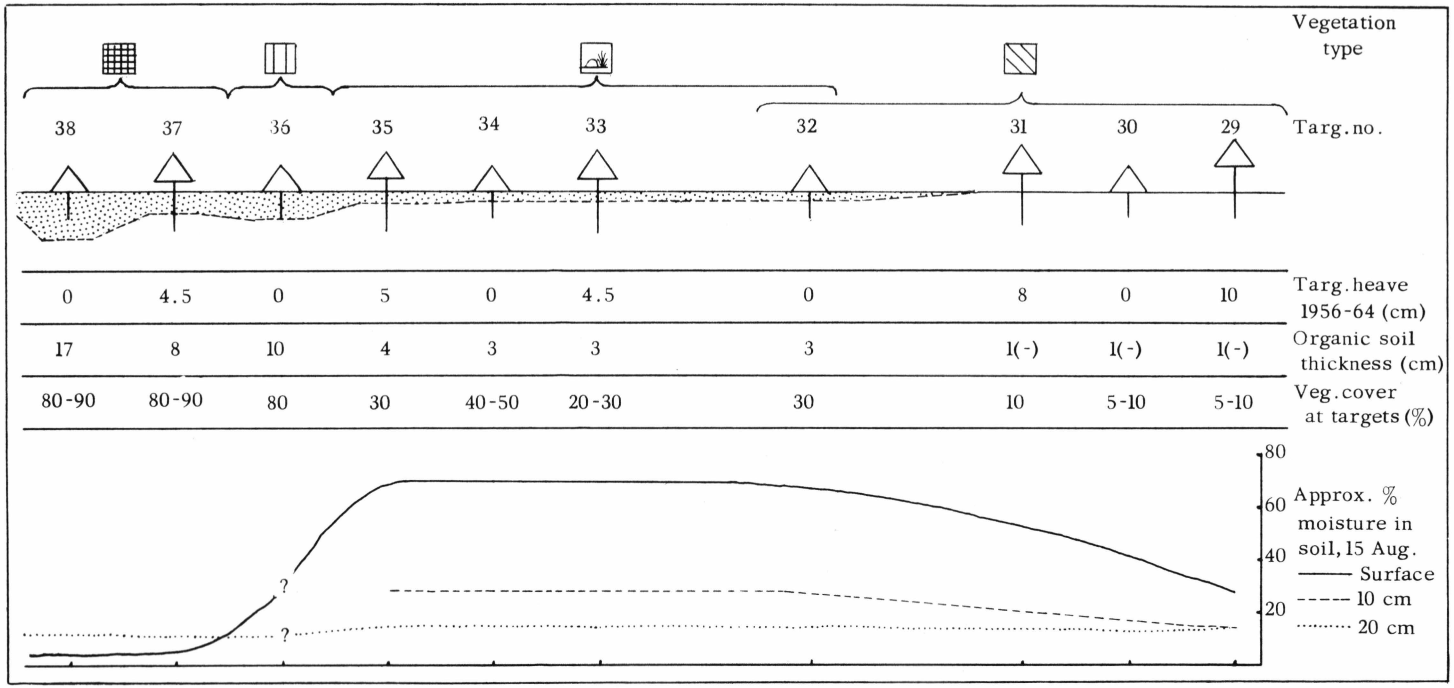

Fig. 5. Target heave, vegetation, organic soil thickness, target insertion depth, and soil moisture relations in "wet" sector of ES 7.

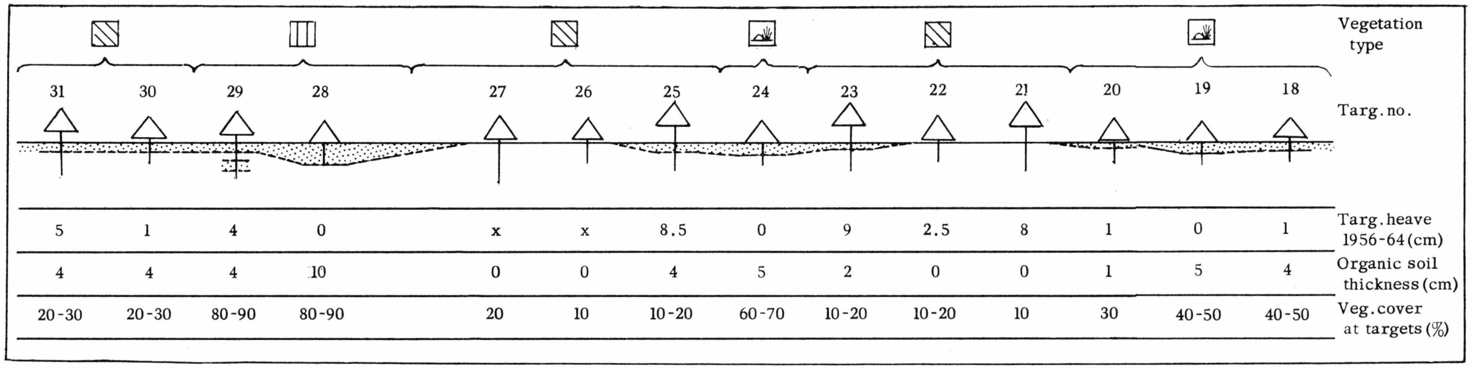

Fig. 6. Target heave, vegetation, organic soil thickness, and target insertion depth relations in "wet" sector of ES 8.

The relationship of heave to depth of insertion of the target pegs in the "dry" sectors seemed a little closer than that of heave to vegetative coverage. In ES 7, 14 targets with 10 cm insertions averaged 0.5 cm of heave, while 12 with 20 cm insertions averaged 1.3 cm. In ES 8, seven targets with 10 cm insertions averaged 0.7 cm of heave, and eight with 20 cm insertions averaged about twice as much (1.5 cm). Reference to Fig. 3 shows that more moisture was available in the diamicton at the 10 and 20 cm levels than at the surface in late summer. This may account for some of the greater heaving of the longer target pegs at the annual freeze-thaw cycle.

The measurements show that there was slightly less heaving in the "dry" sector of ES 7 than in that of ES 8. The average for all target heaves was only 2 mm greater in the latter, but this was consistent with other data showing that ES 8 was slightly more moist than ES 7. The range in the dry sector of ES 8 was also greater than that in ES 7, with two targets (nos. 10 and 17) having heaves of 3 or more cm.

With respect to plant-site relationships, frost heaving in the "dry" sector of the diamicton slope, though it had a role, probably was dwarfed in significance by the excessive desiccation there. Even the 20 cm targets, which penetrated nearly all of the root zone of the vascular plants, were heaved, on the average, only 1.5 cm in the moister ES 8. To assign relative values to relationships between minor differences in vegetative cover and slight differences in heaving under these circumstances seems still more tenuous.

In the "wet" sector frost heaving had much greater and more obvious effects because greater autumn moisture made it more active, and because the absence of restrictive desiccation permitted more plants to appear. The principal problem area of frost heaving was in the "wet" sector, and most of the following discussion will be devoted to it (see Figs. 5, 6, 7).

The average heave of the 12 accepted targets having 10 cm insertions in the "wet" sector during the eight seasons, 1956–64, was only 0.46 cm, in a range of 0 to 2.5 cm. Eight of the targets had no heave, and three were heaved only 1 cm. Thus most of the variation was due to a single target (Figs. 5, 6), no. 22 in ES 8, which was heaved 2.5 cm. This was in an area of thin organic crust. In another area of thin crust, at target 30 in ES 7, there was no heaving of a 10 cm target.

Reference to Figs. 5, 6 and 7 shows that the *average* heave of the 10 cm targets in the "wet" sector, with or without vegetative cover and in spite of greatly increased moisture, was of the same order of magnitude (about half a centimeter) as that in the "dry" sector. This suggests the first tentative conclusion to be drawn from the above data: that the uppermost 10 cm of the soil have been less effective, with minor excep-

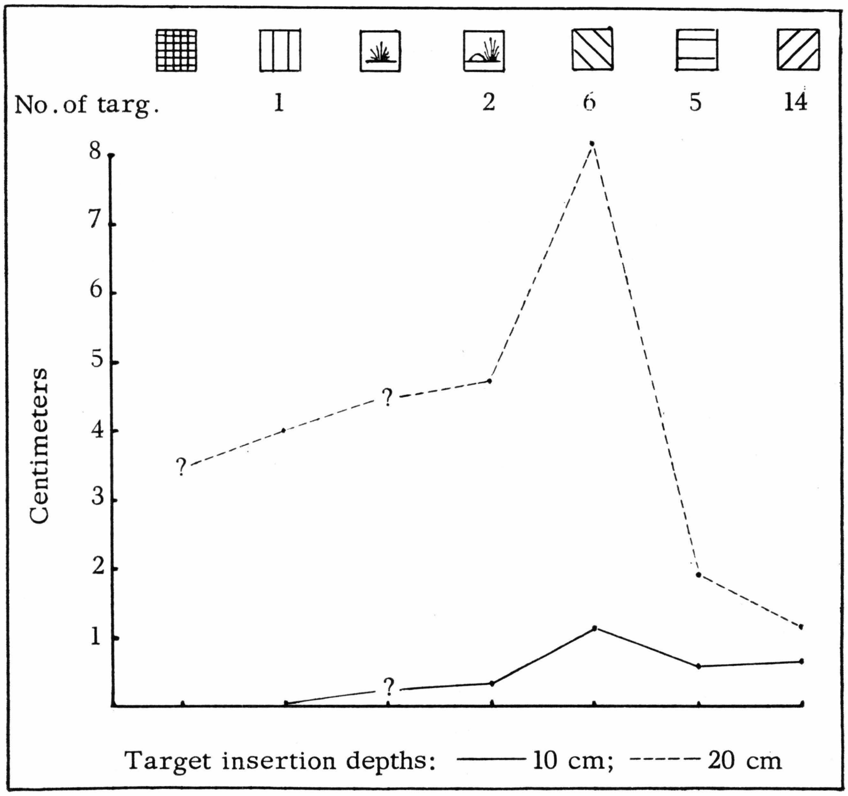

Fig. 7. Target heave, averaged for all accepted targets in each vegetation type on diamicton slope, ES 7 and 8.

tions, than the top 20 cm in heaving the cone-targets. The exceptions have been small heaves in moist diamicton covered with thin organic crust and scattered vascular plants.

Although, as noted above, the 20 cm targets were more heaved in the "dry" sector than the 10 cm targets, their average heave there was still less than 2 cm (Fig. 7). In the "wet" sector their pegs were found heaved up to half their length, but in variable amounts.

Observations of the 20 cm targets in the "wet" sector (Fig. 7, dashed line; Figs. 5, 6) showed a clear maximum of heaving in soils covered on the surface mainly by organic crusts. This was illustrated by targets 29 and 31 in ES 7, and by nos. 21, 23 and 25 in ES 8. Heaving of these targets ranged from 8 to 10 cm.

All other accepted 20 cm targets in the "wet" sector were heaved an "intermediate" amount (4–5 cm). These are: targets 33, 35 and 37 in ES 7; targets 29 and 31 in ES 8. Targets 26 and 27 were eliminated because channeling had eroded their sites. The sites of the "intermediate" group all had two characteristics in common: (1) the uppermost 3–8 cm of the soil were composed of organic materials, and (2) there was a considerably more dense vegetation of vascular plants around the targets than in the organic crust areas. In the latter the coverage of vascular plants usually was 5 to 20 %, but around 20 cm targets with intermediate heaves the cover ranged from 20 % to 90 %. The presence of an organic horizon at the top of the soil profile was not, however, restricted to areas of intermediate heave. At target 25 in ES 8 there were 4 cm of organic material, and at target 23, 2 cm. The actual surface was a crust in both cases, and the targets were heaved 8.5 and 9 cm, respectively.

The principal root zone of the vascular plants being in the uppermost 10–15 cm of the soil profile, it follows that roots in this zone were most likely to be injured by frost heaving if they were in areas covered by damp to wet organic crust and at the same time penetrated the diamicton more than 7–10 cm. In places where the diamicton was covered by 3 to 8 cm of organic material, and there was some vegetation on the surface, roots probably remained relatively uninjured to depths of 12–15 cm beneath the surface. This effect was greatly accentuated wherever very thick moist turfs occurred, such as on turf hummocks. Here many vascular plants were rooted entirely in the organic materials where almost no heaving took place.

Causes for the heave differences among the 20 cm targets may have been due to cover (or partial cover) of vegetation, or to varying thickness of the organic horizon, or to varying soil moisture at the time of autumn freeze, or to various combinations of these factors. Whatever the causes at any particular place, there appeared to be areas on the slope in which the roots of plants were much less subject to injury by frost heaving than in others. These areas were characterized by being damp to wet, by having a well-defined organic soil horizon (3 to at least 8 cm thick) over the diamicton, and by having vascular plants covering at least 20–30 % of the surface (usually 40 % or more). They were found mainly in the hummocky and sedge meadows, in the turf hummocks, and in the heath tundra.

Downslope movement of soils in the ES 7 and 8 area

Instrumental observations and analyses of target movements in ES 7 and 8 have been published by Washburn (1967), and form the basis for the following arrangement of the data in terms of vegetational units. Reference is made to Washburn's paper for a detailed account of the sources of the information.

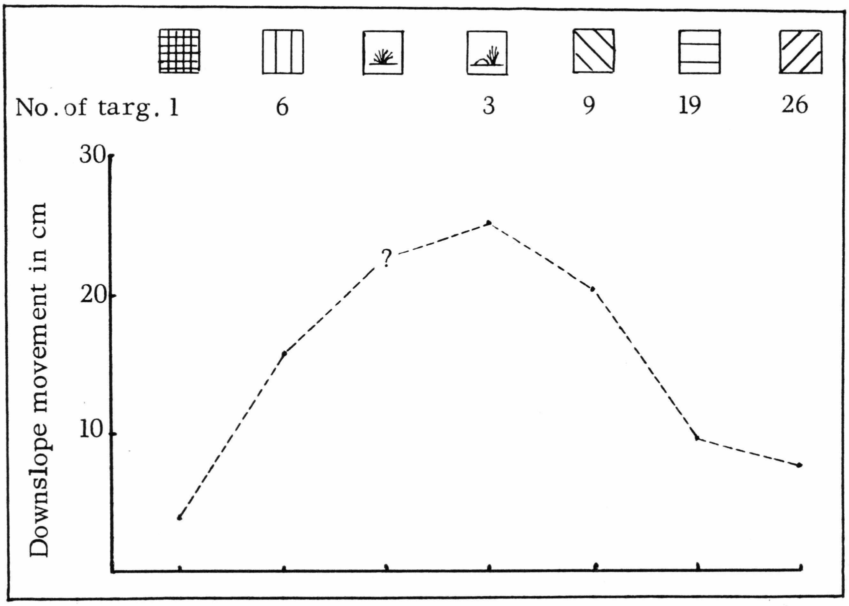

Fig. 8. Total net movement, 1956–1961, averaged for all targets in each vegetation type intercepted by the target lines of ES 7 and 8. Data from WASHBURN, 1967, App. C.

Total net movement of targets

To produce the graph in Fig. 8 the total net movements of all accepted targets in each vegetation type (using both target lines) were averaged. The curve shows a clear peak in the hummocky meadow, and low points in the heath tundra and eastern "dry" sectors. Soils with intermediate movement rates were under the turf hummock vegetation and the wet organic crusts. No targets were in sedge meadow, although one of those in the hummocky meadow was in a site somewhat resembling this vegetation.

Comparison of WASHBURN's Figs. 11 and 19 (1967) shows that Fig. 8 is by no means realistic for all parts of the diamiction slope. In his Fig. 11 the target movements show a rather abrupt increase with increased moisture beginning at target 29 of ES 7. In his Fig. 19 large target movements appear in the vicinity of target 10, in the "dry" sector of ES 8. Therefore separate graphs for ES 7 and 8 were made in the present instance (Figs. 9, 10).

The curve for ES 7 resembles that for the combined target lines, though it shows a lower proportion of movement in the area of damp organic crusts. In ES 8 no heath tundra type was present, and its position in the curve can only be assumed. Because there were no targets in sedge meadow vegetation, the position of the soils of this type on the curve

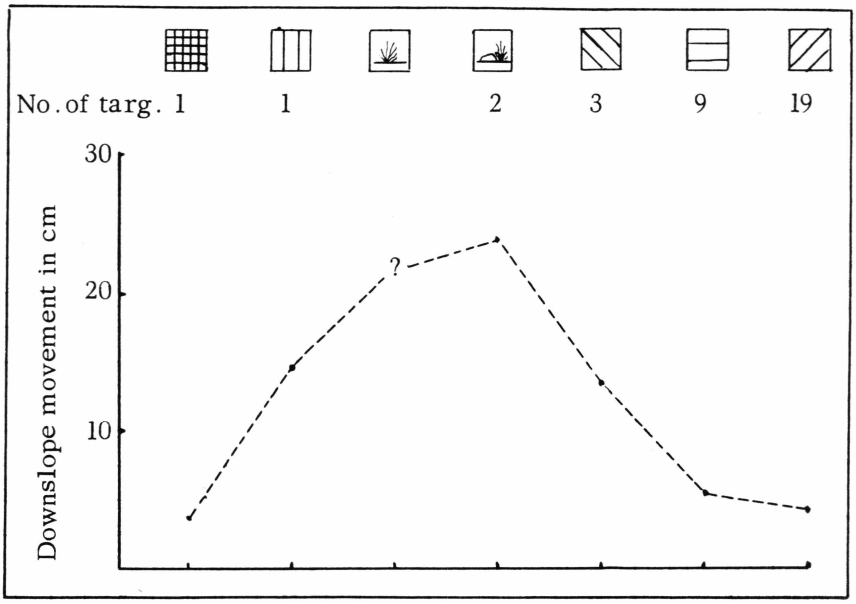

Fig. 9. Total net movement, 1956–1961, averaged for all targets in each vegetation type intercepted by target line of ES 7. Data from WASHBURN, 1967, App. C.

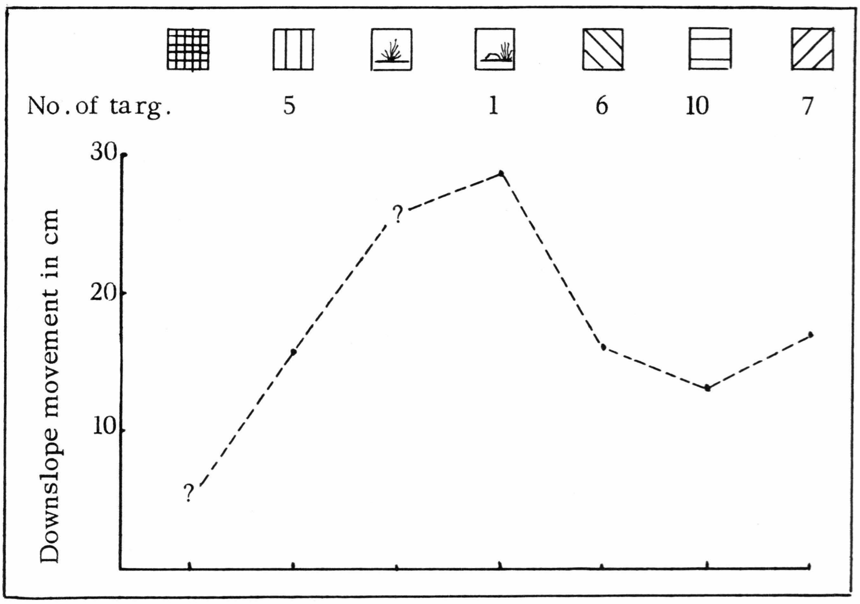

Fig. 10. Total net movement, 1956–1961, averaged for all targets in each vegetation type intercepted by target line of ES 8. Data from WASHBURN, 1967, App. C.

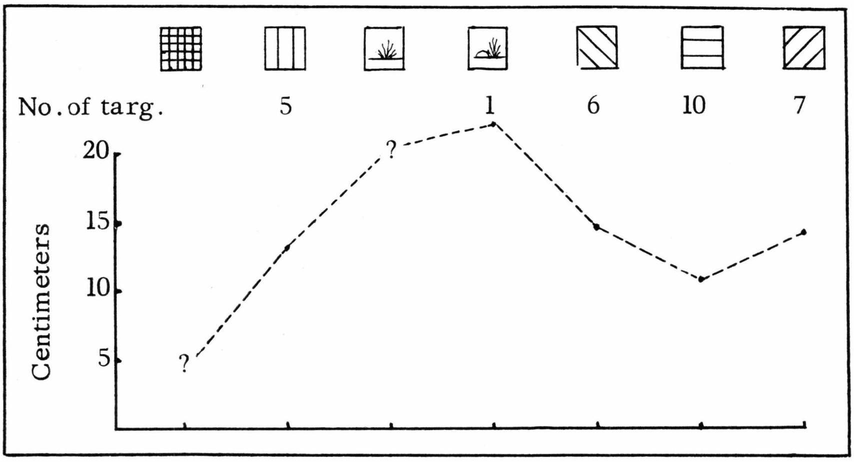

Fig. 11. Total jump (adj.) averaged for all accepted targets in each vegetation type intercepted by target line of ES 7, 1956–1961. Data from WASHBURN, 1967, App. C.

is assumed in the same manner as in the combined graph. The major difference, as indicated by WASHBURN's data, is in the "dry" sector, where intermediate averages appear rather than low ones as in ES 7.

Target jump

An expression of movement and disturbance in the root zone of the soils is in the measurements of "jump" made at each target each year. This term was defined by WASHBURN (1967, p. 17–18) as follows: "The jump is the movement between the last target reading of one year and the first reading of the next. It incorporates the result of ground heaving at right angles to the slope, which is the predominant cooling surface controlling

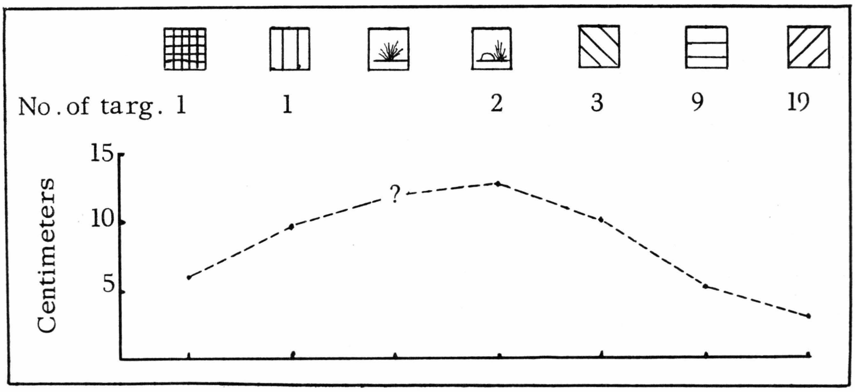

Fig. 12. Total jump (adj.) averaged for all accepted targets in each vegetation type intercepted by target line of ES 8, 1956–1961. Data from WASHBURN, 1967, App. C.

the direction of ice-crystal growth . . . The jump may involve some gelifluction if the first reading of the year was made after the ground around the target had thawed".

In Fig. 11 the total jumps for all accepted targets in each vegetation type intercepted by the target line of ES 7 were averaged, and the results plotted to form the curve shown. The same procedure was used with data from ES 8 to make the curve in Fig. 12. These curves closely resemble those for net downslope movement of the targets (Fig 9 and 10).

The downslope displacement of soil recorded by these target movements was massive rather than surficial. There was a certain amount of tilting of the targets, but none was overturned. Here and there on the slope were small, surficial gelifluction lobes with fronts ranging in height from 5 to 50 cm. In these the surface materials were also actively moving, but the total area of the lobes was small compared to the area of the slope. Thus on most of the surface which was moving downslope at the rate indicated by the targets, there was no obvious indication of motion. Large mats of vegetation were continuous and apparently unbroken in areas of many square meters. Seemingly a mat of vegetation, once formed, can "ride" on the moving diamicton quite safely until the latter is disturbed by an obstruction or a break in slope.

The vegetation

Introduction

The nucleus for the following description of the vegetation is taken mainly from notes made in the immediate vicinity of the target lines of ES 7 and 8, with two exceptions. One of these exceptions is the sedge meadow which is poorly represented in the lines. The other is the turf hummock vegetation, which will be discussed below. The lists given with the target line descriptions will, with these exceptions, therefore not be complete for the vegetation types they represent, nor will they give all the data available on the distribution of the species over the slope. For fuller information on the flora of the types reference should be made to Table 3. Following the description of the target lines will come notes on the vegetation of the map units not represented around the targets.

Table 3 is so arranged that the driest sites on the diamicton are at the right, and become progressively wetter toward the left until the sedge meadow is reached. From this they become progressively drier into the heath tundra vegetation of ES 7, or into the drier diamiction represented at the western end of ES 8. Still farther left in the table are the vegetation types not represented along the target lines. The species are arranged in

Table 3. *Species found in the ES 7 and 8 map area, showing their distribution among the vegetation types. Theorder of listing is from species present in all sites to those found in only one.*

	1	2	3	4	5	6	7	8	9	10
Salix arctica	+	+	+	+	+	+	+	+	+	+
Polygonum viviparum	+	+	+	+	+	+	+	+	+	+
Silene acaulis	+	+	+	+	+	+	+	+	+	+
Saxifraga oppositifolia	+		+	+	+	+	+	+	+	+
Dryas octopetala	+		+	+	+	+	+	+	+	+
Saxifraga cernua	+	+	+		+		+	+	+	+
Carex scirpoidea		+	+	+	+	+	+	+	+	
Vaccinium uliginosum ssp. microphyllum	+			+	+	+	+	+	+	
Carex misandra				+	+	+	+	+	+	+
Trisetum spicatum	+		+		+		+	+	+	+
Pedicularis flammea				+	+	+	+	+	+	+
Draba lactea	+	+	+					+	+	+
Carex rupestris	+			+			+	+	+	+
Poa alpina	+	+	+			+	+	+		
Cassiope tetragona				+	+	+	+	+	+	
Carex nardina	+					+		+	+	+
Minuartia biflora		+					+	+	+	+
Cerastium alpinum	+	+	+					+	+	
Oxyria digyna		+	+				+	+	+	
Epilobium latifolium	+			+		+	+	+		
Equisetum arvense		+			+	+	+	+		
Carex Bigelowii				+	+	+	+	+		
Carex capillaris					+	+	+	+	+	
Tofieldia pusilla				+	+	+	+	+		
Stellaria Edwardsii				+		+	+	+	+	
Ranunculus sulphureus				+	+	+	+	+		
Arctostaphylos alpina	+						+		+	+
Luzula spicata	+				+	+	+			
Kobresia simpliciuscula						+	+	+	+	
Poa glauca	+								+	+
Pedicularis hirsuta	+			+					+	
Euphrasia arctica						+	+		+	
Saxifraga aizoides						+	+	+		
Luzula confusa				+	+			+		
Festuca rubra ssp. cryophila				+	+		+			
Draba alpina		+					+	+		
Poa arctica				+	+		+			
Erigeron humilis		+					+	+		
Juncus biglumis						+	+	+		
Juncus castaneus					+	+		+		
Carex supina ssp. spaniocarpa	+									+
Melandrium affine	+									+
Draba glabella	+									+
Minuartia rubella	+								+	
Draba nivalis	+							+		
Saxifraga caespitosa	+							+		
Pedicularis lapponica				+			+			
Carex Lachenalii						+			+	
Equisetum variegatum							+	+		
Juncus triglumis						+		+		
Poa pratensis ssp. alpigena							+	+		
Eriophorum callitrix						+	+			
Carex parallela						+	+			
Carex microglochin						+	+			
Ranunculus nivalis						+	+			
Colpodium Vahlianum										+
Woodsia glabella	+									
Cystopteris fragilis	+									
Festuca brachyphylla	+									
Betula nana	+									
Arenaria pseudofrigida	+									
Draba fladnizensis	+									
Draba subcapitata	+									
Draba cinerea	+									
Sedum Rosea	+									
Potentilla Crantzii	+									
Potentilla nivea	+									
Potentilla hyparctica	+									
Campanula rotuntifolia	+									
Antennaria canescens	+									
Arnica alpina	+									
Festuca vivipara								+		
Melandrium apetalum ssp. arcticum								+		
Pyrola grandiflora				+						
Ranunculus pygmaeus		+								
Arabis alpina		+								
Lycopodium Selago							+			
Arctagrostis latifolia							+			
Carex norvegica ssp. inserrulata							+			
Luzula frigida							+			
Saxifraga hieracifolia							+			
Saxifraga tenuis							+			
Saxifraga foliolosa							+			
Rhododendron lapponicum							+			
Antennaria Porsildii							+			
Eriophorum triste						+				
Carex atrofusca						+				
Carex saxatilis						+				
No. of spp.	39	15	12	22	22	34	49	40	27	19

a decreasing order of the total number of different kinds of vegetation in which they were found established and growing. Occurrence is given entirely upon the basis of presence or absence.

Vegetation of experimental site 7

The first 17 targets (Fig. 1) at the easterly end of the line of ES 7 were situated on a broadly convex surface the highest part of which was between targets 5 and 10. The surface was marked by faint systems of low, parallel or anastomosing ridges 2–10 cm high. The systems appeared in ground plan as lobate structures with the low ridges becoming broader downslope. The continuity of the ridges was broken here and there by step-like structures where small terraces were formed with more or less vertical fronts 10–20 cm high. These were usually banked by mats of *Dryas* and *Salix*.

For a few days immediately following the disappearance of the snow and basal ice in spring all the surface soils of ES 7 were saturated. The diamicton was mire-like and sticky, and could not be walked on without sinking ankle-deep. Within a few days the convex surface in the eastern part of the target line dried out and became hard. By mid-summer it was usually so firm that digging had to be done with a pick. The area between targets 18 and 28, on a level to slightly concave surface, and receiving water from the snowdrift upslope for a little longer time in spring, remained moist at the surface somewhat longer than the soil under targets 1–17, but it became dry in the latter part of the summer.

The area under targets 1–17 was characterized by mostly bare soil which was on the tops and upper parts of the many low ridges (Fig. 13). The soil was stony, and slightly cracked by the summer desiccation. In many places micro-sorting had occurred, to form miniature nets and stripes of small pebbles. It is doubtful that this sorting was active under the existing moisture regime. The most conspicuous vascular plants were mats of *Dryas octopetala*. Most of these were small, 50 cm in diameter or less, though some were as much as 2 m in greatest dimension. Taproots from these plants were only 5–15 cm beneath the surface, and extended upslope from the main stems. *Salix arctica* also formed small mats, but was not as common or conspicuous as *Dryas*. Next in order of prominence on this part of the slope was the dark gray to black organic crust which covered much of the ground in the shallow depressions between the low ridges. The crust was discontinuous within the depressions, associated with or interspersed with lichens such as *Cladonia pyxidata* and *Stereocaulon sp.* It was also intermingled with the *Dryas* and *Salix* mats, most of which were rooted in the depressions or on the fronts of the small steps.

Fig. 13. Bare soil and *Dryas* mats in *Dryas* — *Carex nardina* vegetation, eastern "dry" sector of ES 7 and 8.

Nine other species of vascular plants were noted in the immediate vicinity of the first 17 targets: *Carex nardina*, *Carex rupestris*, *Polygonum viviparum*, *Minuartia biflora*, *Silene acaulis*, *Draba lactea*, *Draba glabella*, *Saxifraga cernua*, *Saxifraga oppositifolia*. All of the vascular plants, including *Dryas* and *Salix*, were much scattered. Ground cover by these plants ranged from zero to about 45 %, but averaged about 10 %. It is difficult to characterize vegetation in terms of species under these circumstances. This portion is called *Dryas*—*Carex nardina* merely because this combination appeared relatively more conspicuous here than elsewhere in the transect. It was one of the most conspicuous also in terms of area occupied, for it covered about 38 % of the total surface that was mapped. The list of all plants seen in the type totals 19 species (Table 3).

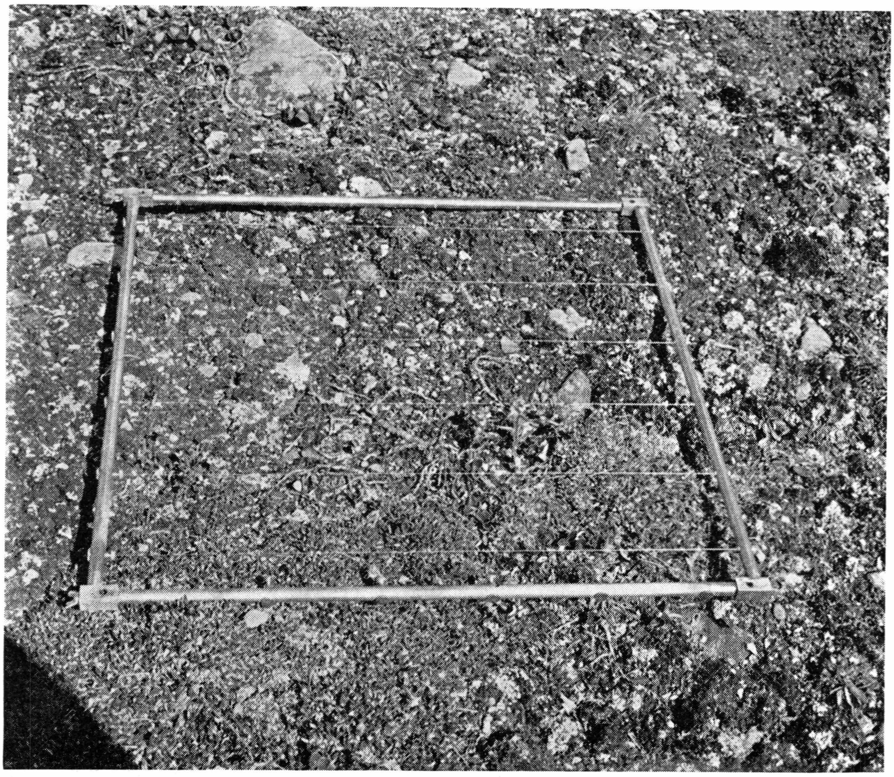

Fig. 14. Quadrat no. 3 (see map, Fig. 1), in *Dryas* — *Carex* — *Polygonum* — organic crust vegetation, in eastern "dry" sector of ES 7 and 8 map area, 9 July, 1958.

The area of targets 1–17 was the driest of two "dry" phases of ES 7. A slightly more moist phase embraced targets 18–28, on the generally level to slightly concave surface (Fig. 14). Although this surface was also ridged, there was much less bare soil, and most of the ground between the mats of vascular plants was covered with organic crust. Mats of *Dryas* and *Salix* were not much larger or more frequent than in the driest area, and there appeared to be even greater mortality among these woody species. A notable feature was the appearance of a few additional species, especially *Carex scirpoidea*, which added materially to the ground coverage. When observed in 1957 and 1958 this vegetation had considerable living moss on the ground surface, but in the dry summer of 1964 the moss was almost entirely dried out.

The following species were seen in the immediate vicinity of targets 18–28: *Trisetum spicatum*, *Carex nardina*, *Carex scirpoidea*, *Salix arctica*, *Polygonum viviparum*, *Oxyria digyna*, *Minuartia biflora*, *Cerastium alpinum*, *Silene acaulis*, *Draba lactea*, *Saxifraga cernua*, *Saxifraga oppositifolia*, *Dryas octopetala*, *Pedicularis hirsuta*. Estimates of the coverage of the

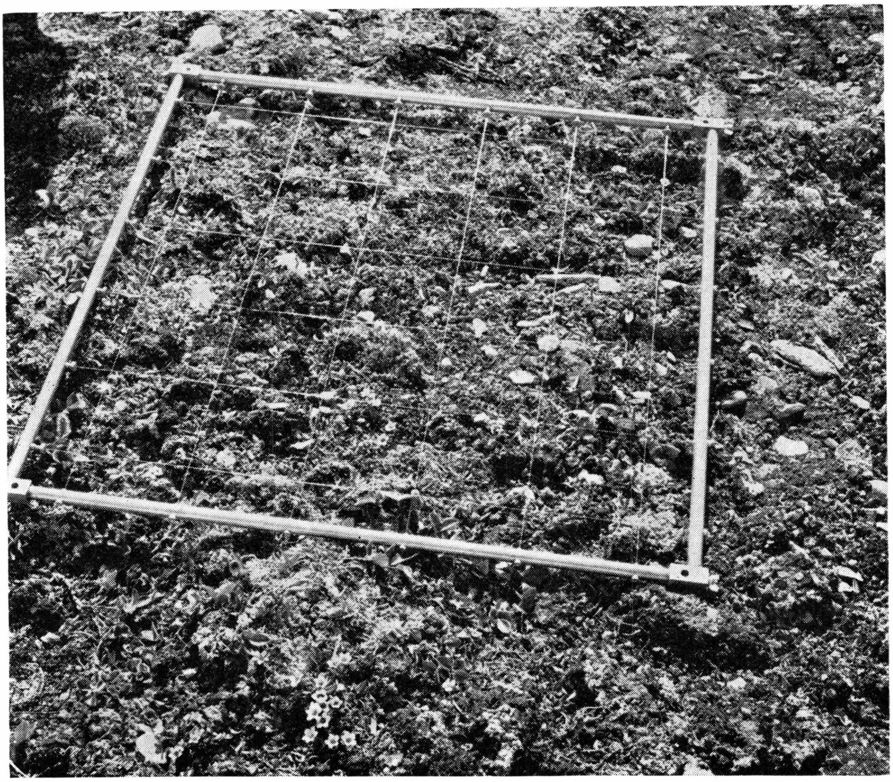

Fig. 15. Quadrat no. 9 (see map, Fig. 1), in vegetation of damp to wet organic crusts, low hummocks and small mats of vascular plants, ES 7 and 8 map area, 29 July, 1958.

ground by these plants ranged from 10 to about 40 %, averaging about 17 %. All the plants were much scattered.

The slightly more moist phase of the "dry" element was, like the drier phase, representative of a vegetation type that is widespread on the diamicton slope. It occupied about 20 % of the mapped area, and 27 species of vascular plants were recorded in it. Thus a total of about 58 % of the vegetation of the mapped area (about 63 % of that of the diamicton slope) was on soils that became surficially dry in mid- or late summer.

Targets 18 to 28 were on a system of low ridges. This system had a rather sharply defined western margin between targets 28 and 29, beyond which the surface had a slightly lower level and was somewhat concave, with boulders and cobbles scattered over it. When seen in the summers of 1957 and 1958 it was saturated throughout most of the frost-free season by water from the snowdrift above; and even in the excessively dry summer of 1964, when the drift was entirely gone by mid-July, the soil was still moist and the mosses were green.

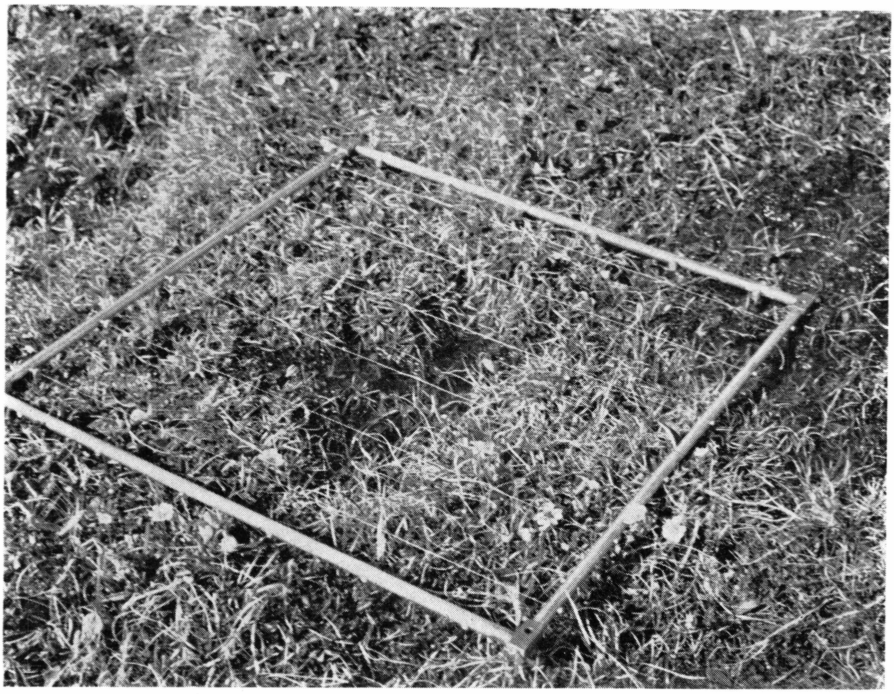

Fig. 16. Quadrat no. 5 (see map, Fig. 1), in hummocky meadow, ES 7 and 8 map area, 9 July, 1958.

The vegetation here was characterized by low moss hummocks or mats with large intervening areas of black organic crust (Fig. 15). Associated with the hummocks and moss mats were clumps of *Vaccinium*, *Dryas*, *Salix*, *Cassiope* and *Carex*. Except in very dry years water was found seeping through the mosses or standing in small pools during much of the summer. The following species were seen in the vicinity of targets 29–32: *Equisetum arvense*, *Equisetum variegatum*, *Poa alpina*, *Trisetum spicatum*, *Carex scirpoidea*, *Salix arctica*, *Polygonum viviparum*, *Oxyria digyna*, *Ranunculus nivalis*, *Ranunculus sulphureus*, *Minuartia biflora*, *Silene acaulis*, *Draba alpina*, *Saxifraga cernua*, *Saxifraga oppositifolia*, *Vaccinium uliginosum*, *Cassiope tetragona*, *Erigeron humilis*. Estimates of coverage of the ground by these plants ranged from 10 to 32 %, with an average of about 19 %.

Thus in spite of a relatively abundant moisture supply the flora remained much the same as in the area of targets 18 to 28 (four more species) and the average percentage of ground covered by vascular plants increased by only 2 %. Mortality among the vascular plants was high. This vegetation was a common one in the map area. A long "zone" of it is shown on the map bordering the "dry" sector and extending over

Fig. 17. View northeast from location near quadrat no. 5. Hummocky meadow and turf hummocks in foreground; damp to wet organic crusts with scattered low hummocks in middle ground; "dry" sector vegetations with much bare soil in background. 11 July, 1957.

most of the distance from the top to the bottom of the slope except for the immediate vicinity of the snowdrift. Other areas appeared on the southwestern parts of the slope. Many lesser ones occurred in the hummocky meadow, but the scale of the map prevented their inclusion. Approximately 16 % of the mapped area was occupied by the type, and a total of 40 species was recorded in it.

The vegetation of the area under targets 29–32 merged imperceptibly, along the line of ES 7, into that of the area under targets 33–35. In the latter the moss hummocks were larger and more prominent. They were more closely spaced, and many of the intervening crusts were more or less clothed with sedges (Figs. 16, 17). Sedges were also common in the vascular flora of the hummocks themselves. The ground was almost continually wet here. In the dry summer of 1964 there was water standing in small pools or flowing gently in small rills among the hummocks in the last week of July, after the snowdrift had entirely melted away. This water was coming from melting ground ice in the trap ridge and talus higher on the slope, and in small part from a light rain late in July.

Twenty-nine species of vascular plants were found in the immediate vicinity of targets 33–35: *Equisetum arvense*, *Equisetum variegatum*, *Festuca rubra* ssp. *cryophila*, *Arctagrostis latifolia*, *Poa pratensis* ssp. *alpigena*, *Poa alpina*, *Trisetum spicatum*, *Carex scirpoidea*, *Carex parallela*, *Carex misandra*, *Carex Bigelowii*, *Juncus biglumis*, *Luzula spicata*, *Tofieldia pusilla*, *Salix arctica*, *Polygonum viviparum*, *Oxyria digyna*, *Ranunculus sulphureus*, *Minuartia biflora*, *Silene acaulis*, *Draba alpina*, *Saxifraga foliolosa*, *Saxifraga cernua*, *Saxifraga oppositifolia*, *Saxifraga hieracifolia*, *Vaccinium uliginosum* ssp. *microphyllum*, *Pedicularis flammea*, *Erigeron humilis*, *Antennaria Porsildii*. This vegetation was a common one on the wetter parts of the slope, and is called "hummocky meadow" on the map. Coverage by vascular plants varied between 10 % and nearly 80 %, but averaged about 43 %, which is more than twice that achieved by the vegetation around targets 29–32. The hummocky meadow covered about 6 % of the mapped area. On the slope as a whole 49 species of vascular plants were noted in it.

The vegetation changed rather abruptly about halfway between targets 35 and 36. Target 36 was among hummocks that averaged larger in size (30–40 cm high, 30–120 cm broad) and were much closer together (Fig. 18). The intervening spaces were reduced to narrow channels. The ground surface began to slope upward to the west at this point, so that the area under target 36 was somewhat less moist than the wet area immediately east of it. Although its soils and mosses were quite moist in late July of the dry season of 1964, and surface water was evident in the area of targets 33–35, none was seen around target 36.

Eighteen species were noted in the vicinity of target 36. *Festuca rubra* ssp. *cryophila*, *Poa arctica*, *Poa pratensis* ssp. *alpigena*, *Trisetum spicatum*, *Carex scirpoidea*, *Carex misandra*, *Carex Bigelowii*, *Luzula confusa*, *Tofieldia pusilla*, *Salix arctica*, *Polygonum viviparum*, *Ranunculus sulphureus*, *Silene acaulis*, *Saxifraga oppositifolia*, *Dryas octopetala*, *Vaccinium uliginosum* ssp. *microphyllum*, *Cassiope tetragona*, *Pedicularis flammea*. The hummocks were nearly covered with rather dense growths of vascular plants, among which the *Vaccinium* was the commonest and most widely distributed. On some hummocks its primary position in the cover was shared by *Salix arctica*, in others by *Dryas octopetala*, or *Cassiope tetragona*, or *Carex Bigelowii*, or by various mixtures of these species. The percentage of the surface covered by vascular plants varied from 70 to about 90 %, averaging about 80 %.

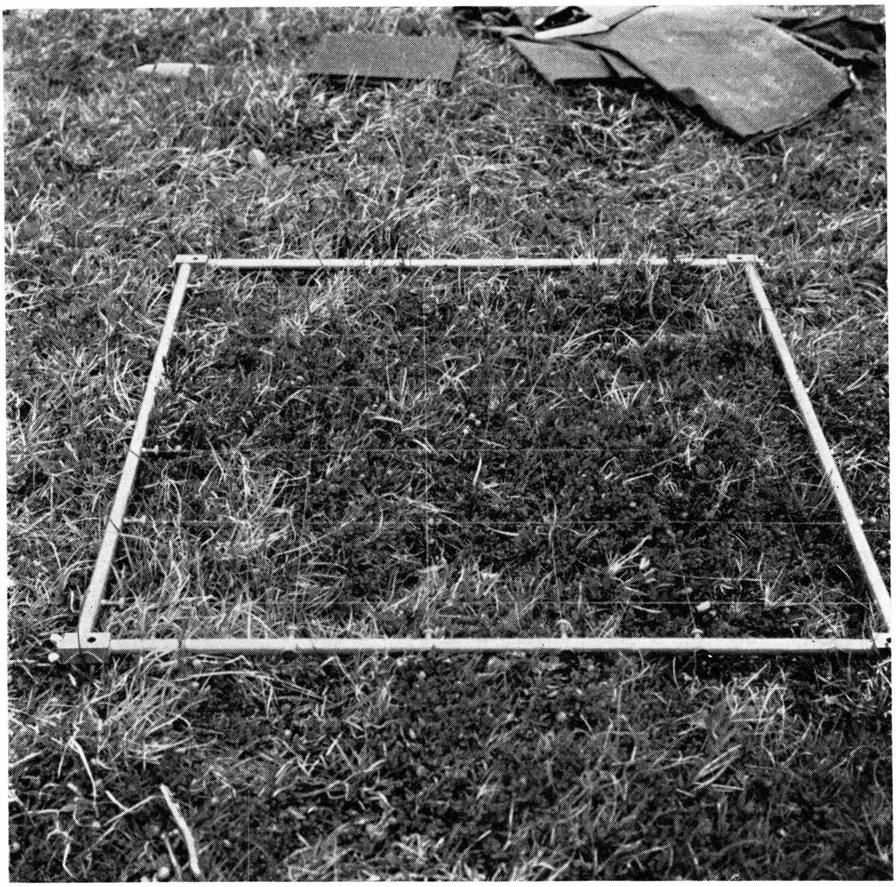

Fig. 18. Quadrat no. 10, in dense turf hummock vegetation near base of talus, ES 7 and 8 map area, 29 July, 1958.

The total area of mature turf hummocks such as are represented at target 36 was only about 3 % of the map area, and only 22 species of vascular plants were seen along the target line in its vegetation type.

The large *Vaccinium* hummocks of the target 36 area merged imperceptibly into those of the well-drained "heath tundra" around targets 37 and 38. Here the hummocks did not appear to rise so high above the general level, the turf was drier, and there was a richer growth of lichens in the intervals between the hummocks. The vascular flora noted in the vicinity of target 36 was nearly all present here, but five species should be added: *Carex rupestris*, *Stellaria Edwardsii*, *Epilobium latifolium*, *Arctostaphylos alpina*, *Pedicularis hirsuta.* The coverage achieved by the vascular plants was 80–90 % of the surface.

The heath tundra was localized in two relatively small areas of the map. One was in the narrow strip about 30 m long around the base of

Fig. 19. View of part of ES 7 and 8 area, looking southeastward from talus. Targets 38–40 of ES 7 in left foreground. July, 1960.

the talus, sampled at targets 37 and 38 of ES 7 as noted above (Fig. 19). The other was near the southwest corner of the map area about 25 m below the westernmost targets of ES 8. In all they covered about 1 % of the mapped surface, and 22 species of vascular plants were found in them.

Targets 39 and 40 were on the lower part of the talus slope (Fig. 19). The soil was dry and gravelly, with a few small bare spots showing around target 39, and much bare soil around target 40 which was higher on the slope. Target 39 was in a large mat of *Arctostaphylos alpina*, which did not go much above this level on the talus. The flora around these two targets was relatively small, and was drawn largely from the drier phase of the talus flora: *Poa glauca*, *Carex nardina*, *Salix arctica*, *Polygonum viviparum*, *Draba nivalis*, *Dryas octopetala*, *Epilobium latifolium*, *Vaccinium uliginosum*, *Arctostaphylos alpina*, *Pedicularis hirsuta*. The vascular plant coverage averaged about 40% around these two targets. When examined in the dry summer of 1964 there was a great deal of mortality among the plants, apparently due to desiccation. Further discussion of the talus flora will be found below. The type as a whole covered about 4% of the mapped area, and 39 species were recorded in it.

Vegetation of experimental site 8

The vegetation along the target line of ES 8, like that of ES 7, can be divided into "dry" and "wet" elements. The "dry" element, corresponding to that surrounding targets 1–28 in ES 7, appeared in ES 8 around targets 1–17. It reappeared in modified form around targets 31–34. The "wet" element embraced all of the remaining target areas: 18–30. The map symbols show that with one exception all of the kinds of vegetation appearing in ES 8 have already been described along the target line of ES 7. Although these descriptions need not be repeated in detail, a few differences should be mentioned.

Along the line of targets the driest phase of the "dry" element (*Dryas—Carex nardina*) did not have so wide an expanse as it did in ES 7. Only eight or nine targets were related to this kind of vegetation. However, the microrelief was much like that farther up the slope, with a series of broadly convex surfaces having their long axes oriented up and down. A short distance below the eastern part of ES 8 these ridges merged into some rather large gelifluction lobes 1–2 m high on their fronts. Just east of a mass-wasting meter installation (MW 8 on the map, near target 1 of ES 8) was a broad shallow gully that appeared to have been formed by an old earthflow movement (WASHBURN, 1967). The broad ridges along the target line were further marked by smaller ridges and faint terracettes.

The flora and ground coverage around targets 1–5 and 7–12 were much like they were around targets 1–17 in ES 7. However, *Arctostaphylos alpina* was seen at targets 10, 11 and 12. *Melandrium affine* was noted at all of the targets, and *Pedicularis flammea* was found at target 11. None of these appeared in the "dry" sector of ES 7, and although they have intermediate or wide tolerances on the moisture gradient, they were commonly found in somewhat more moist sites.

Target 6 was in a shallow depression floored with organic crust and having a vascular flora similar to that around targets 18–28 in ES 7. Between targets 13 and 17 the ground surface sloped gently downward to the west and became gradually more moist. Even so it dried out during the summer. Most of the surface here was also covered with organic crust and the vascular flora was scattered. However, it was noted in the field that beginning with target 13 the mats of *Dryas* and *Arctostaphylos* were large and numerous, giving an appearance of continuity to this type of vegetation that was lacking in ES 7. Again there was evidence among the plants of slightly more moisture than in this kind of vegetation in ES 7. *Carex capillaris* and *Euphrasia arctica* appeared around targets 13–17, and *Carex misandra* was seen not only around these targets but also at target 6. Thus both the driest and the slightly more moist phases of the "dry" sector of ES 8 had suggestions in their vascular floras that growing conditions were somewhat more moist in ES 8 than in ES 7.

Reference to the map (Fig. 1) will show that between targets 17 and 31, ES 8 crossed a series of "wet" vegetations. At the scale used, the map does not do justice to the complexity that actually existed in the vegetation of this area. It was directly below the main source of summer moisture for the slope, the melting snowdrift above the western part of ES 7. Its local terrain was much broken by boulders and by small gelifluction lobes. Some of these lobes were terracettes while others were larger structures 4–5 m broad and having fronts 30–40 cm high. Target 19, for example, was at the lower margin of a small lobe about 30 cm high, while target 20 was on the tread of this lobe. Targets 21–25 were in an area of faint terracettes of varying size, reaching as high as 60 cm on their fronts. Target 27 was at the base of a terracette about 25 cm high situated in a channel where water flowed around both sides of it. Thermocouple String 8B was on a broad and prominent gelifluction lobe a short distance below targets 27–28.

Beginning with target 17 and continuing through target 26 there was a series of combinations of mossy hummocks and organic crust, with or without sedges, rushes and other vascular plants. In general, the thickest turfs in the hummocks were found in the wettest areas, around targets 19–22 and 24–26. Also the richest floras in numbers of species and ground cover were found in these places. It must also be said that in immediately adjacent situations which were almost if not quite as wet as these some of the poorest floras and ground covers were found. These were in the anastomosing areas of organic crust which were ubiquitous throughout. As indicated on the map they were especially abundant between targets 17 and 19, and between 22 and 24. The latter area was particularly notable because it also contained some of the heaviest vegetation of the target line.

In the neighborhood of targets 27–28 was a vegetation called "sedge meadow" on the map. Turf hummocks were entirely absent here, or were only weakly developed. This type did not appear at all in ES 7. It was more extensively developed above ES 7 and between the two experimental sites than it was in ES 8. In the map area as a whole it covered about 6% of the surface. The substratum was primarily of aquatic moss and organic crust. The organic portion of the substratum ranged up to 4–5 cm thick over the diamicton. Until late in most summers the surface was saturated with seeping or slowly flowing water.

The target line of ES 8 crossed only a narrow part of this meadow; therefore the following list of its flora is derived from observations and collections upslope and around TCS 8B below the target line: *Equisetum arvense*, *Eriophorum callitrix*, *Eriophorum triste*, *Kobresia simpliciuscula*, *Carex scirpoidea*, *Carex parallela*, *Carex Bigelowii*, *Carex microglochin*, *Carex misandra*, *Carex atrofusca*, *Carex capillaris*, *Carex saxatilis*, *Juncus biglumis*, *Juncus triglumis*, *Juncus castaneus*, *Luzula spicata*, *Tofieldia pusilla*, *Salix arctica*, *Polygonum viviparum*, *Silene acaulis*, *Saxifraga oppositifolia*, *Dryas octopetala*, *Epilobium latifolium*, *Cassiope tetragona*, *Vaccinium uliginosum* ssp. *microphyllum*, *Euphrasia arctica*, *Pedicularis flammea*.

In some parts of the sedge meadow *Carex microglochin* was the predominant species. In others a mixture of *Carex saxatilis* and *Eriophorum callitrix* took its place. The woody plants were small and inconspicuous, mostly restricted to very low mounds of moss. A few species of lichens were common, notably *Cladonia pyxidata* and species of *Stereocaulon* and *Peltigera*.

Targets 29 and 30 were in the upper part of an area of relatively large, closely spaced turf hummocks similar to that described around target 36 in ES 7. All of the sedge meadow plants in the preceding list were absent from this area, and the hummocks were well clothed with various mixtures of *Vaccinium*, *Salix* and *Dryas*. The moisture regime also appeared to be about the same as that near target 36 in ES 7.

Targets 31–34 were mapped as occurring in "damp ground, with low hummocks, etc. . . .". The surface of the ground along the target line began to rise gradually at about target 29, and continued to do so through target 32 which was on the top of a large lobe-like terrace that dropped off steeply to the southward. Target 31 was in a vegetation of low turf hummocks, much organic crust, and a great deal of mortality among the vascular plants. As would be expected the transition to this condition from the preceding one of dense hummocks around targets 29 and 30 was gradual. There was a 4-meter gap between targets 31 and 32 instead of the usual 2 m. If the intervening target were there it would still have been in the vegetation of low hummocks and organic crust.

The three targets on the top of the lobe were in a small dry area that resembled in surface features and vegetation the "dry" sector on the eastern parts of the slope. The flora, however, suggested that it represented the slightly more moist phase of this element. Such species as *Carex scirpoidea*, *Poa alpina*, *Melandrium apetalum* ssp. *arcticum*, and *Cerastium alpinum* suggested this.

Vegetation on a steep, stony diamicton slope

The stony slope below targets 32–34 in ES 8 was composed of diamicton with pebble- and cobble-sized stones on its surface, and was relatively steep (ca 20–25°). Most of the ground was covered with organic crust, and all vascular plants were small and scattered: *Poa alpina*, *Trisetum spicatum*, *Carex scirpoidea*, *Salix arctica*, *Polygonum viviparum*, *Oxyria digyna*, *Cerastium alpinum*, *Silene acaulis*, *Draba lactea*, *Saxifraga oppositifolia*, *Saxifraga cernua*, *Dryas octopetala*. A striking feature of this area was the evidence of high mortality, especially among the willows. Approximately a third of the surface of the ground was covered by a "lace-work" of dead willow mats. The flora suggests the slightly more moist aspect of the "dry" elements in the eastern part of the map area.

Vegetation of bouldery-stony stream channels

Stream channels along the base of the trap cliffs appeared near the top of the slope and below the theodolite station of ES 8. The streams in these channels were intermittent, and flowed at different times during the season as water was supplied to them. A characteristic feature of their vegetation was a coating of bright green moss covering their beds and often some of the stones that lay in their immediate channels.

The vascular flora usually found scattered in the channels is as follows: *Equisetum arvense*, *Poa alpina*, *Carex scirpoidea*, *Salix arctica*, *Polygonum viviparum*, *Oxyria digyna*, *Cerastium alpinum*, *Minuartia biflora*, *Silene acaulis*, *Ranunculus pygmaeus*, *Draba alpina*, *Draba lactea*, *Arabis alpina*, *Saxifraga cernua*, *Erigeron humilis*. Nearly all of these plants are common in the district. One species, however, came close to being distinctive for this habitat. It was *Arabis alpina*, which was scarcely ever found anywhere else.

Vegetation on the trap cliffs and talus

In Table 3 are listed indiscriminately all the plants under "Talus" that were noted in crevices, on ledges, and on various parts of the talus itself. This group should no doubt be divided into at least two and probably three subgroups.

First was the dry gravelly slope of the talus itself, which had a sparse growth of relatively few species. Closely related to it was the flora and vegetation of the ledges and crevices on the trap cliffs above. However, a few species such as the ferns and *Sedum* were more or less characteristic of this habitat. Finally, at and near the base of the cliffs, where there was greatest protection from excessive insolation and a more reliable moisture supply, the more mesophytic species of the talus were found: *Betula nana*, *Potentilla Crantzii*, *Potentilla hyparctica*, *Campanula rotundifolia*, etc.

Summary of the vegetation at ES 7 and 8

The ES 7 and 8 map area thus contained a large proportion of the kinds of vegetation found in the Mesters Vig district. The nearly barren surfaces of diamicton, dry at the surface in late summer and with scattered *Dryas* and *Salix* mats, were widespread at low levels near the shores of the fjord. The hummocky meadow, with the sedge meadow vegetations related to it, was a common feature of the Mesters Vig landscape wherever a water supply was sufficient throughout the open season to support the growth of sedges and hummock mosses (*cf.* Raup, 1965 B). The dense cover of woody heaths with *Dryas* and *Salix* on relatively well-drained soils had only a small representation in the map area. It was likewise relatively limited in the district as a whole, confined to such places as the tops of till banks, the lower and lateral fronts of large gelifluction lobes and terraces, or the tops of ancient delta remnants. The "talus" vegetation in all its phases was to be found repeatedly throughout the district. Trap cliffs similar to that in the map area were on every hand in the Nyhavn and Labben peninsulas, with many large aprons of talus composed of sandstone, trap, and materials derived from glacial drift. Finally there was a kind of vegetation well represented in the map area that was widespread in the whole district. This was the organic crust mentioned many times in the preceding pages (see below).

Distribution of vegetative ground cover densities in the ES 7 and 8 area

The most detailed studies of vegetative cover density were made in the quadrats located on the map (Fig. 1) and described in an earlier paper (Raup, 1968). Based on these were about 15 other estimates, equally representative of the types of vegetation and scattered over the diamicton slope.

Within any one of the vegetation types mapped the coverage of the ground by vascular plants varied widely. The extent of these variations was noted in the general description of the vegetation and need not be repeated here. The vegetative density of each of the types was defined by the averages given in the above-mentioned general description. Figure 20 shows a graph comparing these averages.

Coverage remained low throughout the two "dry" vegetations (10–17 %), but adequate moisture in the organic crust area increased it

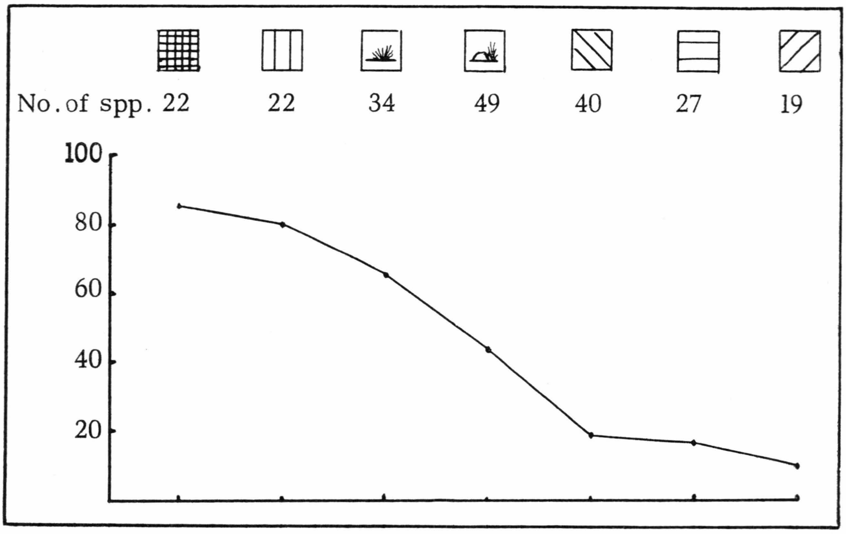

Fig. 20. Comparison of average percentages of ground surface covered by vascular plants in vegetation types on diamicton slope, ES 7 and 8.

only 2 %. Then began a rapid rise which continued with only minor abatement to the densely aggregated turf hummocks and an average coverage of 80 %. But in the latter situation the moisture supply was less than in the areas of sedge meadow and hummocky meadow. In the still more dense heath tundra the moisture supply was even less than under the turf hummock vegetation. Thus the vegetation reached only medium coverage density (43 %–65 %) under conditions of greatest moisture. At medium to low moisture it could reach its greatest cover densities (80–90 %), but it could also remain at low densities (less than 20 %).

Distribution of species in the ES 7 and 8 map area

The distribution of species in the ES 7 and 8 map area will be presented primarily in two ways. The first will be in terms of the simple presence or absence data given in Table 3. The second will incorporate ocular estimates of species frequency made at study sites within the vegetation map units of the area. Emphasis will be placed upon the seven vegetation types intercepted by the ES 7 and 8 target lines on the diamicton soils of the slope east of the talus and trap cliffs. Of the 88 species of vascular plants known to occur in the whole map area, 71 were recorded in the seven vegetation map units intersected by the target lines.

An analysis of species frequency distribution in the map area may be made from the presence-or-absence data given in Table 3. Here the

Table 4. *Distribution of species in the ES 7 and 8 map area with respect to their occurrence in varying vegetation types and area sizes.*

	Total species in map area		
	No. of spp.	%	Av. % of map area
Present in 10 veg. types	3	3.4	100
" " 9 " "	2	2.3	99
" " 8 " "	2	2.3	93
" " 7 " "	4	4.5	85
" " 6 " "	4	4.5	67
" " 5 " "	11	12.5	51
" " 4 " "	3	3.4	49
" " 3 " "	11	12.5	25
" " 2 " "	15	17.0	22
" " 1 " "	33	37.5	6
Totals	88	99.9	

distribution of species among all ten vegetation map units is given. Table 4 shows the numbers of species (and percentages) found in all of the vegetation types, then in nine of the types, then in eight, and so on down to one. It also gives the approximate average percentage of the total map area occupied by the group of species involved in each case. This was obtained by averaging the map unit areas for the individual species in each of the groups indicated in the table.

A striking aspect of this table is the trend of increase in the number of species from those present in all vegetation types (3) to those present in only one (33), accompanied by a parallel decrease in the average areas the species occupy. Those wide-ranging through the vegetation types, occupying eight-ten of them, could be expected to appear in types with both large and small areas, and they occupied between 90 and 100 % of the 2.2 hectares of the map area. But the 33 species (37.5 % of the flora) appearing in only 1 type each were restricted to vegetation map units that averaged only 6 % of the total area. Twenty-four of the 33 were found in one or another of two types ranging in area from 4 to 6 % of the total, while the remaining nine were scattered through five types only one of which exceeded 16 % of the total and three measured 1 % each.

To produce Fig. 21 the total number of species present in each of the vegetation types represented along the target lines was divided by the total number in all of these types (71), and the quotient expressed

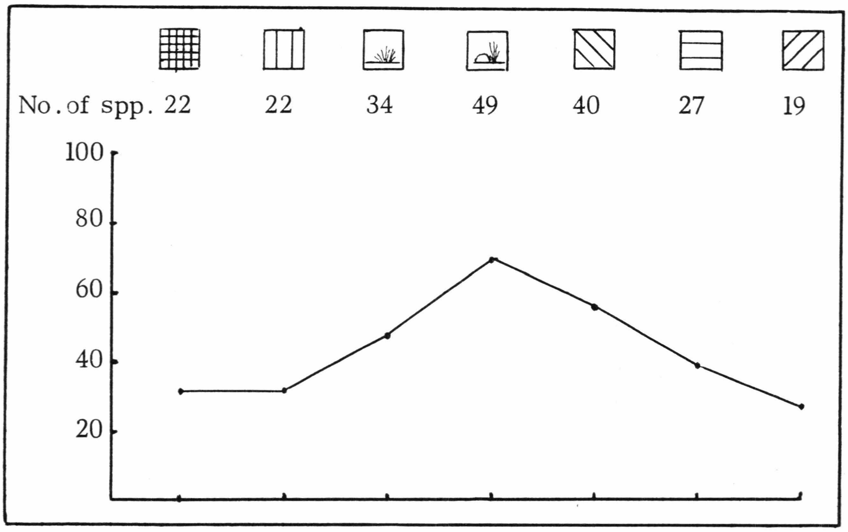

Fig. 21. Percentage distribution of 71 species among vegetation types on diamicton slopes, ES 7 and 8.

in percentages. It should be noted that targets 39 and 40 in ES 7 were located on the talus, and are therefore eliminated from consideration. The graph shows low frequencies of species occurrence on the "dry" sites in the eastern parts of the diamicton slope where the ground cover was exceedingly sparse, and again in the moist to wet areas in parts of the lines where some of the most dense vegetation occurred. The largest numbers of species were in the hummocky meadows and in the damp to wet organic crusts, where the vegetation was sparse to intermediate in density.

In Fig. 22 the species in each of the above seven vegetation types were first grouped into three classes of relative abundance based upon ocular estimates made at study sites within the types. The first group consists of plants that were abundant on the diamicton slope as a whole, or common and locally abundant. The second group, though they may have been locally common here and there, was of occasional occurrence over the slope. The third group contains the small number of species that were genuinely rare in the map area, plus another small group that in a few places were noted as occasional. The numbers of species in each of these three groups in each vegetation type were then divided by the total numbers of species in the types, and the quotients expressed in percentages.

The most striking feature of Fig. 22 is the contrast between the curves for common to abundant plants on one hand, and rare to locally occasional plants on the other. The former showed relatively high per-

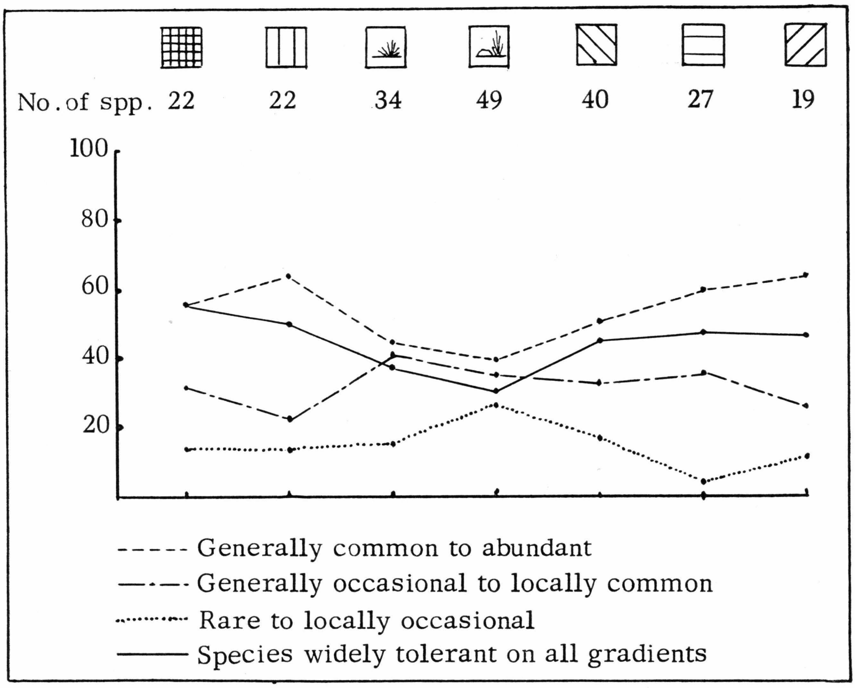

Fig. 22. Percentage distribution of frequency of 71 species among vegetation types on diamicton slope, ES 7 and 8; also percentage distribution of 22 widely tolerant species.

centages in the dense vegetations of heath tundra and turf hummocks at one extreme, and in the very open vegetations of the "dry" sector at the other. They reached their lowest percentages in the sedge and hummocky meadows which were the wettest areas of the slope, and had vegetation of intermediate density. The rare to locally occasional species showed their highest percentages in the hummocky meadow, one of the wettest areas, and the vegetation with the largest flora. They had their low percentages in the very dense and very open types, where the common to abundant species showed their high percentages. Generally occasional to locally common species were intermediate, but their curve trends slightly upward in the sedge and hummocky meadow vegetations.

Some further aspects of Fig. 22 will be discussed later. One of these is the solid line, which connects the percentages of species in each vegetation that are widely tolerant on all of the environmental gradients studied. It has been noted elsewhere (Raup, 1968) that there is a close relationship between abundance and wide tolerance of variation on these gradients. The similarity of trends in the curve for wide tolerance on this slope and in that for common to abundant plants is evidence of this.

Another aspect to be discussed later is the distribution of tolerance percentages in the turf hummock vegetation, which appears to be inconsistent with reality due to sampling limitations.

Behavior of species at ES 7 and 8 with respect to their tolerance of variation in vegetative coverage of the ground, soil moisture, and physical disturbance

Introduction

Basic data for the following analyses were published in the descriptions of the flora of the Mesters Vig district (RAUP, 1965 A), and summarized in a later paper (RAUP, 1968). The reader is referred to these papers for statements of the methods by which the data were obtained and organized. Only a small proportion of the species generally rated as rare in the Mesters Vig district as a whole were found in the ES 7 and 8 area. This had the effect of raising to a relatively high percentage in the map area the species that had frequency ratings of common or greater. It has already been pointed out that there is a clear relationship between relative abundance and the breadth of tolerance displayed by the species on various environmental gradients such as moisture, physical disturbance and vegetative coverage of the ground (GELTING, 1934; RAUP, 1968). In general the species with the wider tolerances of variation in the gradients are the most common and widespread in the tundra landscape (see Fig. 22). Therefore it is to be expected that the 88 vascular plants of the ES 7 and 8 map area will show, when compared to the flora of the district at large, relatively higher percentages of wide tolerance on all the gradients, and lower percentages of narrow tolerance. This indeed proved to be the case, as shown in Fig. 23. It is further emphasized by the facts that all 22 of the species rated as widely tolerant on all of the environmental gradients (RAUP, 1968) were present in the map area, and only three of those rated as narrowly tolerant on all gradients.

If the assumption is correct that the presence and success of the species is determined by the impact of the various environmental factor complexes operating within the ranges of the various inherent tolerances of the species, then one can assume further that general site conditions in the ES 7 and 8 map area do not permit most of the more narrowly tolerant plants to survive there. In short, they have "sorted" the flora of the Mesters Vig district. They permit plants to grow there that have relatively wide tolerances of variation in the amount of ground coverage they can live in, the amount of moisture or desiccation they can withstand, and the amount of physical disturbance their roots or underground stem systems can survive.

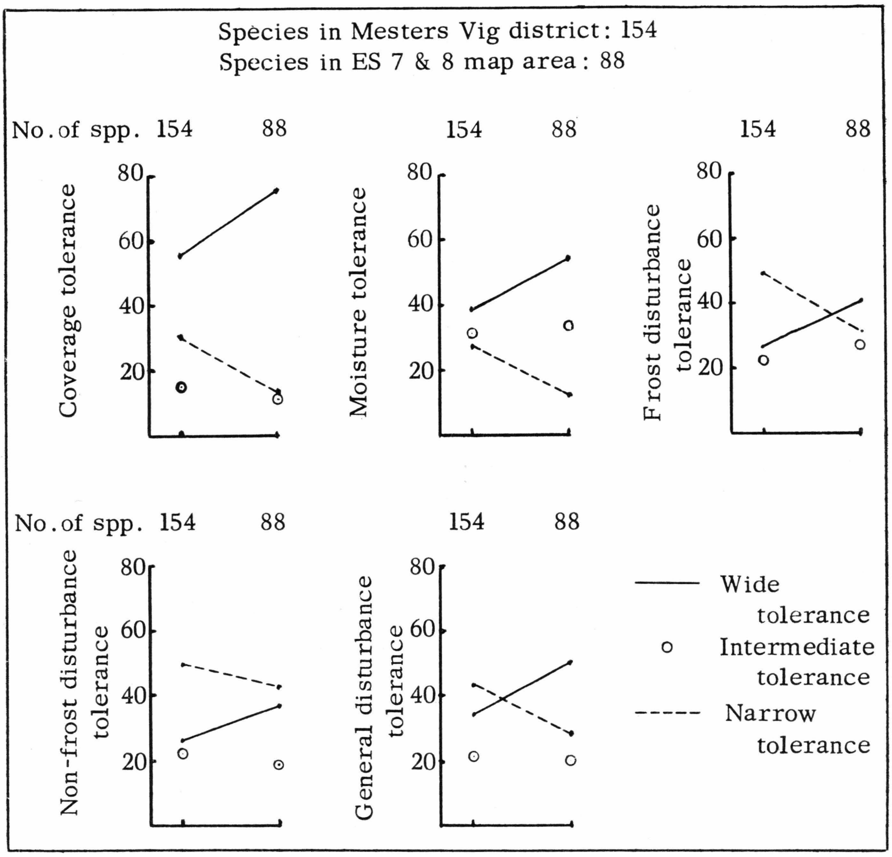

Fig. 23. Comparisons between percentage distributions of tolerance among 154 species in Mesters Vig district and among 88 species in ES 7 and 8 map area.

There were, however, distinct differences of site and vegetation within the map area. These were documented by the material accumulated for the map, and by geomorphic studies (Washburn, 1967). It will be useful to analyze the various elements of the vegetation of the map area in terms of species tolerance ratings.

It was proposed earlier in the present paper that species widely or narrowly tolerant on all the gradients used were not acceptable for comparative studies among the vegetation types. Therefore the following analyses are based only on the behavior of definitive species—those that show something less than universally wide or narrow tolerance in the Mesters Vig district as a whole.

Behavior of species on the coverage gradient

In the vascular flora of the Mesters Vig district as a whole 55.2 % of the species were rated as widely tolerant on the coverage gradient,

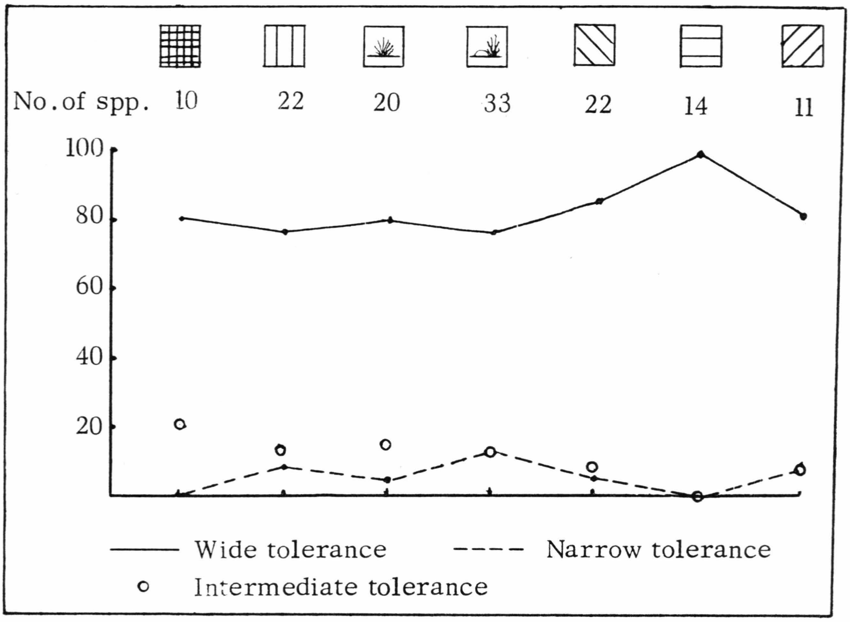

Fig. 24. Percentage distribution of coverage tolerance in species among vegetation types on diamicton slope, ES 7 and 8.

29.9 $^0/_0$ as narrowly tolerant, and 14.9 $^0/_0$ as intermediate (*cf.* Fig. 23). By this is meant that the widely tolerant species were growing in coverage densities ranging through more than two-thirds of the 90 $^0/_0$ cover recognized as possible in the Mesters Vig landscape. Narrowly tolerant species were those found in only one-third of the possible range or less. Species having intermediate tolerance were found in more than one-third of the range, but in not more than two-thirds. These estimates of tolerance give no indication of the probable preference of the species for one or another density.

In contrast to the above figures the 88 species in the ES 7 and 8 map area showed 76.1 $^0/_0$ widely tolerant on this gradient, only 12.5 $^0/_0$ narrowly tolerant, and 11.4 $^0/_0$ intermediate. The contrast is equally striking when the analysis is restricted to definitive species at the scene of the instrumental studies on the diamicton slope (Fig. 24). In none of the vegetation types did the wide tolerance percentages fall below approximately 75 $^0/_0$, and the narrow tolerances did not rise higher than about 13 $^0/_0$. Thus the site as a whole, particularly the diamicton slope, appears to have restricted the flora mainly to species especially capable of growing in both dense and very open vegetation. The proportion of these was so great that any variation they may show among the types of vegetation will be small.

Table 5. *Distribution of species in the ES 7 and 8 map area showing interrelations between their occurrence in varying numbers of vegetation types and their occurrence in "wet" and "dry" sectors of the map area.*

	Present in both "wet" and "dry" elements		Present in "wet" elements only		Present in "dry" elements only	
	No. of spp.	%	No. of spp.	%	No. of spp.	%
Present in 10 veg. types	3	10.0				
" " 9 " "	2	6.7				
" " 8 " "	2	6.7				
" " 7 " "	4	13.3				
" " 6 " "	4	13.3				
" " 5 " "	7	23.3	4	10.8		
" " 4 " "	3	10.0				
" " 3 " "	2	6.7	8	21.6	1	4.8
" " 2 " "	3	10.0	8	21.6	4	19.0
" " 1 " "			17	45.9	16	76.2
Totals	30	100.0	37	99.9	21	100.0

Behavior of species on the moisture gradient

Sectors of the target lines in ES 7 and 8, and elements of the vegetation on the diamicton slope have been referred to repeatedly as "dry" and "wet". With this simple division of the map area the presence or absence data in Table 1 can be sorted into three groups of species: 30 (34.1 %) were seen in both "dry" and "wet" vegetational elements; 37 (42.0 %) were in "wet" elements only; and 21 (23.9 %) were in "dry" elements only. The general distribution of these species among the 10 vegetation map units is shown in Table 5.

The 30 species present in both "wet" and "dry" vegetations were fairly evenly distributed among the nine possible types. However, 22 of them (73.3 %) were found in five or more of the types, these occupying on the average over half the total map area. In sharp contrast, 17 (about 46 %) of the 37 species found only in the "wet" elements of the vegetation were seen in a single type each, and 16 of the remaining 20 in 2 or 3 types each. Four were seen in 5 types, but none with any greater spread in the vegetation. Thus about half these plants appeared to be restricted to approximately 6 % of the map area, and all but four of them to 25 % of the total area or less.

(The dense heath tundra around targets 37–38 in ES 7 is here considered "wet" although it was placed in the "dry" series by WASHBURN (1967) on the basis of its being well drained and associated with generally dry surface soil. The plants, however, were mostly rooted in mosses and turf that retained some moisture even in very dry summers).

Even greater contrast is shown by the 21 species found only in the "dry" vegetational elements. Sixteen of them (76.2%) were seen in one vegetation type each, four in two types each, and one in three types. Thus nearly three-quarters of them were in types that occupied on the average only 6% of the land surface of the map area, and the remainder were on about 25% of the area.

A note of explanation is essential for analyses involving the talus vegetation with respect to "dry" vs. "wet" elements. Fifteen of the 21 species limited to the "dry" elements were found only on the talus or cliffs. The remaining six were seen only on the dry eastern parts of the diamicton slope. Among the species occurring in both "dry" and "wet" elements these proportions were reversed. About two-thirds of these species were seen on the talus and cliffs as well as on the diamicton slope, while the remainder were restricted to "dry" and "wet" elements on the diamicton.

The preceding analysis suggests that there were among the species of the map area two major levels of tolerance of variation in the moisture gradient, and probably one minor one. The species capable of living in both "wet" and "dry" sites can be regarded as widely tolerant, and those restricted to one or the other as having narrow or intermediate tolerance. Table 5 suggests that species limited to wet sites may include some intermediates.

Figure 25 results from the application of general moisture tolerance ratings to the seven vegetation types intercepted by the target lines of ES 7 and 8.

The highest percentages of wide tolerance were clearly in the drier parts of the moisture gradient, and the lowest in the sedge meadows and hummocky meadows. The easterly parts of the diamicton slope were excessively wet for a short time in spring, during and for a short period after the melting of the winter snow. Plants that survived there had to withstand both this spring flooding and the excessive drought that developed later in the summer. The above figures suggest that those with such wide tolerance made up most of the small flora found here.

Nearly as high percentages of wide tolerance were in the turf hummock and heath tundra vegetations, where the cover was relatively dense and the soil moisture, though low in quantity, had a quite different seasonal regime. Although narrowly tolerant plants were absent here, species with intermediate sensitivity were relatively more numerous.

Behavior of species on the disturbance gradients

Although "wet" and "dry" sectors of the moisture gradient were rather obvious in the field in most parts of the ES 7 and 8 map area,

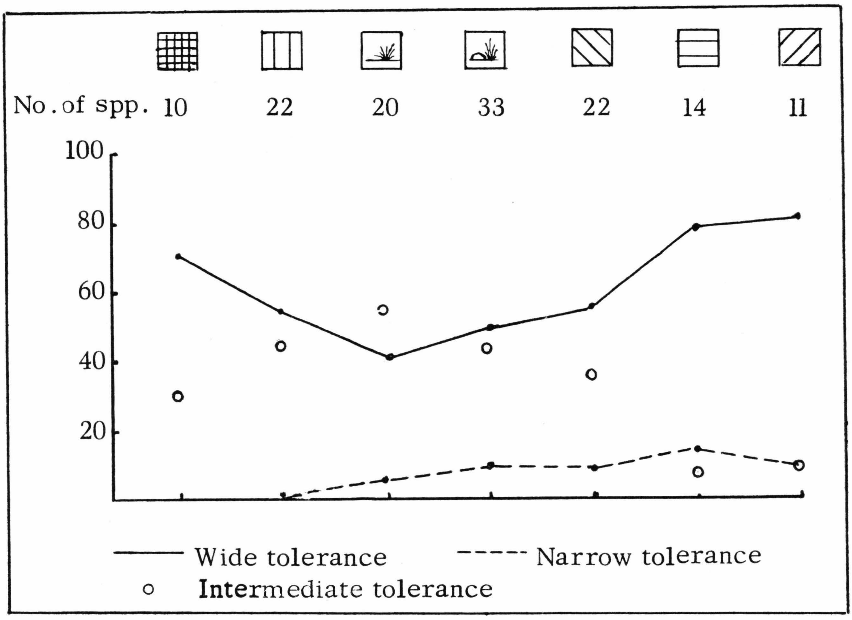

Fig. 25. Percentage distribution of species tolerance on moisture gradient in vegetation types on diamicton slopes, ES 7 and 8.

sectors of equal clarity on physical disturbance gradients were not immediately obvious in the field. A few small active gelifiuction lobes were present in the "wet" sectors as described above, but their effects were localized and difficult to evaluate in terms of total vegetation map units. Evidence of downslope movement in the diamicton soils was on every hand, as well as evidence of frost heaving, but until there was proof that these were actually "processes in being", and until they were quantified at least as to relative rates, they could not be properly correlated with vegetations.

In the course of the Mesters Vig studies parallel observations were made of differences in the kind and relative intensity of physical soil disturbance, and in the reactions of plants to the disturbance. These observations were made in situations where the activity of geomorphic processes was obvious, and where gradients of intensity could be seen. It soon became clear that while many species were relatively indifferent to disturbance of their root-soil relationships, others appeared to be sensitive to them. At least they were not found where physical disturbance in the root zone of the soil could be identified.

As in the case of the moisture and coverage gradients, all vascular species in the Mesters Vig flora were given ratings in terms of their sensitivity to physical disturbance in the soil (Raup, 1968, Table 1, Figs. 3, 11, 12). The terms "wide", "intermediate", and "narrow tolerance", used with respect to the moisture and coverage gradients, give no indication of the preferences of species within the gradients; *i. e.*, a narrowly tolerant species might be restricted to dry sites or to wet sites. In the case of the disturbance gradients, however, there is a difference in the meaning of these terms in that with very few minor exceptions (principally strand plants) the three terms are equivalent, in the order given above, to the behavior of the species on unstable, medium, and stable soils.

The behavior of each species was analyzed with respect to disturbance arising from two causal complexes: frost action and all other geomorphic processes affecting the surficial horizons of the soil. It was recognized that no precise boundary between the two could be drawn in terms of the physical processes involved, for in such frost-induced processes as frost creep there are elements of nonfrost creep, and in earthflow there are some of the disturbance qualities of gelifluction and frost creep. In spite of these imperfections of definition the two aspects of behavior are maintained because they express observed differences among the plants, however unclear they are in many cases. Reference to Table 1 in RAUP, 1968, will show many species rated as widely tolerant of frost-induced disturbance while they are more or less sensitive to nonfrost disturbance; the reverse is likewise true.

An attempt was also made to rate the species on a general disturbance gradient combining frost and nonfrost tolerance ratings (1968, Fig. 13). In the following analysis of the ES 7 and 8 vegetation the various types will be first discussed in terms of their relation to frost and nonfrost disturbance; then the general disturbance gradient will be used. The analysis will be limited to the seven vegetation types on the diamicton slope, and to the 71 species represented in them.

Frost disturbance gradient

Figure 26 is a chart suggesting probable responses of species distribution to physical disturbance due to frost action of various kinds. A notable feature here is the relatively high percentage of intermediates, which were most abundant in the "dry" sectors in the eastern parts of the slope. The most striking features, however, are in the percentage values for wide and narrow tolerances. The largest proportions of widely tolerant species, and the smallest percentages of narrowly tolerant, were in the damp to wet organic crusts and in the heath tundra. In the wettest heavily vegetated—types—turf hummocks, sedge and hummocky meadows—widely and narrowly tolerant ranged between 27 % and about 36 %. Slightly more of the former than the latter were in the turf hummocks, and vice versa in the hummocky meadow. In the sedge meadow they

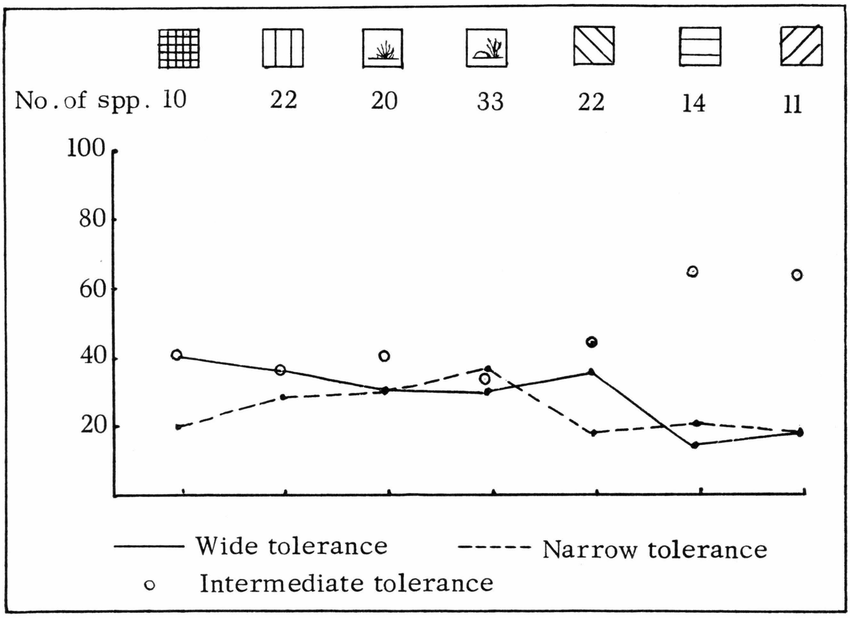

Fig. 26. Percentage distribution of species tolerance on frost-induced physical disturbance gradient in vegetation types on diamicton slope, ES 7 and 8.

were present in about equal numbers. In the "dry" sectors the pattern was quite different, for here the proportions of widely tolerant species were lower than they were in the meadows and hummocks. Strangely, however, the narrowly tolerant species were also low in percentage. The dual nature of the more heavily vegetated, wet sites appears to be reflected in the approximately equal numbers of widely and narrowly tolerant species in them. This will be discussed further in another part of the paper. The preponderance of widely tolerant species in the heath tundra suggests that frost heaving was more injurious there than elsewhere in the "wet" sector.

Nonfrost disturbance gradient

Figure 27 is a graph comparing the tolerance ratings of definitive species on the gradient of non-frost induced disturbance. Striking features of this graph are, first, the relatively high percentages of narrowly tolerant species in vegetations of the "wet" sectors of the slope, coupled with low proportions of widely tolerant species; and second, the reversal of these proportions in the drier parts of the "dry" sectors. Intermediate tolerances on this gradient are consistently low, all of them ranging between 18 % and 28 %.

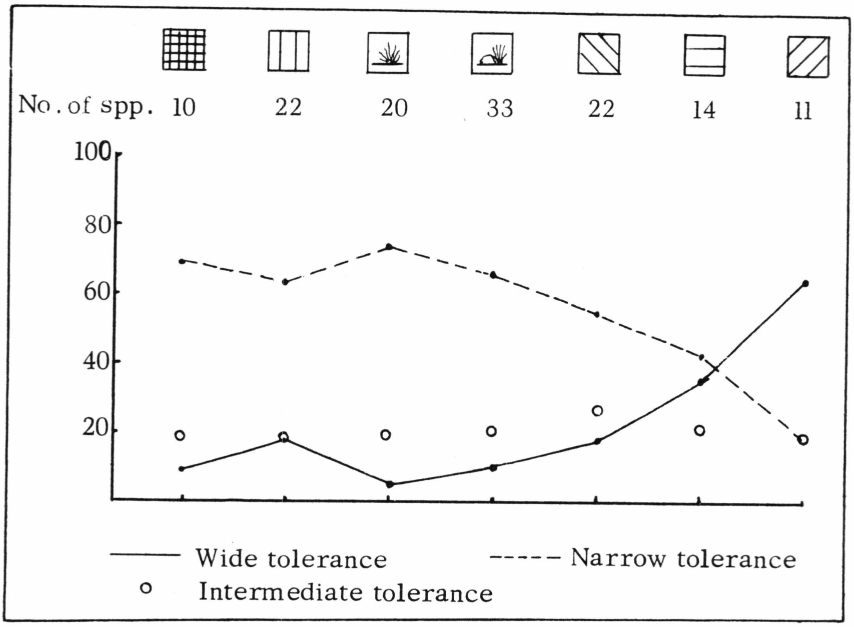

Fig. 27. Percentage distribution of species tolerance on nonfrost-induced physical disturbance gradient in vegetation types on diamicton slope, ES 7 and 8.

General disturbance gradient

When the tolerance of physical disturbance due to various causes is merged and plotted for the 71 species on the diamicton slope in ES 7 and 8 as in Fig. 28, the percentages of wide tolerance relative to those of narrow tolerance are higher on the average than when the causal complexes are plotted separately. The wide tolerances range approximately between 30 % and 73 % while the narrow tolerances range between 9 % and about 36 %. Vegetation types having the highest proportions of their floras capable of withstanding intense physical disturbance of some kind are in the driest eastern sector of the slope (*Dryas* — *Carex nardina*). Those having the smallest proportions of plants widely tolerant of general physical disturbance are the sedge and hummocky meadows and the heath tundra. Vegetations with medium proportions of widely tolerant species are in the slightly more moist phase of the "dry" sector (*Dryas* — *Carex* — *Polygonum*), in the damp to wet organic crusts, and in the turf hummocks.

The proportions of narrowly tolerant species are the reverse of the above in the "dry" sectors, in the organic crusts, and to some extent in the turf hummocks. Otherwise they are not much different from those of wide tolerance. Thus they reflect again the dual nature of the wet, more heavily vegetated sites.

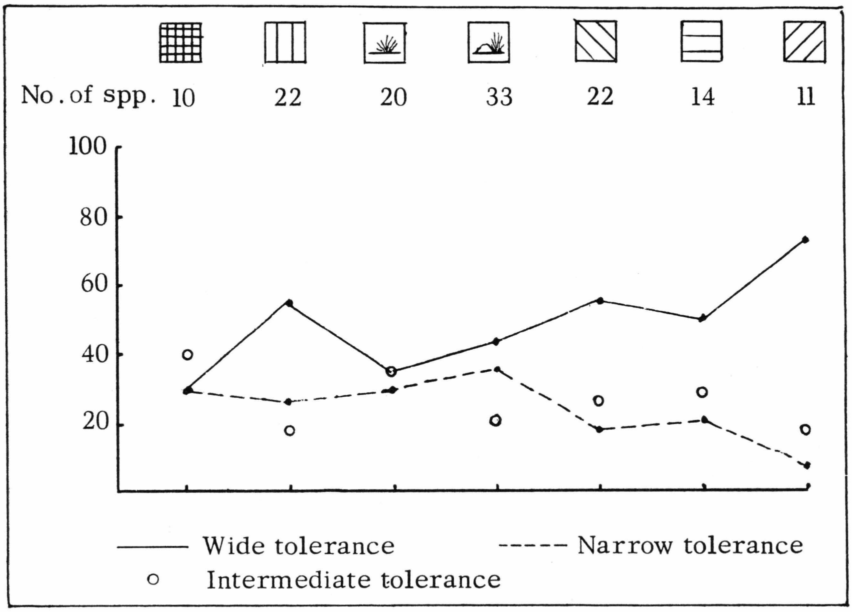

Fig. 28. Percentage distribution of species tolerance on general physical disturbance gradient in vegetation types on diamicton slope, ES 7 and 8.

Discussion of species tolerance

On the coverage and moisture gradients (Figs. 24, 25) the higher percentages of widely tolerant plants suggest sites in which variability in coverage and moisture supply was likely to be relatively large for considerable periods of time. The fact that in general there were higher percentages of species widely tolerant on the coverage than on the moisture gradient suggests that variation on the former may have been greater than on the latter.

On the disturbance gradients (Figs. 26, 27, 28) the higher percentages of narrowly tolerant species suggest the physically more stable sites. In contrast the lower percentages suggest the physically more unstable sites. Further discussion of these graphs will be found below.

The distribution of root and underground stem structures among species in the ES 7 and 8 area

Nearly all of the roots, and all of the underground stems, of the plants growing on the diamicton in the ES 7 and 8 map area are in the uppermost 10–15 (20) cm of the soil. Where the substratum is largely organic, as in the turf hummocks, most of the roots are in the turf though a few penetrate to the mineral soil beneath. Soil factors limiting to the growth of plants, such as desiccation and physical disturbance, are to be looked for in the horizon of root concentration and in the surface materials where germination and establishment must take place.

Evidence that plants are damaged or destroyed by one or another or by combinations of these factors is on every hand. Mortality among species is high in some sites, with some plants killed by desiccation in excessively dry summers, or heaved out of the soil by frost, or partially overturned by moving soil. Still others are dead or in varying states of decline due to damage to their root systems (see RAUP, 1965 B, for discussions of injury to root systems of *Salix arctica*).

The vascular plants of Northeast Greenland have three main kinds of underground parts. First are plants supplied with many fibrous roots. In a few species these roots are more or less fleshy, but usually they are threadlike and bunched. Second are plants with taproots. Many of these are carrotlike, with a few small fibrous rootlets rising from them. Others are long, woody roots, sparingly branched and with few or many small thread-like rootlets attached to them. Third are the plants with true underground stems or "rhizomes". These stems, simple or branched and with a few fibrous roots attached, trail just beneath the soil surface and send up new growth each year from terminal buds. In the vascular flora of the Mesters Vig district as a whole, only about 16 % of the species have well-developed underground rhizomes. The remaining 84 % are about equally divided between species with fibrous roots and taproots.

It is useful to explore the relationship between the form and structure of these underground systems and the physical factors affecting the soils in which they live. In order to do this a few minor modifications were made in the classification of the systems (*cf.* RAUP, 1968). Certain rhizomatous species such as *Carex scirpoidea* and *Hierochloë alpina* have very short rhizomes and numerous fibrous roots. Thus they behave like caespitose, fibrous rooted plants, and they have been placed in that group. Other species, which on structural grounds are rhizomatous or stem tuberous, behave more like taprooted plants. These are *Cystopteris fragilis*, *Woodsia glabella*, and *Polygonum viviparum*.

Another group of modifications arises from the fact that some species have means of vegetative propagation. The propagation is accomplished by runners (above or below the surface of the ground) and/or by rooting at the nodes of the stems. The total number of species in the Mesters Vig flora that achieve it by one means or another is not great (not above 27). Nonetheless, species that have this capacity probably have a definite advantage in situations where physical disturbance is a critical factor, because the spatial scale of this factor is commonly commensurate with the scale of vegetative propagation of

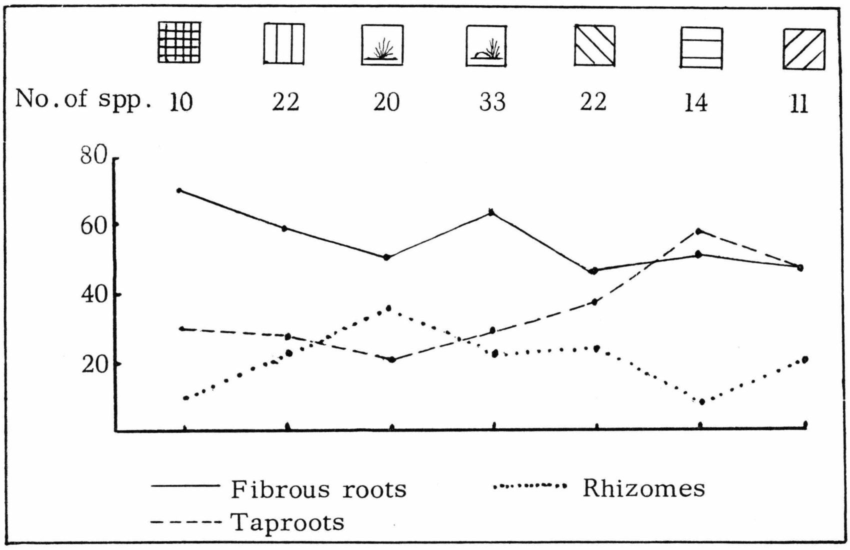

Fig. 29. Percentage distribution of fibrous roots, taproots, and rhizomes in vegetation types on diamicton slope, ES 7 and 8.

the plants. Death of a parent plant could leave one or several progeny thriving.

Therefore in working out percentages of taprooted, fibrous rooted and rhizomatous species in each vegetation type on the diamicton slope in ES 7 and 8 (Fig. 29), the species having above ground means of vegetative propagation have been "weighted" by having their numbers doubled, thus giving them higher percentages. Species having underground runners were not weighted in this way because these runners are subject to the same kinds of injuries as the roots and rhizomes.

It is to be expected that species widely or narrowly tolerant on all the gradients are the least acceptable for comparative studies of root and rhizome distribution. Figure 29 was prepared in the same way as in the studies of the distribution of tolerance ratings, by subtracting the numbers of non-definitive species from the floras of the vegetation types. The proportions of fibrous roots, taproots and rhizomes in the turf hummock vegetation based on species found only on the target lines show the same anomalies that were apparent when this figure was used in comparative tolerance percentages. Therefore the adjusted number of species among the turf hummocks was used here as elsewhere (see below).

Probably the most striking aspects of the graph in Fig. 29 are the curves for taproots and rhizomes. The former reach their lowest percentage in the wettest part of the slope, and their highest percentages in the dry sectors. Although the organic crust areas had a relatively large moisture supply, taprooted plants were relatively more numerous there than anywhere else on the slope except in the dry sectors. These observations suggest that plants with taproots were particularly successful in surviving desiccation, and to some extent in surviving frost heave. Rhizomatous species, on the other hand, reached their highest percentages in the wetter parts of the slope, and were proportionately less numerous in the drier sectors. Definitive fibrous rooted species were consistently more numerous than those with taproots except in the dry sectors, where the two groups showed approximately equal proportions.

Summary and discussion of ES 7 and 8

Having made comparative studies of the vegetation and of various site factors in the ES 7 and 8 area, attempts will now be made to summarize and relate the two bodies of information.

Dryas – Carex nardina

This type is characterized by the lowest ground coverage by plants seen anywhere on the slope (av. approx. 10 %) (Fig. 20). Likewise it has the smallest proportion of the 71 species of vascular plants known to occur on the whole slope (Fig. 21). Definitive species having taproots are about as numerous as those with fibrous roots (Fig. 29), and those with underground rhizomes are well represented relative to those in most of the other types of vegetation.

The smallest differences in tolerance of variations seen among the plants of the diamicton slope were on the gradient of vegetative coverage of the ground. Most of the species were widely tolerant ranging between about 77 % and 100 % in the various vegetation types. Species with narrow tolerances all appeared at levels of 13 % or less (Fig. 24). The relatively high proportion of narrow tolerance in the hummocky meadow, and of wide tolerance in the "dry" sectors and the organic crust areas may have some significance.

Moisture tolerance distribution on the diamicton slope shows greater variation (Fig. 25). The *Dryas* — *Carex nardina* had the highest percentage of species widely tolerant on this gradient, approached only in the *Dryas* — *Carex* — *Polygonum* and in the heath tundra. Species with narrow and intermediate tolerances made up approximately 10 % each.

With respect to tolerance of physical disturbance in the soils the definitive species in the *Dryas* — *Carex nardina* vegetation showed a striking difference of behavior on the frost andnon frost gradients. On the frost disturbance gradient the proportions of widely and narrowly tolerant species were about the same (approx. 18 %). But on the nonfrost gradient there were about three times as many widely as narrowly tolerant species.

Surface soil moisture at mid-August in the *Dryas — Carex nardina* type was lowest of any on the slope except under the heath tundra at the base of the talus (Figs. 3, 4). The surface soil became dry and brittle in late summer and remained so until freeze-up except for an occasional early snow or drizzling fall rain. Analyses in mid-summer, and the presence of a few more hygrophytic species, indicated that the lower parts of the slope such as the eastern part of ES 8 may have retained slightly more moisture in the dry season than the upper parts. As noted by WASHBURN (1967), however, and described elsewhere in the present paper, the early summer moisture supply to the eastern part of ES 8 was much greater than to the eastern part of ES 7. Though both were considered "dry" sectors of their respective experimental sites, and had essentially the same vegetation, they had quite different moisture regimes.

The frost heaving of cone-targets was relatively insignificant in the *Dryas — Carex nardina* type, averaging less than 1 cm (Fig. 7). Downslope movement of these targets differed widely as between ES 7 and ES 8. In the former the average was about 4 cm (Fig. 9), while in the latter it was about 17 cm (Fig. 10). The figures for total jump (Figs. 11, 12) show the same contrast between ES 7 and 8, with a movement in the latter over four times greater than in the former.

In summary, the physical habitat of this vegetation was one of extreme desiccation in late summer following a period in the spring and early summer when the soil was at or above its liquid limit. This early period varied in length from a few days on the upper parts of the diamicton slope to 2–3 weeks on the lower parts. In both cases progressive drying took place from east to west. Judging by the behavior of the targets, frost heaving of objects in the uppermost 10–20 cm of the soil appears not to have been a significant disturbing factor. On the other hand, wherever the diamicton was supplied with enough water to keep it at or above liquid limit for an appreciable length of time, the flow motion of gelifluction may have become a disruptive factor. It is probable that the lower third or half of the area mapped as *Dryas — Carex nardina* was affected by this motion.

Vascular plants capable of withstanding the rigor of such habitat must have a "built-in" tolerance of wide variation on the moisture gradient. Some of them were the obvious "xerophytes" of the Arctic that are characteristic of dry sites, but others, such as *Salix arctica*, have more often been called "hygrophytes". It probably is significant that a relatively high percentage of them had taproots which served to carry them through the dry periods or keep them alive until they could rehabilitate themselves after injury. Although injury from frost heaving in the soil seemed not to menace them seriously, they were subject to physical disturbance each year by differential flow that could have been disruptive.

The plants in this type had the required wide tolerance on the moisture gradient. On the disturbance gradients they appeared to be somewhat selective, for they showed a relatively low percentage of wide tolerance on the frost disturbance gradient (where less was required of them) coupled with about the same number of plants with narrow tolerance. The last two groups suggest a relatively low intensity of frost heaving. On the other hand the presence of a relatively high proportion of species widely tolerant of such nonfrost disturbance as gelifluction, coupled with a relatively lower proportion of species sensitive to this kind of disturbance, suggests that it had a much more significant influence on this vegetation than frost heaving.

The net result of the interplay of plants and site was a small flora restricted to species able to withstand, first, the seasonal extremes of moisture and desiccation, second, the gelifluction mobility of the soil, and third, probably to a minor degree, frost heaving in the soil.

Dryas – Carex – Polygonum

Average coverage of the ground by vascular plants in this slightly more moist phase of the "dry" sector of the diamicton vegetation was a few per cent greater than in the *Dryas — Carex nardina* type (Fig. 20), though it was still low (about 17 %). Most of the type was in shallow depressions and was characterized by organic crusts which, like the soil, became dry in late summer. About 38 % of the total flora of the slope was found in the type (Fig. 21). Species with taproots were relatively more numerous here than elsewhere on the slope (Fig. 29), and slightly outnumbered the species with fibrous roots. Plants with rhizomes were at their lowest proportion (ca 7 %).

Definitive species in this type were all widely tolerant on the coverage gradient (Fig. 24), and about 78 % were widely tolerant on the moisture gradient (Fig. 25). On the disturbance gradients they showed the same trends as those in the *Dryas — Carex nardina* vegetation, though with somewhat less pronounced contrasts in percentage distribution of tolerance groupings. There was the same trend toward a relatively low percentage of plants widely tolerant on the frost disturbance gradient (Fig. 26), and toward a relatively high percentage of plants widely tolerant on the nonfrost gradient (Fig. 27). However, the latter was somewhat lower than appeared in the flora of the *Dryas — Carex nardina* vegetation. Correspondingly similar proportions appeared among the plants with narrow and intermediate tolerances.

Reference to Figs. 3 and 4 indicates that the (1961) mid-August soil moisture conditions in the *Dryas — Carex — Polygonum* were only slightly wetter than in the preceding type. What was said above about seasonal regimes of soil moisture in the *Dryas — Carex nardina* vegetation applies here also. Although in both areas the soil became extremely dry in late summer, it was extremely wet for a relatively short period after snow-melt on the upper part of the slope, and for an appreciably longer period on the lower part. Reference to the map (Fig. 1) will show that in the area sampled by the target lines most of the *Dryas — Carex — Polygonum* type lay west of the slightly drier *Dryas — Carex nardina* type. Thus it lay in the direction of increasing moisture on the slope in general, and might be expected to be, in some aspects at least, a transition area.

The frost heaving of cone-targets in this vegetation type was only slightly greater than in the preceding (av. about 1 cm for all accepted targets, 1956–1964; see Fig. 7). The range was a little greater in ES 8 than in ES 7, as would be expected from the probably slightly greater amount of frost heaving in the spring at ES 8 (*cf.* Washburn, 1967). The difference in downslope movement that appeared between ES 7 and ES 8 in the *Dryas — Carex nardina* type appeared also here, but it was somewhat less pronounced (Figs. 9, 10). The same contrast is apparent in the figures for total jump (Figs. 11, 12). The lesser average movement in the *Dryas — Carex — Polygonum* type in ES 8 appears related to the shorter length of time the targets were exposed (*cf.* Washburn, 1967, Table B V). The targets in the vicinity of T 10, where the maximum downslope movement was recorded in the "dry" sector of ES 8, tended to be exposed about a week or ten days earlier than those from T 13 to T 17 where somewhat lesser movements were measured.

Comparing the physical habitat of this vegetation with that of the preceding type, there may have been slightly more moisture available, though not enough to change the major requirement that plants here must survive severe desiccation in late summer. A little more frost heaving was also apparent in the soils, particularly on the slightly more moist lower parts of the slope, but again the amount was not very great. Disturbance by downslope movement of soil was slightly greater in ES 7, but considerably less in ES 8.

Response of the vegetation to these minor changes in the form of slightly greater cover density (Fig. 20) and number of species (Fig. 21) is understandable. The small difference in the proportions of widely and narrowly tolerant species on the frost disturbance gradient, if significant at all, may be anomalous. One would expect more widely than narrowly tolerant plants because the small increase in moisture over that in the *Dryas — Carex nardina* type might produce a little more frost heaving. However, both types had dry soils in the autumn when heaving was most active, and there was very little heave of cone-targets anywhere in the "dry" sectors. But the prevailing summer desiccation was slightly alleviated, and the trends of the two tolerance curves may here be a reflection of this rather than of reactions to frost heaving. A higher percentage of plants narrowly tolerant on the nonfrost disturbance gradient and a reduction of species widely tolerant on this gradient may reflect a net reduction in gelifluction movement in this type from that found in the *Dryas* — *Carex nardina* (Fig. 27).

A question is raised by the fact that the percentage of species with taproots in this vegetation (57 %; cf. Fig. 29) exceeded that of the preceding type by about 10 %, though the moisture supply may have been slightly greater. In general there appears to be a better correlation between decreasing moisture and increasing taproot percentages than between the latter and other factors. Thus the slightly higher percentage of taproots in the *Dryas* — *Carex* — *Polygonum* type is somewhat anomalous, though the difference may be too small to be significant.

Damp organic crust vegetation

The range of variation in vegetative coverage of the ground in this type was somewhat greater than in the two preceding, but the average remained low (less than 20 %; see Fig. 20). The number of species was considerably increased, to about 57 % of all those occurring on the diamicton slope (Fig. 21). In this vegetation species with taproots were proportionately less numerous than in the preceding types (Fig. 29). From about 57 % in the *Dryas* — *Carex* — *Polygonum* vegetation they fell off to about 36 %. At the same time rhizomatous plants increased by about 15 %.

Reference to Fig. 25 shows that the species widely tolerant on the moisture gradient in this vegetation exceeded the narrowly tolerant by about seven to one. On the frost disturbance gradient relatively high percentages of widely tolerant plants appeared, and proportionately only about half as many narrowly tolerant species (Fig. 26). On the nonfrost gradient the percentage of definitive widely tolerant species dropped to about 18 % while that of narrowly tolerant plants reached nearly 55 % (Fig. 27).

It was noted in an earlier part of this paper that available quantitative data on soil moisture are unrealistic for this type (Fig. 3). Therefore an extrapolated figure was proposed for it (Fig. 4) based upon repeated field observations. Some free water was found on the surface in the middle and western parts of this vegetation on many of the occasions when it was visited. At other times it was either moist or muddy. The difference in moisture regimes between ES 7 and ES 8, pronounced in the eastern part of the latter and considerably reduced in the neighborhood of target 15, largely disappeared in the damp crust vegetation.

A primary feature of the damp organic crust areas was the intensity of cone-target heaving found in them (Fig. 7). The average for all measured target heaves in this type was considerably greater than that seen in any other vegetation on the slope. Downslope movement of targets, on the other hand, showed median values relative to other soils of the slope (Figs. 9, 10). The same was true of total jump (Figs. 11, 12).

Proceeding from east to west across the diamicton slope, the damp crust vegetation appeared to be the first in which desiccation did not become a serious restraint for the growth of plants. The soil was damp to wet throughout the summer and into the autumn. It was wetter in some years than others, and in general was progressively wetter in a westward direction. In theory the increased moisture, with its continuity, should result in much greater density of vegetation, but such was not the case. The average coverage was only about 2% greater than in the preceding vegetation of the "dry" sector. It might be suggested that time of exposure was a significant factor, but some parts of the damp crust vegetation at mid-slope between the target lines were among the first to be exposed in spring. The decline in proportion of species with wide tolerance on the moisture gradient suggests that moisture was not so restrictive as in the "dry" sector. The notable decline in percentage of taproots and the corresponding increase of rhizomes suggest the same things, for the plants here had less necessity for storage through a season of late summer desiccation.

The coincidence of a relatively high percentage of plants widely tolerant on the frost disturbance gradient with the intense frost heaving seen in this vegetation type was evident. Probably more significant was the coincident lower percentage of species more sensitive to frost heaving. This situation may be contrasted with the coincidence of very few definitive species that were widely tolerant of flow in the soil together with a median to high proportion of species narrowly tolerant of this kind of disturbance, and median values for actual movements of the targets (Figs. 26, 27). These proportions and contrasts suggest that the vegetation was fairly well adjusted to the intense frost heaving, the moderate downslope movement and the intermediate moisture that obtained in the site it occupied.

However, in spite of apparent adjustments of the vegetation to the site in the damp organic crust, the vascular plants succeeded in covering, on the average, only about 19% of the ground surface. It was in this type that recent mortality among the plants was most abundant and obvious. One can only surmise that though plants may have become established here the intensity of frost heaving, coupled with some flow, was periodically so great that they were badly injured or completely killed (see below for further discussion).

Hummocky meadow vegetation

Vegetative coverage of the ground increased sharply from about 19% in the damp crust areas to an average of about 43% in the hummocky meadows (Fig. 20). At the same time the number of species reached nearly 70% of all those known to occur on the diamicton slope (Fig. 21). Plants with fibrous roots were here much more numerous than those with taproots (Fig. 29), while the percentage of rhizomatous plants was about the same as in the damp crust vegetation.

Relative to the species in other vegetations on the slope, those in the hummocky meadow were low in wide tolerance and medium to high in narrow tolerance on the moisture gradient (Fig. 25). On the frost disturbance gradient they showed relatively high proportions both of species most sensitive to the disturbance and of species widely tolerant of it (Fig. 26). On the nonfrost disturbance gradient they showed a very low proportion of widely tolerant plants and a very high proportion of narrowly tolerant species (Fig. 27).

With respect to moisture (Fig. 3) the hummocky meadow was the wettest part of the slope according to the August field data collections. Moisture in the sedge meadow may have been closer to that of the hummocky meadow than the data indicate, for the sedge meadow was not sampled in an area of larger development. Free water was seen on the surface or seeping through the mosses or turf of the substrata in the sedge and hummocky meadows throughout most of the summer. It is probable that the mineral horizons of the soil remained at or near the liquid limit through most of the frost-free season. This varied, of course, from year to year, and from place to place on the slope, and from time to time within any one season (*cf.* WASHBURN, 1967).

Cone-target heave data suggest values varying from none to intermediate intensities depending upon whether the heaving was measured entirely in the organic horizons of the soil or in the underlying diamicton (see discussion of cone-target heave, and Figs. 5, 6, 7). Downslope movement of the targets indicated that the soils in this type were the most mobile of any on the slope. The average movement for all accepted targets in the five-year period was about 25 cm (Figs. 9, 10). The figures for total jump in ES 7 and 8 (Figs. 11, 12) also show maximum values in the hummocky meadow.

Assuming that root and underground stem habits are significant with regard to adjustment to moisture conditions, the plants of the hummocky meadow suggest by the proportionate numbers of species with fibrous roots, rhizomes, and taproots, that moisture, per se, was no problem to them (Fig. 29). Figure 25 suggests that plants sensitive to variations in moisture supply, being present here and in the sedge meadow in larger proportions than elsewhere on the slope, probably reflected the lower incidence of these variations that was known to exist. The relatively low proportion of plants widely tolerant of such variations also suggests it.

An apparent paradox appears when the disturbance factors are considered. Here, in soils with the most active downslope movement found anywhere on the slope, frost heaving that reached a median level of intensity, and an abundance of moisture, the plants exhibited an apparently inconsistent mixture of wide, intermediate and narrow tolerance on the disturbance gradients.

In the discussions of cone-target heaving and downslope movement of the soils it was proposed that, in effect, two habitats for vascular plants existed in the more heavily vegetated parts of the diamicton slope. By "more heavily vegetated" was meant the areas having vascular plant coverages of 20–90 % (mainly 40–90 %) and having an organic horizon 3–8 cm thick over the diamicton. These habitats were side by side or in vertical order. The plants occupying them may have been growing so closely together as to have their roots and stems intertwined. Further, there were intergradations between them.

The principal difference between these habitats was in their relative physical stability. Data from the cone-target heave measurements show that plants rooted in the organic horizons probably suffered very little or not at all from frost heaving unless some of their roots penetrated at least 15 cm beneath the surface. Most of those growing in the thick turf of hummocks were rooted almost entirely in this turf. Those in the inter-hummock channels, or in moss-sedge meadows interspersed among the hummocks, were on a relatively thin organic mat (3–4 cm) through which their roots penetrated and entered the diamicton. Some of these plants were subject to heaving. Probably the most extensively and deeply rooted plant on the slope was *Salix arctica*. Although it was growing on the hummocks, its roots entered the diamicton and may have extended 2–3 meters horizontally at depths of 10–15 cm beneath the surface of the organic soil.

Evidence from the movement and attitudes of the targets over the five-year period of observation, together with the continuity of much of the vegetation mat, indicated that the latter was not seriously injured by massive downslope soil movement. Thus, in spite of the mobile nature of the soils, and the amount of frost heaving shown by the targets, the hummocky meadow proved to have, for the plants, some of the most stable sites that the slope afforded. As might be expected from the above analysis, frost heaving appeared to be more restrictive than gelifluction (as represented in nonfrost disturbance). On the frost disturbance gradient the dual nature of the site was most apparent (Fig. 26) for it showed high proportions, relative to those in other vegetations, of both widely tolerant species and species more sensitive to frost heaving. This was rather sharply contrasted with the situation on the nonfrost gradient (Fig. 27). Here the amelioration of the site in favor of species sensitive to nonfrost disturbance, presumably gelifluction, reached an extreme case.

Sedge meadow vegetation

The average ground cover by vascular plants in the sedge meadows was about 65 % (Fig. 20), and about 48 % of the species of the diamicton slope were found in them (Fig. 21). About 30 % more had fibrous roots than had taproots, and there were only about 15 % more fibrous roots than rhizomes. This vegetation was distinguished by having more species with rhizomes than any other on the slope (Fig. 29). It is not known whether this can be correlated with the plants' behavior on the moisture gradient (Fig. 25) where widely tolerant species reached their lowest percentage and where sensitive species were slightly less numerous than in the hummocky meadow.

On the frost and nonfrost disturbance gradients the proportions were roughly analogous to those in the hummocky meadow, though in the former the percentage of species sensitive to frost disturbance is considerably lower (Figs. 26, 27).

Quantitative data on the moisture and disturbance factors are incomplete for the sedge meadows, and can be inserted only by estimate except in the case of moisture. Figures for moisture on 15 August, 1961, were shown in Figures 3 and 4 at about 54 %. This was probably too low for typical sedge meadow which usually was saturated throughout the summer season. It is more probable that the moisture percentage for this type should be about the equivalent of that of the hummocky meadow, or perhaps higher.

The site of cone-target 35 in ES 7 somewhat resembles a sedge meadow habitat, though it was situated in a generally hummocky area. The target was on a mat of mosses, among sedges, and was heaved 5 cm, an intermediate amount (Fig. 5). Target 33, also in an extremely wet site and inserted 17 cm into the diamicton, was heaved 4.5 cm. Target 34, likewise very wet and inserted 7 cm into the mineral soil, was not heaved at all. From these few observations, and notes on the behavior of willows in the turf hummock sequence described elsewhere (RAUP, 1965 B), it seems probable that frost heaving in the sedge meadows, at least in the uppermost 10 cm of the diamicton, was only a moderately active process.

Downslope movement by gelifluction, however, may have been fully as active as in the hummocky meadow.

As a habitat for vascular plants the sedge meadow site had no dearth of moisture throughout the frost-free season. Its diamicton soil remained at or near its liquid limit through most of this period, with free water at the surface much of the time. Such conditions were favorable for the development of mossy turfs in which sedge meadows developed. The turfs produced thicknesses up to 5 cm or more. Plants rooted in these turfs and in the few centimeters immediately beneath them appeared to be less subject to injury by frost heaving than plants rooted in diamicton under the nearby organic crusts. At the same time the turfs formed tough mats that rode intact upon the soil moving downslope by gelifluction.

The relatively high proportions of fibrous rooted and rhizomatous plants may have reflected some vegetational adjustment to the abundance of moisture and relative stability. The dual nature of the site with respect to disturbance factors suggests the same correlations with relatively high proportions of plants sensitive to and widely tolerant of frost disturbance that were made in the hummocky meadow (Fig. 26). The amelioration of the site in favor of species sensitive to nonfrost disturbance appears also to have been extreme in the wet meadow (Fig. 27).

Turf hummock vegetation

Attempts to analyze the flora of the turf hummock vegetation in terms of tolerance ratings exposed an apparent paradox. The paradox was illustrated especially by the behavior of species on the frost disturbance gradient (Fig. 26). Of the 11 definitive species found in the immediate vicinity of the target line only one was narrowly tolerant on this gradient, while five were widely tolerant. Thus the effective indicator plants showed a level of sensitivity to frost heaving that was much higher than would be expected.

Plants rooted solely in the turf of the hummocks were essentially free of disturbance by frost heaving. Those in the narrow inter-hummock channels were likely to suffer considerable heaving in the autumn. Any species growing in the organic horizon, with roots penetrating the diamicton, were frost heaved in varying amounts depending upon the depth of penetration of the roots and upon whether the roots were affected by the more intense heaving that occurred under the crust-covered channel floors.

A survey of all of the 22 species in this vegetation indicated that their tolerances, so far as we can judge by their behavior elsewhere on the slope, permitted nearly all of them to live either on the hummocks or in the inter-hummock channels. Thus for nearly all of them the dual nature of the site was of no consequence. The paradox lay in there being present so few species that were more sensitive to frost disturbance although the thick turf was available to them.

A probable explanation of the paradox is in the sampling methods that were possible in the ES 7 and 8 map area. It was pointed out in an earlier paper (Raup, 1965 B) that the flora of an individual turf hummock is characteristically small, commonly not more than four to six species of vascular plants though the hummock may be densely covered by them. Although about 40 species were found growing on turf hummocks in the Mesters Vig district, this number was accumulated from studies at more than a dozen sites. Some species are common to hummocks on most of the sites, while many more appeared to be randomly scattered. The turf hummock vegetation occupied only about 3 % of the ES 7 and 8 map area, and did not adequately sample the random element in the turf hummock flora. In theory it would be this element that would be most sensitive to disturbance and probably restricted to the thick turf.

As a test of this theory a new list of species for the turf hummock vegetation was formed. The 22 species already used were found listed in the turf hummock flora described by the present author (1965 B). From the latter list all those additional ones were extracted which had also been found elsewhere in the ES 7 and 8 map area. There were 18 of these, making a total of 40 species in the new list. The species in the new list were then analyzed as were those in the original list. Eighteen of them proved to be widely tolerant on all gradients, and were eliminated from consideration. Of the 22 definitive species, eight were widely tolerant on the frost disturbance gradient, and six were narrowly tolerant. Thus the plants most sensitive to frost heaving reached about 27 %, and the widely tolerant ones only about 36 %. This is more nearly the combination expected from what is known of the site and the behavior patterns of the plants. It accentuates, as did the hummocky meadow with respect to frost heaving, the dual quality of the site.

The flora of the turf hummocks as modified in the way described above has been used throughout the comparative studies at ES 7 and 8. The same method for expanding it was used at ES 6 and ES 16.

Coverage of the ground by vascular plants reached an average of about 80 % in this vegetation, though the number of species found in the immediate vicinity of the target lines was relatively low (22), about 21 % of the vascular flora of the diamicton slope (Fig. 21). Plants with fibrous roots greatly outnumbered those with taproots, and the latter nearly equalled those having rhizomes (Fig. 29). Compared to the floras of the sedge and hummocky meadows these figures constituted a decrease of about 12 % in rhizome composition, and an increase of about 8 % in taproot composition.

Data from soil samples collected in 1961 (Figs. 3, 4) indicated a rather "low median" percentage of soil moisture in the turf hummock area of ES 7. It is probable that this was approximately correct for the late summer season. The hummocks were well developed, closely aggregated, with channels between them extending down to mineral soil. Typically developed over diamicton as they were they had earth cores raised under them. In early summer the inter-hummock channels carried running streams, and water was seeping through their basal mosses, but in late summer the channels were merely damp.

Cone-target heave measurements showed heaving only in targets with 20 cm insertions in this vegetation type, and in intermediate amounts (4–5 cm) (Figs. 5, 6, 7). Downslope movement of targets, though appreciable, was about half as much, on the average, as in the hummocky meadow vegetation (Figs. 9, 10). The total jump, averaged for all accepted targets, was about two-thirds as great as in the hummocky meadow (Figs. 11, 12).

Comparing the physical habitat presented to vascular plants by the turf hummocks with that presented by the hummocky meadow, its moisture supply was smaller in quantity, partially limited to the early part of the summer season, and vertically limited to the basal parts of the hummocks and to the inter-hummock channels. The slow movement of the underlying diamicton by gelifluction probably left all or most of the plants undisturbed by this process for relatively long periods of years. On the other hand frost heaving was present at both low and relatively high intensities, giving the dual nature of the site previously mentioned.

Figure 25 shows that the proportion of definitive species widely tolerant on the moisture gradient was relatively low in the turf hummock vegetation (about 55 %). The only types in which it was lower were in the sedge and hummocky meadows, which occupy the wettest parts of the slope. This suggests adjustment of the vegetation to a decreasing water supply (see Fig. 3), which is buttressed by the fact that species intolerant of variation in moisture fell to zero. The behavior of these plants on the frost disturbance gradient, discussed above, reflected the mixture of stable and unstable habitats with respect to frost heaving. Widely and narrowly tolerant plants were present in approximately equal numbers. Plants narrowly tolerant on the nonfrost disturbance gradient maintained a high percentage here (about 64 %) as they did in the sedge and hummocky meadows, while those widely tolerant of this kind of disturbance were present to the extent of only about 18 %. This suggests that the plants in the turf hummock vegetation experienced minor risk of injury from gelifluction movement in spite of the fact that this movement was appreciable (see Figs. 9, 10). The decreased proportion of rhizomatous species from that in the sedge meadows, and the increased percentage of taprooted plants, may be a response to decreased moisture supply (Fig. 29).

Heath tundra vegetation

Vegetative coverage of the ground here reached the maximum for the diamicton slope, averaging about 85 $^0/_0$ (Fig. 20). The more-or-less hummocky turf, composed basically of mosses, was densely clothed with vascular plants. The number of species was relatively small (22). Species with taproots here attained a median percentage of the flora. Reference to Figure 29 indicates that only in the eastern "dry" sector of the slope did they reach higher proportions. Further, the proportion of rhizomatous plants was reduced to a level approached only in the "dry" sector.

Percentages of species widely tolerant on the coverage (Fig. 24) and moisture (Fig. 25) gradients were both high, with no narrowly tolerant species present and relatively small numbers with intermediate tolerance. Twice as many species with wide tolerance of frost heaving as with narrow tolerance on this gradient were present. But on the nonfrost disturbance gradient the proportions were conspicuously reversed. Here there were about seven times as many narrowly as widely tolerant species (Figs. 26, 27).

Available data (extrapolated from samples collected in 1958; see preceding discussion) indicated that the surface materials of the diamicton under the thick turf of this vegetation had a relatively low moisture content in late summer (about 5 $^0/_0$, Fig. 3). They also showed that the soil at a depth of 20 cm had about twice as much moisture at the same time. It will be seen in Fig. 3 that these low percentages were found elsewhere on the slope only in the eastern "dry" sector under exceedingly sparse vegetation. Further, only in the "dry" sector did the surface soil also have less moisture than the deeper horizons. The heath tundra was located at the base of the talus (Figs. 1, 19), and just below the steep southern slope of the large snowdrift. Most of it emerged from the snow relatively early in the season, but its gentle slope downward to the southeast made it relatively well drained. Its diamicton never became desiccated like that in the "dry" sector, and though its water supply was relatively small, it was probably fairly constant throughout the summer.

Cone-target heave data are scanty for this vegetation type. Target 37, with a 20 cm peg, was inserted through 8 cm of organic soil and 12 cm of diamicton. From 1956 to 1964 it was heaved 4.5 cm. Target 38, inserted 10 cm entirely in organic soil, was not heaved. Gelifluction movement is known to have been very small during the five-year period of observation (Fig. 9) (approx. 2–5 cm). At the same time the total jump, combining the effects of frost creep and gelifluction, was considerably greater (Fig. 11). It is probable, therefore, that frost heaving had a role in the plant habitat of the heath tundra (Fig. 7).

In summary, plants growing on the heath tundra site found a moderate but adequate moisture supply that appeared to be fairly constant throughout the frost-free season. The diamicton substratum was relatively free of physical disturbance due to gelifluction. It was subject to moderate frost heaving, most of which probably occurred in the autumn with the major episode of the annual freeze-thaw cycle. Some of the plants were growing in the inter-hummock channels where the turf may have been thin, and they may therefore have been rooted in the diamicton. Others were rooted entirely in the turf. Those in the latter were scarcely if at all injured by the heaving. Those in the diamicton may have suffered some damage, as in the turf hummock areas. Thus the heath tundra shared the dual site quality with respect to the physical disturbance factors.

It is possible that the higher proportion of taprooted plants is a response to the drier site (Figs. 3, 4). It is more difficult to rationalize the preponderance of wide tolerance on the moisture gradient among plants here (Fig. 25), except in general terms. There was a certain amount of fluctuation in the water supply during the growing season. In the "dry" sector it reached a stage that we think of as "desiccation". But we do not know the threshold of this in terms meaningful to the plants, either in the "dry" sector of the slope or in the heath tundra. It may be that the species composition of the latter represented a closer approximation of actual site moisture conditions than the field data on moisture show. There is also the probability that once a dense vegetation is established it modifies the seasonal moisture regime to such an extent that the destructive desiccation of late summer is impossible.

The reversed proportions of species very tolerant and very sensitive to frost and nonfrost induced disturbances are fairly consistent with what is known or assumed with respect to these disturbances. Gelifluction movement was of small consequence to this vegetation, and plants very sensitive to it were growing there in relative safety. A considerable part of the flora was subject to frost heaving, especially the plants rooted in the intervals between the hummocks. The relatively high proportion of widely vs. narrowly tolerant plants on this gradient (2:1) suggests that the frost heaving was relatively intense compared to that in most of the other vegetations in the "wet" sectors. Perhaps it was nearly as intense as that found in the organic crust areas though not as widespread throughout the soil as in the latter.

Development of vegetation on the diamicton slope

The presence of "perched" willows (*Salix arctica*) in the "dry" sector of the diamicton slope, already mentioned, suggests that this area was formerly a part of the "wet" sector. Data to support this concept were presented in an earlier paper (RAUP, 1965 B). The lobate, ridged and stepped micro-relief of the surface in the "dry" sector was further evidence that its soils were formerly much more active than they now are. The timing of this wetness and greater activity was not investigated in the ES 7 and 8 map area, but the appearance of the willows suggested that the change occurred within the last 60–75 years.

Assuming that this change took place, the flora and vegetation of the "dry" sector may be regarded as essentially residual. The principal change in the site has been the loss of moisture from annual snow-melt. This has stopped the activity of the soils due to frost heaving, frost creep and geliflucton, and the plants have suffered severely from desiccation. The latter has reduced the flora to a small scattering of species most of which have wide moisture tolerance.

In the "wet" sector there appeared to be enough moisture in the soil for plants throughout the season, but this has given rise to intensive frost heaving in the diamicton which, in turn, appeared to be potentially lethal to plants. Nonetheless the flora was richer in species and the vegetative cover more dense in the "wet" than in the "dry" sector, although the relationship is not a linear one.

The preceding treatment of the whole vegetation of the ES 7 and 8 area has been, in effect, an attempt to rationalize "residuals". It has been assumed that the site factor complexes, operating within the inherent tolerance ranges of the species, have "sorted" the latter into the vegetation types. Beyond this assumption has been an apparently simpler one: that the species were there to be sorted. In view of the fact that an adequate moisture supply *per se* seems not to be sufficient for the development of a vegetation, and that combined with frost it may be lethal to plants, the question of how vegetation was first established on the diamicton becomes essential.

There is circumstantial evidence that the early stages in the development of the vegetation should be looked for in the "wet" sector of the slope. If the "sorting" referred to above has occurred, the largest number of species available for the process is in the "wet" sector, particularly in the hummocky meadows. Nearly all of the 71 species of the diamicton slope were found in the "wet" sector or in both "wet" and "dry" sectors. Only six species were confined to the latter.

Further evidence of a "sorting" process is in Fig. 22, which shows relatively low percentages of species with wide tolerance (on all gradients) in the sedge and hummocky meadows paralleling similarly low percentages of common to abundant species. This group was mixed in these vegetations with species of lesser tolerances and frequencies which here reached their highest percentages. In either direction the vegetation assumed smaller floras usually with high percentages of widely tolerant species and lower percentages of sensitive ones; the sites may have become lethally unstable for the plants, or lethally dry, or both.

The situation in ES 7 and 8, although it contained the elements essentially as described in the preceding paragraph, was not as "symmetrical" as there assumed. Reference to Fig. 20 shows that vegetative ground cover density did not fall off with increasing desiccation and decreasing numbers of species in the western part of the diamicton slope. Rather it increased in that direction. Although there was some instability in the soil it was not as great as in similar moisture regimes in the eastern part of the "wet" sector. A reason for this may be found in the organic horizon of the soil overlying the diamicton, and leads to the belief, expressed by WASHBURN (1967), that the vegetation, once started, materially modifies the frost heaving in the soil.

Studies of the origin and development of turf hummocks in the Mesters Vig district (RAUP, 1965 B) presented an analysis of vegetation, soil, moisture, and thermal regimes below melting snowdrifts analogous to the situation at ES 7 and 8. Wet meadows with moss substrata developed on the organic crusts of snow-beds produced low turf hummocks which then grew into more or less continuous hummocky masses of thick turf by proliferation of more mesophytic mosses. These gradually deteriorated by desiccation, erosion, and frost heaving. The intervals between them were covered for a time by organic crusts. There was evidence that frost heaving was of medium to low intensity in this sequence during the mossy sedge meadow stage, and that it began to become more active when the hummocks were well formed and the water channeled between them. It was particularly active in the soil of inter-hummock intervals which were near enough to the source of water to remain moist throughout the summer. When the latter intervals became dry in late summer the frost activity appeared to cease or be reduced to a minimum.

There was evidence that this sequence of turf hummock origin, development, maturity and deterioration was a dynamic one, motivated by gradual retreat of perennial snowdrifts and other sources of surface moisture. Occurring over a period of years, this has resulted in progressive desiccation of slopes.

Judging by the evidence at hand with respect to the frost heaving process, the situation on the ES 7 and 8 diamicton slope in which the surface materials were most stable for the establishment of vascular plants was in the "moss mat" that develops in sheet flow areas below snowdrifts. Here the substratum was basically organic and constantly irrigated throughout all or most of the open season. Sedges, a few grasses and other herbaceous plants appeared in it, and low hummocks of moss formed upon which willows and other woody species became established. Gelifluction of the underlying diamicton may have gone on with little or no disturbance to the vegetation. The observed behavior of targets 33 and 35 at ES 7 was evidence of this. Frost heaving occurred, but it appeared to have been relatively inactive in the root zone of the soil, probably the uppermost 15 cm.

As the hummocks grew larger, and the inter-hummock channels were more prominently developed, the vegetation on the floors of the latter was reduced to thin organic crust. Frost heaving may have been relatively intense in these channels depending upon how closely they came to mineral soil. Plants rooted in the hummocks were free of frost heaving. Thus both stable and unstable habitats were produced in close association.

In the turf hummock sequence described earlier (RAUP, 1965 B) the front of the retreating snowdrift which activated the progression of changes moved directly upslope. As the older hummocks became farther removed from the source of summer moisture they deteriorated and became farther apart. Inter-hummock areas finally lost their late summer moisture entirely and became essentially stable. In the ES 7 and 8 area the elements of this sequence were all present, but they were greatly expanded and somewhat modified. This was due to the fact that the water-producing snowdrifts melted back diagonally across the upper and middle parts of the diamicton slope. Therefore each phase of the hummock sequence was skewed eastward and marginally though in modified form because the amounts of water delivered by the drifts decreased eastward as well as downslope, and the periods of their availability were shortened in both directions.

It is probable that the hummocky meadow vegetation was in part a phase in the development of the turf hummocks, and in part a phase in their deterioration. As it appeared around targets 33–35 it seemed to be the former, but target 32 seemed to be in an area of small deteriorating hummocks surrounded by organic crusts. The large marginal areas of organic crusts that lay below the snowdrift in Fig. 1 may be regarded as a greatly expanded "inter-hummock channel" phase of the hummock sequence. They were kept moist late in the season by progressive snow-melt from the two major drifts. The slightly more moist phase of the "dry" sector, which bordered the organic crusts on the east, got some of this water but not enough, so that it dried out before the end of the summer. Mention was made earlier of perched willows in the driest areas of the "dry" sector, suggesting that at no distant time it also had been well watered by a much larger extension of the upper snowdrift than now obtains.

A proposed developmental sequence of vegetation on the "wet" areas of the diamicton slope is as follows. An available starting point was in mats of aquatic mosses or organic crusts continually bathed by sheet flow water from snowdrifts throughout all or nearly all of the frost-free season. This has developed through a sedge meadow to a turf hummock vegetation; then by deterioration of the latter, and by the expansion and modification of its stable and unstable elements, the hummocky meadow and organic crust areas have formed. Apparently the vegetation can remain dense only so long as there is abundant surface water to maintain the basal mosses of the turf hummocks or to replenish the sequence continually with new meadows in inter-hummock channels as the latter develop. In the more usual event the hummocks gradually dry out and erode away while the inter-hummock channels enlarge.

Because of the extended water supply on this slope the hummocky meadow, consisting of hummocks in varying states of growth and disintegration, interspersed with crusts variously overgrown with sedges, was in reality a mixture of all of these vegetations. However, in nearly all of it there was an organic soil horizon from an earlier more dense cover, and frost heaving was greatly ameliorated in the root zone. The net result was a vegetation of medium density consisting of a relatively large number of species, a comparatively large proportion of which were rather sensitive to physical disturbance factors.

Marginal to the hummocky meadow, or to the turf hummock vegetation, the expanded organic crust areas have lost their turf hummocks entirely, or the latter have been reduced to small remains. The organic horizon was also gone and the crust lay on mineral soil. Here the frost heaving was intense and lethal. There appeared to be ample moisture for the plants, and for a time in spring water was flowing over the surface. But continuous flow did not occur, and mats of aquatic moss have not formed. It is probable that occasionally there has been a series of years in which such a flow has come and a few plants were established, only to be killed later by frost heaving.

EXPERIMENTAL SITE 6

Introduction

The relation of vegetation to geomorphic processes in experimental site 6 presents problems that differ materially from those in ES 7 and 8. This is due to several causes: (1) its smaller vascular flora; (2) a much smaller area involved in the investigation; (3) the prevailingly moist to wet condition of the whole site; and (4) a greater uniformity in the effects of the processes upon the lives of the plants than was found in ES 7 and 8.

Data and methods used in the following analyses are from sources similar to those used at ES 7 and 8. Specific information on them will appear as the need arises in the following discussions.

Topography and soils

The general location and structure of experimental site 6, and the mass-wasting phenomena illustrated by it, were described by WASHBURN in No. 4 of the present series of papers (1967). A brief description of the site was also included in No. 1 (WASHBURN, 1965). Several of the turf hummocks discussed in paper No. 3 (RAUP, 1965 B, p. 33–42) were located in the immediate vicinity of ES 6, and a photograph of the site appeared as Fig. 1 in that paper. For more detail than is found in the following brief account the reader is referred to these sources.

Experimental site 6 was in a shallow valley between two trap knobs (MS 78 m and MS 120 m) at the southeast end of the Nyhavn hills. A small stream, fed from the hills to the northwestward, flowed eastward through this valley near the base of MS 78 m, which was the southernmost of the two knobs. In doing so it subtended the southern border of the ES 6 area, at an altitude of about 45 m above sea level. Experimental site 6 was about 0.6 km east of ES 7–8, and about 30 m lower in altitude (see map, Pl. 1, RAUP, 1965 A). The target line of ES 6 extended northwesterly from the base of a low bedrock knob (53 m alt.) to near the base of another low knob with an altitude of about 60 m (see Figs. 30, 31). A small stream flowed southward through the area, intercepting the target line near its eastern end. This stream had a poorly defined channel system, spreading over 3–4 m during the spring thaw, but confined to

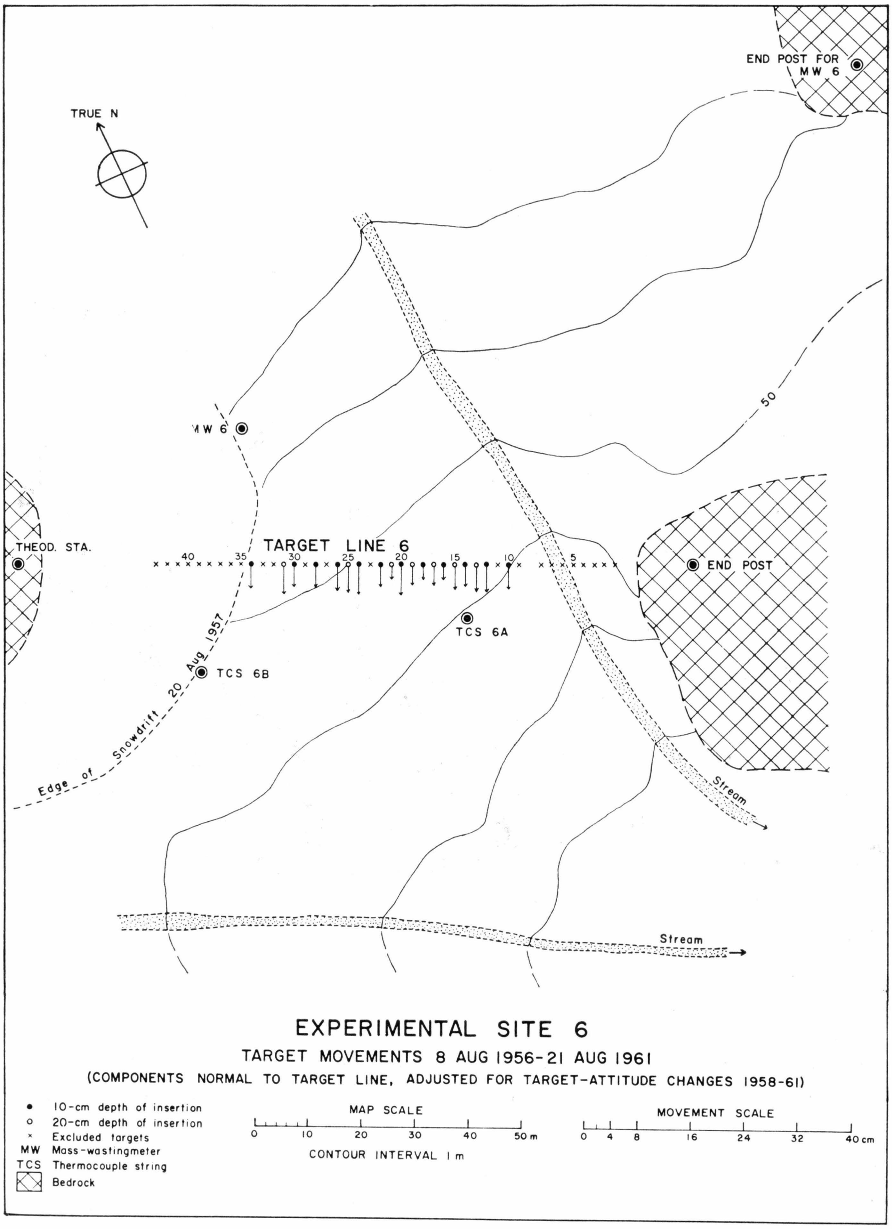

Fig. 30. Map of experimental site 6, showing topography, target line, and downslope movement of targets, 8 Aug., 1956, to 21 Aug., 1961. From WASHBURN, 1967, Fig. 6.

a narrow depression in the vicinity of targets 5 and 6 later in the season. At most it was only a few centimeters deep.

The gradient in the vicinity of the targets was 2.5°–3°, averaging about 2.5°. The soils ranged from gravelly-clayey-silty sand to silty-

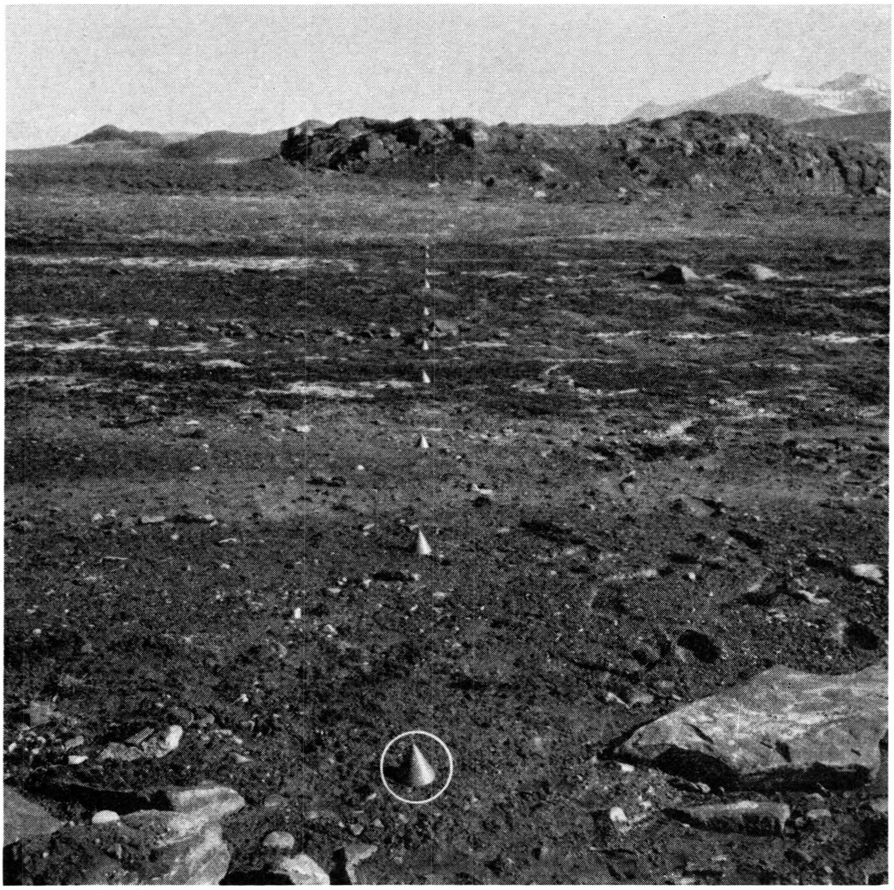

Fig. 31. Experimental site 6. View southeast along target line from below theodolite station (see map, Fig. 30). Circled target is no. 43. 14 Aug., 1956. From WASHBURN, 1967, Fig. 8.

sandy gravel. UGOLINI, in 1964 (personal communication), described the soil textures in the eastern part of the line (T1–T20) as silt loams, and those in the western part (T20–T40) as varying to sandy clay loams. The fines in the uppermost 20 cm ranged from 10 to 52 %, but at depth the silt and clay content increased. The material was shell bearing below about 80 cm. The surficial horizons were entirely non-calcareous.

The moisture supply and its distribution

Moisture to the vicinity of the target line, other than immediately along the small stream near the eastern end, was from two main sources during the open season. One was seepage from the long gentle slope to the north. The other was melt-water from a large snowdrift that developed each year in the lee of the low bedrock knob which bordered the area

Target number (SE at 1)	21	20	19	18	17	16	15	14	13	12	11	10	9		8	7	6	5	4	3	2	1
Transect of vegetation.																						
Vegetation type.	Sedge meadow	Ground cover	Ground cover	Ground cover	Ground cover	Ground cover	Ground cover	Turf hummocks	Ground cover	Turf hummocks	Ground cover	Ground cover	Ground cover		Mineral soil	Sedge meadow		Moss turf		Turf hummocks	Mineral soil	Grassy herb meadow
Position of targ. 12 Aug, 1964, and approx. organic layer at targets.																						
Target heave. 1956-64(cm).	1.5	0.5	5.0	0	5.5	1.5	4.5	0	4.0	0		3.0	9.5			4.5				2.0	0.5	0.5
Organic soil thickness (cm).		8	8		5±		3+		3±			0.5	2							3+		3
Veg. cover at targets(%).	50-60	40-50	30-40	30-40	30-40	40-50	30-40	30-40	30-40	30-40	30-40	30-40	20-30			20-30		5-10	20-30	80-90	30-40	70-80
Excluded targets.											x				x	x	x	x	x			

Target number (NW at 43)	43	42	41	40	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	23	22
Transect of vegetation.																						
Vegetation type.	Mineral soil		Mineral soil	Mineral soil	Aquatic mosses	Ground cover	Ground cover	Mineral soil	Ground cover	Aquatic mosses	Ground cover	Ground cover	Turf hummocks	Sedge meadow	Ground cover	Turf hummocks	Turf hummocks	Sedge meadow	Sedge meadow	Sedge meadow	Sedge meadow	Sedge meadow
Position of targ. 12 Aug. 1964, and approx. organic layer at targets.																						
Target heave 1956-64 (cm).	2.0		7.5		4	1			6.5	2	10.5	4	3.5	0	11.5	0.	5.0	0.5	6.5	1.5	6.0	1
Organic soil thickness(cm).			0						1		2			3±	1				9		4	
Veg. cover at targets (%).	0		1-	0	0	5-10	5-10	0	5-10	5-10	20-30	30-40	30-40	50-60	33-40	60-70	70-80	70-80	80-90	80-90	40-50	60-70
Excluded targets.	x	x	x	x	x	x	x	x	x		x	x					x				x	

Legend:

- Sedge meadow, over ground cover of moss, organic crust, or low mossy hummocks.
- Turf hummocks, with shrubby and herbaceous vascular plants.
- Ground cover primarily of organic crust, with occasional mats of living moss; scattered vasc. plants.
- Grassy herb meadow.
- Aquatic mosses in shallow pools or slow streams.
- Moss turf in damp to wet stream channels; few vasc. plants.
- Mineral soil bare or with few widely scattered vascular plants.
- Organic layer in the soil profile.

Fig. 32. Transect along target line of ES 6, showing variations in vegetation, target heave, density of vascular plant cover, and thickness of organic soil.

on the west. With the distal edge of the drift approximately at right angles to the target line and melting back progressively across the slope, and with seepage water coming to the whole target line from upslope, the entire area remained wet or very moist throughout the summer.

Comparative data on the moisture content of the soils along the target line are too scanty to form a graph showing whatever differences may have occurred. On 30 July, 1958, samples taken at about 5 m downslope from T17–18 showed ca 353 % water at the surface, 18 % at 10 cm depth, and 20 % at 20 cm. On the same day, at about 5 m downslope from T36–37, samples showed ca 244 % water at the surface, 23 % at 10 cm, and 27 % at 20 cm. At 10 m downslope from T15–17, in the vicinity of Thermocouple string (TCS) 6 A, samples were taken on 13 July and 7 August, 1961. On 13 July there was 252 % water at the surface, 240 % at 5 cm, 36 % at 10 cm, 13 % at 20 cm, and 7 % at 50 cm. On 7 August there was 38 % at the surface, 29 % at 5 cm, 18 % at 10 cm, 32 % at 20 cm, and 8 % at 50 cm (see Washburn, 1967, App. F).

Although there was great variation in soil moisture from season to season and from year to year at ES 6 as in most parts of the Mesters Vig district, as previously stated this area remained generally wet to very damp at the surface throughout. It was examined repeatedly in all of our field seasons, and even through the excessively dry summer of 1964 was damp to wet underfoot.

It is probable, however, that the moisture supply was not entirely uniform along the target line. Ugolini, while excavating the targets on 12 August, 1964, detected a progressive deterioration, from east to west, of a platy structure in the uppermost 20–30 cm of the mineral soil. This he associated with increasing wetness toward the west. He also noted that gley conditions were more pronounced toward the west, also related to increasing moisture. According to Ugolini's notes, gleying in the soils became fairly prominent and more or less continuous in the neighborhood of targets 17–19. It was also in this general area that sedge meadow began to predominate over turf hummock vegetation, and where an organic horizon more than 3 cm thick became fairly continuous over the surface of the mineral soil (Fig. 32). As previously noted, Ugolini placed a transition from silt loams in the eastern part of the area to sandy clay loams in the western part in the same general vicinity (near T20).

Cone-target heaving in ES 6

The cone-targets of ES 6 were placed in their original positions on 8 August, 1956, and final measurements of heave were made on 12 August, 1964. Also on 12 August, 1964, every fifth target (beginning at T1) was excavated, plus all other targets that were heaved more than 5 cm.

Although the heaving and settling of the targets had been measured repeatedly during the instrumental observations between 1956 and 1961, the data used here represent only the net heave of the targets in the eight-year period, 1956–64. These data, with related information, are presented in Fig. 32.

Information on the kind and density of vegetation around the targets was derived from a transect described below. Data on the thickness of the organic layer over the mineral soil are from UGOLINI's field notes, made at the time of the excavations in 1964. These are supplemented by a few gathered by the writer while making the transect, and the remainder are extrapolated from data on neighboring target areas.

In his analysis of the physical processes active in cone-target heaving at ES 6, WASHBURN (1967) excluded 19 targets from his calculations. He considered that the data on them lacked precision or continuity, or that their behavior was due to processes other than frost heaving. Figure 32 shows that most of the excluded targets were in the area of the shallow stream channels near the eastern end of the target line (T4–T8), and in the area immediately marginal to or under the snowdrift at the westerly end of the line (T32–T43). In the channel area T4, 5, 6 and 8 were all entirely out of the ground in 1964 or nearly so. All were subject to spring flooding by melt-water. Target 11, on the other hand, was situated among turf hummocks on organic crust with occasional patches of bare soil, and did not appear to be subject to washing. Targets 36, 37, 40 and 42 were all out of the ground in 1964, and were considered by UGOLINI as having been "washed out". They were in shallow channels with slowly flowing streams at the time of observation in 1964. There was some discontinuity in observations on T35–43 because the snowdrift did not melt back far enough in some years to expose them.

Thus the heave data are extremely questionable in some cases, while in others their precision is merely doubtful. Considering the general effect of heaving upon the life of the plants it seems reasonable to retain some of the doubtful cases in the present calculations. Of the excluded targets those retained are T7, 11, 23, 27, 32, 33, 35, 37, 38, 39, 41.

On the basis of the heaving data shown in Fig. 32, three intensities of heaving are proposed: high, intermediate, and low. In high intensity the net heave of the targets, 1956–1964, was 6.5 cm or more; intermediate intensity ranged from 3 cm to 6 cm; and low intensity included heaving of 2 cm or less. This division is arbitrary.

Eight targets were heaved 6.5 cm or more (assuming that T11 and T37 were heaved out of the ground). These were numbers 9, 11, 25, 29, 33, 35, 37 and 41. All of these were 20-cm targets, and if they had organic horizons beneath them the latter were less than 3 cm thick (with one exception). All of them were in vegetative coverage of 30–40% or less (with one exception). All were on organic crust or bare soil (again with one exception). The exception mentioned was the same target in all cases, no. 25, which seemed to be anomalous. It was in a sedge meadow over an organic layer up to 9 cm thick, and the cover was 80–90 %. All of the figures for target heave were rounded to the nearest half-centimeter. The actual measurement on T35, for example, was 6.5 cm, but for T25 it was 6.3 cm. Had it been 6.2 cm, T25 would have fallen into the intermediate category of heave used in this analysis, and would be grouped with T23 and T27 (see below). Therefore its significance in the high intensity group was more apparent than real.

Eleven targets had intermediate heaves (nos. 7, 10, 13, 15, 17, 19, 23, 27, 31, 32 and 39). All were 20-cm targets except two, nos. 10 and 32. Seven were on organic layers 3 cm or more thick (nos. 13, 15, 17, 19, 23, 27 and 31). Four of these seven rested on crust (nos. 13, 15, 17 and 19). One of the seven, no. 23, was in sedge meadow, and two others, nos. 27 and 31, were on turf hummocks. The other four of the eleven intermediates were on organic layers less than 3 cm thick (nos. 7, 10, 32 and 39). Target 7 was in sedge meadow, and T39 was in aquatic moss with gently flowing water. Targets 10 and 32 appeared to be exceptions to the rule that 10-cm targets do not heave this much (3 and 4 cm), and will be discussed further in another place.

Sixteen targets were heaved 2 cm or less (nos. 1, 2, 3, 12, 14, 16, 18, 20, 21, 22, 24, 26, 28, 30, 34 and 38. It is doubtful that T43 is significant). Thirteen of the sixteen were 10-cm targets. Of these thirteen, four were on organic crust (nos. 16, 18, 20 and 38); two were on hummocks (nos. 12 and 14); eleven were in vegetative cover of 30 % or more (nos. 2, 12, 14, 16, 18, 20, 22, 24, 26, 28 and 30); one was in wet moss with running water (no. 34). The remaining three were the 20-cm targets, nos. 1, 3 and 21. Target 1 was over an organic horizon 3 cm thick and in vegetative coverage of approximately 80 %. Judging by its vegetation and topographic position it is probable that it was in a somewhat drier situation than any of the other targets. Target 3 was on a low hummock in vegetative coverage of about 90 %. The organic horizon immediately beneath it probably was at least 3–4 cm thick. Target 21 was in a sedge meadow, in vegetative coverage of approximately 50–60 %. The organic layer beneath it was estimated at 6–8 cm, judged by the measured thicknesses at T20 (8 cm) and T23 (4 cm).

Discussion of cone-target heaving

The most intense heaving (6.5 cm or more) was seen only in targets having 20-cm insertions. WASHBURN (in press) reached the general conclusion from his studies of the Mesters Vig data on heaving "that progressively greater depths of target insertion to 20 cm correlate with progressively greater heaving, other factors remaining equal". He stated that "all the heave data from the experimental sites are consistent with the Hamberg-Beskow hypothesis". "As indicated by HAMBERG (1915, p. 609), the maximum upfreezing an object undergoes during a single freeze-thaw cycle is proportional to the object's 'effective height', which is the vertical dimension of the buried portion frozen to, and therefore heaved with, the adjacent material".

Factors other than the depth of insertion, however, were not constant, and gave rise to variations of heave in targets of the same insertion depths. The conditions other than insertion depth that appear to favor the greatest intensity of heave (6.5 cm or more) were the following, all present simultaneously:

1. Insertion in soils having organic layers less than 3 cm thick over the mineral soils.
2. Situation of the targets on organic crusts, or on bare soils, or on soils covered with very thin mats of living moss not inundated by running water.
3. Situation of the targets in vascular plant coverages of 30–40 % or less.

It is assumed that in all cases the soils remained moist or wet throughout the summer and into the autumn freeze-up.

If these criteria are valid, their opposites should also be effective. Such inhibiting factors may be listed as follows:

1. The presence of an organic layer in the soil 3 cm or more thick.
2. The presence of sedge meadow vegetation.
3. Vegetation of densities well above 30–40 %.
4. Vegetation of aquatic mosses in gently flowing water.

These conditions, functioning individually or together, should limit heaving in varying degrees.

Heaving of intermediate intensity (3–6 cm) was confined, except for T10 and T32, to targets with 20-cm insertions. At six of these nine 20-cm targets only one of the above-mentioned factors limiting to heaving was functional; at one target two were functional; and at the remaining two (three if T25 is included among the intermediates) three of the factors functioned together. The most pervasive of the four factors listed was the thicker organic layer in the soil, which appeared at eight of the ten targets.

Both of the 10-cm targets that were heaved to intermediate amounts (T10, 3 cm; T32, 4 cm) were in situations particularly favorable for heaving. Both were over relatively thin organic layers (1–2 cm), situated on organic crusts, and in vascular plant coverages ranging from 20 % to 40 %.

The behavior of the intermediately heaved targets with respect to the factors described suggests that there was an interplay among the latter, some favoring and others limiting to heaving. The resultant determined the amount of heave at any given target.

It would be expected from the general conclusions reached by WASHBURN with respect to frost heaving in the Mesters Vig district (see above) that most of the 16 targets with low intensity of heaving (0–2 cm) would have 10-cm insertions. All but two of the 13, in addition to their short pins, had at least one factor limiting to heaving operative at their sites (two had one; four had two; and five had three). Two had two factors favorable to heaving, four had only one, and five had none, other than their short pins. Two targets in this group, nos. 2 and 38, both had all three of the major factors favorable to heaving operating together, thus closely resembling T10 and T32 in the intermediate group. However, they were heaved only 0.5 cm and 1.0 cm, respectively.

All of the 20-cm targets in the low intensity group (T1, T3, T21) were in situations where the inhibiting factors were all functional simultaneously. An apparent exception was T43, but this was excluded because of its doubtful validity.

Figure 33 gives the distribution of average cone-target heaves in varying thicknesses of the organic horizon that overlay much of the mineral soil in ES 6, in the varying percentages of ground cover by vascular plants, and in the various types of vegetation. In two cases vegetation types were combined where their effects upon heaving appeared to be approximately equivalent, and where their combinations had little effect upon the average heaves. Among the 20-cm targets, ten were on organic crusts and averaged 9.7 cm of heave. Only one target was on essentially bare soil, with a heave of 7.5 cm, well within the range of the preceding ten (4–20 cm). Averaged with the latter, it made the average heave for the combination 9.5 cm. Similarly, only one 10-cm target was on bare soil. Averaged with the six that were on organic crust, it changed the average heave of the latter from 1.67 cm to 1.75 cm. Turf hummocks and mats of aquatic mosses in gently flowing water were entirely different habitats, but their effects upon the heaving of the 20-cm targets seemed to be about the same. Three of these targets on turf hummocks were heaved on the average 3.5 cm (range 2–5 cm), while one in aquatic moss was heaved 4 cm, thus moving the average 1.2 mm. Among the 10-cm targets the aquatic moss seemed a little less effective as an inhibitor of heaving than the turf hummocks, so that a single target in this habitat altered the average by a centimeter.

The sharp difference between the amounts of heaving in the 20-cm and 10-cm targets is clearly shown in Fig. 33. The response of the 20-cm target heaving to the effects of external factor combinations is also shown, together with the failure of the 10-cm targets to respond to the same factors.

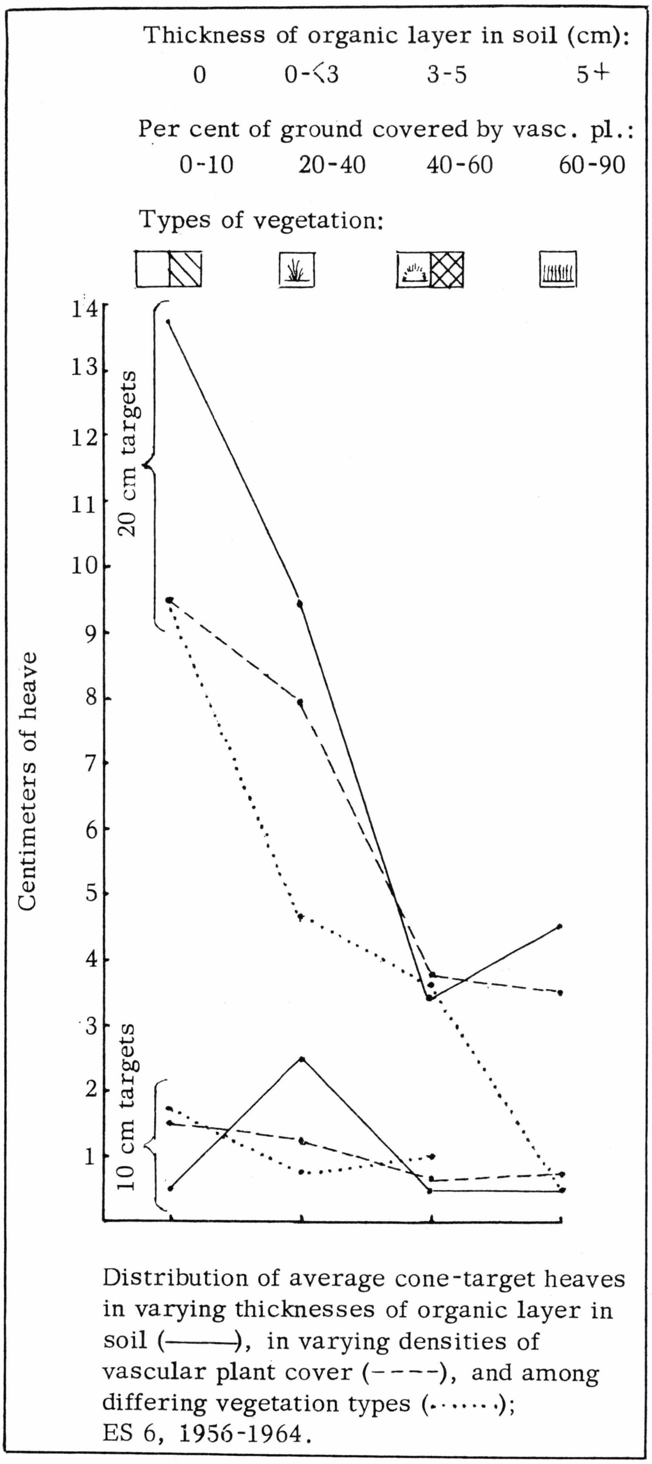

Fig. 33. Distribution of average cone-target heaves at ES 6 (1956–1964) in varying thicknesses of organic soil, varying densities of vascular plant cover, and differing vegetation types.

The above analysis suggests merely that there was a general relationship between target heave and the factors favorable and inhibitive to target heaving, definable in broad categories of intensity. Knowledge of the factors is not sufficiently precise to refine the analysis much further. Also, data on variations in the moisture factor along the target line are inadequate. It is probable that were these data available many of the variations of heave within the three major categories would be rationalized.

The fact that eight of the ten targets having 20-cm insertions (including T25 in the intermediate group) appeared to be influenced by an organic layer 3 cm or more thick, and that the heaving in six of them appeared to be inhibited principally by this factor, suggests that the presence and relative thickness of an organic layer may be of primary significance. It also suggests the possibility of using the data at hand to assign relative values to the factors outlined above. Figure 34 was designed to test the relevance of these suggestions.

The sharp difference in amount of heaving between most of the 20- and 10-cm targets strongly suggests that their behavior relative to the external factors should be analyzed separately. All but two of the 10-cm targets were confined to the low heaving intensity group, while all but three of the 20-cm targets were confined to the intermediate and high intensity groups. No 10-cm targets were found with heaving of high intensity. Therefore in Fig. 34 separate series of graphs are given for 20-cm and 10-cm targets. Because the main purpose of these graphs is to bring out relative values for factors favoring or inhibiting target heave, the figures for the three accepted 20-cm targets with low intensity of heave have been grouped with the intermediates.

Among the 20-cm targets in the high intensity group about eight times as many were on soils with thin organic horizons (less than 3 cm) as occurred on soils with thicker organic layers (3 cm or more). About 4.5 times as many were on open sites like thin organic crusts or bare soil or very thin mats of moss as were in the denser vegetative cover of sedge meadow or turf hummocks. Only about three times as many were in vascular plant coverages of 30–40 % or less as were in denser coverages. The graphs show that these proportions are about the same for the 20-cm targets with intermediate and low intensities of heaving, but all in reverse order.

The graphs suggest that the relative thickness of the organic layer probably was the most significant of the three factor complexes considered. Second was the presence or absence of some kind of fairly dense plant cover, whether it be of heavy mats of moss such as occur in turf hummocks, or wet sedge meadows which commonly have a mat of mosses as a substratum. Related to such cover were mats of aquatic mosses

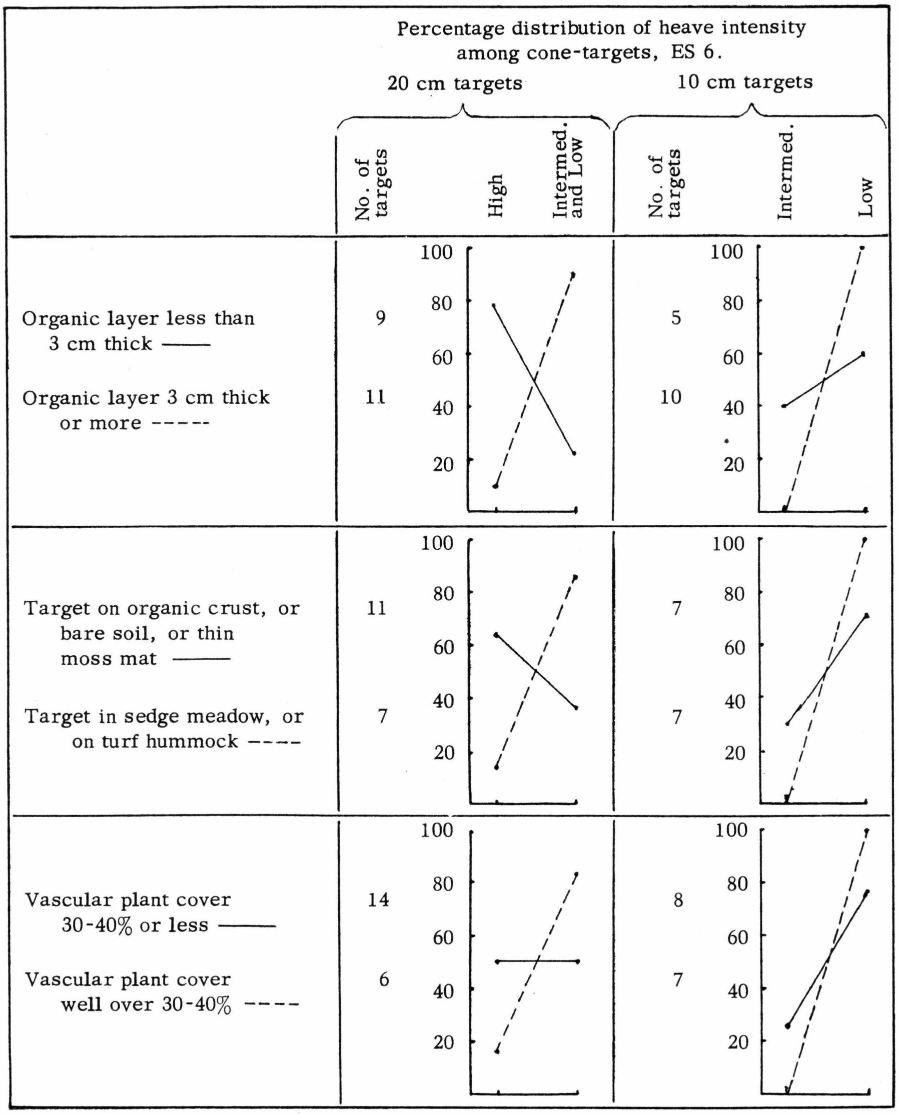

Fig. 34. Percentage distribution of cone-target heave intensity at ES 6 with respect to thickness of organic soil and to kind and density of vegetation.

bathed by seepage water or sheet flow. Third in significance seems to be the relative density of whatever vascular plant cover may have occurred.

The most striking aspects of the graphs for the 10-cm targets are their similarity and the fact that the contrasting effects within the opposing factor pairs showed relatively small differences. The most pronounced of these differences was in the factor complex of the thickness of the organic horizon, a result which supports the conclusion suggested above—that this was the most significant. In general, the similarity and lack of contrasts in these graphs suggest that the 10-cm targets were much less sensitive to variations in the external factors than were those with 20-cm insertions. This seems to have been the case whether they were on crust or bare soil, or in vegetation of varying densities. They appeared only slightly more sensitive to variations in the thickness of any organic horizons that may have been in their soils.

Comparison with ES 7 and 8

Evidence from cone-target heaves in ES 6 permits conclusions essentially the same as those reached in similar studies in the wet sectors of ES 7 and 8. Because most of the roots of the plants were in the uppermost 15 (20) cm of the soil, frost heave injury to them, and variations in the amount of injury, are to be looked for in this zone. The heaving of the targets gives only relative values that may be applicable to root injury. The major difference between the 10- and 20-cm targets suggests, as in ES 7 and 8, that roots in the uppermost 10 cm of the soil, whether the latter is organic or mineral, are much less subject to injury than those that go more deeply and have greater length. Those that penetrate to 15 or 20 cm are likely to be injured particularly if there is little or no organic horizon in the soil, and if the surface is bare or covered by organic crust. Thicker organic layers in the soil, or denser vegetative covers of moss or vascular plants, or combinations of these may greatly reduce the chances of root injury.

The average heave of the accepted 20-cm targets in ES 7 and 8 (1956–1964) was almost identical with the average of the 20-cm targets considered in ES 6. The heave of the 10-cm targets averaged about twice as much (1.03 cm) in ES 6 as in ES 7 and 8 (0.46 cm). This difference was small and may not be significant. Although, as noted, precise moisture data are not available, field observations suggested that ES 6 retained more moisture in the surface soils throughout the summer and autumn than ES 7 and 8. The more gentle slope at ES 6, and the larger drainage area above it, tended to maintain the supply and thus increase the probability of disturbance by volume changes in the soil due to freezing and thawing. It is also notable that the range covered by the averages was wider in ES 6 than in ES 7 and 8. In the former, assuming that some of the targets were heaved entirely out of the ground, the range among the 20-cm targets was 0.5–20 cm, while in ES 7 and 8 it was only 4–10 cm. Among the 10-cm targets it was 0–4 cm in ES 6, and only 0–2.5 cm in ES 7 and 8.

Although the average net heave of the targets in ES 6 and in 7 and 8 was essentially the same, there was evidence that the total activity of the process may have been slightly less in ES 6. This is because the area in ES 6 that was affected by heave-inhibiting factors is a little less than in ES 7 and 8. Using the same unit of measure in the latter that was used in the transect of ES 6—an area of about 4 square meters for each target—about 4% more targets were in soil with 3 cm or more of organic material in ES 6 than in 7 and 8. Likewise about 6% more were in vegetative cover of 40% or greater, and about 11% more were in sedge meadow or on turf hummocks. Though these differences were not concerned with the amount of heaving in individual targets, their total effect may have had some influence upon the general selection of the flora.

Downslope movement of soils at ES 6

The movement of soils downslope at ES 6 resulted from mass-wasting processes and also, in the stream channel areas, from erosion and deposition of the surficial sandy and silty materials. Washburn (1967) has described and analyzed the mass-wasting processes, basing his analysis upon instrumental observations between 1956 and 1961. The following data on this kind of movement are derived from his work.

Mass-wasting

All but 19 of the 43 targets originally placed were excluded by Washburn in his final study of downslope movement. Reference to Fig. 30 shows that the 19 used were well away from the channel area in the easterly part of the target line, and away from the area at the west that was exposed by the melting of the snowdrift.

The total net downslope movement of these targets ranged from 3 cm to 7.1 cm, and the mean was 4.9 cm. This gave a mean annual rate of 1.0 cm per year. The principal processes in this movement were gelifluction and frost creep. The total gelifluction movement ranged from 0.4 cm to 2.9 cm, with a mean of 1.4 cm. The "jump" (see Washburn, 1967) included the movement due to the annual freeze-thaw cycle, and was the major element in the frost creep. The total jump ranged from 2 to 8.8 cm, with a mean of 6 cm. None of these observations on downslope movement showed any appreciable difference in the behavior of 10-cm and 20-cm targets.

Two general aspects of these soil movements are noteworthy: (1) they were relatively small compared to those in the wet sectors of ES 7 and 8; (2) they showed a relatively uniform minor variation along the section of the target line sampled by the non-excluded targets. It is probable that the more gentle slope accounted for the first, and the generally moist to wet condition of the whole area accounted for the second.

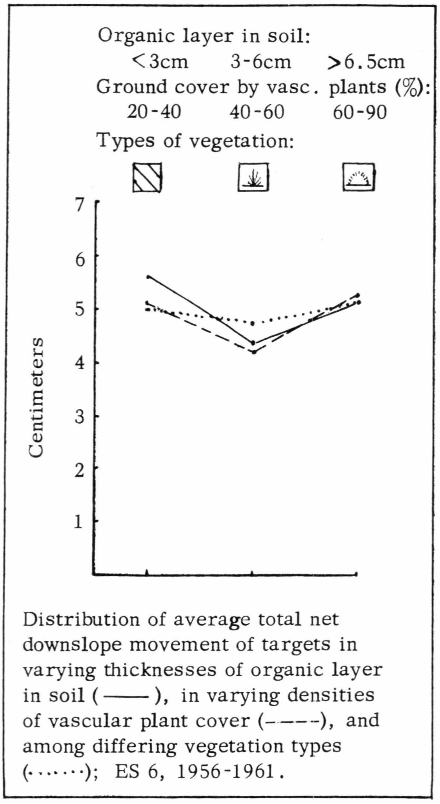

Fig. 35. Distribution of average total net downslope movement of targets at ES 6 in relation to varying thickness of organic soil, varying density of vascular plant cover, and to kinds of vegetation.

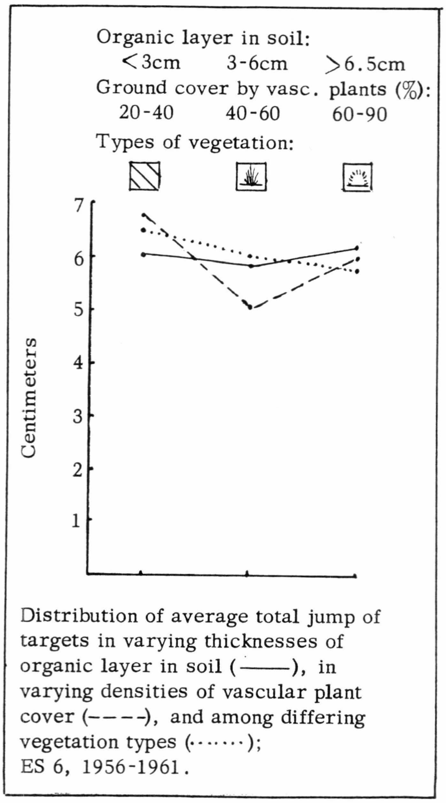

Fig. 36. Distribution of average total jump of targets in relation to varying thickness of organic soil, varying densities of vegetation, and differing vegetation types.

Attempts to correlate the movement behavior of these targets with the vegetation and the three external factor complexes used in the analysis of heaving brought out only minor differences, and supported the idea of a general uniformity of downslope movement in the soils. For example, eight of the targets were on organic crusts, with an average total movement of 5 cm. Six were in sedge meadow with an average movement of 4.78 cm, four were on turf hummocks, with an average movement of 5.13 cm, and one was on an aquatic moss mat (T 34), with a total movement of 4.15 cm. Excluding T 34, which was a single representative of a type, and somewhat isolated from the others, the range among these averages was only 0.35 cm. Two targets were over soil organic layers less than 3 cm thick, and showed an average total movement of 5.63 cm. Seven were over organic horizons 3–6 cm thick, with an average movement of 4.39 cm, while ten were over organic horizons 6.5 cm thick, or more, with an average total movement of 5.14 cm. Here the range of averages was a little greater (1.24 cm), but still relatively minor. Similarly small differences appeared in the target movements with respect to density of cover by vascular plants. Comparative figures for total jump show comparable lack of significant differences.

Figures 35 and 36 contain the analysis described in the preceding paragraph. Factor values represented by single targets (in all cases T34) have been excluded. The slightly lesser movement that appeared consistently among targets on 3–6 cm of organic soil, in vascular plant densities ranging from 40 to 60 %, and in sedge meadow vegetation, suggests that some other factor (or factors) operated to modify the sequence that seemed to be effective in the case of target heaving.

Erosion and deposition

Small stream channels were noted in the vegetation transect made in 1957 (see below) as occurring between T3 and T8 (see Fig. 37). The most prominent of these on 14 July was about 50 cm wide and 5–10 cm deep, with T6 standing in it. Lesser ones were about 40 cm west of T3 (dry on 14 July), and near T8 (with a small running stream on 14 July). Target 7 was in sedge meadow bathed by sheet flow on a low divide between the channeled streams seen at T6 and T8. Target 5 was in a shallow silty depression about 50 cm east of the running stream which contained T6.

Evidence of sedimentation was abundant in the area embraced by these channels. Thin coatings of silt were on the targets, on patches of organic crust, and on the branches and persistent dead leaves of plants. Turf hummocks in the channel area were found to be impregnated with sand and silt, indicating that during their growth they were subject to flooding whereas those along the target lines beyond T8 had minimal quantities of mineral material in them (Raup, 1965 B, p. 58–59).

At the time of final study, 12 August, 1964, T4 had been washed or heaved out of the ground (or both). Target 5 was also out of the ground and gave evidence of having been washed out by the stream. Target 6 was lost, apparently washed away. Target 7 had remained essentially intact in its sedge meadow, but T8 was entirely out of the ground. Its position by the side of a rather well-defined channel makes it probable that erosion was at least partially responsible for this.

The present writer saw the targets from T34 to T43 exposed only once, in the summer of 1964. In two seasons of record they were not exposed at all (1957, 1960), while in the others not until late summer after the author's departure from Mesters Vig. Notes made in 1964 show that T36 was out of the ground. It was located in a shallow stream and

Fig. 37. View of ES 6, N from just below east end of target line; small stream channels in foreground; turf hummocks just beyond channel area, merging into sedge meadow toward margin of snowdrift. Photo 8 Aug., 1957.

presumably was washed out. Target 37, also out of the ground, was on organic crust and had a previous record of heaving. It is presumed here to have been heaved out. Target 38 was in a thin mat of living mosses, and appeared to be intact, as did also T39 which was in a mat of aquatic mosses bathed in slowly flowing water. Target 40 was in a shallow channel with a running stream, and apparently had been washed out. Target 41 was on bare silty clay loam with pebbles and cobbles, wet to saturation. Target 42, also on bare wet soil, was out of the ground, presumably washed out; and T43 was still standing in bare wet soil. The water for this western end of the target area came from the melting snowdrift which had only recently disappeared. There was little evidence of the erosion and sedimentation seen in the easterly part of the site.

Actual physical disturbance of the plants and the soils by the processes of stream erosion and/or deposition at ES 6 probably was limited to the vicinity of targets 3 to 8 and 36 to 43. Target 2 was low in altitude and not much above the stream. It may have received some silt in spring. Most of the activity at the easterly end of the target line occurred during spring snow-melt, when most of the remaining surface of ES 6 was still covered with snow and basal ice. Only the channel area was then open and subject to stream action. The target areas above 34–35 were affected only in mid- or late summer, and only in the seasons when they were exposed. Never did they experience the larger volume of rapidly flowing water that the easterly channels did.

With the data at hand it is possible to do no more than propose a gradient of three intensities of stream activity that may have affected the growth and survival of the plants. At one extreme was essentially no activity, represented by the area of targets 9 to 34–35, and including T1. The other extreme of intensity for ES 6 was represented by T4, 5, 6, 8, 36, 40, and 42. All of these targets were out of the ground, either washed out or partially so. Target areas that might be considered "intermediate" in this respect were T2, 3, 7, 37, 38, 39, 41, and 43.

The vegetation of ES 6

No map of vegetation types, similar to that for ES 7 and 8, was made for ES 6. A rather detailed transect, approximately 2 m wide, was made along the target line on two occasions: 14 and 25 July, and 8 August, 1957; and 12 August, 1964. The last target exposed by the melting of the snowdrift by 8 August, 1957, was no. 32. Consequently the vegetation around all targets from 33 to 43 (incl.) was noted only in the 1964 botanical records. The transect shown in Fig. 32 represents a combination of these two sets of notes.

Forty-five species of vascular plants were found in ES 6. Table 6 gives a list of them, and their distribution, on a presence or absence basis, among the vegetation types recognized, and also among the subdivisions of the environmental gradients of density of vascular plant cover, thickness of the organic layer over the mineral soil, intensity of disturbance by frost heaving, and intensity of disturbance by erosion and deposition.

The flora was about half the size of that found in the 2.2 hectares of the ES 7 and 8 map area, and it is evident from Table 6 that a large proportion of the species were found to be widely distributed through the vegetation types and through the gradients of coverage, thickness of the organic layer in the soil, and disturbance factors. Seventeen of

Table 6. *Species found in ES 6, showing their distribution among types of vegetation, vascular plant coverage densities, thicknesses of organic soil, and varying intensities of physical disturbance.*

	Types of vegetation						Coverage of the ground by vascular plants				Thickness of organic layer over mineral soil			Physical disturbance factors					
														Target heave			Erosion and deposition		
							0-20%	20-40%	40-60%	60-90%	0- 3cm	3-5cm	5cm	High (6.5cm)	Med. (3-6cm)	Low (2cm or less)	"High"	"Med."	"Low"
Equisetum arvense	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Equisetum variegatum			+	+	+			+	+	+	+	+	+	+	+	+			+
Festuca vivipara			+	+	+	+		+	+	+	+	+	+	+	+	+		+	+
Festuca rubra ssp. cryophila		+			+	+	+	+		+	+	+				+	+	+	·
Poa pratensis ssp. alpigena		+			+		+										+		
Poa arctica		+	+		+		+	+			+			+	+	+		+	+
Poa alpina		+	+			+	+	+		+	+	+		+		+	+	+	
Poa glauca		+					+										+		
Trisetum spicatum		+	+	+	+	+	+	+	+	+	+	+		+		+	+	+	+
Arctagrostis latifolia				+					+			+				+			+
Eriophorum Scheuchzeri		+	+		+		+	+			+			+	+		+		+
Eriophorum triste	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+
Carex scirpoidea		+	+	+	+		+	+	+	+	+	+	+		+	+		+	+
Carex parallela				+	+			+	+	+		+	+		+	+			+
Carex Lachenalii		+			+	+	+			+	+	+				+	+	+	
Carex Bigelowii			+		+		+	+			+	+			+				+
Carex misandra			+	+	+			+	+	+	+	+	+	+	+	+			+
Carex capillaris			+	+	+			+		+		+	+		+	+			+
Carex saxatilis			+	+	+			+	+	+	+	+	+	+	+	+			+
Juncus biglumis			+	+	+		+	+	+	+	+	+	+	+	+	+	+		+
Juncus triglumis			+	+	+			+	+	+	+	+	+	+	+	+			+
Luzula arctica			+	+				+	+		+	+		+		+			+
Luzula confusa					+														
Salix arctica		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Koenigia islandica			+				+				+			+					
Oxyria digyna		+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+
Polygonum viviparum		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cerastium alpinum		+			+	+	+	+		+	+	+				+		+	
Minuartia biflora		+	+		+	+	+	+		+	+	+		+	+	+	+	+	+
Minuartia stricta				+					+			+				+			+
Silene acaulis		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Ranunculus nivalis		+	+		+	+	+	+		+	+	+		+		+	+	+	+
Ranunculus sulphureus		+	+		+	+	+	+		+	+	+		+		+	+	+	+
Draba alpina		+			+	+	+	+		+	+	+				+	+	+	
Draba lactea				+		+			+	+		+				+		+	+
Saxifraga oppositifolia				+	+					+		+	+		+	+			+
Saxifraga foliolosa	+						+				+					+			+
Saxifraga hieracifolia			+		+			+			+		+		+				+
Saxifraga cernua						+				+		+				+		+	
Dryas octopetala			+	+	+			+	+	+	+	+	+	+	+	+			+
Cassiope tetragona				+	+					+			+			+			+
Vaccinium uliginosum			+	+	+			+	+	+	+	+	+	+	+	+			+
Pedicularis flammea			+	+	+			+	+	+	+	+	+	+	+	+			+
Pedicularis hirsuta			+		+			+					+			+			+
Erigeron humilis						+				+		+				+		+	

the 45 species (37.8 %) were found to be widely tolerant in the Mesters Vig district as a whole on the gradients of coverage, moisture, and physical disturbance (both frost and nonfrost induced). The flora was made up overwhelmingly of species that were common to abundant in the district as a whole. Thirty-three of them (73.4 %) ranged from common to abundant. Ten (22.2 %) were occasional, but locally common. Only two (4.4 %) were regarded as rare in the district, and these were also rare at ES 6. Not only was the vascular flora limited mainly to common species but also to species with preferences for wet or very damp sites, except for plants with wide tolerances on the moisture gradient.

With so small a number of species, and these so widely tolerant and wide-ranging on the environmental gradients for which data are available, it is probable that the calibrations of neither the external factors nor the tolerance ratings of the species are sufficiently refined to draw very clear relationships. Nonetheless the site as a whole had achieved a certain selection of plants from the flora of the district, and analyses of the inherent tolerances of the plants with respect to local factors may throw light on how this has come about.

These analyses have been approached in two ways: First in terms of three rather broadly and imperfectly defined types of vegetation that were highly generalized; and second, in terms of individual target areas within the transect, which were then grouped by common vegetational or habitat characteristics. The two approaches were rationalized as follows.

It is possible to see in photographs of ES 6 (Fig. 31; see also Washburn, 1967) and in the transect (Fig. 32) roughly defined patterns of vegetation. One of the most prominent vegetational differences appeared around T18–19. Approximately from T9 to T19 (incl.) the targets were among turf hummocks, while from T20 to about T32 (incl.) they were in variously constituted sedge meadows. From T32 to about T38 the ground cover by vascular plants was extremely scanty, and most of the area was characterized by organic crusts. These three types were the only conspicuous ones in the transect. Types occupying lesser areas were present, as will be noted below.

Closer examination of the actual plant habitats surrounding the targets showed that the generalized types described above commonly did not reflect true conditions. Most of the targets in the turf hummock area, for example, were on organic crusts, and so were the plants immediately around them. Some of these crusts were very thin over mineral soil (less than 2 cm), while others had an organic horizon 3–5 cm thick beneath them. In some of the sedge meadows there were relatively thick organic layers over the mineral soil, while in others the latter was covered merely by thin organic crust. These local differences among the target areas appeared to be related to differences in individual target behavior, particularly those concerned with frost heaving (see above). They suggest that analogous differences might have occurred among the plants associated with the individual targets.

Thus the second system of analysis treats the individual target areas, grouping them in terms of their actual local situations. In this process six fairly well-defined vegetation types appeared: sedge meadow, turf hummock, organic crust, aquatic moss mat, grass-sedge meadow, and nearly barren soil. The first three are the types noted above, but here their distributions were intermingled. Turf hummock vegetation, for example, was limited to those areas in which the targets were actually on hummocks. The other three types were more highly localized and of limited areal extent. The largest of them was that of nearly barren soil, for it included the channel areas near the eastern end of the target line.

The local conditioning factors used in the analysis were, in addition to the types of vegetation, the density of vascular plant cover, the thickness of the organic layer over the mineral soil, the intensity of disturbance by frost heave, and the intensity of disturbance by stream erosion and deposit. Physical disturbance due to gelifluction appeared to be minimal at ES 6, and was regarded as negligible so far as the plants are concerned.

Distribution of species in experimental site 6 with respect to their tolerance of variation in vegetative coverage of the ground, soil moisture, and physical disturbance

Introduction

Methods used in presenting and analyzing data here are the same as those used for ES 7 and 8, to which the reader is referred. As in the former case, the graphs in Figs. 38 and 39 are based on numbers of species that have been reduced by subtracting the number of species in their appropriate categories which are widely tolerant on all the gradients studied and are thus regarded as non-definitive. No species narrowly tolerant on all gradients were found in this flora.

It should be emphasized that these graphs are no more than suggestive, and that they contain a "built-in" source of error and confusion. For example, on the frost disturbance gradient an increase in the proportion of species narrowly tolerant of frost heaving parallel to increasing density of plant cover is the expected reaction to the decreased heaving that usually accompanies increased density. This increased density also usually accompanies a thicker organic horizon though this is not always the case because organic soils may be largely covered by organic crusts with low densities of vascular plant cover. Also, dense

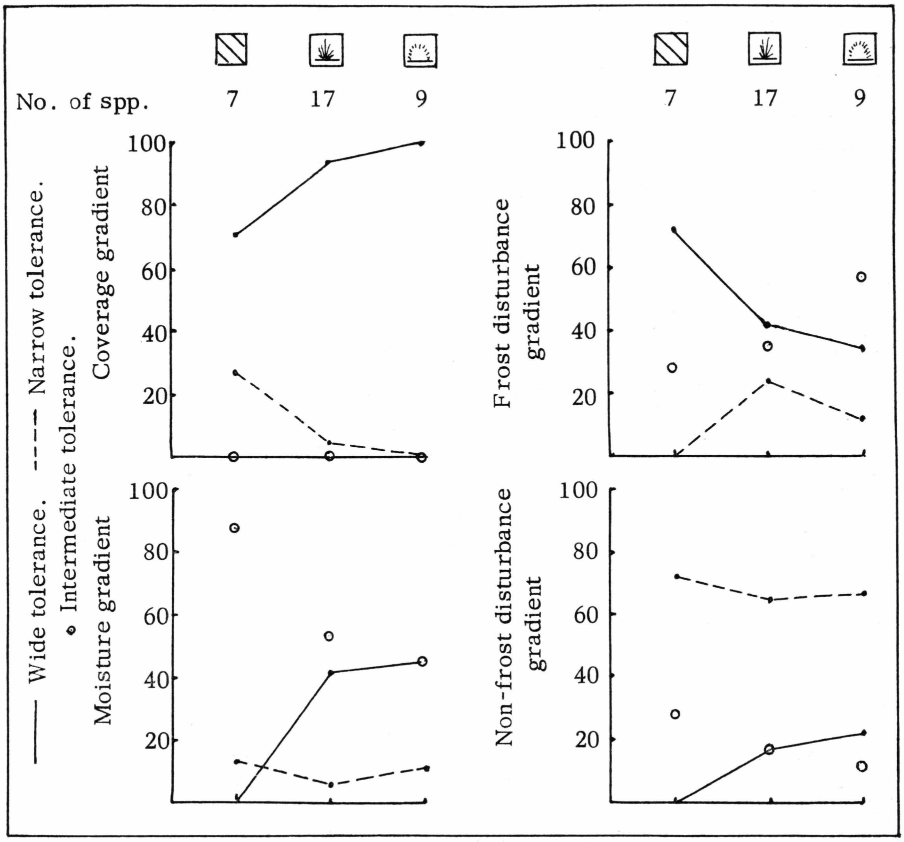

Fig. 38. Percentage distribution of species tolerance on coverage, moisture, and physical disturbance gradients in the three principal vegetation types at ES 6.

vegetations may occur on relatively thin organic horizons. Species combinations formed in this way tend to mix the effects of single factors, to produce apparent paradoxes in habitat selection by the species. It is probable that the mixtures tend to "flatten" the curves in some cases, making the minor variations in them difficult or impossible to interpret.

Analysis in terms of generalized vegetation types

Figure 38 gives the distribution of species tolerance percentages on the coverage, moisture, and physical disturbance gradients in each of the three most conspicuous vegetation types. The curves in these graphs suggest the mixture of vegetation types mentioned above.

Behavior of species on the coverage gradient

The graph for the coverage gradient reflects the prevailingly high proportion of definitive widely tolerant species in the Mesters Vig flora as a whole. However, the proportion was not as high in this case as in many others (see Fig. 39, below). Furthermore, it was not clear why there should be more in the sedge meadow and turf hummocks than in the organic crusts. Nor was it clear why there should be so large a number of more sensitive species in the organic crusts.

Behavior of species on the moisture gradient

On the moisture gradient the absence of any definitive widely tolerant species in the organic crust areas, and a relatively large number of species more sensitive to variations in the moisture supply, was to be expected in so wet a site. But although the sedge meadow was almost if not quite as wet, there was a notable increase in the number of widely tolerant plants here on this gradient, and a small decrease in more sensitive species. The turf hummock area might have been expected to have also a considerable number of sensitive species, and it does. Thus the flora of the organic crust area behaves as expected, but those of the other types show inconsistencies which may be attributed to their mixed nature.

Behavior of species on the disturbance gradients

The same, in part, may be said of the frost disturbance gradient. The organic crust area was known for relatively intense frost heaving, and should have had a relatively high percentages of plants widely tolerant of this kind of disturbance. It should have had relatively few that were sensitive to frost heaving. This proved to be the case, and the percentages were more nearly equal in the sedge meadow as expected. In the turf hummocks there should have been still fewer widely tolerant species, and there were; but the plants more sensitive to heaving also decreased rather sharply, whereas there should have been as many or more than in the sedge meadow. It was said earlier that many of the actual target areas among the turf hummocks were covered by organic crusts, and it is probable that the mixture of their flora with that of the hummocks reduced the percentages of sensitive species here. A similar situation was found in the turf hummock areas at ES 7 and 8.

The nonfrost disturbance gradient appeared to involve erosion and deposition by the small streams almost exclusively. It had little or no visible effect in most of the three areas considered here, though there may have been slight washing in the eastern part of the hummocks and in the western part of the organic crust zone. The analysis suggests that the latter was actually the most stable in this respect. In the crusts the number of narrowly tolerant species reached its highest percentage, and there were no definitive widely tolerant ones. An increase in widely tolerant species in the turf hummock area suggests that the streams may have had some effect on the plants there. A conspicuous feature of this

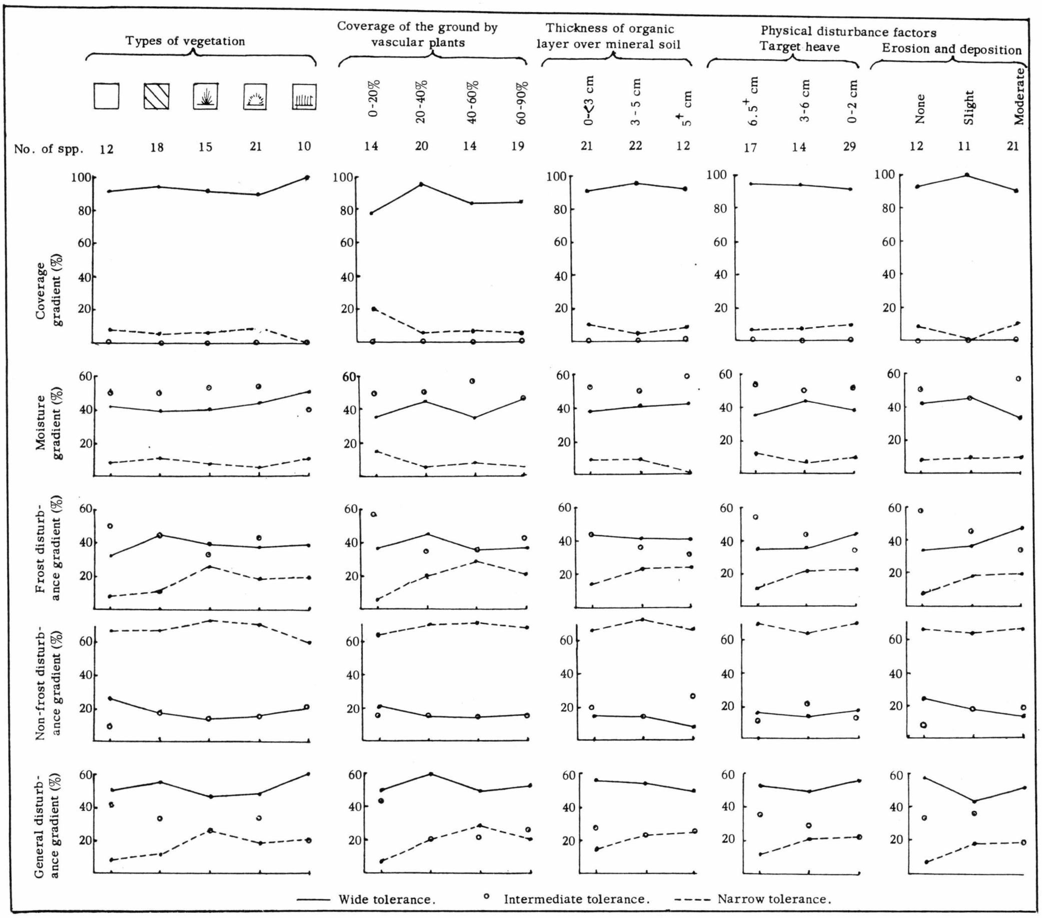

Fig. 39. Percentage distribution of species tolerance at ES 6, analyzed for individual target areas with respect to differing vegetation types, ground coverage by vascular plants, thickness of organic soil, and intensity of physical disturbance.

graph, seen also on others for the nonfrost disturbance gradient, is in the large numbers of narrowly tolerant species in proportion to those with wide tolerance.

Analysis in terms of individual target area vegetations

Behavior of species on the coverage gradient

In all cases except one the definitive widely tolerant species on this gradient exceeded the narrowly tolerant by factors ranging from about 10 to over 18 (Fig. 39). The exceptional case was that of the lowest percentage of vascular plant cover (0–20 %), where the factor was about 3.7. Plants narrowly tolerant on this gradient showed consistently low percentages, from 0 to 21.4 % and averaging about 7.3 %. In fact only four species in the entire flora of the transect were narrowly tolerant of variations in coverage. One was noted as rare in the Mesters Vig district, and the other three as occasional or locally common.

Other differences shown by the application of the external factor gradients to the inherent tolerance characteristics of the plants with respect to coverage appeared to be minor. All but the single exception noted above stayed within a range of about 10 %.

Behavior of species on the moisture gradient

The behavior of the species tolerance groups on the moisture gradient with respect to the other factor gradients studied showed relatively minor variations. In all cases the plants most sensitive to variations in the factors were less prominent than those of wide tolerance. The range of difference between these two groups, however, was not as great as that found on the coverage gradient. In nearly all cases the factors range from 3 to 10. Variations in individual curves of moisture tolerance were too small to be significant.

Behavior of species on the physical disturbance gradients

The frost disturbance gradient: It has been shown above that among the external factor complexes injurious to plants in ES 6 the one producing the most readily measurable variations was frost heaving. Its relative intensities were gauged by the amounts of cone-target heaving, and were shown to be related to the depth of the target insertions, to variations in the thickness of the organic horizon over the mineral soil, and to the nature and density of the vegetative cover. It might be expected that under these circumstances the plants would be selective in their distribution along the target line consistent with the tolerance ratings on the gradient of physical disturbance due to frost heaving.

Evidence for this, though it appeared, as in the case of the moisture gradient, mainly as directional trends in the curves for narrowly tolerant plants, was fairly consistent. The curves for these species showed upward trends from sites with nearly bare soil or organic crusts toward sites with denser vegetation in sedge meadows and turf hummock areas; from sites with thin organic soil horizons to those with thick horizons; and from sites with relatively greater cone-target heave intensity to those with lesser intensity. In the sites with least heave there were 1.5 to 5 times as many species sensitive to this kind of disturbance as in sites with maximum heaving.

The curves for widely tolerant plants on this gradient would be expected to show downward trends, suggesting that sites with least heaving would have had the smallest percentages of plants very tolerant of such disturbance. However, these curves, though they show some minor variations, are nearly level except for the one on cone-target heaving which trends upward rather than downward. The curves for sites of differing intensities of erosion and deposit were also equivocal, showing upwards trends in both from sites with no disturbance to those with a moderate amount. With respect to frost disturbance, however, areas with little or no erosion contained a mixture of micro-sites. Though these areas contained sites with relatively dense vegetation and low heave intensities, they also included much of the land occupied by organic crusts where heaving was intense. Consequently the curves here can be expected to be equivocal.

The curves based upon vegetation types are notable for a median proportion of species very sensitive to frost heaving, and a relatively large number of widely tolerant ones in the organic crust type. In ES 7 and 8 the most intense heaving was in this type. One might expect the same effects in the "bare" ground type, but this included several habitats in ES 6, some of which were subject to intense heaving and some were not. Some were bathed with sheet-flow at the time when heaving might have occurred, and their plants would not have been much affected.

The nonfrost disturbance gradient: The plants of the ES 6 area were distinguished throughout for high percentages of narrow tolerance on the nonfrost disturbance gradient. These were accompanied by relatively low percentages of definitive widely tolerant species. The difference between these values ranged from about 40 % to as much as 60 %. The principal processes producing this kind of disturbance were downslope movement of the surficial soils by gelifluction, and subaerial erosion and/or deposition by the streams.

It is probable that the gelifluction movement (av. ca 1 cm/yr.) was here relatively insignificant as an agent disturbing to living plants. The small amount that occurred was rather uniform. Observations at ES 7 and 8 indicated that fairly dense mats of vegetation such as occurred in several parts of ES 6 tended to reduce the disturbing effects of whatever movement of this kind there may have been.

Erosion and deposition were for the most part confined in space to the stream channels and their immediate environs, and in time to a short period in spring when snow and basal ice helped to keep them in the channels. Of the seven target areas considered to have had a moderate intensity of disturbance, four (T4, 5, 6, 8) were in the easterly channels of the line. All the species noted in them were in the channels or on their margins, or on small deposits of alluvium recently laid down or reworked by the small streams. The other three areas (at T36, 40, 42) were all on the poorly vegetated surface toward the west end of the target line, much of it under snow throughout many summers. Targets 40 and 42 had no vascular plants around them, and T36 had only one (*Poa alpina*) which made no addition to those listed near the eastern end of the line. All of these moderate intensity areas had active streams in them.

Half (9) of the species listed for the channel areas were widely tolerant, six of them wide on all gradients. Of the remaining nine, one was intermediately tolerant of nonfrost disturbance and the other eight were narrowly tolerant. If the application of the tolerance rating in this way is valid, it suggests that the moderate intensity was quite low in comparison to the nonfrost disturbance the Mesters Vig flora undergoes elsewhere in the district. The flow in the small streams that crossed the target line was indeed small, and its confinement to a short period in spring before most of the flora began active growth probably accounted for its small effect upon the vegetation.

Variations within the curves on the nonfrost disturbance gradient probably are of small significance in view of the great preponderance of definitive narrowly tolerant species. An element of uniformity was brought by the more or less uniform gelifluction, and the variations probably were caused by varying combinations of the highly localized data on erosional areas with data not so localized. Also most of the data for the moderate intensity erosional sites appeared nowhere else.

The general disturbance gradient: Analyses on the general disturbance gradient, as might be expected, "averaged" the effects seen on the frost and nonfrost gradients. The sharp reversal in the percentages of species narrowly and widely tolerant on the two gradients essentially disappeared, suggesting that in the vegetation as a whole nonfrost disturbance plays a small role.

Distribution of roots and underground stem structures among species in ES 6

The distribution of the underground parts of the plants in ES 7 and 8 suggested that increasing moisture favored higher percentages of rhizomatous plants and lower percentages of taprooted species, though both reactions may have been due in part to lesser frost heaving in the more dense vegetation of the wettest parts of ES 7 and 8. The prevailingly wet to very moist conditions throughout ES 6 seem to have had an analogous effect upon its whole flora. It has been noted elsewhere (RAUP, 1968) that in the total flora of the Mesters Vig district only about 16% of the species had well-developed rhizomes, while the remaining 84%

were about equally divided between those with fibrous roots and taproots. In ES 6, 22 % of the species had rhizomes and about 47 % had fibrous roots, leaving about 31 % with taproots. When only the definitive species are counted, the general effect of the site is even more striking: rhizomatous, 28.6 %; fibrous rooted, 57.1 %; taprooted, 14.3 % (numbers not weighted for vegetative propagation).

Variations in the proportions of the three underground root and stem systems along the gradients of vegetation type, coverage, organic layer and disturbance factors were present, as they were in some of the tolerance ratings (see Fig. 40, in which only definitive species were used in the analyses). Taprooted species remained in the minority on all the gradients, equaling or superceding the rhizomatous at only two points. Nowhere did they rise above about 23 % of the flora, and their range of variation throughout was less than 6 %. Thus they provided almost nothing useful for comparative study, and suggest general uniformity in the relatively high moisture supply to the whole site. On the other hand fibrous rooted and rhizomatous species showed differences on the gradients ranging from 12 % to 30 %. Because the percentages of taprooted species were nearly similar within each gradient, the curves for fibrous rooted and rhizomatous species are essentially mirror images. The rhizomatous plants probably were most sensitive to variations in the moisture, disturbance and vegetative gradients, and are therefore the most useful for comparisons.

Rhizomatous species were proportionately most numerous in sedge meadow vegetation (Fig. 40). They reached their lowest percentage in the grassy meadow at the eastern end of the target line in which the soil was drier in summer than in any other type. In the consistently wet part of the site they were least numerous in the organic crust areas where frost heaving usually was greatest. They were intermediate between these two in turf hummock vegetation and in nearly bare soil. Heaving was also intense in some of the nearly bare soil areas, but with respect to this factor this type was mixed, for some of the areas were dried out in late summer or bathed with flowing water, and probably were not subject to intense heave.

On the coverage gradient (Fig. 40) rhizomatous plants showed the highest percentage in vegetative densities of 40–60 %, which is apparently anomalous because one would expect them to be most numerous in the densest vegetation. However, nearly all of the higher densities were in the sedge meadows (Fig. 32) and the average for all of them was about 62 % of ground coverage. Most of the remainder of the denser cover was on turf hummocks, and averaged about 55 %. Thus the rhizomatous species, most numerous in these two types, showed the highest coverage tolerance near the upper limit of the 40–60 % category which

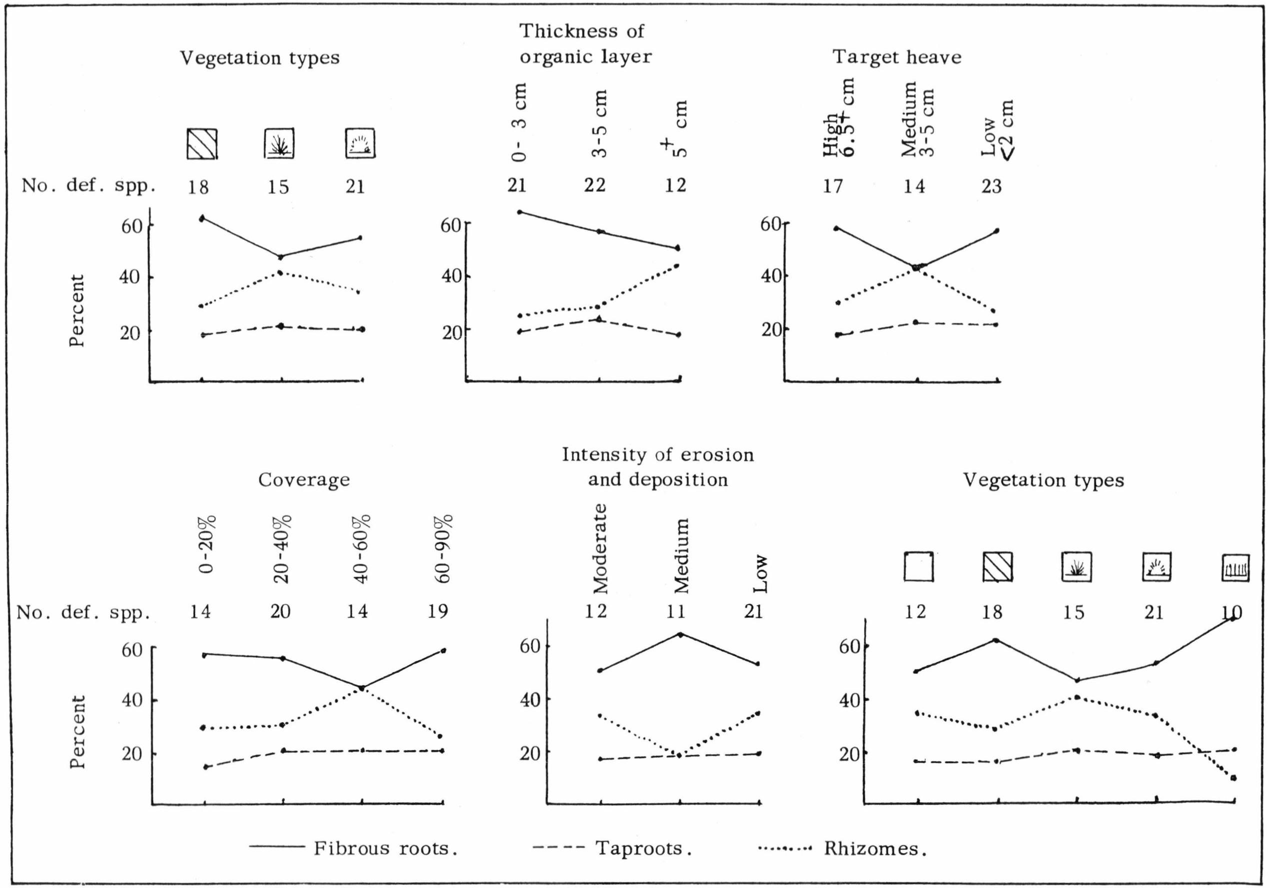

Fig. 40. Percentage distribution of fibrous rooted, taprooted and rhizomatous species at ES6 in differing types of vegetation, thicknesses of organic soil, vascular plant coverage, and physical disturbance.

included the average density for these types. When vegetations with densities of 60–90 % are considered alone the average was about 76 %, but only half of the target areas among them were in the sedge meadows preferred by rhizomatous plants. The others were in turf hummocks or in the drier grassy meadow at target 1, both of which had smaller proportions of these plants.

Many of the differences described above are small, but they suggest that high moisture content accompanied by a thick organic layer over the mineral soil was more effective in raising the proportion of rhizomatous species than was the factor of coverage density.

The behavior of the species on the gradient of frost heaving (Fig. 40) also presented an apparent anomaly. The three intensities of heave were each found in a mixture of vegetations. In the most intensely heaved 20 cm target areas the vegetation was principally in organic crusts (4 targets) or in nearly barren ground (1 target). Only two of the seven targets in this category were in a vegetation favorable to rhizomatous plants (sedge meadow). Therefore the low percentage of these plants seen in Fig. 40 is the expected one. In the medium heave category three of the eight target areas were in sedge meadow (2) and turf hummock vegetation (1), and one in open ground bathed with water. Thus about half of these areas were favorable to rhizomatous plants, and the curve shows an expected rise. Only three 20 cm targets were in areas of low heave intensity, one each in sedge meadow and turf hummocks, and one in the grassy meadow at target 1. The first two suggest a percentage of rhizomatous plants that would be at least as great as in areas of intermediate heave (40–50 %), but Fig. 40 shows an even lower percentage than in areas of high heave intensity. A suggested explanation of this anomaly is that the very small proportion of rhizomatous plants at target 1 (Fig. 40) was sufficient to lower the proportion of them in the mixed group of sites that exhibited low heave intensity.

The most anomalous distribution of root systems is seen in Fig. 40, in which three roughly defined intensities of disturbance by erosion and deposition are used. It has been said earlier that the actual amount of effective disturbance by these factors was not great. Probably it injured the plants only in the most active of the small stream channels, all of which had very small scattered floras or none at all. These channels were wet in spring, but commonly their soils became relatively dry in late summer. Frost heave data for the targets located in the most active channels are not available, for the targets appear to have been washed out. But it is possible that heave injury to plants in these areas was not as great as in the organic crusts where autumn moisture probably was more regularly abundant. If the streams were flowing in the autumn, this also would lessen frost heaving in their channels at the time of freeze-up. Thus the relatively high percentage of rhizomatous plants in the channels may be accounted for by the abundant moisture and freedom from frost injury during at least the major part of the growing season.

The large area of sedge meadow and hummock vegetation, which was essentially undisturbed by erosion, was also moist to wet throughout the summer and contained the vegetation types that had the highest percentages of plants with rhizomes. The relatively high proportion of these plants in this low disturbance intensity (Fig. 40) was therefore to be expected. The relatively low percentage in areas of "medium" intensity is not readily explainable unless by the fact that the seven target areas involved were highly variable in vegetation type, showed a relatively large proportion of high and intermediate heave intensities, and a relatively low representation of vegetation types particularly favorable to rhizomatous plants.

Summary and discussion, ES 6

It is clear from the preceding analyses that the geographic sorting of species along the target line of ES 6 in terms of tolerance ratings was not well defined, whether the working units were generalized vegetation types or groups of similar individual target areas. At several points in the analyses, however, there were indications that although there may not have been much variation along the target line, the site as a whole has functioned as a sorting mechanism. Table 7 presents numbers of species and percentages to illustrate the extent of this sorting.

Before making any of the computations shown in the table 39 species were excluded. Twenty-two were widely tolerant on all gradients, and the remaining 17 were narrowly tolerant on all gradients. They were therefore regarded as non-definitive. No species were found to be intermediately tolerant on all gradients. Only the numbers of definitive species were used throughout. The percentages show the ratio, for example, of the definitive widely tolerant species on the moisture gradient found in ES 6 to the total number of these species on this gradient in the whole Mesters Vig flora. Thus the table gives comparative percentage figures of the extent to which ES 6 as a whole has drawn upon the species "pools" in the three tolerance ranges as the latter apply to the factor gradients.

A general view of Table 7 shows that the narrowly tolerant species with respect to the coverage, moisture and frost disturbance gradients were represented by the lowest percentages of the definitive species available. The reverse was the case with respect to the nonfrost disturb-

Table 7. *Comparison of the floras of ES 6 and the whole Mesters Vig district in terms of their species tolerance ratings on coverage, moisture, and physical disturbance gradients, showing the extent to which ES 6 as a whole has drawn upon the total tolerance groups of the district.*

	Widely tolerant species			Intermediately tolerant species			Narrowly tolerant species		
	No. of spp. in Mesters Vig flora, excl. all widely tol.	No. of spp. in ES 6	%	No. of spp. in Mesters Vig flora	No. of spp. in ES 6	%	No. of spp. in Mesters Vig flora, excl. all narrow tol.	No. of spp. in ES 6	%
Coverage gradient	63	24	38.1	23	0	0.0	29	4	13.5
Moisture gradient	39	10	25.6	48	14	29.2	28	4	14.3
Frost disturbance gradient	21	11	52.4	35	12	34.3	59	5	8.5
Non-frost disturbance gradient	20	4	20.0	35	5	14.3	60	19	31.7

ance gradient, where the narrowly tolerant species were represented by the highest percentage of those available (see Fig. 39). Conversely, the widely tolerant group was represented by the highest percentages of available definitive species on the coverage and frost disturbance gradients, and the lowest percentage on the nonfrost gradient. On the moisture gradient there was a slightly larger percentage of species with intermediate tolerance, consistent with the large proportion of these plants in the flora generally.

Probably the most significant single external factor determining the distribution of plants in the Mesters Vig tundra is the moisture supply. It affects the lives of the plants not only directly, but indirectly by its influence upon the rates and kinds of physical disturbance in the soils. The general abundance and uniformity of the water supply to ES 6 throughout the growing season has already been stressed, and probably provides a basic reason for the general uniformity in the selection and behavior of the plants.

The total vascular flora of ES 6, due to the prevailingly high moisture content of the site, was drawn from two major groups: those with the widest tolerance on the moisture gradient, of which there are 61 in the whole flora of the Mesters Vig district, and those whose moisture preferences were in sites with high and medium moisture. Of the 61 species with wide tolerance, 27 were found in ES 6. These cannot be considered definitive with respect to the selective capacity of the site on this gradient. Seventy species in the total flora of the district have shown preferences for medium, medium-to-wet, and wet habitats. From these came the remaining 18 species in the ES 6 flora: 6 with medium moisture preferences, 5 with medium-to-wet, and 7 with wet. No species with preferences in the drier part of the moisture spectrum were seen.

The ES 6 habitat drew upon the defintive species with relatively high moisture preferences in the Mesters Vig flora (wet and medium-to-wet) to the extent of about 35 % of those available. It had of those with medium moisture preferences only about 13 % of those available, and none of those with preferences for less moisture.

The general paucity of the ES 6 vascular flora was thus due partly to its being drawn in considerable measure from the plants with preferences for the wetter habitats, and also partly to the small size of the area. The actual area involved in the detailed study of ES 6 was only about 200 sq. m, a small fraction of that used at ES 7 and 8. A primary result of this small size was that most of the vascular plant cover was made up of the ubiquitous species of the Mesters Vig flora. No less than 33 of the 45 species (73.3 %) are common in the district as a whole, or are abundant. Only two are rare, and the remaining 10 are occasional but locally common. The common to abundant group contained all of the 17 species that were widely tolerant on all gradients. Experience with the rare to occasional species, which have mixed tolerance ranges, has demonstrated repeatedly that finding more of them requires not only a wider range of habitats than ES 6 affords, but also more space. Even with habitats available they are scattered in the landscape and may or may not be present in expected places.

With respect to the disturbance factors the site as a whole appeared to have selected plants from two rather widely differing tolerance groups. The relatively high percentage of species narrowly tolerant on the non-frost disturbance gradient contrasted with the median percentage of these more sensitive species on the frost disturbance gradient (see Fig. 39). Gelifluction movement along the target line has been shown to be small and relatively uniform; most of the little that occurred was rendered innocuous to plants by more or less continuous mats of vegetation.

Disturbance by stream erosion and deposition was highly localized in space, and confined in time to a period before much active growth occurred. Consequently disturbance by nonfrost factors appeared to be of little significance in ES 6, and most plants intolerant of this kind of disturbance grew there with impunity.

On the other hand, frost induced disturbance was known to be present because of the observed heaving of the targets, and the heave element in the annual measurements of target jump. But much of the effectiveness of the heaving, so far as the plants were concerned, was reduced by relatively thick organic layers over the mineral soil and/or vegetative cover of varying kinds and densities. The general result, for the site as a whole, seemed to be frost induced disturbance of intermediate intensity, with a few areas of organic crust, or nearly barren damp ground, showing high intensity. The tolerance analyses are reasonably consistent with this, and the plants of ES 6 showed a relatively low representation of species narrowly tolerant on the frost disturbance gradient, and relatively high percentages in the intermediately and widely tolerant groups.

Although the site as a whole has selected more widely than narrowly tolerant plants from the Mesters Vig flora, the differences were not very great except in the case of the frost disturbance processes (see Table 7). Even when the percentages were reversed, as in the nonfrost gradient, the difference in percentage was by a factor of only about 1.6. On the coverage gradient it was about 2.8, and on the moisture gradient about 2.0. On the frost disturbance gradient 11 of the 21 definitive widely tolerant species available appeared in ES 6 (52.4 %), while only 5 of the 59 narrowly tolerant species appeared (8.5 %). Thus this difference was by a factor of about 6.1.

The above findings lead to the tentative conclusion that the most effective restraints upon the size of the flora of ES 6 were the relatively abundant water supply which eliminated species with preferences for the drier habitats, and the small size of the area which eliminated a great many rare and occasional species whose distribution is spotty. Among physical disturbance factors, frost heaving appeared to be partially effective in limiting the flora, and nonfrost disturbance to have little or no serious effect. Within the area the only factor that seemed capable of affecting materially the local distribution of the plants was frost heaving. However, the evidence that it did so was not all unequivocal. Areas in which organic crust was the predominating ground cover demonstrated it rather clearly, but its gradient was confused by the mixture of habitats that occurred in many target areas. Furthermore, it was intimately related to the varying density of the vegetation and the thickness of the organic horizon in the soil. Both of these, with observed differences in the soil profiles and the distribution of root and underground stem systems, suggest minor variations of soil moisture along the target line that were not measured.

The transect of the vegetation in ES 6 (Fig. 32) bears a strong resemblance to that of a typical "wet meadow—turf hummock system" in the Mesters Vig district (RAUP, 1965 B, p. 63, Figs. 18, 19). An area of organic crusts bordered the snowdrift and underlay its margin (targets 33–38). Beyond this was a zone of sedge meadow, commonly on a substratum of moss, and in some places there were mats of aquatic mosses with almost no vascular plants (T20–T32). Low ("incipient") turf hummocks appeared in this area (T31 and T28) which became generally larger and more numerous at increasing distances from the margin of the drift. An area of larger, more densely aggregated hummocks followed (T19 to about T12–13). In the easterly part of this zone the hummocks began to thin out, and between T12 and T8 they were increasingly far apart, showing evidence of decay and disintegration.

A similar sequence could be seen in the map area of ES 7 and 8, greatly modified by the behavior of the principal source of water, a large snowdrift that projected across the system at a pronounced angle. The turf hummock system at ES 6 was also modified by the behavior of the moisture supply, but apparently to a much smaller extent. The principal difference in vegetational development between the two areas arose from the fact that ES 6 had two major sources of moisture both of which were continuous throughout the season, while the ES 7 and 8 area had only one. Had there not been drainage from the valley north and northwest of ES 6, the transect would have shown progressive desiccation eastward from the margin of the snowdrift, and the turf hummocks in the vicinity of T1 to T12 would have been greatly reduced or entirely eliminated. Continued water supply from the valley, as seepage or small stream flows, partially maintained these hummocks. The only complete destruction has been in the actual channels of the most active of the small streams, and even here a few hummocks have survived or been newly constructed on the channel margins by silt accumulation in the growing mosses.

To be consistent in the above interpretation of ES 6 vegetation, it is necessary to assume that within the past 60–75 years the general water supply from both sources has decreased materially (RAUP, 1965 B, p. 96–99). Presumably the showdrift was formerly larger and/or maintained a large flow of melt-water during more years. At the same time more and larger drifts in the valley above the site would have been delivering more seepage water and flowage in the channels.

On the other hand, the top of the present drift came nearly or quite to the top of the low trap knoll behind which it formed. It is possible that this has always set a limit to its height, and thus a limit to its eastward extent. If this is the case there may have been very little progression of vegetational zones in the wet meadow—turf hummock system described above. Rather there would have been gradual, though only partial, desiccation more or less *in situ.*

The soil profiles described by Ugolini lend support to this view. An organic layer over the mineral soil accumulates more rapidly under sedge meadow than under turf hummock vegetation. The latter is characterized rather by the dissection of the organic layer, and its eventual removal except under the hummocks themselves. In sedge meadows the layer accumulates, and if the water supply is fairly constant it continues to do so. The relatively thick accumulation of the organic horizon in the sedge meadow zone of ES 6 suggests that the process has been continuous there for many years. The layer was much thinner in the turf hummock zone except in the hummocks. Probably more significant is the evidence of gleying that Ugolini found under the targets westward from T 17–19. This suggests a rather long-continued high water table under a humic horizon.

EXPERIMENTAL SITE 17

Introduction

Experimental site 17 was a large and conspicuous gelifluction lobe at an altitude of about 750 m on the easterly slope of Hesteskoen. The total area involved was approximately 500 sq. m. The site was described in considerable detail by WASHBURN in paper No. 4 of the present series (WASHBURN, 1967, Figs. 38–42). The reader is referred to his paper for more data than will be given here.

The vegetation of ES 17 was first described on 21 July, 1956. On 5 August, 1957, further detail was added and the axial and transverse lines of cone-targets were installed. The first observations of target movement were made on 16 July, 1958, with a few more notes on vegetation. Final observations of vegetation were made on 11 August, 1964, when the targets were excavated.

Topography and soils

The gradient of the general surface of the mountain slope in the immediate vicinity of ES 17 ranged from 15° to 23° (Fig. 41). This surface was composed principally of pebbles and cobbles. The lobe was about 20 m wide at the widest part, and approximately 30 m long (up- and downslope) (Fig. 42). The length was difficult to determine accurately because the upper part merged imperceptively with the surrounding surface. The lobe front at the lower end was as much as 3 m high in places, with a slope commonly exceeding 45°. In some places the front was vertical or overhanging. The lateral margins were of varying steepness, gradually becoming lower and less steep upslope until they disappeared at the upper limits of the structure. The tread of the lobe had a slope of about 12° over nearly all of its surface.

The lobe was composed of a very stony diamicton, mainly a clayey-silty-gravelly sand, containing fines to the extent of 24 % to 34 %. It was located near the upper limit of glacial erratics on Hesteskoen, and probably its materials were in part derived from till. However, fragments

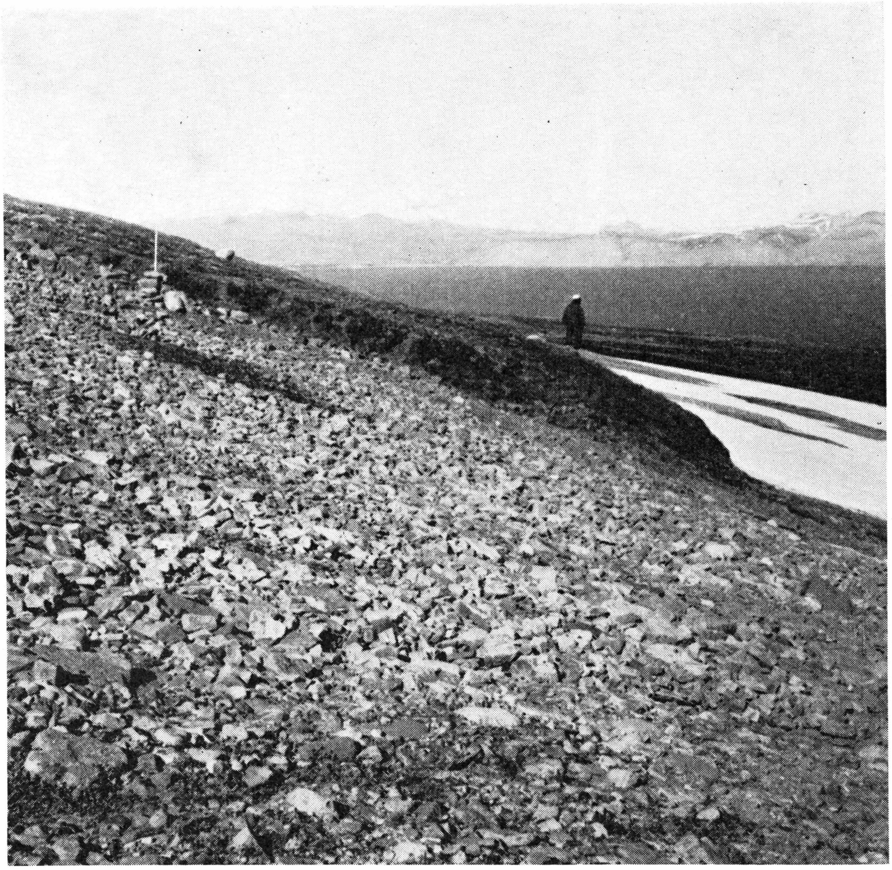

Fig. 41. Experimental site 17, on east slope of Hesteskoen. View north, 5 Aug., 1957. From WASHBURN, 1967, Fig. 39.

wedged from the local sandstone bedrock were incorporated in it. The diamicton of the tread was somewhat coarser towards the surface than below, and contained an abundance of pebbles and cobbles (Fig. 43). There were a few isolated small boulders on the surface.

The front of the lobe at its lower edge was composed of two topographic elements (Fig. 44). The uppermost of these, occupying roughly the upper half of the front, was a hummocky surface formed by densely vegetated masses of soil. These masses were irregular in shape and size, ranging from a few centimeters up to 50 cm in average diameter. They were commonly separated by narrow channels through which water flowed down from the tread. The hummocks of soil and vegetation sometimes overhung the lower section of the front. The lower part of the front was composed of the same materials, but showed little of the hummocky structure. It was covered by a nearly continuous, dense mat of vegetation.

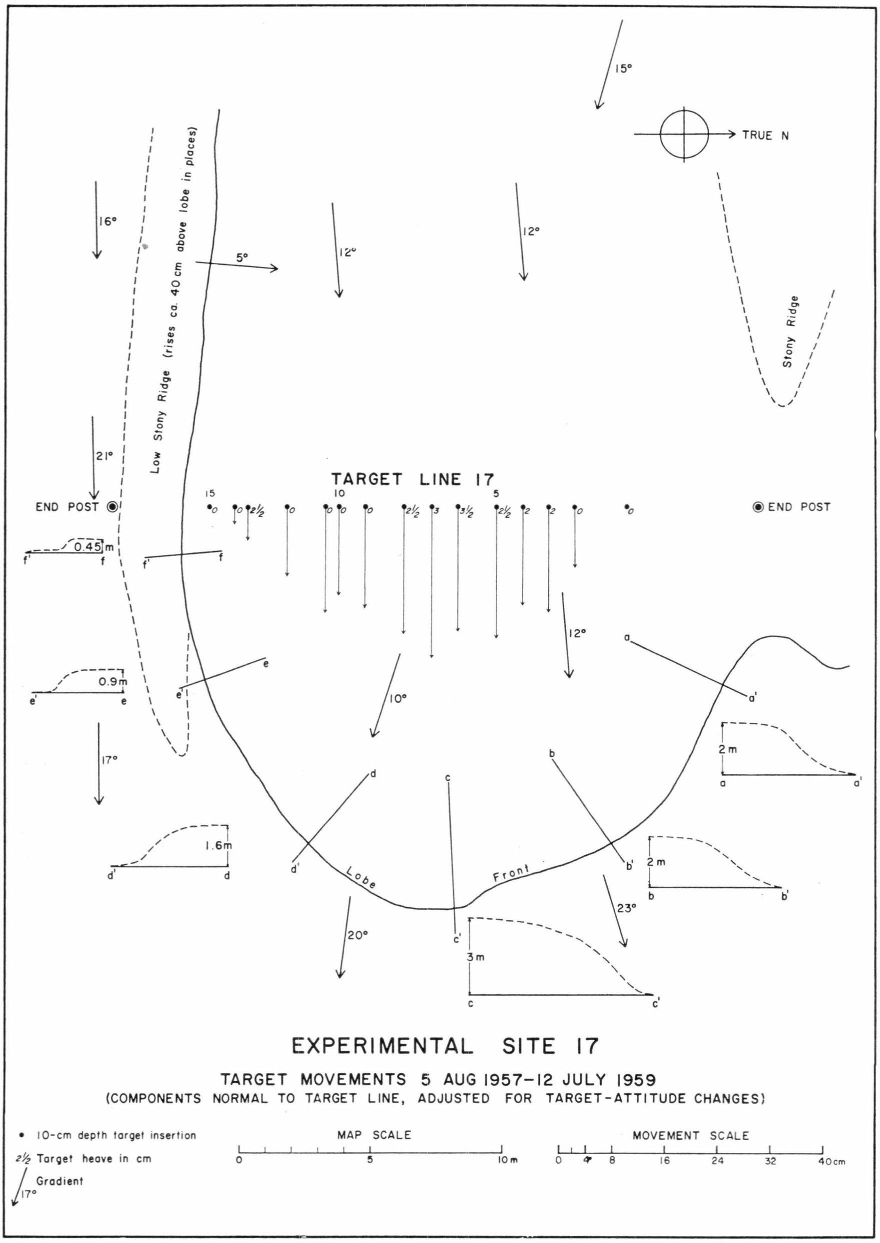

Fig. 42. Map of ES 17, showing transverse target line and target movement from 5 Aug., 1957, to 12 July, 1959. From WASHBURN, 1967, Fig. 38.

Fig. 43. Surface of gelifluction lobe tread, ES 17. Photo 21 July, 1956.

The lateral margins of the lobe were of diamicton, and were also fairly well covered with vegetation (Fig. 45). As noted above, the margins gradually lost height and steepness upslope, and the vegetation became less dense.

Moisture and its distribution at ES 17

The site was not visited enough times during any one season to make possible a precise description of the seasonal moisture regime. However, on all visits during July or August the central part of the tread and the front were found always to be wet or very moist, commonly with water running over the surface in small rills or seeping through the vegetation on the front. A few moisture determinations were presented by Washburn (1967, Table F VI) based on samples from the tread. They were collected on 16 July, 1958, 27 August, 1960, and 17 August, 1961, and showed

Fig. 44. Front of gelifluction lobe, ES 17, showing hummocky upper section overhanging the lower section, 5 Aug., 1957.

that soils from the central part of the tread, in the vicinity of targets 2, 5–6 and 7, all had notably higher water content both at the surface and down to 10 cm than did any of the soils near T 13–14 which were in the southern marginal zone of the tread. The steep lateral margins of the lobe were found to be progressively drier upslope from the front, so that about halfway between the lower end of the lobe and the southern end of the target line a certain amount of dry creep could be seen in the surface fines of the diamicton.

On the tread, as suggested by the moisture determinations above, the diamicton was progressively drier from the central portion toward the lateral margins. The surface materials were also slightly drier in the lower axial part of the lobe a meter or two just above the frontal break in slope, probably due to a lower water table in this area.

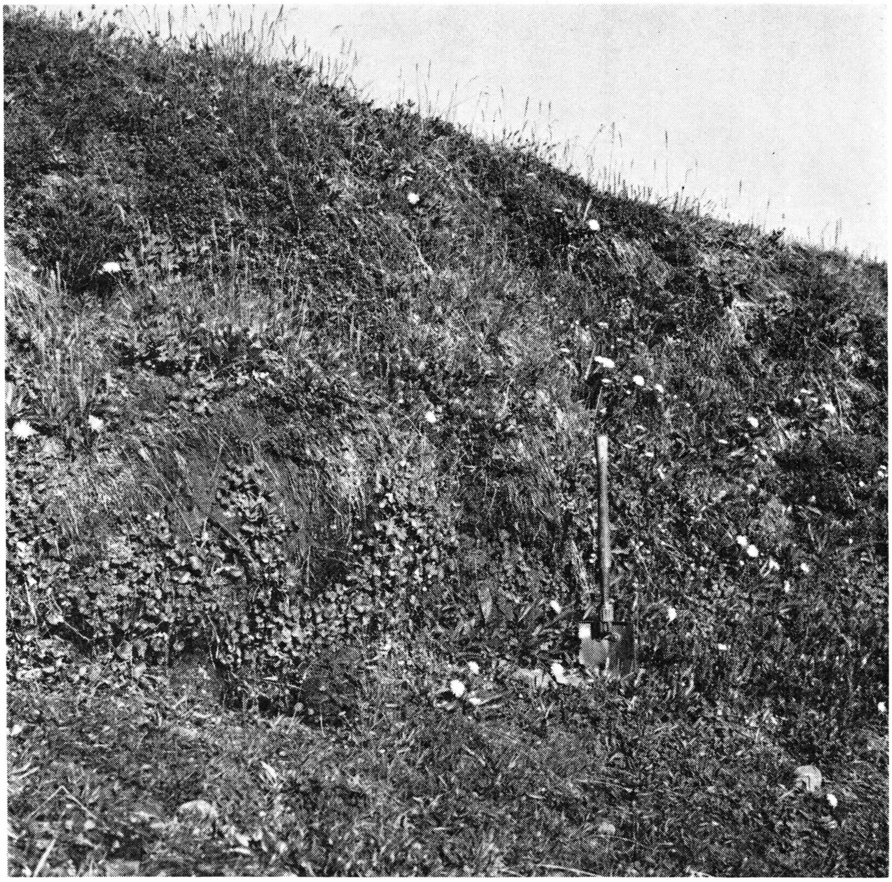

Fig. 45. Lateral bank of gelifluction lobe, ES 17. Photo between sections d and e on map, Fig. 42, 5 Aug., 1957.

The sources of moisture appeared to be, as in other parts of the district, in melting snow and thawing ground. WASHBURN's observations on snow conditions may be quoted (*l. c.*, p. 87): "Snow conditions in the vicinity of the lobe were quite variable, but massive drifting was common. In 1956 there was no snow near the lobe on 21 July; in 1957 none on 5 August; in 1958 none (at least on the lobe) on 16 July; and in 1959 none on 12 July; however, in 1960 the lobe was completely covered on 6 June and probably considerably later, and had snow patches within 10 m as late as 29 August".

In the dry summer of 1964 there was no snow on the lobe or in the vicinity. In the latter parts of most of these summers the rather abundant moisture on the lobe must have been coming from the thaw of snow and frozen ground upslope, though in each case drifts in the immediate neighborhood would have provided a large amount of moisture in the earlier parts of the open seasons.

From the above observations it is reasonable to assume that the driest parts of the lobe were the lateral margins, particularly those situated well above the rounded lower portion. These areas also embraced the stony diamicton in the lateral margins of the tread. They were the first to lose their surface moisture in summer, and probably became relatively dry in more summers than other parts of the lobe. The wettest part of the lobe probably was the lower segment of the steep front. Its diamicton was covered by dense vegetation and it was partially protected from drying winds and sun by its low position on the front, often beneath overhanging hummocks, and by its easterly exposure on the mountainside. At the same time it received most of the drainage from the central portion of the lobe. In the dry summer of 1964 this area was moist to wet.

Between these two extremes were variations in water supply the effects of which on the growth of plants may be roughly estimated in terms of desiccation. Areas subject to partial desiccation, from least to most, probably were the central portion of the tread, the moving soil on the northeast marginal slope, the lower border of the tread (just above the break in slope), and the hummocky upper segment of the front of the lobe. It is likely that in many summers snowdrifts above the lobe supplied so much water that these differences were of little consequence, but in others, such as that of 1964, they were critical in the lives of some species.

Cone-target heave at ES 17

The heave of the cone targets in the transverse line at ES 17 from 5 August, 1957, to 17 August, 1961, ranged from zero to 7.0 cm. Most of the heaving was in the central area of the lobe where targets 3–9 (incl.) were located. Target 8 was out of the ground and disqualified, though it may have been heaved out. The average heave for the 14 accepted targets in this line was 2.8 cm, while the average for the six targets in the central area was about 4.9 cm. In contrast, the average for the marginal targets (T1, 2, 10–15) was 1.1 cm. Considering that all the targets in this line had 10-cm insertions, and that such targets were known to have minimum heave at other experimental sites, the extent of the heaves in the central portion of ES 17 was relatively large. The lesser heaves toward the margins of the lobe were consistent with the smaller moisture supply observed in these areas, and also with the lesser extent of downslope movement there.

An axial line of 9 targets was also established on 5 August, 1957, extending at approximately right angles to the transverse line. It reached about 5.5 m above this line and about 7.5 m below it, and consisted of targets with 20-cm insertions. Thus it extended longitudinally through the part of the tread that exhibited the greatest heaving. Two of the targets were disqualified because of excessive disturbance. The net heave of the remaining seven averaged 9.2 cm of heave, with a range of 5.5 to 16.5 cm, between 5 August, 1957, and 17 August, 1961.

The targets were excavated on 11 August, 1964. At that time most of them were tilted downslope, a few were completely out of the ground, and those in the central part of the tread had moved much farther downslope than they had in 1961. Also heaving in this area had progressed to an even greater extent than was recorded in 1961 (See Fig. 46).

From these limited data on cone-target heaving it can be inferred that there was considerable disturbance in the uppermost 10–20 centimeters of the soil due to frost heaving. WASHBURN suggested (*l. c.* p. 92) that "the altitude of the lobe and its orientation towards the northeast argue for more frequent freeze-thaw cycles . . . than at ES 7–8". From this it might be inferred that volume-change activity in the root of the soil was relatively greater than in the latter area.

There probably were local differences in the amounts of frost heave effective for the survival of plants indicated by the differing heaves of the targets at ES 17. The greatest damage to roots probably was in the central area of the tread, while there was very little toward the drier lateral margins. Observations made on individual target behavior (UGOLINI, Field Notes) showed that within the area of most intense heaving targets situated on bare soil or organic crusts were heaved more than those in local mats of "mosses and *Salix*", etc. On the other hand, where barren or nearly barren soil was frequently or consistently bathed by sheet wash or rills the heaving was also inhibited. Plants growing on the small isolated turf hummocks scattered over the tread were no doubt relatively free of heave injury, as were those on the more heavily vegetated front and steep marginal slopes of the lobe.

Downslope movement of soil

The most rapid downslope movement recorded for the experimental sites in the Mesters Vig district was in the central area of the lobe at ES 17. The maximum here was 23.5 cm in the period between 5 August, 1957, and 12 July, 1959, giving a rate of 12.4 cm per year (Figs. 42, 46). As in the case of target heaving, the greatest movement was in the central area of the lobe, tapering off to approximately zero in the marginal areas (see WASHBURN, 1967, for a more detailed account of the movement). A large share of this movement was no doubt due to gelifluction, but

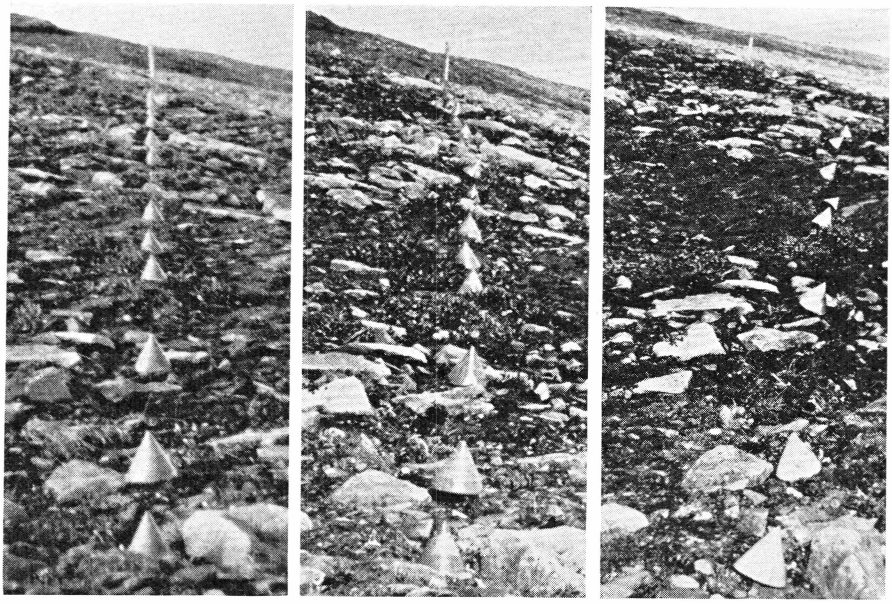

Fig. 46. Transverse target line of ES 17, showing downslope movement from Aug., 1957, to Aug., 1964. Left: 5 Aug., 1957; center: 16 July, 1958; right: 11 Aug., 1964.

the evidence cited above for frost heaving indicates that in the central area, where both heaving and downslope movement were at their maximum, frost creep also was of major importance.

The structure of the front of the lobe was evidence of the continuing downward movement of the surface materials. As these materials approached the crest of the front they appeared to have been partially checked in their advance, probably by lowering of the water table. They reached sufficient stability to be covered with fairly dense vegetation consisting of proliferating mosses in which vascular plants had become established. They had acquired a hummocky structure with channels between the hummocks carrying small rills from the surface of the lobe. As more material came down from above, the hummocks became broken and pushed farther down, often to an overhanging position from which they eventually fell. In some places, notably on the northeasterly margin of the lobe, the frontal slope was more gentle and had the character of a "mud flow" consisting of much disturbed soil.

The marginal side slopes of the lobe, particularly the lower parts, appeared to be "relics" from earlier positions of the front, progressively more stable the farther they were from the existing front. They appeared to be undisturbed by current downslope movement of soil except near the active front of the lobe where there was sufficient moisture for frost creep or gelifluction.

It is probable that gelifluction movement here caused but little injury to plants. Downslope movement in the central part of the tread was "semi-liquid", allowing root and underground stem systems to adjust themselves. Thus the plants tended to "ride" with the soil, their risks appearing at breaks in slope or at obstacles that might interrupt their passage. A certain amount of injury could be expected from these sources, the most important of which at ES 17 was on the upper part of the front where the hummocky vegetation was subject to disintegration. Even this, however, was to a great extent relieved by the fact that most of the species grew in the turf and remained relatively undisturbed by movement of the masses in which their roots were embedded.

Downslope movement of materials by dry creep was observed on the steep southern marginal slope of the lobe, but no attempt to measure it was made. The vegetation was broken here and there by small "streams" of the sliding diamicton, with plants being undermined or inundated.

Although downslope movements of soil appeared to cause little injury to the plants at ES 17, a rough scale of their injurious effects can be constructed from the preceding observations. These movements (due to gelifluction and dry creep) are considered in the analyses below as nonfrost induced disturbances.

The most stable soils in this respect probably were those of the lower segment of the front of the lobe. They had in the past received material from above and were in process of being buried very slowly by more. Much less stable, but not much more injurious to plants, were the fast-moving semi-fluid soils of the central portion of the tread, and the flowing soils on the northeasterly part of the front. The upper part of the front seemed to be slightly more injurious to root systems than the tread, probably due to the physical dissection and dislocation of the hummock masses there. It is probable that the most injurious nonfrost process active on the lobe was not gelifluction, but the dry creep seen on the southerly marginal banks.

The vegetation at ES 17

Fifty-nine species of vascular plants were found growing on the gelifluction lobe which constituted experimental site 17. Thus, within these 500 sq. meters there were about 38 % of all the known species in the Mesters Vig district. The flora of the lobe was derived overwhelmingly from species regarded as common to abundant in the Mesters Vig district. No less than 40 of the 59 species (67.8 %) were rated as common to abundant throughout the Mesters Vig tundra. Fifteen species (25.4 %) were regarded as occasional or merely locally common, and only 4 species (6.8 %) were rare or locally occasional in the district as a whole. If a division of frequencies is made at the level of those species which are rated as common anywhere in the tundra, even locally, then 52 (88.1 %) might be regarded as common to abundant and only 7 (11.9 %) as rare to occasional. In the Mesters Vig district as a whole, on the other hand, rare to locally occasional plants reach a percentage of 21.4 %, and occasional to locally common plants reach 33.8 %.

Table 8 contains a list of the vascular plants seen at ES 17, and gives their distribution in terms of presence or absence among the principal habitats defined in the field. For purposes of description and analysis these habitat-vegetation complexes have been arranged in four groups based upon topographic and/or vegetational similarities.

First is the open, scattered vegetation of the central portion of the tread of the lobe. Included with it are the plants of the moving soil on parts of the northeast front, where the flora was much the same, and the habitat had many features in common.

Second is the upper, hummocky segment of the front of the lobe. Vegetation of similar structure and content was found on the small turf hummocks scattered over the axial part of the tread of the lobe. Third is the vegetation of the lower segment of the front of the lobe. It was restricted to a relatively small area and appeared to be unique in the site as a whole. The fourth vegetation is that found on the south and southeast marginal slopes of the lobe. It is probable that this type should be subdivided at one or more points along the side of the lobe, but field data are not adequate to do it. A characteristic feature of the site here was increasing dryness upslope, and the vegetation of the dry southern margin of the lobe tread in the vicinity of the target line has been included with it for purposes of analysis.

Scattered vegetation on the lobe tread

Throughout the central, axial portion of the tread of the lobe were rather widely scattered plants growing as individuals or small groups. There were occasional small mats of living moss or organic crusts, but most of the soil was bare. It was stony on the surface, and marked by small lobate structures, 1 to 3 or 4 cm high. At the times of most of our observations it was bathed by shallow rills or small areas of sheet flow (Fig. 43). Coverage by vascular plants probably did not average more than about 20 %. The following species were the most common ones in this scattered vegetation: *Poa arctica*, *Luzula arctica*, *L. confusa*, *Salix arctica*, *Melandrium apetalum* ssp. *arcticum*, *Ranunculus nivalis*, *Saxifraga cernua*.

The vegetation of the tread tapered off to fewer and even more widely scattered species toward the margins of the lobe. The reduction

Table 8. *Species found at ES 17, showing their distribution in the principal habitats.*

	On tread of lobe		On moving soil, north-east slope of tread	On lobe front		On south and southeast margins of lobe	
	Plants all scattered	Plants on turf hummocks		Hummocky upper slope	Lower slope	On southeast banks	Dry stony south margin of tread
Equisetum variegatum	+			+			
Festuca brachyphylla	+						+
Festuca rubra ssp. cryophila				+			
Poa pratensis ssp. alpigena					+		
Poa arctica	+	+		+		+	+
Poa alpina	+				+		
Poa glauca				+		+	
Trisetum spicatum				+	+	+	+
Eriophorum triste		+					
Kobresia myosuroides						+	
Carex nardina							+
Carex scirpoidea	+	+		+			
Carex rupestris						+	
Carex Lachenalii					+		
Carex Bigelowii				+			
Carex misandra	+	+	+				
Carex capillaris		+					
Juncus biglumis	+		+				
Juncus triglumis		+					
Luzula arctica	+		+				
Luzula confusa	+				+		+
Salix arctica	+	+		+		+	+
Salix arctophila						+	
Betula nana					+		
Oxyria digyna				+	+		
Polygonum viviparum	+	+		+	+		+
Cerastium alpinum	+			+		+	+
Cerastium cerastoides					+		
Minuartia biflora					+	+	
Silene acaulis	+				+		
Melandrium apetalum ssp. arcticum	+			+	+		
Melandrium affine				+			
Ranunculus nivalis	+				+	+	
Ranunculus pygmaeus	+				+	+	
Draba alpina	+						
Draba Gredinii	+			+			
Draba nivalis						+	
Draba lactea	+		+				
Draba glabella				+		+	
Draba crassifolia				+			
Cardamine bellidifolia			+				
Saxifraga oppositifolia	+						
Saxifraga foliolosa	+						
Saxifraga nivalis	+				+	+	
Saxifraga cernua	+				+	+	
Sibbaldia procumbens					+		
Potentilla Crantzii					+		
Potentilla hyparctica						+	
Dryas octopetala		+	+	+		+	
Empetrum hermaphroditum		+					
Epilobium latifolium					+		
Cassiope tetragona	+	+				+	+
Vaccinium uliginosum ssp. microphyllum		+		+			
Pedicularis flammea		+					
Pedicularis hirsuta	+					+	
Erigeron humilis				+	+		
Arnica alpina						+	
Taraxacum arcticum	+			+		+	
Taraxacum brachyceras					+		

was most conspicuous toward the lateral margins where the soil was much drier and there were no turf hummocks. The plants were likewise more scattered and reduced in number of species in the slightly drier soil just above the break in slope at the crest of the steep front of the lobe. Above the central portion of the lobe, where water issued either from thawing ground or a remnant snowdrift, there was a green carpet of moss covering much of the surface. The following species were found growing in this wet moss: *Poa alpina*, *Luzula confusa*, *Salix arctica*, *Oxyria digyna*, *Ranunculus nivalis*, *Saxifraga cernua*.

The northeasterly marginal slopes of the lobe were in places less abrupt than the eastern margin and consisted of the "mud flow" soils mentioned above. These appeared to be disturbed by frost heaving and downslope movement that may have been even greater than that in the central portion of the tread. Two species were found there that were not seen among the scattered flora of the tread: *Cardamine bellidifolia* and *Dryas octopetala*. In the ensuing analyses the flora of this site has been included with the more open aspect of the tread flora.

Hummock vegetation of the tread and upper lobe front

The vegetation of the east front, as previously noted, can be divided into upper and lower segments (Fig. 44). All of it was relatively dense, in most places reaching cover densities of 80–90 %. It remained wet or moist throughout all or most of the open season, receiving drainage from the central part of the tread. The upper portion was hummocky and much broken by small rills which in many places exposed the mineral soil between the irregularly shaped hummocks. The latter, commonly overhanging, occasionally fell off the front. The basic vegetation of the hummocky surface was of moss in which grew a tundra vegetation of both woody and herbaceous vascular plants. The following were the commonest species found on this upper part of the front: *Poa arctica*, *Trisetum spicatum*, *Salix arctica*, *Oxyria digyna*, *Polygonum viviparum*, *Melandrium apetalum* ssp. *arcticum*, *Vaccinium uliginosum* ssp. *microphyllum*, The *Salix* and the *Vaccinium* alternated as primary species.

Here and there on the surface of the tread were small turf hummocks formed by proliferated moss polsters. They were of varying size and shape, but none were more than 5 to 10 cm high. Individual hummocks usually had only 3 to 6 species of vascular plants, but taken together the following species were their commonest inhabitants: *Poa arctica*, *Carex scirpoidea*, *Salix arctica*, *Polygonum viviparum*, *Vaccinium uliginosum* ssp. *microphyllum*.

Vegetation of the lower segment of the lobe front

The basic vegetation of the lower part of the front of the lobe was also a mat of mosses inhabited by vascular plants the cover density of which was approximately the same as that of the upper part. This area remained wet or very moist throughout the summer, supplied with seepage water from above. The most common species of vascular plants found here were: *Poa alpina*, *Trisetum spicatum*, *Oxyria digyna*, *Polygonum viviparum*, *Ranunculus nivalis*. The surface was not hummocky like the upper segment, and much of it was overhung by the latter. The area involved probably was not more than 10–15 m long by 1–1.5 m wide, extending around the base of the frontal slope of the lobe. The vegetation was distinguished by the absence of most of the woody species of the tundra.

Vegetation on the south and southeast marginal slopes

The soils on the lateral margins of the lobe were not accessible to the principal moisture supply which came down through the central portion, and therefore were progressively drier upslope from the lower front. On the southeasterly side of the lobe the steep marginal slopes were covered with relatively dense vegetation which gradually thinned out westward up the mountain slope, with a gradual change in species composition (Fig. 45). A few species demanding large moisture supplies disappeared, and a few less demanding ones came in. At about halfway between the front of the lobe and the south end of the target line the cover density had dropped from approximately 90% to about 60%. Above this point it fell off to much lower percentages. Common or distinctive species on this southeasterly margin were the following: *Poa glauca*, *Poa arctica*, *Trisetum spicatum*, *Festuca brachyphylla*, *Kobresia myosuroides*, *Salix arctophila*, *Draba nivalis*, *Draba glabella*, *Saxifraga cernua*, *Potentilla hyparctica*, *Arnica alpina*.

In the vicinity of the southern end of the target line the marginal vegetation of the tread, occupying a strip only 1–2 m wide back of the crests of the side slopes, appeared more closely related to the vegetation of these slopes than to that of the tread. In subsequent analyses, therefore, its plants will be grouped with those of the southerly marginal slopes.

Distribution of species in ES 17 with respect to their tolerance of variation in vegetative coverage of the ground, soil moisture, and physical disturbance

Introduction

The types of vegetation at ES 17 were much more sharply defined and easily seen on the ground than at ES 7 and 8 or at ES 6. It might be expected from this that differences in the behavior of their plants with respect to environmental gradients would also be more sharply definable. Although this is to some extent true, its effectiveness is reduced by two factors: the total numbers of species involved, and the relative numbers of definitive species.

At ES 7 and 8 the total number of species in the flora of the diamicton slope was 71. Twenty (28.2 %) of these were found to be widely tolerant of variations on all of the environmental gradients used for analysis and one (1.4 %) was universally narrowly tolerant. At ES 6, in a much smaller area, there was a total of 45 species of which 17 (37.8 %) were found to be widely tolerant on all of the gradients and none narrowly tolerant on all gradients. At ES 17, of the 59 species in the flora 20 (33.9 %) were widely tolerant on all gradients and 4 (6.8 %) were narrowly tolerant on all gradients. Thus ES 17 shares with ES 6 the characteristic of having an intermediate proportion of species that can be regarded as definitive in comparative studies of behavior on the environmental gradients (see ES 15). At ES 7 and 8 there were 50 of these definitive species, while at ES 6 there were 28, and at ES 17, 35. As noted earlier, these differences were probably caused in considerable measure by differences in the areas involved in the sites. Many of the more definitive species were among the less common ones in the tundra vegetation, and although these may have been widespread in the district as a whole they were poorly represented in small areas. In contrast, the most widely tolerant and nondefinitive species are among the common to abundant plants of the tundra, and are those from which the floras of the small areas were principally derived.

The methods used in the following analyses are those followed in discussions of the two preceding sites. The general behavior patterns of the 59 species as observed in the Mesters Vig district as a whole were applied to their distribution in the various site-vegetation complexes available to them at ES 17. These more or less generalized types are the four which were described above in the section on vegetation. Before beginning the analysis, the 20 species regarded as widely tolerant on all gradients (coverage, moisture, frost and nonfrost disturbance) were eliminated from consideration as being nondefinitive, and likewise the

4 species narrowly tolerant on all gradients. These 24 species were as follows.

Widely tolerant on all gradients:

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

Narrowly tolerant on all gradients:

Salix arctophila	*Draba crassifolia*
Cerastium cerastoides	*Sibbaldia procumbens*

Figure 47 contains graphs showing the percentage distribution of tolerance on the various gradients for each of the 4 types of vegetation. The percentages have been derived as in previous analyses, giving figures for definitive widely and narrowly tolerant species as ratios of the actual numbers of these species to the total numbers of definitive species in their respective vegetation types.

Behavior of species on the coverage gradient

In general, the Greenland sites appear to require a large proportion of their plants to have a wide tolerance of variation on the coverage gradient. The prevalence of these plants in all sites studied suggests this. The graph in Fig. 47 shows that, even with the elimination of all non-definitive species, the species widely tolerant on this gradient far outnumbered those that were very sensitive to variation in coverage. Differences within the graph are not easily explained, although it might be said that species growing in very dense vegetation subject to occasional physical disruption would require a wider tolerance than those growing in continuously open vegetation. If this is true it would account for there being a lower percentage of widely tolerant species among the scattered plants of the lobe tread than on the hummocky upper part of the main lobe front. The lower part of the main lobe front was also densely covered with vegetation, but was essentially without disturbance, and should

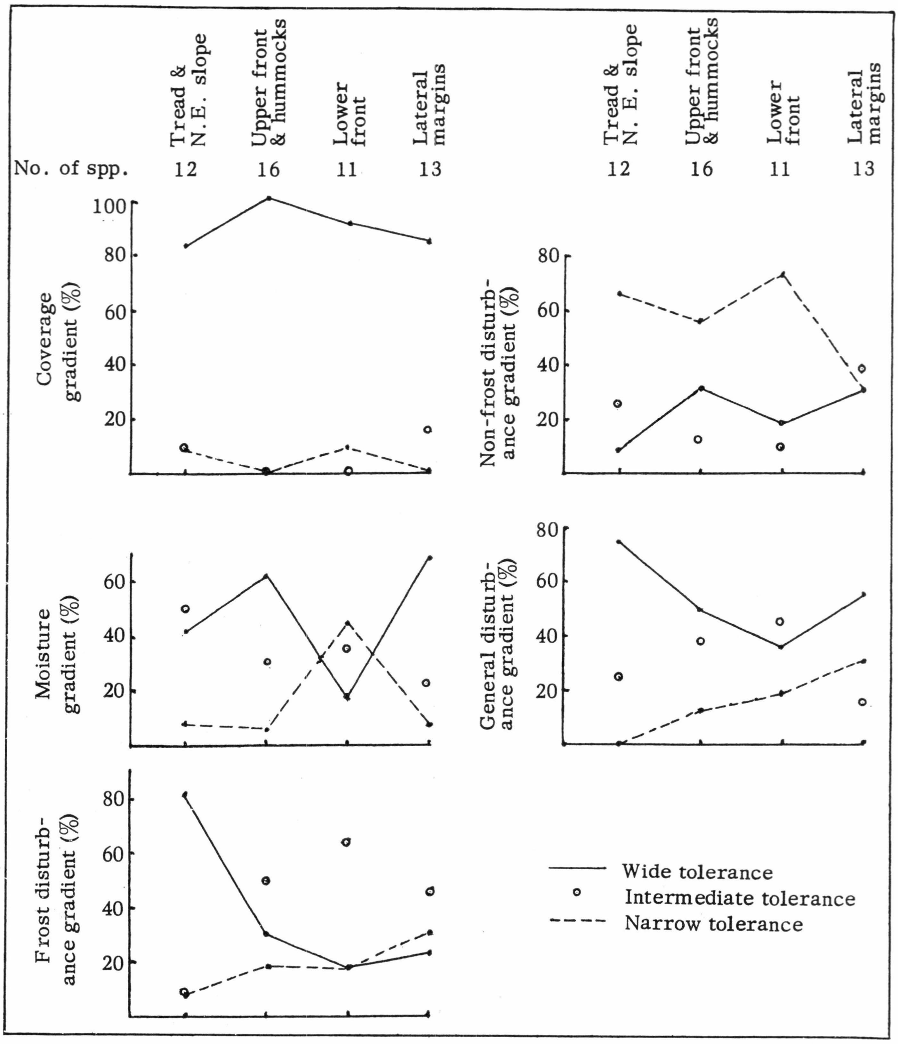

Fig. 47. Percentage distribution of species tolerance in the principal habitats at ES 17, in relation to coverage, moisture, and physical disturbance gradients.

also have relatively fewer widely tolerant plants on this gradient, as it has. Following the same reasoning, the steep southern slope of the lobe might be expected to have more plants widely tolerant of coverage variation because of greater disturbance, but it actually had slightly fewer than the lower part of the main front. However, the southern slopes carried a mixture of coverage densities, and the figures at hand may not be realistic for it. The number of species in the narrowly tolerant category on this gradient was small but it reflected the interpretations suggested above. The absence of narrowly tolerant species on the southern margins supports the suggested influence of disturbance which was not shown by the percentage of widely tolerant ones.

Behavior of species on the moisture gradient

References to preceding notes on moisture distribution in ES 17 indicate that the water supply was relatively abundant in the axial part of the lobe, extending from top to bottom. However, within this distance there were variations dependent upon topography and exposure, giving rise to a certain amount of desiccation on the tread of the lobe during the latter part of the summer season, and even greater drying on the crest of the lobe front during the same season. The lateral margins of the lobe were notably drier than the axial portion, especially the steep southerly banks in mid- and late summer. It is possible to construct a gradient of variations in seasonal moisture supply on which the widest range would be on the lateral margins, and the narrowest on the lower part of the lowermost front of the lobe which remains wet or very moist throughout the summer. Intermediate between these extremes, and nearest to the lateral margins in range of variation, would be the hummocky areas on the crest and upper segment of the front of the lobe. Between this and the narrow range of the lower front would be the more moist axial portion of the tread which became partially dried out on the surface in the latter parts of some summers.

When the behavior patterns of the plants on the moisture gradient are applied to species found in these four vegetation complexes as in Fig. 47, they appear to be reasonably well sorted according to their expected reactions. It is at once striking that the area most regularly supplied with moisture throughout the season, the lower part of the front of the lobe, harbored the lowest percentage of definitive widely tolerant plants. At the same time it had much the highest percentage of species that are least permissive of variations in moisture supply (the narrowly tolerant species). Judging by the high moisture content of this locality in the excessively dry summer of 1964, plants growing there probably suffered from desiccation only on very rare occasions if at all. They did not require wide tolerance of variation on the moisture gradient, and species of narrow tolerance could survive without difficulty.

The largest percentage of species widely tolerant of moisture variation were also in the expected sites, in the vegetation of the upper part of the main lobe front and on the southerly lateral margins of the lobe. It would be expected that the latter of these sites would have a slightly higher percentage of widely tolerant species than the former, and this proved to be the case. A very low percentage of narrowly tolerant species was on these southerly banks where it was expected.

The vegetation of the tread had a median percentage of widely tolerant species on this gradient, thus suggesting its intermediate position in moisture variation between the upper part of the main front and the lower part. The percentage of definitive narrowly tolerant species on the tread faintly reflected its intermediate position, but expectation would give these species a somewhat higher percentage than they had.

Behavior of species on the frost disturbance gradient

The only site complex on the lobe in which frost heaving could be assigned a major influence upon the vegetation was in the axial portion of the tread and on the more gently sloping "mud flow" areas of the northeasterly frontal slopes. In all of the other sites frost heaving appeared to be greatly reduced in effectiveness by dense cover of vegetation or by lack of moisture.

This difference is clearly reflected by the behavior patterns of the plants when they are applied to the species contents of the four vegetation types. Only on the tread and its related northeast slope soils did the definitive species widely tolerant of frost disturbance greatly outnumber those which seem to find difficulty in surviving this kind of disturbance (Fig. 47). In sharp contrast the floras of the lower part of the front of the lobe and of the southerly banks had very few plants widely tolerant of frost disturbance, and relatively high percentages of definitive species narrowly tolerant. The flora of the upper part of the main front of the lobe had a somewhat higher percentage of species widely tolerant on this gradient, suggesting that it may have been intermediate with respect to frost action. However, it had about the same percentage of species sensitive to this kind of disturbance as did the lower segment of the main front and the southerly lateral slopes.

Behavior of species on the nonfrost disturbance gradient

It has been said above that physical disturbances due to gelifluction and dry creep, which are the principal nonfrost induced processes likely to be effective at this site, probably have considerably less effect upon the lives of the plants than do the frost induced disturbances. It is probable that the sites most affected were the drier parts of the southerly marginal banks of the lobe where a certain amount of dry creep appeared. At most this was localized. A little injury may have been caused by breakage of underground stems and root systems during the breakup of the hummocky masses of vegetation on the upper part of the front of the lobe, and there may have been a slight amount of injury to the plants slowly riding downslope in the semi-fluid soils of the tread.

Analysis of species content in the various types (Fig. 47) indicates that in general the definitive widely tolerant species were in the minority while the more sensitive species seemed to live with impunity. The principal exceptions to this were in the expected places. By far the lowest percentage of narrowly tolerant species on this gradient was found on the southerly margins of the lobe where dry creep was undermining or inundating plants here and there. A relatively high percentage of the widely tolerant plants was also found here. The most completely stable situation probably was in the lower portion of the front of the lobe, and here was not only the highest percentage of narrowly tolerant species but also a relatively low percentage of widely tolerant ones. A lower percentage of the former, and a high percentage of widely tolerant species, were found in the hummocky upper part of the main front. The vegetation of the tread suggested that it was about as free from this kind of injury as the lower front. It had a very low percentage of widely tolerant species, and a relatively high percentage of narrowly tolerant ones.

Behavior of species on the general disturbance gradient

It is of some interest that the widely tolerant species with respect to disturbance in general greatly outnumbered the narrowly tolerant ones on the tread and its related soils (see Fig. 47). This suggests that frost heaving may have been of considerable significance in limiting the vegetation of that part of the lobe.

Root and underground stem systems at ES 17

Figure 48 shows the percentage distribution of species having fibrous roots, taproots, and underground rhizomes in the four vegetation types at ES 17. The definition of these root and stem systems is the same as that used in earlier analyses.

As in the Mesters Vig district as a whole, species with rhizomes were present in very small numbers, and about equally distributed throughout the various types in this experimental site. Plants with taproots were clearly in the ascendancy except in the lower segment of the main front of the lobe. This was due in some measure to the fact that the common woody plants of the tundra, many of which are taprooted, were absent from this vegetation. On the other hand, these plants probably were most abundant in the hummocky vegetation on the upper part of the main front, and here they showed the highest percentage.

Experience at ES 7 and 8, where contrasts between dry and wet sites could readily be seen, suggested that plants with taproots were

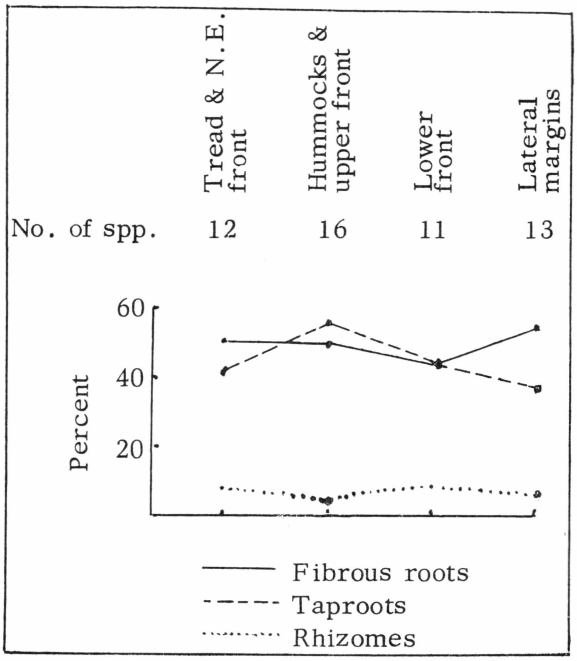

Fig. 48. Percentage distribution of fibrous rooted, taprooted, and rhizomatous species in the principal habitats at ES 17.

somewhat better able to withstand seasonal periods of desiccation than were those having fibrous roots. The curve in Fig. 48 for taprooted plants is roughly consistent with this suggestion, for the least variation in moisture supply was toward the bottom of the front of the lobe and greater variations were found on the southern margin, on the tread, and on the hummocky upper part of the front. The correspondence is not precise, for one would expect a higher percentage of taprooted plants on the southern marginal banks than was actually found there. The curve for fibrous rooted plants shows roughly a reverse image of that for the taprooted species, as would be expected under the circumstances. It is of interest to note that the general trends of these two curves are, respectively, the reverse of the curves for species with narrow and wide tolerance on the moisture gradient.

The relatively high percentage of taprooted species at ES 17 as a whole probably is accounted for by the large proportion of its flora that grew in sites subject to some form of physical disturbance and/or to at least partial desiccation. These sites included the steep banks on the lateral margins of the lobe, the upper segment of the front, the lateral margins of the tread, and in occasional seasons the axial portion of the tread. Again utilizing observations at ES 7 and 8, such sites appear to be more permissive to species with taproots than to those with fibrous roots.

Summary and discussion of ES 17

Experimental site 17 was on a massive lobate structure composed of diamicton, on the easterly slope of Hesteskoen near the upper limit of glacial deposits. Above it, and covering most of the summit and upper slopes of the mountain, was a "felsenmeer" of large angular sandstone boulders. The surface of the slopes around the lobe was covered with pebbly gravel in which was extremely sparse vegetation. This was surficially dry. The tread of the lobe also had sparse plant cover, so that the whole lobe would have been difficult to define at a distance were it not for the "garland" of green vegetation draped around its lower and lateral margins.

The lobe owed its existence and form to an abundant water supply from higher on the slope. This water probably was coming in part from late-lying snow, and in part from ground ice under the mass of sandstone debris above. Washburn (1967) concluded from his study of gelifluction phenomena in the Mesters Vig district that this process was active only in relatively fine textured soils with a water supply sufficient to bring them to their liquid limit or above it. Lobes like that at ES 17 were common on the mountain slopes (Fig. 49), but usually they could be defined as separate, more or less isolated structures, suggesting that their water supplies were also separate concentrations of flow. Such a concentration of water, supplied to the mass of diamicton deposited by glacial ice on the mountainside, probably started the growth of the ES 17 lobe and many others like it. It is assumed that the supply was large enough and sufficiently constant from year to year to continue the growth to the size described in this paper.

Size limits for these gelifluction lobes are unknown. Many were seen on the lower slopes of the mountains that appeared to be stable or nearly so. Their treads were covered with dense tundra vegetation. However, others seemed to be intermediate in stability. It is assumed that stability was caused primarily by the lessening of the water supply. This would be accomplished by altering the "channel" systems that formed the original flow concentrations, or by a general trend toward a warmer and drier climate. The presence of the most stable lobes at low altitudes, and gradually less stable ones at progressively higher levels, suggests the latter. The size of the lobes might be determined in part by the rate of progressive general desiccation over time, and within any single lobe by the total volume and/or seasonal distribution of its water supply. The larger it became the greater would be the loss from evaporation and diffusion at greater distances from the water source. Major aspects of these processes were seen in miniature at ES 15.

Fig. 49. Large gelifluction lobes on southeast slope of Hesteskoen; alt. ca. 500 m. Photo 18 July, 1958.

The vegetation of the lobe at the time of observation seemed to be differentiated primarily in response to water supply, and secondarily due to variation in the intensity of physical disturbance. Most of the water supply was in the axial part of the lobe, and the densest vegetation was on the front. As indicated at other sites, adequate water supply does not ensure a dense vegetation, for the central axis of the tread of the lobe, though as wet as the front, had a low density of cover. This seems to have been due in part to rapid gelifluction, but probably in greater part to the intense frost heaving there.

The lateral margins of the tread were much more stable with respect to gelifluction and frost heaving, but the desiccation which was the principal cause of the stability was also inhibiting to plant growth. Consequently the outer margins of the tread showed vegetative densities as low or lower than those in the axial portion.

The lower lateral "fronts" of the lobe, though outside the main course of moisture flow, had acquired a dense vegetation earlier in the life of the lobe, and appeared to have retained much of this density by inhibited evaporation, lower intensities of disturbance, and probably by seepage of water from ground ice in the lobe itself. The soils were progressively drier upslope, while the vegetation became much less dense and acquired more xerophytic species.

The vascular flora was made up primarily of species common to abundant in the Mesters Vig tundra. The sorting of the species among the various habitats was fairly consistent with their observed behavior throughout the district on gradients of coverage, moisture and physical disturbance.

The early stages in the development of large gelifluction lobes may be surmised from observations of small ones such as were seen in the "wet" sections of ES 7 and 8, and at ES 15. In these situations local concentrations of water flow appear to start more rapid gelifluction in small areas of diamicton. These commonly occur under mats of aquatic mosses, or in sedge meadows developed on saturated moss mats. The existing vegetation is soon disrupted or inundated by a build-up of diamicton which is dammed at the lower end by some small obstruction. The latter may be a larger and more stable mass of vegetation, or a change to coarser texture in the mineral soil, or perhaps a cobble or boulder. After the original insulating vegetation mat is broken, and when the lobe is built up so that it is no longer continually bathed by running water, the tread of the lobe becomes subject to increasingly intense frost heaving which further inhibits recolonization by plants. At the same time the front of the little lobe remains well supplied with water, but has much less frost heaving. Accordingly it develops a relatively stable vegetation.

By this process the essential features of the vegetation patterns of small gelifluction lobes seem to be formed. Given a much larger and more constant water supply such as occurs high on the slopes of Hesteskoen, it appears reasonable to assume that the large lobes began as did the small ones noted above, and had similar developmental processes. However, at some point in the growth of the large lobes they began to have internal permafrost tables and formed steep frontal slopes, with surficial materials being pushed downslope to overhanging positions as at ES 17. Such large lobes were then able to extend far beyond the saturated moss mats or sedge meadows in which they probably started, and inundate relatively dry gravelly slopes. This seems to have occurred at ES 17.

Fig. 50. Experimental site 15, showing lines of target dowels on the small gelifluction lobe. Photo 28 July, 1957.

EXPERIMENTAL SITE 15

Introduction

Experimental site 15 was a small gelifluction lobe situated at an altitude of about 92 m in the northern edge of the ES 7 and 8 map area (see Fig. 1). Instrumental observations for the study of mass-wasting processes at ES 15 have been described by Washburn (1967), and will be only summarized here. Two lines of dowels were placed in the site on 28 July, 1957. One extended longitudinally from the upper end of the lobe through the central portion to a point a few centimeters below the front. The other crossed this approximately at right angles in the wider part of the lobe near the lower end (Fig. 50). The dowels were aligned

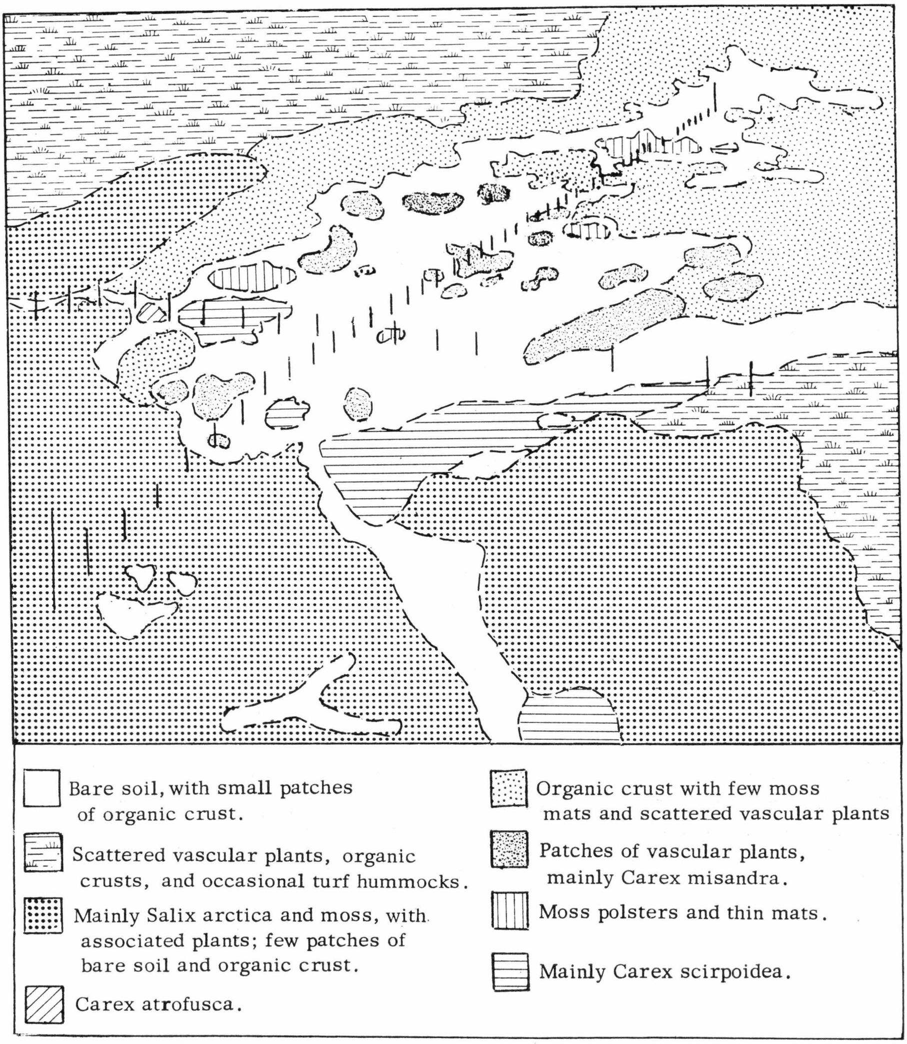

Fig. 51. Map of vegetation at ES 15, showing locations with respect to dowel lines. Compare Fig. 50.

by strings tied to end posts driven as deeply as possible into the diamicton. The insertion of the dowels was 10 cm except in a few instances where they were stopped by stones. The spacing was also 10 cm. Heave, tilt and lateral movement were then "read" in subsequent seasons through 1960. In 1964 the site was excavated.

The flora and the distribution patterns of the vegetation were first described on 28 July, 1957. On 31 July, 1958, a rather detailed map was made showing the distribution of species and species groups on the tread and margins of the lobe (Fig. 51). The site was visited on many other occasions to observe the effects of annual and seasonal variations in moisture supply, frost action and erosion. Small gelifluction lobes of this kind are numerous in the Mesters Vig district, and may be observed in all stages of development.

Topography and soils

The slope gradient, which ranged from 10° to 14° at ES 7 and 8, became more gentle above these sites and was only 4° in the vicinity of ES 15. The diamicton was much less stony than lower on the slope. The soil of the lobe was analysed for size fractions in the central areas of the tread and of the front (WASHBURN, 1967). In the former it was described, to depths of 5–10 cm, as clayey-gravelly-sandy silt, with 53–54 % fines, while in the latter it was coarser, ranging from clayey-gravelly-sand-silt with 47 % fines to gravelly-sandy-silt with 44 % fines. The liquid limit in these soils ranged from 15 to 17 % moisture, and the plastic limit from 11 to 12 % moisture.

The lobe at ES 15 was in some respects a miniature replica of the one at ES 17. Its long axis extended up- and downslope about 6 m (approx. N–S) although the upper part merged with the surrounding slope so as to make the upper limit somewhat indefinite. It was 2–3 m wide near the rounded lower end. Its margin was irregular on the southerly side, and appeared to merge with other small lobate structures in that direction. The lobe front was about 8 cm high, with a gradient of 12°–14°. The tread of the lobe had a gradient that averaged about 3°.

Moisture supply

Experimental site 15 derived its moisture from the same massive snowdrift system that supplied the ES 7 and 8 area. A part of this drift lay a few meters farther upslope than the one shown on the map in Fig. 1. In some seasons the site was kept saturated with melt-water, while in others it was merely damp in late summer. In dry summers such as that of 1964 the surface of the tread was dry in August. Repeated observations indicated that the site in general was well supplied with water, and in the terms used at ES 7 and 8 would be called "wet". However, local differences in moisture regimes were seen within the site, and these were of considerable significance to the local distribution of the plants and to the varying intensities of effective geomorphic processes. Thus the moisture supply at the site must be examined in two ways: (1) for variation in total supply throughout the site, and (2) in terms of local seasonal regimes.

A few moisture determinations were made in the surface materials of the tread: 1958—9 July, 28 July, 30 August, 19 September; 1960—23 June, 10 August. In all samples the moisture content (w) was at or above the liquid limit of the soil, ranging from 15 % to 169 %. All of the data were taken in relatively wet summers when the snowdrifts remained late and supplied melt-water through the latter parts of the open seasons.

Of immediate significance for the establishment and survival of plants was the varying amount of summer desiccation in different parts of the site. This will be discussed further under frost heaving, for the amount of moisture available in the surficial soils at autumn freeze-up has a primary influence upon the intensity of heave. Water supply to the site probably was most evenly distributed throughout the summer in the soils on the frontal slope of the lobe. The wettest soils in spring appeared to be on the lobe rather than its lateral margins, but they suffered a certain amount of surficial desiccation on the tread during dry summers. Although plants might germinate in these soils in wet years or while the soils were wet in spring, survival of seedlings in the periodic summer desiccations was hazardous. The total amount of water available to the tread of the lobe probably was greater than that to the lateral margins, but its seasonal distribution made it less effective in supplying moisture to the plants. Soils in the lateral margins were also desiccated to some extent in summer, but apparently less so than those in the semi-barren soils of the tread. Although it is not possible, with the data at hand, to make an accurate comparison between the regimes of moisture, *per se*, on the tread and in the lateral margins, its net effectiveness probably was not much different in the two areas. A difference, if one occurred, probably made the water supply in the margins somewhat less effective than on the tread. Though summer desiccation was less on the margins, so also was the supply, and the result could well have been even less reliability than appeared on the tread.

Dowel heaving at ES 15

Frost heaving of dowels at this site appears to have been relatively intense. WASHBURN (*l. c.*, p. 74–77) noted that the heave of those accepted as valid for measurement ranged from 0 to 9 cm, but pointed out that many missing dowels probably were heaved out of the ground, thus implying a heave of 10 cm. The number of these missing dowels was large, for 65 were originally put in: 40 in the axial line and 25 in the cross line. Among the total of 65 only 30 were finally used for measurement of heave. Some of the dowels had to be disregarded because of excessive lateral and downslope movement. This was true especially in the upper part of the axial line, where identification of individual dowels with their initial positions was in some cases virtually impossible. Probably a few were pulled up by geese. Only those still standing, and in positions approximating their original spacings and alignments were used by Washburn in his assessment of heave. The average heave for these 30 dowels was 3.4 cm (28 July, 1957–4 June, 1960).

Washburn observed that "in general the heave was least where there was vegetation". This can be documented further with data from photographs (Figs. 53 and 54) and the map of the vegetation patterns (Fig. 51). Of the 30 dowels used for heave measurement, 17 were in vegetation of vascular plants, either on the borders of the lobe or in isolated patches on the tread. Their average heave was 1.3 cm, with a range of 0 to 5.0 cm. The remaining 13 dowels were in bare soil or (in very few cases) in soil with a thin cover of organic crust. These were heaved, on the average, 6.1 cm, with a range of 3 to 9 cm. Thus the average heave of dowels in bare soil or on crust was about four and a half times as great as that in soil bearing a vegetation of vascular plants. Nearly all of the dowels that were entirely out of the ground were among those placed in bare soil, and most of them were found in the immediate vicinity of their original positions. Therefore if it is correctly assumed that many of them were heaved out, not only would the average heave for the whole area be considerably increased but also the relatively greater heave in bare soil than in vegetated would be even more striking than the above figures indicate.

Although these comparative values for heave in vegetated and non-vegetated soils are averages, with relatively wide ranges, the extent of overlap was actually small and restricted. The total overlap was only 2 cm, and this was found in only five dowels. One located in vegetation was heaved 5 cm, but the other 16 were heaved 2.5 cm or less. Four in bare soil were heaved 3.0, 3.5, 4.0 and 4.5 cm, while the remaining nine were heaved 5.5 to 9 cm. These notes suggest that even in a small area such as ES 15, where much of the vegetation pattern was fragmented into small units that were no more than 10–20 cm in diameter, the coincidence of frost heaving intensity with vegetative cover was quite close.

Six dowels were measured for heave on the front or crest of the lobe and 13 on the tread. The six on the front averaged 2.1 cm of heave while those on the tread averaged 5.5 cm. Analogous differences appeared when the dowels in open and vegetated soils were averaged separately. The data suggest that the frost heaving was about twice as intensive on the tread as it was on the front. These findings are consistent with the higher percentage of coarse materials in the uppermost 5–10 cm of the soil on the front compared to the soils of the tread (see above). Further, the break in slope at the crest of the front probably lowered the water table slightly on the frontal slope and decreased the supply of moisture for frost heaving.

Injury to plant root systems by frost heaving at ES 15 probably was least intense on the lobe front where the soil had less fines than on the tread, where there was rapid run-off, and where the water table was somewhat lowered. The densest cover of vascular plants was there, and the most species. Data from the dowels indicate much less heaving than on the tread. No instrumental data are available on heaving in the soils of the lateral margins. Consequently comparison of this heaving with that of the tread or the front must be done through the vegetation and by extrapolation from similar sites elsewhere in the vicinity.

Most of the tundra lateral to the lobe at ES 15 had a comparatively low density (20–40 % coverage by vascular plants). A large proportion of the ground was covered with thin, black to very dark gray organic crusts on which the vascular plants were scattered. There were occasional small polsters or thin mats of living mosses and a few lichens, the latter mainly species of *Cladonia*. The soil was wet in spring and early summer and remained moist into the autumn except in dry years when the uppermost horizons became fairly well dried out. Experience in the organic crust areas of ES 6, 7 and 8 (Figs. 5, 6, 7, 32, 33) showed that sites of this kind were subject to intensive frost heaving.

Washburn (1967) stated that "Most of the heaving [of cone-targets and dowels] probably occurred in the autumn as indicated by the following facts: (1) The greatest heaving was commonly in places that tended to remain wet throughout the summer because of lingering snowdrifts and were therefore particularly favored with moisture during the autumn freeze-up; (2) most of these places tended to be protected from spring freeze-thaw cycles by lingering snow; (3) even places that were commonly snowfree and wet in the early spring (for example, part of the east sector of ES 8, ES 9) showed relatively little heaving; (4) low temperatures following thawing are more characteristic of autumn than spring".

Facts (1) and (2) in the preceding paragraph adequately describe the general situation in the vicinity of ES 15. Washburn's observations also emphasized the primary importance of the seasonal moisture regime for varying the intensity of frost heaving. He cited the extreme cases of ES 9 and the eastern part of ES 8 where diamicton resembling that at ES15, barren of plants or with very low cover density, was extremely wet for a time in spring but became dry and hard by late summer. In these places there was very little heaving, presumably because the surface soils usually did not contain enough moisture at autumn freeze-up to produce it.

The lobe soil at ES 15 resembled that in the eastern "dry" sectors of ES 7 and 8, but it rarely (if ever) became as dry in late summer. Nonetheless, in relatively dry summers such as occurred in 1956, 1959, 1961, 1964 it formed a hard crust on the surface which was firm to a depth of 2–3 cm. Below this the diamicton retained a degree of plasticity. The surficial soils marginal to the lobe were also subject to this partial desiccation, but to a smaller extent. The net result may be that averaged over a period of years the marginal soils went into the autumn freeze-up with more moisture available for heaving in the upper 10–15 cm than did the lobe soils. Although heaving is known to have been relatively intensive on the lobe, it may have been even more so, and more injurious to plants, in the thinly vegetated marginal soils with their common covering of organic crusts. However, this difference, if it occurred, probably was a small one.

Downslope movement at ES 15

Observations in the wetter parts of ES 7 and 8 indicated that all of the surface materials were slowly moving downslope (Fig. 52). It may be assumed that those in the wet area embracing ES 15 were also in motion, though the rate is unknown. Therefore all measurements of movement at ES 15, made with reference to stakes set in the soils adjacent to it, can be relative only to the stakes and do not show true rates of movement.

The difficulties with the identity of the dowels that appeared in the measurement of heave applied equally to the estimation of downslope movement. WASHBURN (1967) believes the measurements were accurate to ± 0.2 cm in the transverse line, and to ± 1 cm in the axial line.

The dowel lines indicated two elements in the movement of the surface materials of the lobe. The major element was downslope through the axial portion. It was clearly evident in July, 1958, after the dowels had been in place for one year, and was approximately 5 cm in the vicinity of the axial line. In 1960 this had increased to about 9 cm. The dowels in the transverse line had formed a rather symmetrical bow-shaped arrangement, convex downslope, with the cord, by 1960, about 9 cm from the arc approximately at the axial line. WASHBURN estimated the mean rate of movement in this lower axial area at 3.1 cm per year. That the axial downslope movement was the major element, and extended rather uniformly through most of the central part of the lobe, was indicated by the fact that as long as the dowels in the axial line were not excessively heaved and remained upright they maintained approximately uniform spacing (Fig. 53).

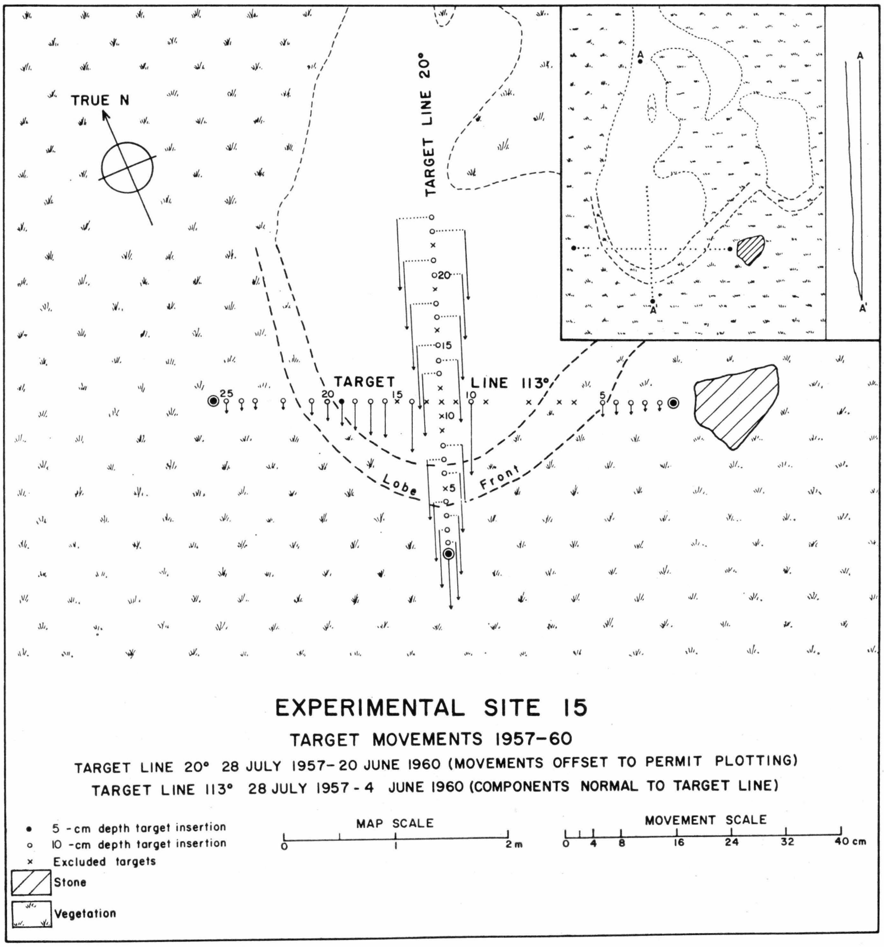

Fig. 52. Map of experimental site 15, showing downslope movement of dowels, 1957–1960. From Washburn, 1967, Fig. 28.

A secondary element in the movement also appeared during the first year and was later accentuated. This was due to the tendency of the lobe to bulge outward toward the southeast (Washburn, *l. c.*). The evidence for it was in two areas of lateral displacement southeastward in the axial dowel line (Figs. 54, 55). The uppermost extended approximately from dowels 35–36 to the upper end stake, and was so violent in 1957–58 as to eliminate most of the dowels in that interval. Not only had the gelifluction movement been extremely active, but there was also evidence of considerable washing and silting. The other main area of lateral displacement was between dowels 19–20 and 29–30. Here the dowels had maintained their vertical positions and regular spacing, but showed a well-defined curve southeastward away from the original line.

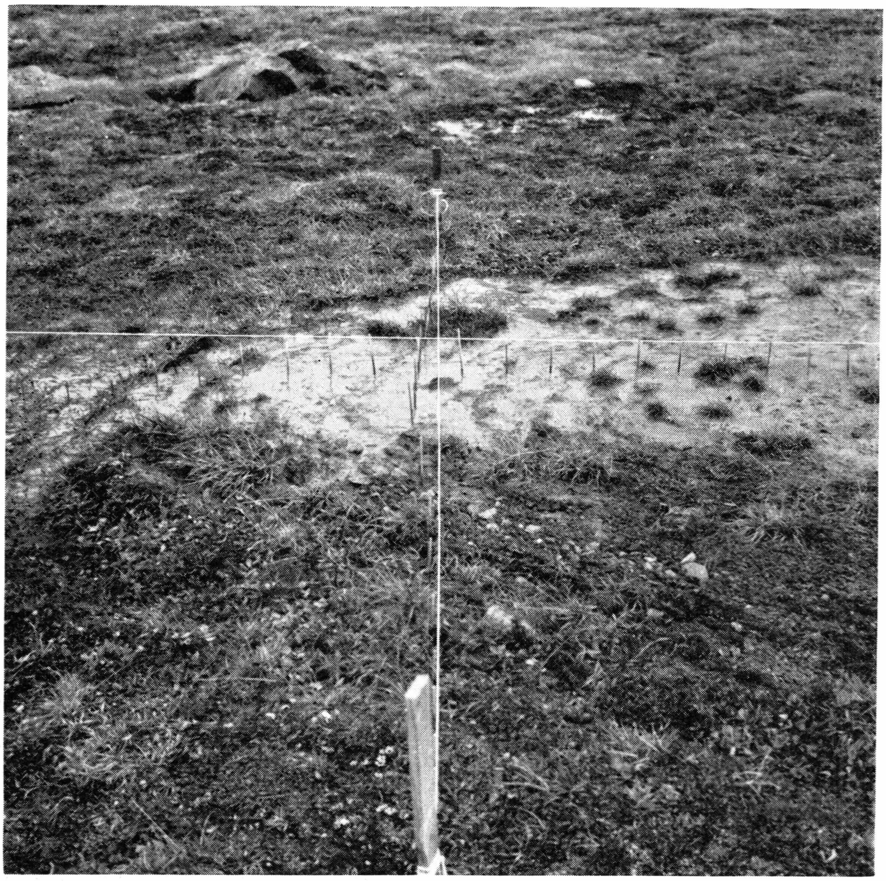

Fig. 53. Frontal part of small gelifluction lobe at ES 15. Note bow-shaped displacement of transverse dowel line after one year. Photo 8 July, 1958.

By 1960 this displacement had reached a maximum of about 15 cm. A small displacement in the same direction also occurred in the dowels between nos. 30 and 35, but though it appeared in the first year it was not much enlarged in later seasons. These dowels were on a vegetated area which appeared to be a "peninsula" separating two parts of the southeastward bulge of the lobe.

WASHBURN has pointed out that evidence of movement was seen not only in the dowel lines but also in the vegetation that was associated with them or could be located from them. Comparison of Figs. 53, 54, and 55 show that individual patches of vegetation ranging in average diameter from 10 to 50 cm moved downslope as more or less intact units. The movement of the vegetation patches appears to have been at about the same rate as that of their associated dowels. Thus they moved most rapidly in the axial line of the lobe, and at progressively slower rates

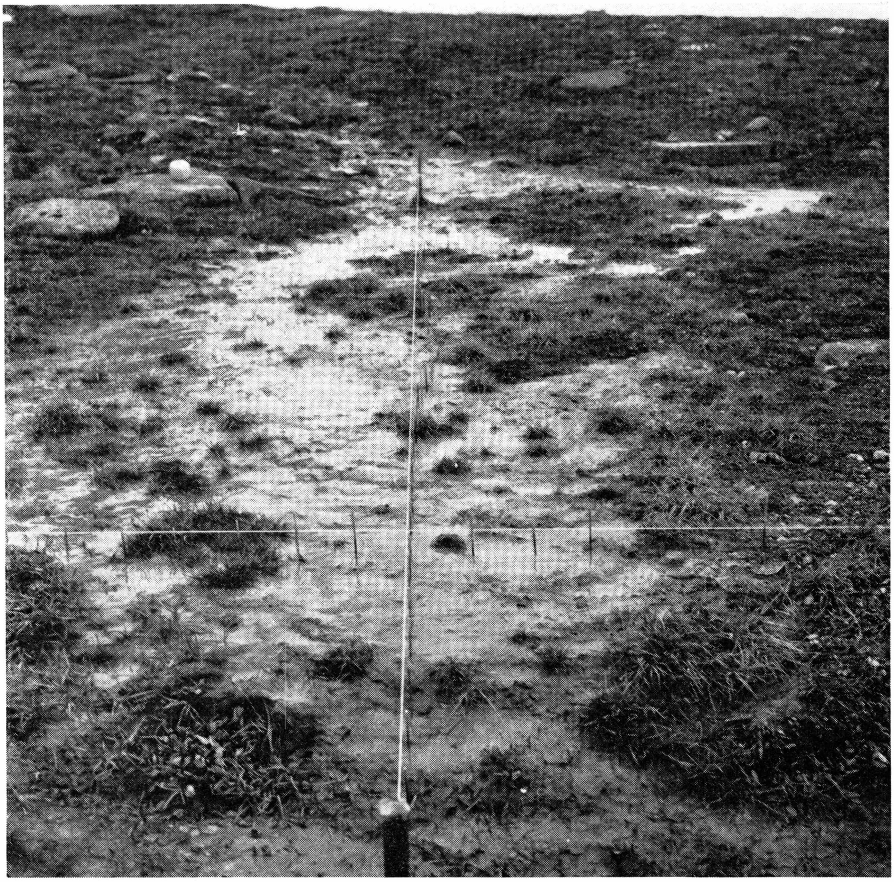

Fig. 54. Gelifluction lobe at ES 15, showing lateral displacements in axial dowel line after one year. Photo 8 July, 1958.

toward the lateral margins except where the more rapid rate was extended southeastward in the bulges.

There seems to have been some differential movement of the soil in the axial line. As noted above, the major downslope element of motion was rather uniformly distributed in this line northward to about dowel 35, and seems to have carried with it not only the dowels but also the vegetation of the "peninsula" between the two parts of the southeastward bulge. Comparison of Figs. 54 and 55 shows, however, that the curve in the dowel line between nos. 19–20 and 29–30 occurred in essentially bare soil, and had the effect of moving the dowels nearer to a patch of vegetation. This patch was on the margin of the "peninsular" area, and appears not to have moved in the same direction. It suggests that the "peninsula", though its soil was moving downslope along with the whole

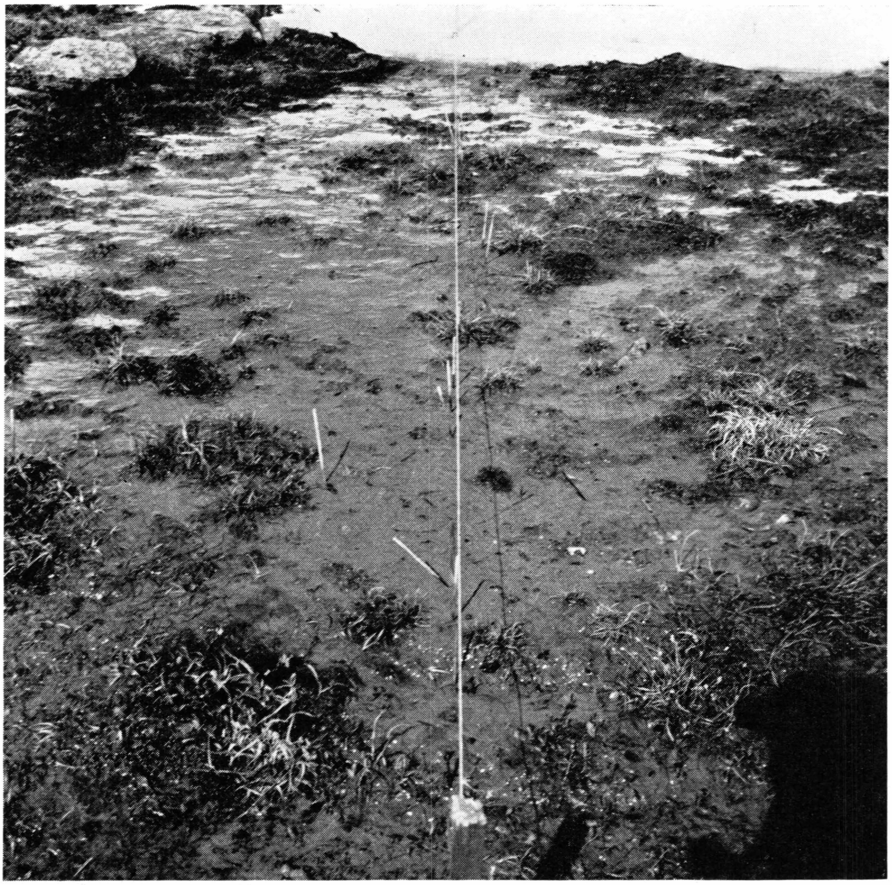

Fig. 55. Gelifluction lobe at ES 15 showing displacement of dowels after three years. Photo 20 June, 1960.

mass of the axial part of the lobe, was able to maintain greater stability in its directional orientation than were the areas above and below it. Whether the vegetation was cause or effect in this case in unknown. In view of the known variability of coarse vs. fine fractions in the soils of the vicinity, one is led to suspect that the "peninsula" contained slightly better drained soil, thus giving it slightly lower liquid and plastic limits.

The vegetation at ES 15

The flora of ES 15 is a small one due to the small area of the site (about 10 sq. m) and to the prevalence of disturbed soil. Only 18 species of vascular plants were found on the gelifluction lobe and the surfaces immediately marginal to it. They are listed in Table 9.

Table 9. *Species found at ES 15, and their distribution among the principal habitats represented.*

	On tread of lobe		Lateral margins of lobe	On front of lobe	
	Isolated patches	"Peninsular" area		Crest	Frontal slope
Equisetum variegatum		+	+		+
Eriophorum triste					+
Carex scirpoidea	+	+	+	+	
Carex Bigelowii		+	+		+
Carex misandra	+	+	+	+	+
Carex capillaris					+
Juncus biglumis	+	+	+		
Juncus triglumis	+			+	+
Juncus castaneus	+				+
Salix arctica	+	+	+		+
Polygonum viviparum	+	+	+		+
Silene acaulis			+		+
Saxifraga aizoides	+				+
Saxifraga oppositifolia		+	+		+
Saxifraga caespitosa					+
Dryas octopetala					+
Epilobium latifolium		+	+		
Pedicularis flammea			+		+

This table shows that most of the species were on the frontal slope (83.3%) and on the lateral margins (61.1%), and that the "peninsular" area extending into the lobe from the easterly side had much in common with the vegetation of the lateral margins. It also shows that the sparsest floras were in the small patches on the tread of the lobe (44.4%) and in a narrow rim of vegetation on the crest of the front (16.7%).

With respect to vegetative density, the variations ranged from zero in much of the lower axial portion of the tread to coverages of 60–80% on parts of the frontal slope. The photographs (Figs. 50, 51, 54) show that patches of plants on the tread were smallest and farthest apart in a broad area extending southeastward from the end of the "peninsula" to the crest of the front at the lower end of the axial dowel line. From this central area toward the lateral margins they increased in size and frequency, but there was little change in their species content.

A rating of vegetative densities for the site is approximately as follows: lower axial part of tread, 0–10 %; marginal part of tread (with isolated patches of plants), 0–30 %; lateral margins of lobe, 20–40 %; crest of lobe front (central part of front), 0–40 %; frontal slope of lobe (central part, vicinity of axial dowel line), 10–40 %; frontal slope (lateral portions), 40–80 %.

Behavior of species at ES 15 on gradients of vegetative coverage of the ground, moisture, and physical disturbance of the soil

The small number of species at ES 15 makes analyses such as were used at the preceding sites difficult and of questionable significance. It has been customary to rule out as nondefinitive those species that have wide or narrow tolerance of variation in all of the gradients used for analysis. By this ruling no less than 10 of the species in Table 9 must be eliminated, leaving only eight that are entirely valid for estimating species-site relationships.

The difficulty of assessing these relationships may be seen, in part, by further examination of Table 9. All of the species at the site were found on the lateral margins or the frontal slopes of the lobe; and all of the species in the "peninsula" were in one or the other or both of these places. Further, all of the few species in the sparse floras of the patches and the crest of the front were also found either on the lateral margins or the frontal slopes. The combination of these various distributions with the elimination of nondefinitive species leaves only three definitive species on the tread of the lobe, three on the lateral margins, and eight on the front; and in most cases these definitive species were found at the same time in supposedly different habitats such as the isolated patches and the lateral margins or on the frontal crest or slopes.

When all of the species at ES 15 are considered together, and their behavior on the various gradients compared as in Fig. 56, results appear that are at least suggestive. There were no narrowly tolerant plants at ES 15 except on the nonfrost disturbance gradient. Only one of the 18 species had demonstrated, in its selection of habitats, any preference with respect to density of vegetative cover, and this species was intermediate (found in about two-thirds of the coverage range). Only four of the 18 had shown preferences for anything less than wide ranges of variation in the moisture supply, and these also were intermediate in their selectivity. The same proportions hold for the frost disturbance

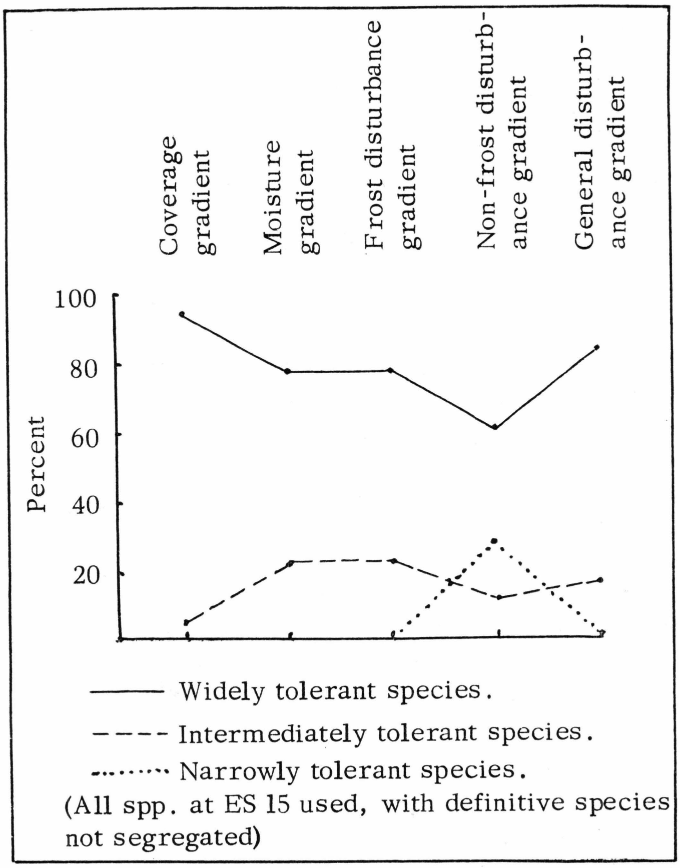

Fig. 56. Percentage distribution of species tolerance at ES 15 (all spp.) on gradients of coverage, moisture, and physical disturbance.

gradient, suggesting that the flora of the site as a whole was well adjusted for survival from injury due to rather intense frost heaving.

Behavior of the species on the nonfrost disturbance gradient shows a conspicuous modification of the proportions noted above. Five of the species were noted as narrowly tolerant of this kind of disturbance, two as intermediately tolerant, and 11 as widely tolerant. The principal nonfrost process causing disturbance here was the gelifluction movement. The selection of species for the site as a whole suggests that injury due to this process was much less than that due to frost heaving, for over half the definitive species and nearly a fourth of all the species had shown preference for soils relatively undisturbed by gelifluction. However, the presence of 11 widely tolerant species and two intermediates suggests that a certain amount of injury was to be expected.

When the disturbance factors are grouped together, as in the general disturbance gradient, 15 species were widely tolerant and three were intermediate. Thus on this gradient the effect of the narrow tolerance of four species on the nonfrost gradient fails to appear, suggesting that the net reaction of the flora to the gelifluction factor may be intermediate in spite of the relatively high percentages of definitive narrowly tolerant plants on the nonfrost gradient.

Although the detailed results of the above analysis are speculative, two outstanding facts emerge: (1) Over half the flora of the site (10 spp.) is of species widely tolerant on all the gradients; (2) all of the remaining species (8) show intermediate tolerance on the various gradients except on that of nonfrost disturbance where five species are narrowly tolerant. These facts suggest that the site as a whole has not permitted the establishment and growth of species that are, at the same time, (1) restricted to a narrow range in the coverage gradient; (2) restricted to consistently very wet or very dry sites; (3) restricted to soils that remain physically undisturbed for periods of many years. The behavior of the plants suggests further that with respect to physical disturbance, although the site did not permit plants that were very sensitive to frost heaving and thrusting (narrowly tolerant), it did harbor a few species that seemed unable to survive disturbance by nonfrost induced processes.

It follows that the vegetation of ES 15 was made up overwhelmingly of species with wide tolerances. The largest number of intermediately tolerant species reached on any of the gradients was four (22.2 %). Behavior differences among subdivisions within the site can therefore be looked for, with the possible exception of the nonfrost disturbance gradient, only in relatively small percentage variations in the incidence of wide and intermediate tolerance, of which the former probably is most significant.

Still more speculative results come, therefore, from analyses of subdivisions in the flora of ES 15 (Fig. 57), but they supplement those in Fig. 56 and are likewise suggestive. In Fig. 57 the floras of isolated patches on the tread of the lobe, and on the crest of the frontal slope are grouped together. The floras of the lateral margins of the lobe and of the "peninsular" area that projects from the southeast margin are likewise merged because they were much the same and appeared to have approximately similar habitats. The frontal slope flora makes a third division. In Fig. 57, as in Fig. 56, species widely tolerant on all gradients were not eliminated from the analysis, because to have done so would have produced even smaller numbers to work with, and greater uncertainty in the results.

Nearly all of the 18 species at the site were rated as widely tolerant on the coverage gradient, found at one place or another in the Mester Vig district in more than two thirds of the possible range of variation in vascular plant cover (Fig. 57). The single exception was *Saxifraga*

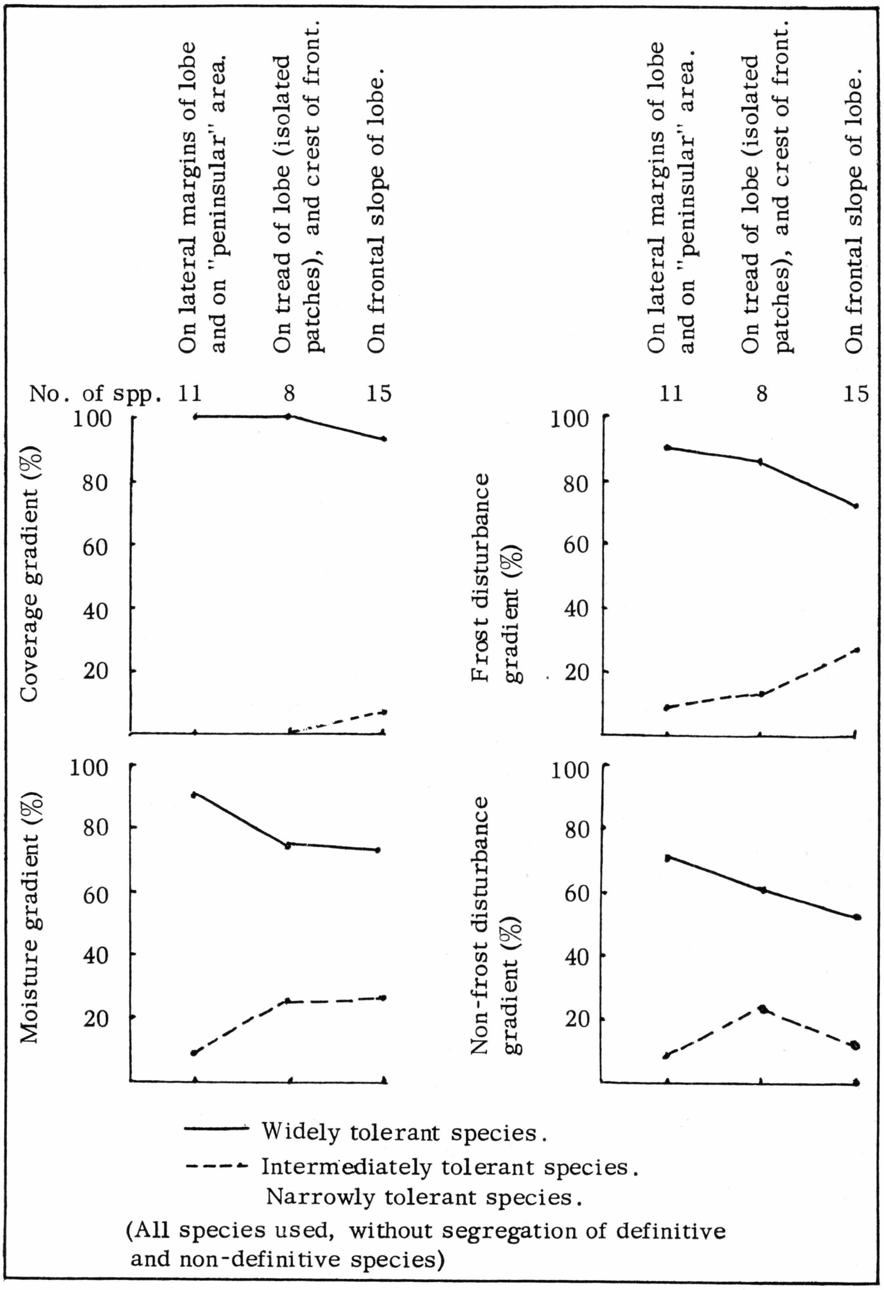

Fig. 57. Percentage distribution of species tolerance in the principal habitats at ES 15, in relation to coverage by vascular plants, moisture, and physical disturbance.

caespitosa, an intermediate on this gradient, found in one of the less densely covered parts of the frontal slope.

The graph for the moisture gradient shows a larger proportion of widely tolerant species and a lesser one of intermediates in the lateral marginal vegetation than on the tread (Fig. 57). This would suggest that the marginal habitat was more subject to variations in moisture supply than the tread. No data are available with which to prove that this was the case, but observations of differing moisture supply and desiccation have suggested that there may have been little difference between the two areas, or if a difference occurred it may have resulted in slightly more effective seasonal variation in the marginal than in the tread soils (see above, under Moisture supply). The trends of the curves for widely and intermediately tolerant species are continued into the flora of the frontal slope. Though the percentage differences are small, the trends are in the expected direction, for the frontal slope probably is less subject to moisture variation than any other part of the site.

Similar trends are seen in Fig. 57 in the graph for the frost disturbance gradient. Here the percentage differences between the marginal and tread vegetations are smaller than on the moisture gradient, but the differences between both of these and the vegetation of the frontal slope are more pronounced. As in the moisture regimes, a good comparison of frost heaving intensities between the tread and marginal soils is impossible with existing data (see above, under Dowel Heaving). But in view of the slightly more reliable moisture supply in the surface soils of the lateral margins at autumn freeze-up, the plants growing on the margins may have reflected a slightly more injurious frost heave there. The somewhat less frost heaving known to have occurred on the frontal slope is reflected by the considerably lower proportion of widely tolerant species found there.

The most significant suggestions derived from the graph for the nonfrost disturbance gradient are (Fig. 57): (1) that narrowly tolerant species appeared at all, even in very small numbers, in the disturbed soils of this site; (2) that they made up the lowest percentage of the flora on the lobe tread where gelifluction was most active; (3) there were, proportionately, nearly three times as many of them on the frontal slopes as on the tread, and the frontal slopes probably were the parts of the site least disturbed by gelifluction; and (4) the frontal slopes also showed the smallest proportion of widely tolerant species, which is also consistent with the least gelifluction activity. Comparisons of percentages for the tread and lateral marginal vegetations are not so consistent with expected results. The figures show a slightly larger proportion of narrowly tolerant species at the margins than on the tread, and this is consistent with the lesser gelifluction known to occur there. But a smaller proportion of widely tolerant species should have appeared on the margins than on the tread, whereas the reverse is evident on the graph.

It should be emphasized that all of the above analyses of species behavior on the various gradients are based upon very small numbers and are therefore subject to much uncertainty. At best they indicate general trends which may be useful for comparison with other sites.

Root and underground stem systems

Among the 18 species of vascular plants at ES 15, four have underground rhizomes while the remaining 14 are about equally divided between fibrous and taprooted plants (the number of taprooted species adjusted for species with vegetative reproduction; see Raup, 1968). The proportion of rhizomatous species is somewhat higher (22.2 %) than in the whole Mesters Vig flora, possibly a reflection of the generally wet site.

Analysis of the distribution of underground systems among the three habitats described above can give no definitive results because of the tolerance ratings and small numbers of the species concerned. All but one of the seven fibrous rooted and taprooted species on the tread of the lobe are widely tolerant on the crucial moisture and frost disturbance gradients, leaving only a single fibrous rooted species that can be considered definitive. All but one of the nine fibrous and taprooted species in the marginal vegetation are likewise widely tolerant on these gradients. Eleven of the 15 species on the frontal slope have these types of systems, and eight of them are widely tolerant of frost disturbance and moisture variation. Thus there are not enough definitive species in the three habitats for comparison.

Summary and discussion of ES 15

In the discussions of ES 17 the problem of initial stages in the development of large gelifluction lobes and their vegetation was briefly treated. It is probable that ES 15 represents one way in which these initial stages appear. Not only does it contain the microrelief of a lobe "in embryo", but also a simple pattern of vegetation in which the floristic elements are relatively undifferentiated.

Assuming that the gelifluction activity of the small lobe at ES 15 was dependent upon an adequate supply of water delivered from a specific source, in this case a small stream from a melting snowdrift, it could be expected that the greatest activity would be in the main course of the stream where the greatest volume of water was present and moving.

Marginal to this, other factors being equal, the volume of water would be less, and the gelifluction movement less rapid. These things were demonstrated at ES 15 by the rounded form of the lobe front and by the bow-shape acquired by the transverse line of dowel targets. Gelifluction effects upon the vegetation were therefore most intensive in the axial part of the lobe tread, and were progressively less intense toward the lateral margins of the tread.

Frost heave effects could not be expected to be so clearly differentiated. Heaving was relatively intense in the axial portion of the tread, as shown by the dowels. Though the axial area appeared to receive the largest supply of water, it also had the least cover of vegetation and dried out at the surface to varying degrees during late summer. The marginal areas, though they received less water, carried more insulating vegetation and tended to hold their moisture through the summer more effectively. Injurious effects of heaving upon plants may have been greater, therefore, in the marginal zones than in the axial part of the tread, and probably were balanced against a combination of lesser heave injury and more desiccation in the axial portion.

The vegetation pattern suggests that the combination of late summer partial desiccation, a considerable amount of frost heaving, and relatively intense gelifluction activity was the cause for the bare soil and scattered vascular plants in the axial part of the tread. Toward the lateral margins the individual plants or small patches of vegetation were a little larger and closer together. Still farther from the axis the patches were much larger and tended to merge, and finally formed the more or less continuous marginal vegetation of the lobe.

If the preceding analysis of the moisture regimes is valid, although there probably was more intensive frost heaving toward the margins it was more than offset, so far as the plants were concerned, by a smaller seasonal variation in moisture supply and by less gelifluction activity.

Excavations at ES 15 and vicinity in 1964 suggest a concentration of finer textured materials in the lobe. Whether this was due to sorting in the process of lobe formation, or the development of the lobe was due to a preexisting concentration of fines is unknown. In any case the lobe had been built up to a tread slope only about 1° less than that of the surrounding areas. Thus the difference in ground level between the tread and marginal surfaces in the part of the lobe above the lower front was insignificant, and lateral banks were essentially nonexistent except on the rounded lower front. There was very little evidence that the front was overriding the surface below it. Rather it appeared to have been halted early in its development by an accumulation of pebbles and cobbles that continued to build up in place.

The selection of species for the flora appeared to reflect the partial differentiation of the environmental factors and the small size of the area. At ES 17 the area involved was about 50 times as large as at ES 15, and the vascular flora was about three times as large. The flora at ES 15 was derived from species widely or narrowly tolerant on all gradients (55.6 %) to a considerably greater extent than at ES 17 (40.7 %). Experimental sites 7 and 8, with an area of about two hectares on the diamicton slope, had only 29.6 % of its species widely (or narrowly) tolerant on all gradients. At ES 17 and ES 7 and 8 it was possible to demonstrate a significant amount of sorting among definitive species in the micro-habitats in terms of the observed tolerance ratings of the species. Only suggestions of such a differentiation were possible at ES 15. Only eight of the species there could be considered to be in any sense definitive, and most of these were ineffective because they showed intermediate tolerances on some of the gradients.

With a larger water supply and a steeper gradient the small lobe probably would continue to enlarge, and would begin to override the surfaces below it. With time enough under these circumstances it would acquire a larger flora and more clearly differentiated micro-habitats. The flora could then be more effectively sorted according to its habitat preferences, as it was found to be at ES 17. Some medium-sized lobes in the "wet" sector of ES 8 appeared to be intermediate stages in this sequence though no detailed studies of their floras were made. Some on the diamicton slope below ES 8 seemed to have been halted by desiccation.

EXPERIMENTAL SITE 16

Introduction

Experimental site 16 was unique among the sites described in this paper in having an exceedingly low moisture content throughout. It consisted of a west-facing talus slope composed of relatively dry grus, located on the easterly border of a small dell a short distance west of the summit of trap knob 112 m, in the Nyhavn hills (Fig. 58). Its altitude lay between the 100 m and 110 m contours (see Pl. 1 for location on map).

A line of dowel targets was established across the grus slope on 17 August, 1957, approximately 7 m above the base of the slope and roughly parallel to the contours (Figs. 58, 59). The ends of the line were posts set in bedrock outcrops. The original number of dowels, set 10 cm apart, was 68, inserted alternately to depths of 5 and 10 cm. Varying numbers of dowels proved unacceptable for measurement, due to disturbance by animals, or to the weight of the snow, or to disturbance by wind. More 5 cm dowels were lost than 10 cm. By 18 August, 1961, only 40 % of the former remained standing, while nearly 90 % of the latter were still up.

The grus was so unstable that the targets could not be approached via the slope itself without disturbing the normal creep of the surface materials. Consequently no direct measurements of attitude, heave and downslope movement could be made until 29 May, 1960, when a bank of firm show still covered the slope nearly up to the target line. This made close approach and direct measurements possible. Final measurements were made on 18 August, 1961, when the site was abandoned.

A mass-wastingmeter and thermocouple strings were established on 15 August, 1957 (see map, Fig. 59). Moisture content of the grus was determined from samples collected 15 August, 1957; 9 July, 1958; 23 June, 10 August, and 18 September, 1960; and 13 July and 24 July, 1961 (*cf.* Washburn, 1967).

The vegetation of the site was first described on 28–29 July, 1957. This description included not only the grus slope but also the summit of MS 112 m, especially the area immediately above site 16. Notes on the

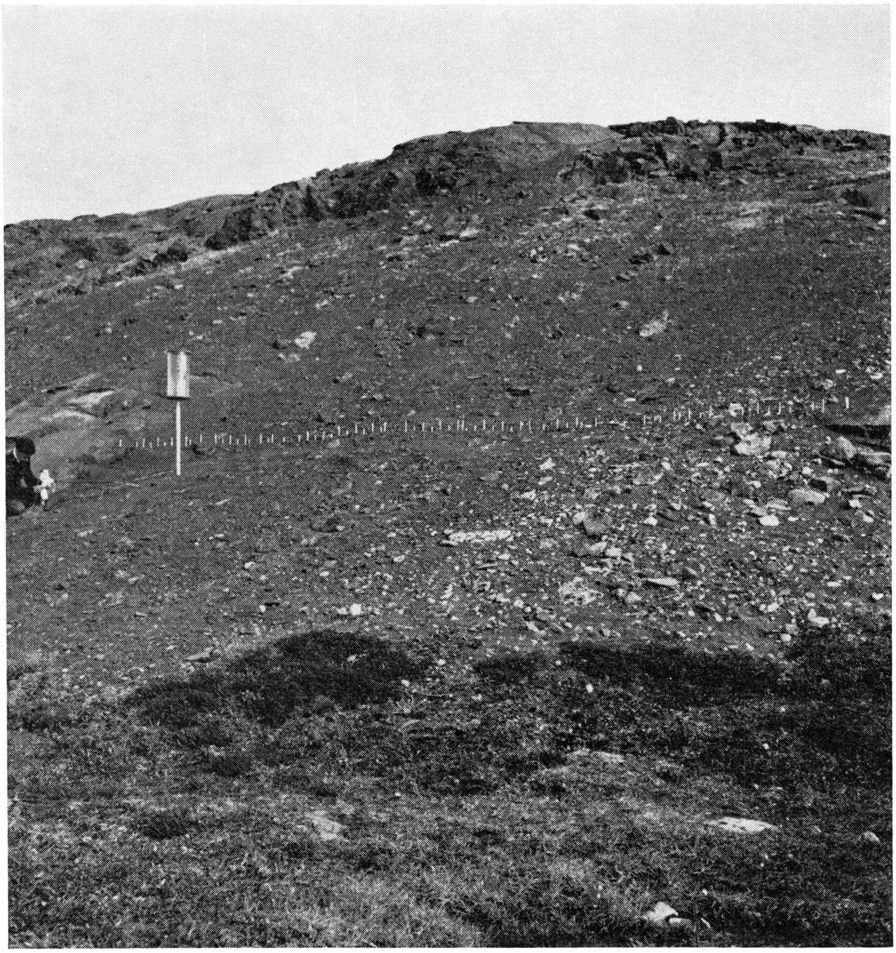

Fig. 58. Experimental site 16. View northeast, diagonally upslope. Target line extends between trap outcrops in middle ground; mass-wastingmeter 16 is below target line at left; 22 Aug., 1957. From WASHBURN, 1967, Fig. 33.

vegetation at the foot of the slope were made on 28 July, 1957, in connection with the study of turf hummocks (RAUP, 1965 B, p. 44–66, Fig. 8). These areas were visited on several occasions in subsequent years. Further notes on the summit vegetation above the site were made on 26 May, 1960.

Site 16 itself was exceedingly small and had a scanty vegetation. Only 7 species of vascular plants were found on the main part of the grus slope. A closely related habitat was on the outcropping ledges, also covered by loose grus but sometimes with lesser slopes. Even with the addition of the ledge grus flora the total number was only 13 species.

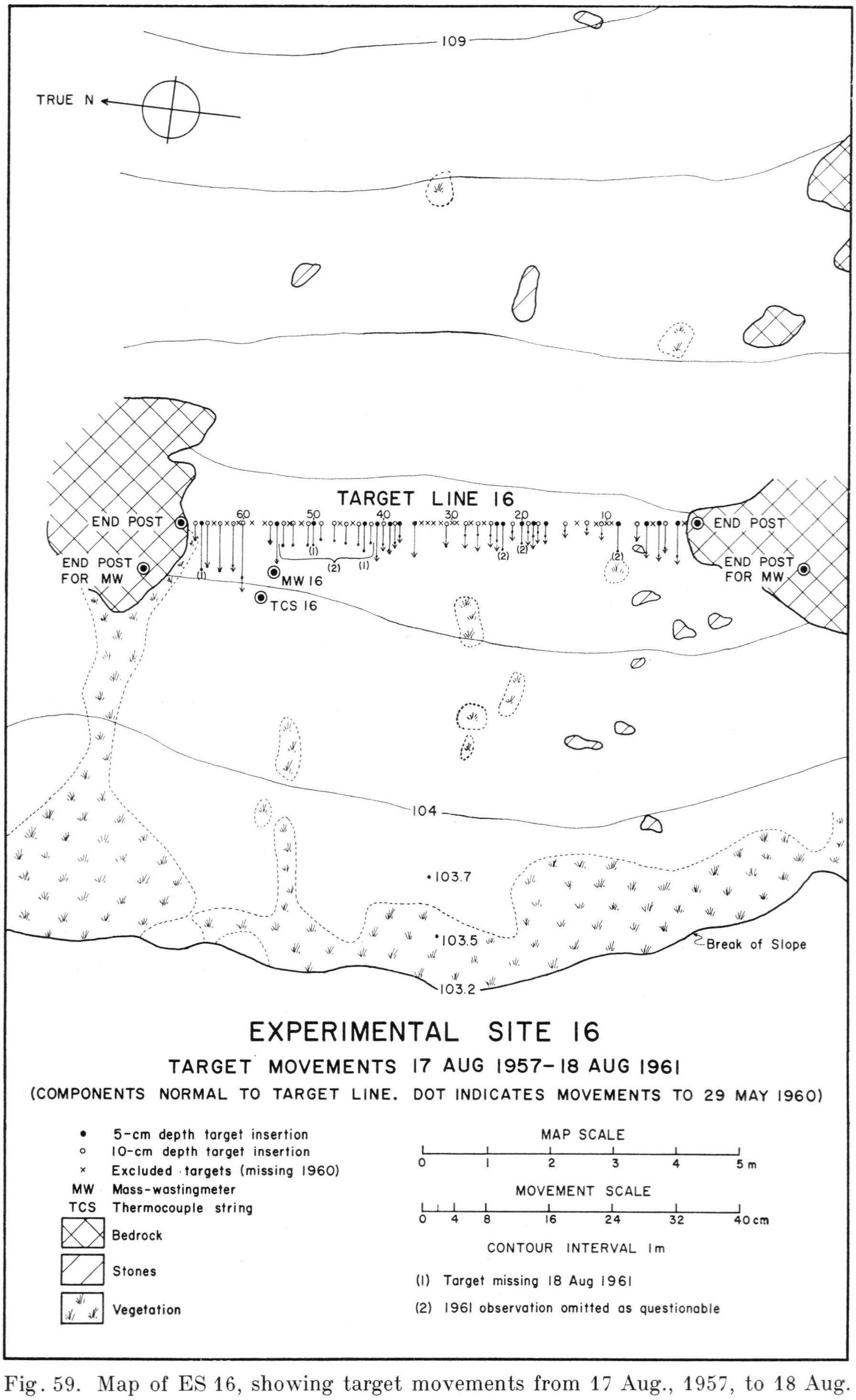

Fig. 59. Map of ES 16, showing target movements from 17 Aug., 1957, to 18 Aug. 1961. From WASHBURN, 1967, Fig. 35.

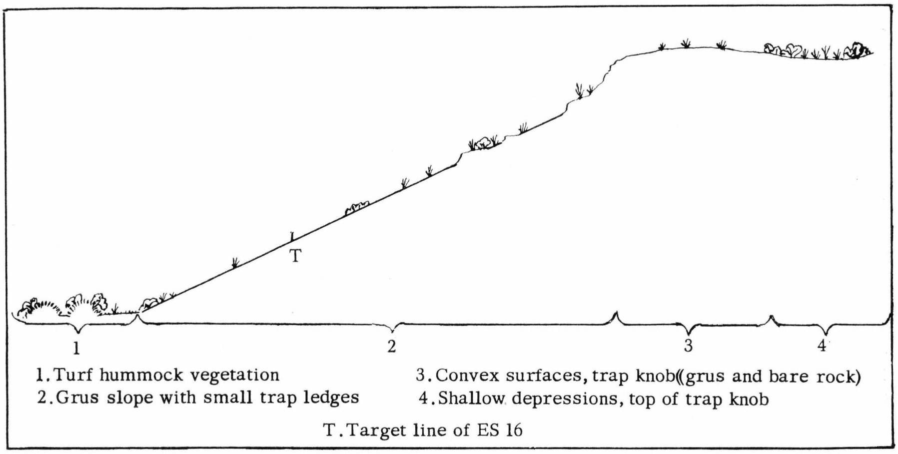

Fig. 60. Diagrammatic transect through ES 16, approximately at right angles to the target line, showing the four habitats used in the accompanying analysis.

The distinctive character of this vegetation can best be seen by contrasting it with other types that are immediately adjacent to it. Therefore the following analyses will be based on four types: turf hummock vegetation at the foot of the slope; the grus slope itself, including the grus-covered ledges; the low rounded knolls on the summits above the grus slope; and the relatively moist shallow depressions between these knolls. Figure 60 is a diagrammatic section of the slope and its adjacent surfaces, indicating the vegetational subdivisions noted above.

Topography and soils

The angle of the grus slope ranged from 22° to 29°, with an average of about 25°. The trap rock of the knob was coarse-grained, breaking up to form a gravelly sand (grus). The surface grus ranged in grain size up to 4 mm, containing about 15% of pebble sizes, and lesser quantities of cobbles and boulders. The boulders were erratics composed of granitic rocks. The surface materials were coarser than those at depth, but all had very low percentages of fines. The grus was thin at its upper limits, but at the sites of the mass-wastingmeter and the thermocouple strings (Fig. 59), near the foot of the slope, it was 91 cm thick (see Washburn, 1967, p. 78–79).

The grus slope was interrupted in several places by outcropping ledges of bedrock (see map, Fig. 59). Above the slope the top of the knob was gently rolling, with alternating convex and concave surfaces. Some of the convex surfaces were of bare rock, while others had a thin soil of grus. The shallow depressions were floored with thicker grus usually covered by a humus horizon and bearing vegetation of considerable density. The soil in the depressions also contained some fine sand and silt derived from small local deposits of diamicton closely resembling that found at ES 7 and 8. The floor of the dell at the foot of the grus slope was of diamicton also resembling that of ES 7 and 8. It sloped gently downward to the north, and was covered with a turf hummock vegetation.

The moisture supply

The principal source of moisture to the grus slope was from melting winter snow. With its southerly exposure the slope was exposed relatively early in the summer, and progressively from the top downward. Drying of the surface materials, once they were exposed, went forward rapidly due to insolation and to excessive drainage within the grus. Thereafter the grus remained dry throughout the summer except for infrequent light rains or thin coverings of snow which melted quickly.

The earliest samples for moisture determination were taken on 23 June, 1960, from points 1 to 1.5 m downslope from the mass-wastingmeter. They showed no moisture in the uppermost 10 cm of the grus. On 10 August of the same year, samples at the same place showed 2% moisture (w) at the surface and 4% at 5 and 10 cm, while on 18 September there was 4% at the surface and at 5 cm, 3% at 10 cm, and 5% at 20 cm. At the same location in 1961 there was 2% at the surface and at 5 cm depth, 3% at 10 cm, 6% at 20 cm, and 5% at 50 cm. By 24 July, 1961, this place had become a little drier, with 1% from the surface down to 10 cm, 3% at 20 cm, and 4% at 50 cm. The highest moisture value determined was 14% in the uppermost 3 cm in the excavation for the mass-wastingmeter on 15 August, 1957. This value was localized in the surficial materials, for at 18–22 cm there was only 3%, at 38–42 cm 2%, and at 69–73 cm 5%. Precipitation records for 1957 show that the 14% near the surface was due to a recent light rain.

Thus the available moisture records show that during most of the summer the water content of the grus ranged from 0% to 6%. They also suggest that summer precipitation wets only the surficial material, and that this moisture is quickly diffused or evaporated.

The slightly convex or flat surfaces on top of the knob above the grus slope were almost if not quite as dry as the latter (Fig. 64). Some were swept bare of soil by the wind, or covered by layers of grus ranging in thickness from 1–2 cm to 10–20 cm. These soils were exceedingly dry during the summer, subject to disturbance by wind, and poorly vegetated. The coverage by vascular plants was considerably greater than on the grus slope, but contained about the same number of species.

Depressions in the top of the knob contained much more moist soils than the convex surfaces. Not only did they collect runoff from the surrounding surfaces, but their finer textured soils were more retentive of the moisture received. They were collection areas for the finer materials blown out of the grus above, and also contained some silt from the scattered patches of diamicton mentioned above. Further, their topographic positions gave them some protection from the wind, resulting in smaller losses from evaporation than were prevalent on the convex surfaces.

The diamicton under the turf hummocks at the foot of the grus slope was moist whenever it was examined. The moisture was from drainage from surrounding slopes, melting ground ice, and from snowdrifts that lingered upslope from it until mid- or late summer.

Although no samples were analyzed for moisture except on the grus slope, it is possible with the general observations noted above to rate the four habitats just described in terms of moisture supply. The wettest site was that of the turf hummocks. Next were the depressions in the trap knob. Water loss during the summer season probably was greater here than under the turf hummocks, though the inter-hummock channels in the latter may have been fully as dry late in the season. Much drier than either of these sites were the convex surfaces on the knob. Moisture difference between these areas and the grus slope probably was not great. Which was the driest is uncertain, but it is probable that there was slightly more moisture on the slope than on the high surfaces.

Available data do not permit precise comparisons with moisture distribution in other experimental sites. However, a general comparison with ES 7 and 8 is possible. Judging by vegetation and by field observations, the soil moisture of the turf hummock area near the base of the grus slope was roughly equivalent to that in the turf hummock areas at ES 7 and 8. In the latter place the dry weight percentage of solids was estimated as intermediate between that in the sedge meadows and the heath tundra, or about 30 % in mid-August, 1958. In the driest portions of the ES 16 area (on the grus slope and on the convex surfaces of the knob above) the soil moisture was roughly equivalent to the late summer content in the dry eastern sectors of ES 7 and 8, though the textures of the soils are quite different. Thus it may be inferred that the total range of soil moisture in the ES 16 area probably was between 0 % and 30 %. For the life of the plants the dry portion of this range probably was considerably drier than the dry sectors of ES 7 and 8 because the latter area had a wet period in spring and early summer while at ES 16 the grus became desiccated almost immediately after it was exposed.

Frost heaving at ES 16

Frost heaving of dowels in the ES 16 target line was small, though it was perceptible and measurable in nine of the 54 dowels that were considered acceptable for such measurement (WASHBURN, 1967, p. 84–85). It was noted earlier that detailed measurements of heave and downslope movement usually were not feasible because of the looseness of the grus. The following data on heave were taken after the targets had been in place only one year, 17 August, 1957, to 8 September, 1958.

There were 31 acceptable 10 cm dowels and 23 acceptable ones with 5 cm insertions. Most of the heaving occurred among the 10 cm dowels, where three were heaved 1 cm each, one 2.5 cm, and three 0.5 cm each. Only two of the 5 cm dowels were heaved: one 1 cm and one 0.5 cm. Thus the average heave of all the 10 cm dowels was 0.29 cm, and the average for all 5 cm dowels was 0.07 cm. The average for all 54 dowels was 0.16 cm. All of this heaving was found within about 1.5 m of either end of the dowel line. Compared to the heaving in finer textured soils elsewhere in the Mesters Vig district, its effect upon plant survival probably was minor.

Using frost heave measurements elsewhere as a guide, the heave in other parts of the ES 16 area studied here can be rated approximately. The wettest area, which also had the most fine-textured soils, was that of the turf hummocks. However, sites of this kind contain two habitats with respect to heaving (see discussions under ES 7 and 8 and ES 6). Targets with most or all or their pins in the moss or turf of the hummocks showed little or no heaving, while those penetrating the mineral soil, especially in the inter-hummock channels, were heaved several centimeters. Thus heaving in the hummock area at ES 16, rated generally as intermediate, probably had the greatest effects among the sites at ES 16. The depressions in the top of the knob also had some fine-textured soils, and heaving could be expected to be less there than among the hummocks because of greater desiccation in late summer. Heaving in the grus on the convex surfaces of the knob probably was as low as on the grus slope.

Downslope movement at ES 16

Two sets of measurements to evaluate downslope movement of dowels were made at ES 16. One of these was on 29 May, 1960, when a bank of snow below the line made a close approach possible. The other was on 18 August, 1961, when the site was abandoned. Figure 59 shows these two measurements (WASHBURN, 1967, p. 84–85) (see also Figs. 61, 62). Only 46 dowels were considered acceptable.

Fig. 61. View along target line of ES 16, showing movement of dowels from 17 Aug., 1957, to 31 May, 1960. From WASHBURN, 1967, Fig. 37.

The range of movement values, to 18 August, 1961, was 1.4 cm to 10 cm. The 5 and 10 cm targets moved at about the same rate (average for 5 cm dowels, 3.6 cm; for 10 cm, 3.8 cm). The average annual rate was about 1 cm per year. The movement was most rapid near the north end of the target line where the slope was steepest (about 29°). WASHBURN (1967, p. 86) proposed that gelifluction on this slope was of no consequence, and that the movement was by the process of dry creep. He concluded that there was little disturbance at depth, and that the movement by creep was much slower than by gelifluction in saturated soils, even where the latter occurred on much less steep slopes.

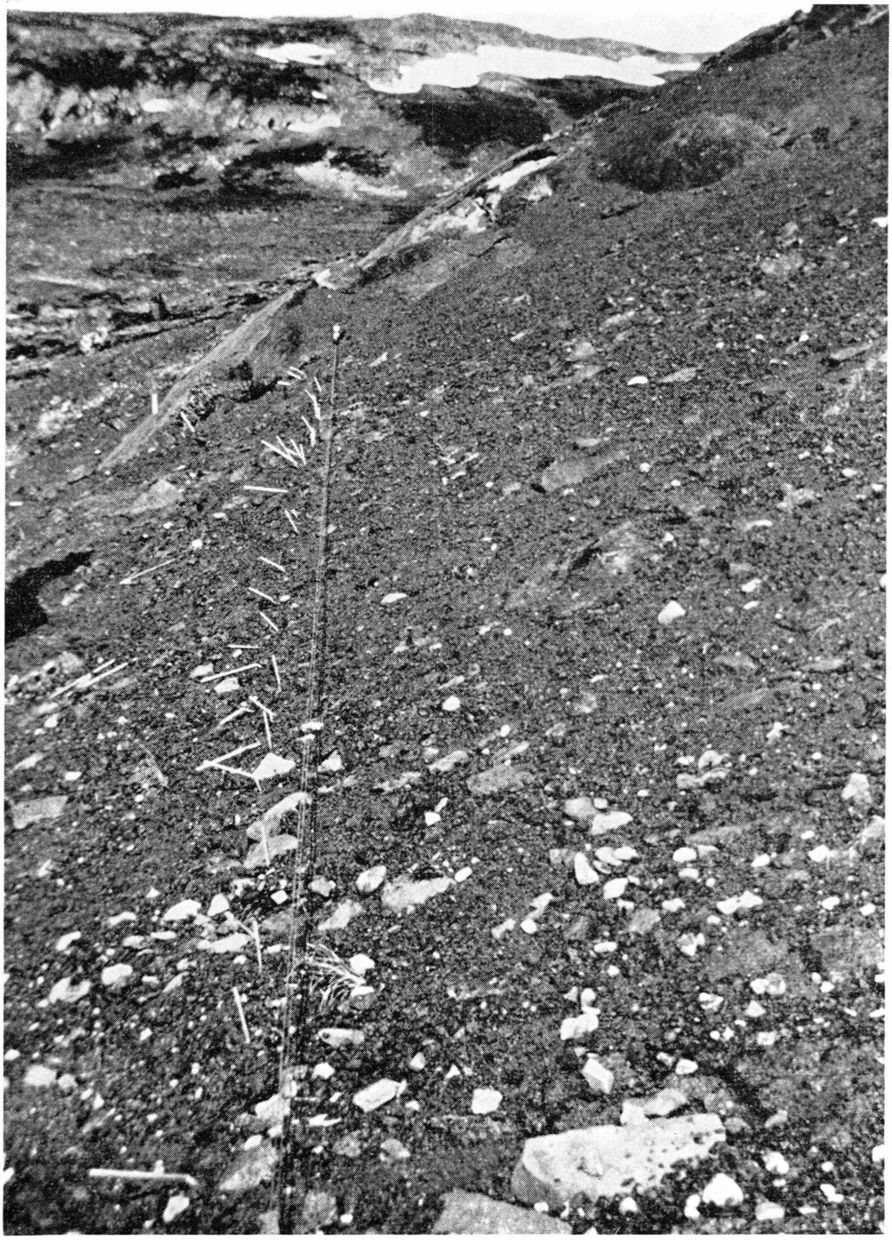

Fig. 62. View along target line of ES 16, 18 July, 1964.

Both dry creep and gelifluction are regarded in these analyses as nonfrost disturbance factors. In the ES 16 area gelifluction probably was of minor importance to plants. The turf hummocks probably were moving downslope to the northward, but judging by the estimated moisture content of the soil the movement probably was relatively slow. The only other place where gelifluction might have occurred was in the shallow depressions on the knob. Lesser moisture content there in mid- and late summer, and probably also lower gradients and less fines, probably resulted in less movement than in the turf hummocks. Dry creep occurred also on the convex surfaces of the knob, though the lower gradients of the latter made the movement much less rapid than on the grus slope. On the other hand deflation and deposition by wind were no doubt much more active than on the target line slope.

From the standpoint of plant survival, injury due to nonfrost disturbance can be rated as follows: The most stable site probably was that of the turf hummocks, and next was in the depressions in the trap knob. Of the two areas subject to creep and wind action, the grus slope, less subject to violent winds, may have been somewhat more stable than the convex surfaces on the knob.

The vegetation at ES 16

Forty-six species of vascular plants were found in the area used for comparative studies in the immediate vicinity of ES 16. Table 10 contains a list of these species and shows their distribution among the sites shown in Fig. 60.

The grus slope, scene of the dowel line, had an open vegetation of widely scattered plants (Fig. 63); *Carex nardina*, *C. supina* ssp. *spaniocarpa*, *Salix arctica*, *Dryas octopetala*, *Epilobium latifolium*, *Vaccinium uliginosum* ssp. *microphyllum*. *Dryas* formed small mats 15–60 cm in diameter and 0.5 to 3 m apart. The sedges were scattered as individual plants or small groups. The creeping grus was slowly inundating the vegetation at the lower margins of the slope, and the few plants in the moving grus clearly showed the effects of the same process. It was common to find small tufts of *Carex nardina* bent over and held down by pebbles up to 2 cm in diameter.

Outcropping ledges of trap on this slope were partially covered on the upper surface with the creeping grus, here probably moving at a somewhat slower rate due to decreased angles of slope. In addition to the species noted above, the following were found on these ledges: *Calamagrotis purpurascens*, *Kobresia myosuroides*, *Melandrium affine*, *Draba nivalis*, *Dr. glabella*, *Potentilla nivea*, *Campanula rotundifolia*. For purposes of analysis these species are grouped with those on the steeper grus slope, making a total of 13 for the creeping grus habitat.

Among the other three habitats used for comparison the one most closely related to the grus slope was on the convex surfaces of the top

Table 10. *Species found at ES 16 and vicinity, showing their distribution among the habitats seen on the grus slope and on the neighboring turf hummocks and trap knob.*

	Turf hummocks	Grus slope	Trap ledges, upper grus slope	Trap knob (grus and crevices)	Shallow depressions in trap knob
Woodsia glabella				+	+
Cystopteris fragilis				+	+
Festuca brachyphylla				+	
Poa arctica	+				+
Poa glauca	+			+	
Trisetum spicatum	+				
Calamagrostis purpurascens			+	+	
Kobresia myosuroides			+		
Carex nardina	+	+	+	+	
Carex rupestris				+	+
Carex Bigelowii	+				+
Carex supina ssp. spaniocarpa		+	+	+	
Carex misandra	+				+
Carex capillaris	+				+
Luzula arctica	+				+
Luzula confusa	+			+	+
Salix arctica	+	+		+	+
Betula nana					+
Oxyria digyna	+				+
Polygonum viviparum	+				+
Stellaria Edwardsii	+				
Cerastium alpinum	+			+	
Arenaria pseudofrigida					+
Minuartia rubella				+	
Silene acaulis	+				+
Melandrium affine				+	
Papaver radicatum			+	+	+
Draba alpina	+				
Draba nivalis			+		
Draba lactea	+				+
Draba glabella			+		
Draba cinerea				+	
Braya purpurascens					+
Sedum Rosea				+	
Saxifraga oppositifolia	+			+	+
Saxifraga tenuis				+	+
Saxifraga cernua	+			+	+
Potentilla nivea			+		
Dryas octopetala	+	+	+	+	+
Epilobium latifolium	+	+	+	+	
Pyrola grandiflora					+
Cassiope tetragona	+				+
Arctostaphylos alpina					+
Vaccinium uliginosum ssp. microphyllum	+	+			+
Pedicularis hirsuta	+				+
Campanula rotundifolia			+	+	

of the trap knob (Fig. 64). Some of these surfaces were low-domed and barren of vascular plants except for a few species found in crevices. Others had a few centimeters of grus forming a thin soil. The grus was variable in texture, from very coarse sand to coarse sand mixed with finer sands. On the coarsest grus there were only a few scattered plants of *Carex nardina*, an occasional small mat of *Dryas octopetala*, *Salix arctica*, or *Saxifraga oppositifolia*, and a few individuals of *Poa glauca*

Fig. 63. Mats of *Dryas octopetala*, and small tufts of *Carex* on grus slope at ES 16, 18 July, 1964.

and *Melandrium affine*. There was a great deal of mortality in the *Dryas*. The finer textured grus had a more varied flora, though it still did not cover more than about 20 % of the ground. In addition to the species found on the coarse grus, the following were on the finer textured material: *Festuca brachyphylla*, *Calamagrostis purpurascens*, *Carex rupestris*, *C. supina* ssp. *spaniocarpa*, *Luzula confusa*, *Cerastium alpinum*, *Minuartia rubella*, *Papaver radicatum*, *Draba cinerea*, *Saxifraga tenuis*, *S. cernua*, *Epilobium latifolium*, *Campanula rotundifolia*. The most abundant and prominent species here were *Carex nardina*, *C. rupestris*, *Dryas octopetala*, and *Salix arctica* with the sedges conspicuous enough to form a thin, green "sward". Largely confined to rock crevices were *Woodsia glabella*, *Cystopteris fragilis*, and *Sedum Rosea*. In the following analyses all the species (22) on these convex surfaces are grouped together.

Fig. 64. *Carex nardina* and *C. rupestris* scattered in thin grus soil on rounded trap knob above ES 16, 29 July, 1957.

Shallow depressions in the top of the trap knob had a thicker cover of plants, with densities estimated to range between 20 % and 60 %. They contained a shrub tundra in which the following species were most conspicuous: *Vaccinium uliginosum* ssp. *microphyllum*, *Dryas octopetala*, *Salix arctica*, *Arctostaphylos alpina*, *Cassiope tetragona*, and *Betula nana*. Soils in these depressions were varied, but all were characterized by finer textures and much more moisture than were seen on the convex surfaces. Some not only had fine sands in them but also clayey silts derived from small patches of diamicton deposited on the knob. Table 10 indicates the 27 species found in the depressions. No attempt was made to sort them according to micro-habitats, though this would no doubt be possible.

Notes on the turf hummock vegetation were confined to a small area in the immediate vicinity of the foot of the grus slope. The list of vascular plants in this area contained only seven species, which is far from realistic for this vegetation (see discussion of the turf hummock flora in RAUP, 1965 B, p. 100–104, and in the present paper under ES 7 and 8). The notes were made in 1957, before the random nature of species distribution among mature turf hummocks was fully realized. Otherwise a wider area would have been utilized. Therefore the turf hummock flora used in Table 10 was formed as for ES 7 and 8. Twenty-four species in the list of turf hummock plants (RAUP, 1965 B, p. 101, Fig. 40) were found in the ES 16 study area, and these included all of the seven found among the turf hummocks at the foot of the grus slope. Table 10 lists these 24 species, which are used in the ensuing analyses as more representative of hummock vegetation than the seven found in the small area originally studied.

Vascular plant densities in the turf hummock vegetation were estimated at 60% to 90%. The primary species were *Cassiope tetragona*, *Salix arctica*, *Dryas octopetala* and *Vaccinium uliginosum* ssp. *microphyllum*. The hummocks were mature, with well-formed inter-hummock channels usually floored with organic crusts.

The behavior of species at ES 16 and vicinity on the coverage, moisture and physical disturbance gradients

Figure 65 shows the behavior of species in the four segments of the transect at ES 16 used in the present study. The numbers of species used in each segment were derived, as in the preceding analyses, by subtracting from the total floras the species widely tolerant on all gradients. No species narrowly tolerant on all gradients were found in this area. A general view of the graphs indicates that the behavior patterns in the two dry segments (the grus slope and the convex surfaces on the trap knob) are more nearly related to each other than to the patterns in the two moist segments (the turf hummocks and the shallow depressions on the trap knob).

Behavior on the coverage gradient

As in other analyses on this gradient, widely tolerant species consistently showed much higher percentages than narrowly tolerant ones. Within the different vegetations the greatest variation in coverage was found in moist areas, and in these the definitive widely tolerant species showed the highest percentages (Fig. 65). Estimated coverages suggest that there was somewhat more variation in the turf hummock vegetation

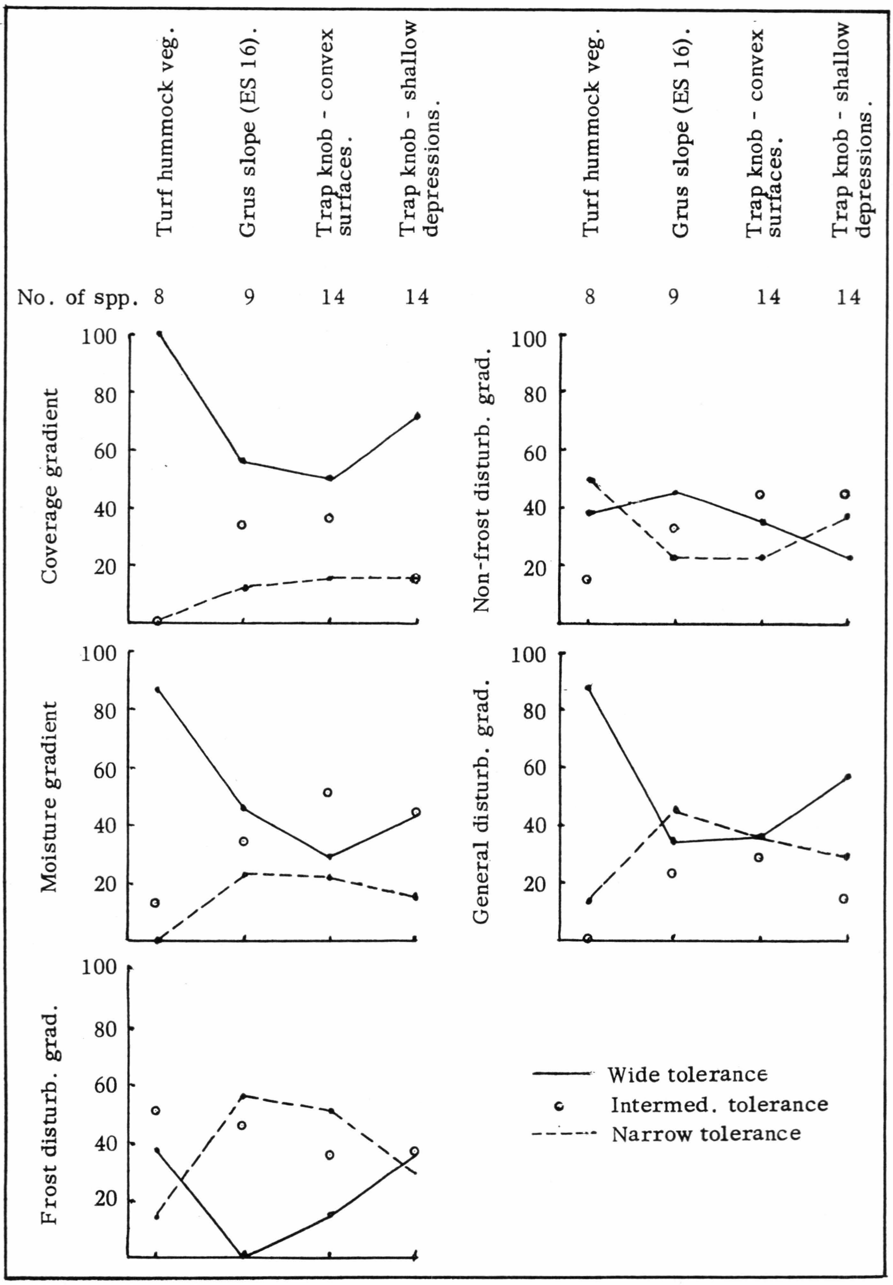

Fig. 65. Percentage distribution of species tolerance in the principal habitats at ES 16 and vicinity, in relation to gradients of vascular plant coverage, moisture, and physical disturbance.

than in the moist depressions on the trap knob. Consistent with this there was a lower percentage of widely tolerant plants in the knob depressions, and a higher percentage of narrowly tolerant plants.

Behavior on the moisture gradient

Behavior on this gradient is also based on the capacity of the species to withstand variation in an environmental factor—in this case moisture supply. The least variation was in the dry sites (Fig. 65). They lost nearly all of their moisture very early in the growing season and remained relatively dry throughout the summer. Occasional precipitation during the open season produced only surficial soil moisture, and this was quickly dissipated. On the other hand the moist sites were more subject to year-by-year variations in their water supplies, and to variations in their seasonal regimes. Moisture supplied by snow-melt lasted longer into the summer due not only to larger initial supplies but also to their finer textured soils. Further variation came from localized differences in the vegetation, *i. e.* turf hummocks vs. inter-hummock channels.

The general behavior of the species on the moisture gradient was consistent with these differences in variation. The lowest percentages of widely tolerant species, and the highest percentages of narrowly tolerant ones, were on the dry grus slope and on the convex surfaces of the trap knob. The highest and lowest percentages respectively of widely and narrowly tolerant species were in the turf hummocks and in the trap knob depressions. The selection of species for these two sites suggests that there was considerably more variation in the former than in the latter. This may have been the case, for the knob depressions tended to be poorly drained, and may have held their moisture through the open season more effectively than the turf hummock area which was on a gentle slope.

Behavior on the frost disturbance gradient

The process most injurious to plants on this gradient was frost heaving. Because its effectiveness depends upon adequate moisture for the formation of interstitial ice, particularly at autumn freeze-up, and because a fine-textured soil holds more water than coarse sands, the dry areas at ES 16 and vicinity should have had the least frost heaving and shown the least frost injury to plants. The group of definitive species found on these sites showed low percentages of plants widely tolerant of frost heave injury, and relatively high percentages of narrowly tolerant species (Fig. 65). On the grus slope there were no widely tolerant species, and on the convex knob surfaces only about 15 % of the species were widely tolerant. On the other hand between 50 % and 60 % were species extremely sensitive to frost heaving. Observations of dowel heaving showed that it was slight on the grus slope. Plants sensitive to it (narrowly tolerant) could therefore live there with impunity, other things being equal. The species selection for the convex knob surfaces suggest that there may have been slightly more heaving there than on the grus slope.

In the moist sites the above proportions were reversed, showing more widely than narrowly tolerant species in both places. However, the differences in percentage were not great, suggesting the mixed nature of these sites. Densely vegetated areas such as turf hummocks and heath tundra usually showed little heaving, while immediately adjacent soils covered by organic crusts may have been heaved violently.

Behavior on the nonfrost disturbance gradient

It has already been noted that the most effective disturbance factor on the grus slope was dry creep, with deflation by wind probably second in importance. On the gently rounded convex surfaces of the trap knob wind deflation and deposition may have been the more significant factors. In the moist areas there was no doubt some gelifluction movement, more under the turf hummock vegetation than in the knob depressions. The curves for species selection on the nonfrost disturbance gradient are generally consistent with these observations (Fig. 65). There were about twice as many definitive widely as narrowly tolerant species on the grus slope, and about a third more on the convex knobs. These proportions suggest that narrowly tolerant species were considerably less successful in these dry sites than widely tolerant ones. Again the proportions were reversed in the moist sites, where narrowly tolerant plants were most successful. Gelifluction apparently was a less effective disturbing agent here, as elsewhere in the Mesters Vig district, than frost heaving.

Behavior on the general disturbance gradient

The graph for this gradient, in summarizing the behavior of species on the frost and nonfrost gradients, suggests that disturbances injurious to plants were more prevalent in the moist sites than in the dry (Fig. 65). Widely and narrowly tolerant species were about equally represented in the dry sites, while in the moist sites the species very sensitive to physical disturbance were greatly outnumbered by the widely tolerant ones. Again the species selection has indicated more injurious disturbance in turf hummocks than in the knob depressions.

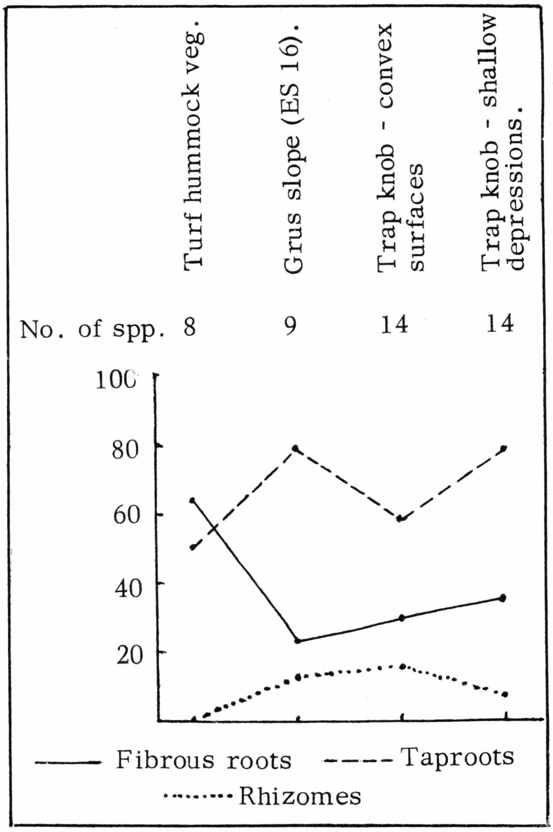

Fig. 66. Percentage distribution of fibrous rooted, taprooted, and rhizomatous species in the principal habitats at ES 16 and vicinity.

The distribution of root and rhizome systems in the ES 16 area

Figure 66 shows percentages of definitive species with fibrous roots, taproots and rhizomes in the four study sites at ES 16. If the assumption is tenable that taprooted plants are more resistant than fibrous rooted or rhizomatous species to desiccation and physical disturbance, the preponderance of taproots in the ES 16 area probably can be accounted for. The lowest percentage of taproots was in the turf hummock vegetation which was one of the moist sites. On the other hand one of the highest percentages was also in a moist site, in the trap knob depressions, which is anomalous. High and median percentages were in the dry sites where they would be expected. The relatively higher percentages of rhizomatous species were in the dry sites where physical disturbance by frost action was notably low, and where nonfrost disturbance though clearly present was not intensive. Higher proportions of rhizomes have usually occurred in very wet sedge meadows, but these were non-existent in the ES 16 area. The curve for fibrous rooted plants is consistent with expectation, for a high percentage of them was in the turf hummock vegetation, and an intermediate proportion in the knob depressions. The lowest percentages of them were in the dry sites.

Summary of species behavior on the environmental gradients at ES 16

This summary emphasizes the selection of species found on the site for which the most precise data are available: the grus slope which yielded information on the movement of dowel targets. The grus was exceedingly dry, with samples showing 0% to 6% moisture (w) throughout most of the growing season. It was composed mainly of relatively coarse trap sand which was moving downslope by dry creep at a mean rate of about 1 cm per year. Frost heaving was present on some parts of the slope, but was minimal throughout. The average heave of 31 10-cm dowels was only 0.29 cm in one year, and the average for 23 5-cm dowels was 0.07 cm, making the average for all accepted dowels 0.16 cm.

The vegetative cover was extremely scanty, ranging from 0% to 10% (estimated). On most of the slope it ranged from 0% to 5%. Thirteen species of vascular plants were found there. Of these, four species were rated as widely tolerant on all the gradients studied, leaving nine species that could be considered definitive.

Relative to more moist sites in the vicinity, the percentage of species widely tolerant of variation in vegetative cover was low, and the percentage of species narrowly tolerant on this gradient fairly high. This would be expected in a site where variation in density was scanty and apparently had continued thus for a long time with very little variation.

Variation in the moisture gradient locally, seasonally, or from year to year was also relatively small. However, it appears to have been sufficient to bring to the site nearly twice as many species widely as narrowly tolerant of moisture variation.

With frost heaving minimal in the grus the definitive species growing there could be relatively safe from this kind of physical disturbance. All of the flora consisted of species narrowly or intermediately tolerant on this gradient.

The reverse was true for nonfrost induced disturbance, in this case the dry creep demonstrated by the downslope movement of the dowels, and probably also slight deflation by wind. The site contained about twice as many species widely tolerant of nonfrost disturbance as species sensitive to this disturbance.

There were nearly three times as many taprooted as fibrous rooted species on the grus slope. This probably reflected the extreme desiccation, and to some extent the effective physical disturbance by dry creep. The percentage of rhizomatous plants was low, as in the Mesters Vig flora generally. But relative to other sites near ES 16 it was fairly high, possibly reflecting minimal disturbance by frost heave and a friable soil easily penetrated by growing shoots.

Among the adjacent sites used for comparison in the preceding analyses the convex surfaces on the trap knob most nearly resembled the grus slope in the selection and behavior of the plants. The tolerance ratings of their plants suggest that they may have been slightly drier, but also a little more subject to frost heaving. The latter could be due to slightly more moisture in spring and autumn though the total effective moisture for the growing season might be less. The species ratings suggest that there was slightly less nonfrost disturbance than on the grus slope. The taproot percentage, probably reflecting relatively great desiccation and physical disturbance, was somewhat lower than expected for the dry trap knob flora. There seems to have been a little more frost disturbance there, and a little less nonfrost disturbance. Also it probably was a little drier. These factors, in balance, probably would have reduced the taproot proportion to some extent.

ORGANIC CRUSTS IN THE MESTERS VIG DISTRICT

A conspicuous feature of the Mesters Vig landscape is the prevalence of thin organic crusts that cover, in the aggregate, many hundreds of hectares of the ground surface. They have been mentioned in nearly all of the descriptions of experimental sites in the preceding pages. The only exception was the grus slope at ES 16, where they were not seen. They were so abundant in the sites, and in the Mesters Vig district generally, that they deserve special attention. Photographs of them may be seen in Figs. 14, 15, 17 and 31 of the present paper, and in several pictures by WASHBURN (in press). They appear also in RAUP, 1965 B, Fig. 16, where they occupy a snow-bed habitat.

The crusts varied from dark gray to black in color, though in places they had a tinge of green in them. They occurred in patches of all sizes, ranging from small areas only a few centimeters wide to large expanses covering many hectares. Occasionally their surfaces were quite smooth, but in nearly all cases they had a microrelief of small "nubbins" 1–5 cm high and 2–20 cm broad, or low ridges showing parallel or concentric arrangements. The crusts were usually 1–5 mm thick, and usually overlay mineral soil though they sometimes rested on a humic horizon (as at ES 6). They were found on soils ranging in texture from gravel to clayey silt.

When wet or moist the crusts were flexible, easily torn apart, and somewhat gelatinous on the surface. If the soil was firm beneath, this made them slippery to walk on. When in such a condition they had their darkest color. When dry they were dark gray, hard and brittle, often showing the polygonal crack patterns of the underlying soil. Most of the small nubbins and wrinkles on the surface when dissected were found to be filled with mineral soil of the general substratum, but occasionally some were found that were empty, as though the soil had shrunk away from their interiors.

The crusts were found in moisture regimes ranging from those in which surface water was available for only a short time in spring (one or two weeks during and immediately after snow-melt), to those in which water was abundant throughout the season. A certain amount of moisture, even though small, appeared to be necessary for their formation. The only situations in which they were not seen were on coarse-textured soils that became dry almost immediately after the melting of the snow, by rapid evaporation, surface drainage, or by percolation.

In nearly all cases, whether wet or merely moist, the crusts were sparsely populated by vascular plants, the coverages by these plants ranging from less than 1 % to about 40 %. Average would be about 20 %. The vascular flora was characteristically scattered, though it reached greater density in some sedge meadows and in upland shrub tundra.

The specific nature of the Mesters Vig organic crusts is imperfectly known, and will require more study than we have been able to give it. Dissection and microscopic examination have indicated that their basic ingredients, making up most of their volume, are the blackened remains of dead bryophytes, mainly mosses. Apparently the most important living ingredient is a gelatinous blue-green alga of the genus *Gloeocapsa*, which no doubt gives the crusts their slippery quality when wet. A few filamentous blue-green algae were also present, and there was a black lichen, *Polyblastia gelatinosa*, though this was found in exceedingly small quantity. A few green fronds of living mosses and hepatics were sometimes found in the otherwise dark mass of a dissected bit of crust. Two species of mosses have been identified in it: *Campylium stellatum* and *Ditrichum flexicaule*; and six species of liverworts: *Anastrophyllum minutum*, *Cephaloziella* (*cf. arctica*), *Gymnomitrium corallioides*, *Lophozia quadriloba*, *Lophozia* (subg. *Leiocolea*) sp., *Solenostoma polaris*. All of these plants were present in very small numbers.

At the margins of small streams and pools apparent transitional stages from black organic crusts to green moss mats were found. The following mosses were collected in these living green mats: *Anoectangium tenuinerve* and *Ditrichum flexicaule*. Trivial quantities of seven species of liverworts were also found: *Anthelia juratzkana*, *Sphenolobus minutus*, *Lophozia quadriloba*, *Blepharostoma trichophyllum*, *Scapania cuspiduligera*, *Solenostoma* (? *polaris*), *Tritomaria quinquedentata*.

Thus among the collections made, three species were found to be common to the crusts and to living moss mats at their margins: the moss *Ditrichum flexicaule*, and the hepatics *Lophozia quadriloba* and *Solenostoma polaris*. This suggests that the crusts may be moss mats deteriorated by desiccation, and it also proposes an origin for the dead bryophytic matrix which forms most of the crust.

Crusts superficially similar to those seen at Mesters Vig have been described frequently in arctic and alpine regions. Descriptions and photographs published by GJAERVOLL (1956, p. 229–233) in his studies of Scandinavian alpine snow-beds indicate that he found them widespread there. He also cited accounts by KALLIOLA (1939, p. 165) and SÖYRINKI

(1938, p. 53) of their occurrence in the mountains of Finland. STEINDORSSON (1945) mentioned them repeatedly in his description of the vegetation of the Central Highland of Iceland. All of these observers correlated the development of the crusts with extreme snow-bed conditions, *i. e.*, sites in which snow lies very late in spring or into the summer. The principal plants in them have been noted as one or two species of liverwort: *Anthelia juratzkana* or *Gymnomitrium varians*, the first of which is by far the most common.

There appears to be no necessary relationship between the occurrence of the Mesters Vig crusts and late-lying snow. They do occur in extreme snow-bed habitats, below snowdrifts that continue melting back throughout all or most of the summer. But they are also abundantly developed on surfaces that are exposed by the earliest thaws. They were observed in the spring of 1960 emerging from deep snow side by side with densely vegetated shrub tundra, the border between the two coming out from under the melting front of the snow at right angles to the latter. *Anthelia juratzkana*, as noted above, was collected at Mesters Vig but in very small numbers. Also it appears to be associated with marginal living mats of moss rather than with the crusts. A species of *Gymnomitrium* was found in the crusts but formed an insignificant part of them.

Causes for all of the micro-relief in the surface of the crusts are not clear. In cases of small ridges formed in more or less concentric patterns over fine textured soils the mechanism may be flow of the soil and consequent wrinkling of the moist surficial crust. On the other hand the crust may have formed after the mineral soil had already acquired its microrelief. The manner of development of nubbins is uncertain, and has been discussed at some length by WASHBURN (in press). It was quite common to find the nubbins disrupted, with the crust torn and the mineral soil exposed. The areas so disturbed usually were small, each involving only 1–3 sq. dm. The exposed mineral soil had all appearances of disturbance by needle ice. In some other areas where dense tundra vegetation had been disturbed by comparatively recent surficial breakage and slipping so that one or more square meters of mineral soil were exposed, organic crust had covered the bare soil. From these observations it was concluded that whatever the cause of the microrelief, it probably was not greatly affected by the presence or absence of the crust. Rather, the crust covered the surface provided the latter remained moist enough, and provided its disturbance intensity permitted the crust to remain intact. This conclusion was buttressed by the fact that some active surfaces were found with nubbin and concentric wrinkle structures, but entirely without crusts.

The origin of the crusts is suggested by their distribution with respect to other phenomena noted in the district. They are most highly developed on soils that retain some moisture throughout the summer, exemplified by ES 6, the "wet" sectors of ES 7 and 8, the marginal tundra around ES 15, and large expanses around ES 3 and 9. On damp sandy flats near the shore of the fjord at the mouth of Tunnelelv they have formed nearly continuous cover over wide areas. They were present, however, in the "dry" sectors of ES 7 and 8 where they were in minor depressions, became very dry in summer, and were much fragmented. They were found on the well-drained loams of till knolls where Arctic Brown soils have developed. There they were often only partially covered by vascular plants, and were associated with many foliose and fruticose lichens. There were broad expanses of them on the river terraces about the mouth of Tunnelelv. On the highest of these terraces (17–25 m) they were domed and cracked into polygonal forms 10–30 cm broad, partially covered and interspersed with lichens. The vascular flora, except for patches of *Cassiope*, was exceedingly sparse. On the lower terraces the crusts were more moist, less domed and cracked, and had the characteristic nubbin micro-relief seen in sheet flow areas on the uplands.

Evidence from several sources has indicated a period of general desiccation in the Mesters Vig district during the last 60–75 years (Raup, 1965 B; Washburn, 1967). The principal result has been a gradual decrease in summer moisture delivered to surface soils by the melting late-lying snowdrifts and ground ice. If this has been the case large areas of the surface were formerly moist throughout the summer, and suitable for the development of moss mats. It is not impossible that the crusts, made up primarily of dead bryophytes and decaying very slowly in the arctic climate, have resulted from the general desiccation.

GENERAL SUMMARY AND CONCLUSIONS

Introduction

The analyses and discussions in this paper suggest lines of attack upon two interrelated problem complexes. The first of these embraces the old question of how the "fjaeld-mark", as it was defined long ago in Greenland by WARMING and others, is caused and maintained as a kind of vegetation. The second was stated in the Introduction to the present paper and is concerned with the validity and usefulness of the analytical methods used here. The medium in which these problems have been approached has been the combined study of vegetation and geomorphic processes at five experimental sites illustrating mass-wasting in the Mesters Vig district.

Analyses presented in the preceding pages were based first upon instrumental data and general observations at the five mass-wasting sites published by WASHBURN (1967), and second upon botanical observations made concurrently by the writer not only at these sites but also in the Mesters Vig district at large. The present summary will attempt to bring these data together and draw tentative conclusions from their interrelationships.

In the course of the study an effort was made to define some physical factors of the environment that were believed to inhibit the growth of vascular plants. At the same time the ranges of tolerance to variations in these factors exhibited by the species were defined in general terms. The interrelations between the limiting physical factors effective in the five sites and the distributional behavior of the species were then explored.

It was recognized at the outset that analyses in terms of a few selected factors would be imperfect because of interrelations with other factors that were not measured. Such factors were both external and internal to the species. External ones, broadly categorized, would have included varying nutritional supplies to the plants, Ph differences in the soils, and factors of local climate near the ground. Internal factors would have included the varied genetic ecotype development in the species, the incidence and local distribution of polyploidy, and the characteristics of different species with respect to rates of photosynthesis and to phenology.

Certain phases of these factors were dealt with cursorily. There were, for instance, minor sources of calcium in some soils such as the shells embedded in the fjord-bottom clayey silts exposed at low altitudes. However, the total effect of calcium from all sources was not large enough greatly to affect the content of the flora. Several measurements of Ph were taken in the surficial soils, but they showed only minor differences. Two of the experimental site areas had local climates that closely resembled each other—7 and 8, and 15. Experimental site 6 was somewhat similar but less exposed. The grus slope at ES 16, and the rounded upper slopes of the adjacent trap knoll were both extremely dry situations and were especially well exposed to warm sun and dry winds. Experimental site 17, situated on a northeasterly mountain slope, showed the effects of altitude in the relative shortness of the growing season for plants.

The geomorphic processes treated most were frost heaving and gelifluction, which appeared to be of primary significance in most of the sites. Dry creep was characteristic only of ES 16, but minor occurrences of it were seen at ES 17. Erosion and deposition by wind probably were of some importance at ES 16, though adequate measures of them were not made. The effects of stream erosion and deposition were present in ES 6 and to a minor degree in ES 7 and 8, 15 and 17. But these effects appeared to be minor in comparison to those of frost heaving and gelifluction. Several other active geomorphic processes common in the Mesters Vig district were not found in the sites reported upon here. These were earth flow, the action of slushers, erosion and deposition by larger streams, etc. The effects of these processes upon the vegetation will be discussed in other papers.

Correlations between species tolerance ratings and habitat differences within the experimental sites were treated in the general discussions of the various sites. These will not be reviewed here, but an attempt has been made to draw up comparative correlations involving all the sites (Figs. 71, 72, and 73). Only the definitive species have been used in these analyses. Habitats in ES 15 were not included in the figures because their small numbers of definitive species were not adequate for comparative purposes. No graph was made for general comparison of plant behavior on the coverage gradient. The wide tolerance of most of the species to variations on this gradient was evident in the analyses of individual sites and habitats. Although there were minor percentage differences in tolerance ratings among the habitats, no consistent relationships with coverage densities or physical factors could be seen. With minor exceptions all habitat data used were derived from situations where instrumental observations of the geomorphic processes were available.

In the case of the moisture gradient a threefold division was made in the extent of variation experienced by the plants in the various habitats: narrow, median, and wide (Fig. 71). The division is somewhat arbitrary, with the median category merely separating the extremes. Within each of the three broad divisions are habitats drawn from different experimental sites, generally arranged to show increasing variation. Similar threefold divisions were made for the gradients of frost and non-frost disturbance of the soils (Figs. 72 and 73), in these cases high, median and low, referring to decreasing intensities of the disturbances.

Comparisons among the experimental sites brought out the significance of areal size and habitat differentiation as factors limiting the numbers and kinds of species present. The following discussion will begin with these factors and then proceed to those believed to limit the germination and growth of species and the development of the plant cover.

Limiting factors:

1. Size of area and extent of habitat differentiation
2. Water supply and desiccation
3. Soil texture
4. Frost heaving
5. Gelifluction
6. Dry creep
7. Erosion and deposition by wind and water.

It is probable that the order used in nos. 2–7 of the above list approximates a descending order of effectiveness among the limiting factors in the five experimental sites. Item 1 is difficult to evaluate, but may exert an overall determining influence in the smaller sites.

Influences of area size and habitat differentiation

The number of species found in the flora of each of the sites appeared to be closely related to the size of area involved (Fig. 67). The map area embracing ES 7 and 8 contained 88 species of vascular plants, over half the total flora of the Mesters Vig district. These combined sites had an area of approximately 2.2 hectares (22,000 sq. meters). Experimental site 17, with an area of 500 sq. meters, had 59 species in it, a little less than 40 % of the flora of the whole district. Experimental sites 16 (and vic.) and 6, with approximately 400 and 200 sq. meters respectively, had 46 and 45 species respectively, about 30 % of those in the district flora. Finally, site 15 with 10 sq. meters had only 18 species in it, approximately 12 % of the total district flora.

Area	2.2 ha.	500 sq. m	400 sq. m	200 sq. m	10 sq. m
Site nos.	7 & 8	17	16	6	15
No. of spp.	88	59	46	45	18

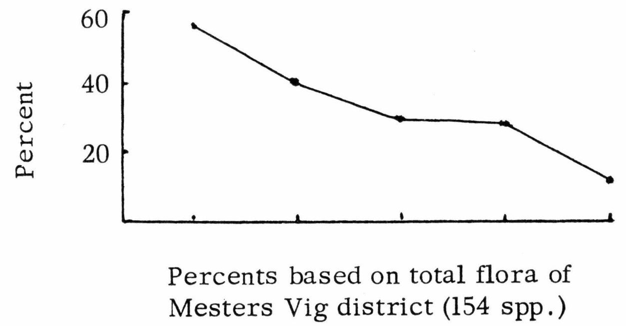

Fig. 67. Graph showing the relationship of area size to numbers of species found in the experimental sites.

It was difficult to judge in all cases the extent of differentiation of habitats within the experimental sites, but it is probable that the descending order of areas shown in Fig. 67 is approximately that of habitat differentiation, from greatest to least. Although the habitats along the target lines at ES 7 and 8 sometimes showed indefinite boundaries, there were rather clearly defined habitat differences not only between the "dry" and "wet" sectors, but also between local areas differentially affected by frost heaving and mass-wasting processes. Experimental site 17, though it had rather sharply defined habitats on the tread and margins of the gelifluction lobe, had a limited total array of habitats represented. The grus slope at ES 16 was in itself relatively undifferentiated, but the vicinity of the site, which was also used in the analysis, showed an extent of differentiation that was judged to be somewhat less than that seen at ES 17. Experimental site 6 was considerably less differentiated within itself than ES 17 or the vicinity of ES 16. However, the general wetness of the whole site favored a relatively high proportion of moisture loving species, and thus raised the size of the flora to a larger number than found in areas of similar size and greater habitat differentiation. Experimental site 15 was not only the smallest in area but probably also had the least differentiated habitats. It was a small, "embryonic" gelifluction lobe,

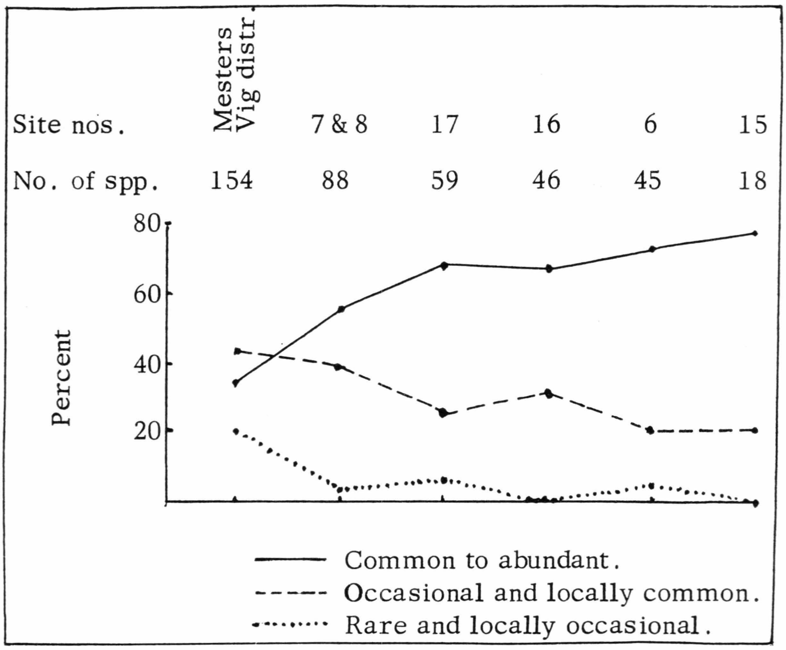

Fig. 68. Graph showing the relation of species frequency distribution to size of area in the experimental sites.

with variation in habitat highly localized in the central part of the tread and in the narrow strip of more dense vegetation on its low front.

The relative sizes of the site areas were also reflected in the distribution of the frequency of occurrence of the species. Figure 68 shows the percentage distribution among the sites of three frequency classes: common to abundant; occasional to locally common; rare to locally occasional. The percentages of these classes are given also for the Mesters Vig district as a whole. As the areas and floras became smaller, with progressively less differentiated habitats, the percentage of the common to abundant species increased from a low of about 35 % in the whole Mesters Vig district to a high of about 78 % in ES 15. Occasional to locally common species occurred more frequently in the district as a whole than the common to abundant species. At ES 7 and 8 these relationships were reversed, and the curve for occasional to locally common species showed a general decline to about 22 % at ES 15. Rare to locally occasional species were present in the whole district to the extent of about 21 %, but throughout the experimental sites they ranged from zero to only about 7 %.

The size and habitat differentiation of the experimental sites could be related to the proportional representation of species tolerance ranges in the sites. Figure 69 gives comparative percentages of definitive species

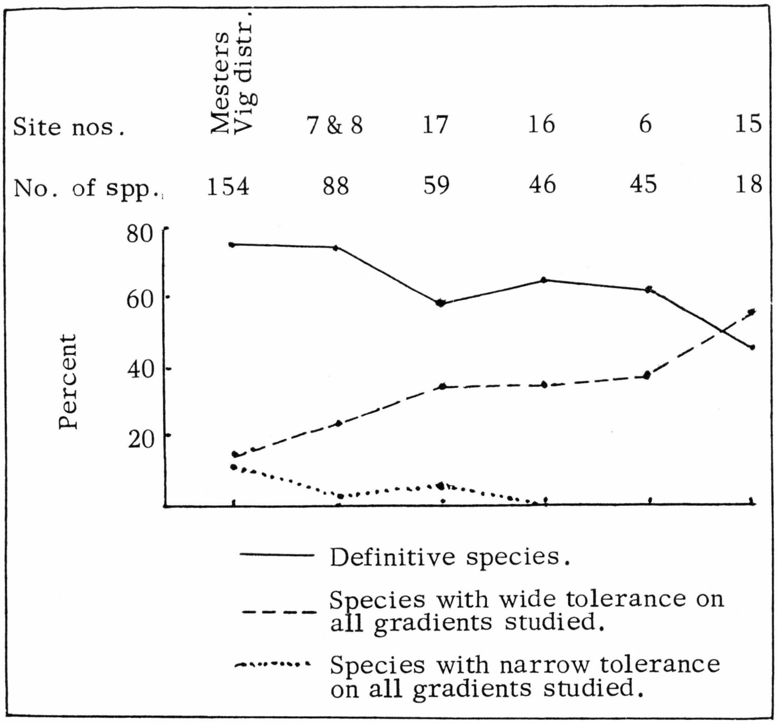

Fig. 69. Graph showing the relation of area size to the general distribution of species tolerance in the experimental sites.

within each of the experimental sites, and of species with wide and narrow tolerances on all the gradients used for analyses. In the Mesters Vig district as a whole the definitive species made up about 75 % of the total flora. Compared to the floras of lesser areas, these species showed a general decline from their high proportion in the district as a whole to about 44 % in the smallest area and flora. A break in the evenness of this curve appears at ES 17 where the definitive species showed only about 59 % of the total flora of the site.

Species with wide tolerance on all gradients showed a contrasting curve, the lowest point of which was at about 14 % in the district as a whole. From here there was a general increase in the proportions of them which, with about 56 % of the flora, outnumbered the definitive species at ES 15. Species narrowly tolerant on all gradients, although there were about 11 % of them in the district as a whole, ranged from zero to about 7 % in the larger sites, while in ES 16, 6, and 15 there were none of them.

As an example of the interrelations among the effects of area size, habitat differentiation, frequency of occurrence, and the distribution of tolerance ratings, Fig. 70 was constructed. The same order of area size

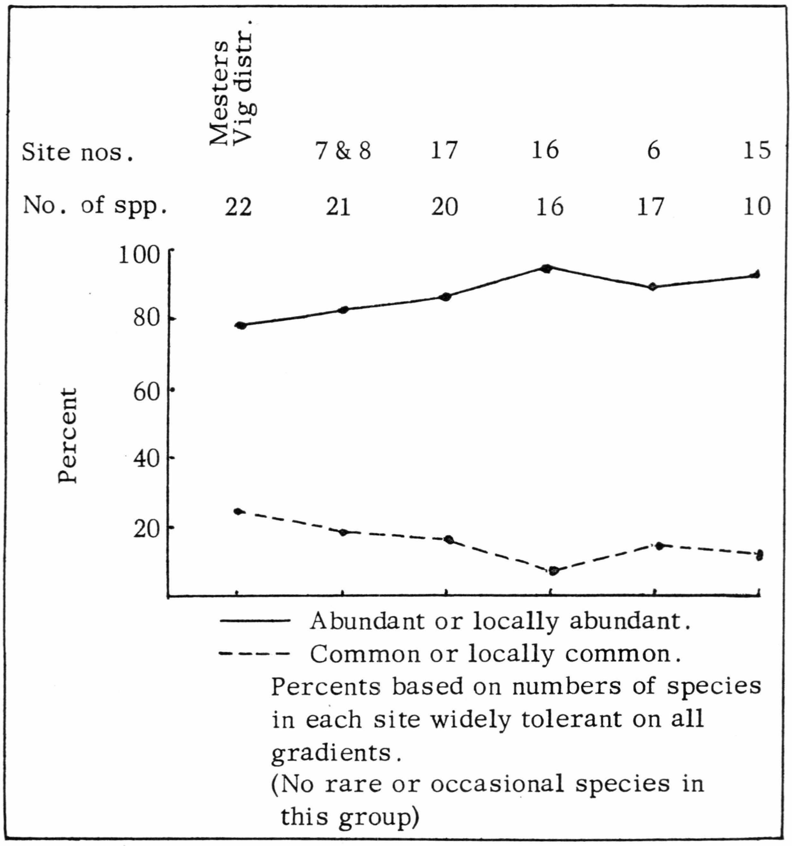

Fig. 70. Graph showing some relations among area size and differentiation, species tolerance, and frequency distribution in the experimental sites.

was used in this graph as in the preceding ones, but the number of species in each experimental site was restricted to those widely tolerant on all gradients. A twofold division of frequency classes was made in this case: species abundant in the Mesters Vig tundra, or at least abundant locally; and species common or locally common in the tundra. No occasional or rare species were found among those widely tolerant on all gradients. It was to be expected that the abundant species would show by far the highest proportions, but there also appeared a modest though rather consistent increase in their proportions from the largest to the smallest areas. Experimental site 16 showed a minor exception to this, with about 94 % of its wides in this category as against 88 % in ES 6 and 90 % in ES 15. The reason for this is not entirely clear, though it can be suggested that the generally low moisture content of the site, and the rather high intensity of physical disturbance may have caused the selection of a high proportion of widely tolerant species. The curve for common or locally common species is, of course, a mirror image of the curve for abundant species. In the Mesters Vig district as a whole there were about 23 % of these species and at ES 15 about 10 %.

It is thus evident that the numbers and kinds of species found in the experimental sites were determined in considerable measure by the areal size and extent of habitat differentiation in the sites. These factors, independently of those directly limiting to the growth of the plants, appeared to have accomplished an initial and basic selection of species available for site and habitat analyses.

Effects of moisture supply and desiccation

The Mesters Vig observations tend to support in large part SØRENSEN's conclusion (1937) that the quantity and continuity of moisture supply was of first importance to the behavior of the vegetation. Second for him were the relative extent and thickness of the winter snow cover; and in third place he put "solifluction" in which he included all frost heaving and mass-wasting processes. The information available on snow cover in the Mesters Vig district has already been discussed (RAUP, 1965 A, p. 8–9; 1965 B, p. 28–30; WASHBURN, 1965, p. 21). It indicated that differential snow cover in the district was of much less significance than the geomorphic processes of SØRENSEN's "solifluction". Moisture supply and desiccation were of large significance not only because of the direct use of water in the physiological processes of the plants but also because of their varied effects upon the geomorphic processes inhibiting to the plants.

Most of the moisture effective in the lives of the plants in the Mesters Vig district came from melting snow or thawing ground, principally the former. The winter snow rested upon a relatively thin layer of "basal ice" which covered the surface of the ground in a number of places. The soil immediately beneath this basal ice was solidly frozen throughout the winter and remained so until the spring thaw removed the snow and ice. At the edge of a melting snowdrift there were sometimes 1–2 cm of surficially thawed ground beneath the edge of the ice. Once out from under the snow and ice the ground thawed rapidly to depths of a meter or more depending upon the soil texture and the coverage of vegetation and organic horizons. The melting of the general winter snow cover left the well-drained surface soils wet or moist for a relatively short time due to rapid evaporation in the dry air. Continued moisture through a part or all of the growing season for plants depended, therefore, upon the presence of remnant snow in the form of drifts, or of melting ground ice. In most seasons many of these drifts persisted throughout the summer, sending melt-water downslope from them. There was clear evidence that the size and effectiveness of the sources of moisture had been declining gradually over the past 60–75 years (*cf.* WASHBURN, 1965, p. 21–24; RAUP, 1965 B).

On surfaces watered by sheet flow from the broad fronts of melting snowdrifts the vegetation demonstrated roughly concentric zonations and developmental sequences (RAUP, 1965 B). Among the experimental sites described in this paper these were seen in modified forms at ES 7 and 8 and ES 6. Where melt-water was more narrowly channeled, raising the moisture content of the diamictons in localized areas, gelifluction was accelerated and lobes were formed. The lobe treads, if active, harbored scattered plants or none, while the fronts and lower lateral margins carried relatively dense cover. Experimental site 17 typified the larger, more highly developed of these lobes and ES 15 the smaller "embryonic" ones. Experimental site 16 had no source of water supplying its grus slope except that which came from spring snow-melt or occasional light rain. Its very well drained soil quickly became dry and remained so. Its vegetation was restricted to a few scattered plants capable of withstanding the extreme desiccation and the disturbances due to dry creep and wind.

Habitat differentiation within the experimental sites appeared to be controlled mainly by seasonal and spatial regimes in the water supply. The "wet" and "dry" sectors of ES 7 and 8 were segregated by the fact that the water supply was continuous throughout the summer in the former and limited to one to three weeks in spring in the latter. Differences within these sectors were closely related to local topography and to distances from the water sources. Habitats were progressively drier with increasing distances from the sources. The zonation of vegetation reflected these differences, variously modified in detail by geomorphic processes which also reflected the water regimes.

Another modification of the vegetational zonation below a snowdrift was seen in ES 6 where melt-water from the adjacent drift was supplemented by drainage from a broad valley above the site. Thus no "dry" sector appeared, and the vegetation was limited to "wet" ground types. A small stream running through the site caused a minor and highly localized differentiation of habitats.

On the gelifluction lobes habitat differentiation was most highly developed at ES 17 where a relatively large and fairly continuous summer water supply kept the lobe enlarging and overriding the cobbly surface below it. It had become a conspicuous topographic feature on the mountain slope. Most of the water moved over and through the axial part of the tread and the front. The soils of the tread were progressively drier lateral to the axis and the sides were progressively drier upslope from the wet front. These moisture differences were reflected in rather clearly defined vegetation types; and small lobes, with small water supplies, probably were limited in the same way. The lower part of the tread at ES 15 was forming a relatively dry crust in late summer of some years, and excavation of the front showed but slight overriding of the slope below. These things suggest that ES 15 may already have reached nearly its maximum size and habitat differentiation. Many similar small lobes in the immediate vicinity of this site had ceased to be active. In this case also the types were modified by the geomorphic processes that kept the lobe active.

The small lobe at ES 15 had only the beginnings of a vegetation pattern similar to that at ES 17. Its most heavily vegetated part was its front, about 8 cm high. Lateral banks were scarcely evident. Most of the gelifluction movement was in the longitudinal axis of the tread, which was relatively narrow though it widened somewhat toward the front. Except in the partially barren axial portions, the tread vegetation of the lobe merely merged laterally with the sparse vegetation of the adjacent tundra.

The large active lobes have continued to grow as long as they had an adequately high water supply. Stabilization probably has resulted from general reduction of the water supplies, or from enlargement of the lobes great enough to reduce the moisture reaching their lower portions.

A summary of species behavior on the moisture gradient in the various sites (excl. ES 15) appears in Fig. 71. Narrow variation was found in habitats which retained their moisture throughout most or all of the open season, or lost their moisture very early in the season almost immediately after snow-melt and then remained dry throughout the summer and autumn. The sedge and hummocky meadows in ES 7 and 8 and ES 6, most of the organic crust areas in ES 6, and the axis of the lobe tread at ES 17 were examples of the first of these. The second type was best illustrated by the grus slope at ES 16. The proportions of widely tolerant species remained in general between 40 and 50 °/₀ in all of these habitats, while the percentages of narrow tolerance remained relatively low, most of them below 10 °/₀. As in most of the Mesters Vig district plants of intermediate tolerance showed about the same percents where the moisture variation during the season remained low. Habitats with a median position in the range of moisture variation were in the organic crust and turf hummock areas of ES 7 and 8. These habitats were both in the "wet" sector, but both occurred toward its drier margins. Situations with wider variation in moisture supply were illustrated by the "dry" sector and the heath tundra at ES 7 and 8, and by the margins of the tread of the large gelifluction lobe at ES 17. Percentages of widely tolerant species averaged very little if any higher in the median group than under conditions of narrow variation. However, narrowly tolerant

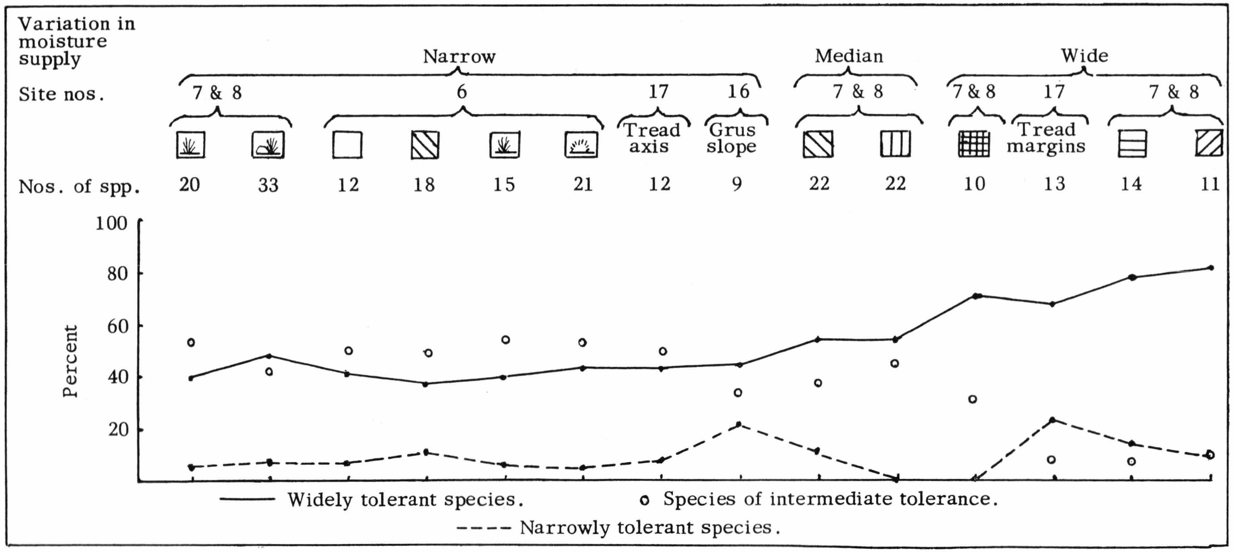

Fig. 71. Summary of the distribution of species tolerance on the moisture gradient in the principal habitats of ES 6, 7 & 8, 16, 17.

plants fell to zero in one of the habitats included in the median group, suggesting conditions that were more rigorous. In the four habitats showing wide variation the percentages of widely tolerant plants rose to between 70 and 80% of the floras, while the narrowly tolerant plants retained relatively low percentages (Fig. 71).

Influences of soil texture

The quantity and behavior of the moisture supply were highly conditioned by the texture of the soils. Soil texture therefore appeared to be the second major determining influence upon the vegetation found in the sites.

With the exception of ES 16, the soils of the experimental sites reported in this paper were relatively fine-textured diamictons which showed relatively minor variations. Data on this were published by WASHBURN (1967, App. D). Most of these diamicton soils were silty sands or sandy silts, with varying lesser fractions of gravel and/or clay. A minor exception appeared in ES 6 where there was some silty-sandy gravel and silty sand. The general uniformity among the sites was also shown by the liquid limits of the soils. In ES 7 the average was about 19% moisture (w), in a range of about 14% to 32%. In ES 8 the average was also about 19% in a range from 12% to 32%, with a single sample showing 51%. At ES 15 the average was 16% in a range of 15% to 17%. At ES 17 the average was about 19% in a range of 19% to 20%. At ES 6 where the textural variation was somewhat greater the average liquid limit was about 29% in a range of 16% to 57%. The grus slope at ES 16, composed as it was of sandy gravel, gravelly sand, and silty-gravelly sand, was too coarse and well drained to show evidence of any plasticity.

The diamictons of ES 7 and 8, 15, 17, and to a slightly lesser degree of ES 6, were thus subject to gelifluction at moisture percentages ranging for the most part between 12% and about 32% and averaging 19% except at ES 6. Water supplies within these amounts were available in one or more parts of all of the experimental sites except ES 16. The rate and amount of the gelifluction were dependent upon degree of slope and upon the amount and continuity of the water supply. Frost heaving and frost creep were active in most diamictons under these conditions.

Among the experimental sites having diamicton soils, therefore, major differences due to soil texture could be looked for only at ES 6, and even there to a minor extent. The difference between all of these sites and ES 16 was a large one. The coarse grus at ES 16, coupled with a very small water supply, eliminated gelifluction and nearly all frost heaving. Dry creep, however, was active in this soil, which was also disturbed by wind to a minor degree.

Effects of frost heaving

Frost heaving probably was present to some degree in all the soils of the Mesters Vig district, caused by the formation of ice lenses and interstitial ice, and by the resulting increase in the volume of the surficial soil materials. Roots embedded in the soils were likely to be broken or injured by differential movements of the soil particles or masses. Depending upon the relative violence and frequency of the heaving, plants might suffer only minor checks to their growth; on the other hand they might be killed either by an accumulation of injuries or by being heaved out of the ground.

Frost heaving was most intense in clayey-silty diamicton soils that were moist to wet at the time of autumn freeze-up. It was least in gravelly-sandy soils that had no continuing water supply during the open season. The principal factors tending to increase or decrease frost heaving, other things being equal, thus appeared to be variation in soil texture and/or soil moisture. The effects of moisture supply were in turn highly conditioned by the seasonal regimes of moisture and the incidence and violence of freeze-thaw cycles. These cycles were few in number and usually of low intensity in spring, and though also few in number during late summer and autumn, were violent at the time of autumn freeze-up (WASHBURN, 1967). Soils whose moisture supply was abundant in spring and early summer, but which were nearly dry at freeze-up, therefore were heaved to a minor extent.

Other factors tending to reduce the intensity of heaving were coverage by thick vegetation and/or organic soil horizons, and inundation by flowing water. In the presence of moisture and texture conditions conducive to frost action, heaving was most intense in soils that were nearly or entirely bare of vegetation, or where the cover consisted primarily of thin organic crusts. It was least in the thicker organic soils such as occurred in turf of hummocks. Heaving occurred in the mineral soil beneath growing hummocks, in places forming earth cores, but most of the plants on these hummocks were rooted in the turf. Soils continuously bathed by running water during freeze-thaw cycles were heaved intermediately or very little.

Figure 72 compares the varying intensities of frost induced disturbances (primarily frost heaving) in the several habitats with the percentage distribution of wide, intermediate and narrow tolerances of the definitive

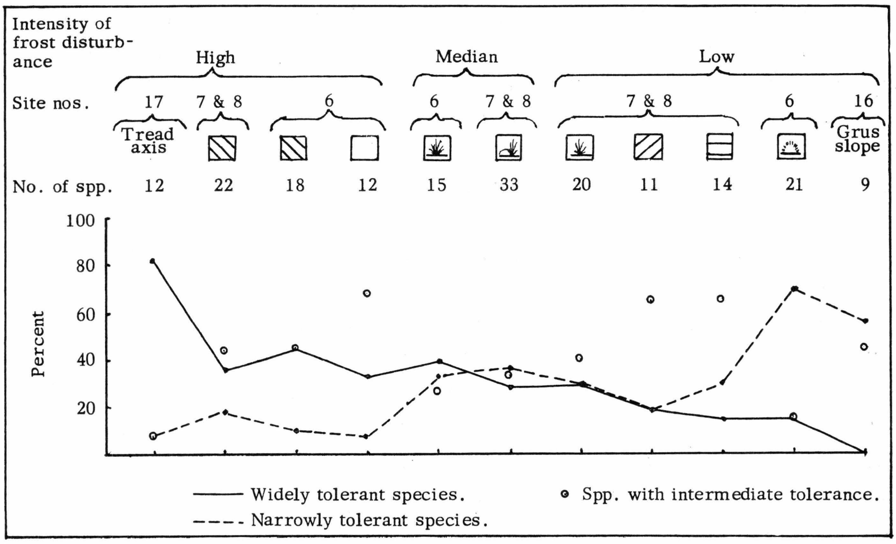

Fig. 72. Summary of the distribution of species tolerance on the frost disturbance gradient in the principal habitats of ES 6, 7 & 8, 16, 17.

species on this gradient. In this case the assumption would be that habitats with the higher intensities of frost heaving should have the higher percentages of plants best able to survive this kind of disturbance (widely tolerant). In contrast, the habitats should show the lowest percentages of species narrowly tolerant of this kind of disturbance. The highest intensities of frost heaving probably were seen in the axial portion of the gelifluction lobe tread at ES 17. Next would come the organic crust and bare soil areas of ES 7 and 8, and ES 6. Areas of observed low heave intensity were in the "dry" sector and the sedge meadows of ES 7 and 8, and in the turf hummocks of ES 6. It is probable that the lowest heave intensity seen among the five sites studied was on the dry grus slope at ES 16. The graph shows a general trend downward in the percentages of widely tolerant plants from about 83 % on the tread axis at ES 17 to zero on the grus slope at ES 16. At the same time there was a general upward trend from the tread axis of ES 17 in the percentages of narrowly tolerant species. They reached about 70 % in the turf hummocks of ES 6 and remained above 50 % on the grus slope at ES 16.

The tread axis of ES 17 contained all the conditions favoring intense heaving: a relatively fine-textured diamicton, an essentially continuous water supply, and the soil barren or with thinly scattered plants and organic crusts. Some of the more barren areas in ES 6 and 15 had similar conditions. The "wet" sectors of ES 7 and 8 were characterized by a moisture supply which, though it varied in quantity, was continuous.

The wettest part had some of the denser vegetation types. The eastern part of the "wet" sectors had somewhat less moisture though it was ample for the development of vegetation. However, this area showed the highest intensity of frost heaving of any part of the slope, and its vegetative density was very little greater than in the nearby "dry" sectors. It is probable that the frost heaving caused so much injury and/or mortality that the plants were prevented from developing a dense vegetation. This area was characterized by thin organic crusts which covered most of the ground surface. Similar situations were seen in parts of the target line of ES 6, and on much of the surface immediately surrounding the small gelifluction lobe at ES 15.

Frost heaving showed only median to low intensities in the wettest parts of ES 7 and 8 and ES 6. In these habitats the presence of an organic horizon in the soil and denser vegetation appeared to restrict it. There were some areas that demonstrated marked differentials in the amount of frost heaving. This was particularly true in areas of mature or maturing turf hummocks where the inter-hummock channels extended down nearly or quite to the mineral soil. Heaving in these channels was relatively intense, but under the adjacent hummocks it was small or at most median in intensity. Thus in such areas plants extremely sensitive to frost heaving and those widely tolerant of it could exist side by side.

The soils of the "dry" sectors, though they had enough moisture in spring or early summer for the formation of interstitial ice, experienced comparatively little frost heaving because of the lower intensity of freeze-thaw activity during these periods. At the time of fall freeze-up, having already lost their moisture, they again experienced insignificant frost heaving even though the major cause of heaving, the annual freeze-thaw episode, would otherwise have been effective. Thus the summer desiccation in the "dry" sectors of ES 7 and 8, which are representative of large areas in the Mesters Vig district, appeared to have been a major factor preventing the development of more than a very thin cover of vegetation. This was effective even though the soils had a large water-holding capacity. Situations not unlike it were found on parts of the tread of the gelifluction lobe at ES 17, and on the small lobe at ES 15, though in these two cases the extent of desiccation was not as great except on the lateral margins of ES 17. Less frost heaving was noted on the front of the lobe at ES 15 than on the tread, due in large part to the somewhat coarser texture of the soils there, and the denser vegetation. Although no instrumental data were available to support it, the behavior of the plants on the front of the lobe at ES 17 indicated that it apparently also had much less frost heaving than the axial part of the tread. Frost heaving was an insignificant factor limiting to plants on the grus slope at ES 16. Both here and in the "dry" sectors of ES 7 and 8, even in the absence of organic soils and dense vegetative cover, plants with median to narrow tolerance of heave were preponderant in the floras.

The influence of gelifluction

When the species tolerance ratings were made on the gradient of nonfrost disturbance it was first assumed that gelifluction should be included among the frost induced processes. Later, as a result of WASHBURN's intensive studies of mass-wasting, it became clear that gelifluction could be measured as a separate process which could be independent of the mechanical effects of the frost heaving responsible for creep. Thus, being activated by a high water content in the soil rather than by repeated short-term freeze-thaw cycles, it did not entail the injurious effects resulting from these cycles. It is in this sense that gelifluction was included among the nonfrost processes in the final tolerance ratings, even though some of its water supply came from the melting of ice lenses which had induced the frost action. In many places the main supply of water came from snow-melt. It was thought whatever injurious effects resulted from gelifluction would be reflected in the sorting of plants on the nonfrost disturbance gradient.

Tolerance ratings of species on the nonfrost gradient were arrived at mainly from observations of the behavior of the species with respect to geomorphic processes not discussed at length in this paper. These processes showed obvious and dramatic inhibiting influences, though at any given time they were more or less localized in the landscape. Deflation and deposition by wind were clearly altering the vegetation on the windswept sandy delta remnants near the mouth of Tunnelelv, on sand dune areas of the Labben peninsula, and on occasional sandy beaches along the shore of the fjord. Slushflows occurred periodically on the lower slopes of the mountains, associated with the spring thaw. These slushflows were particularly destructive in the gullys from which they issued, and on the fans deposited by them. Earth flow, with its characteristic breakaway scarps, though highly localized, was widespread on the mountain slopes, and disrupted the vegetation much more violently than gelifluction. Wherever larger streams occurred they were destructive to plants on their banks and flood plains.

Figure 73 contains an apparent paradox. In most of the habitats represented, even in some of those where gelifluction was known to be very active, species intolerant of nonfrost disturbance showed percentages consistently much higher than those for widely tolerant species. The paradox lies in these high proportions of species believed to be especially sensitive to nonfrost disturbance. Two notable exceptions

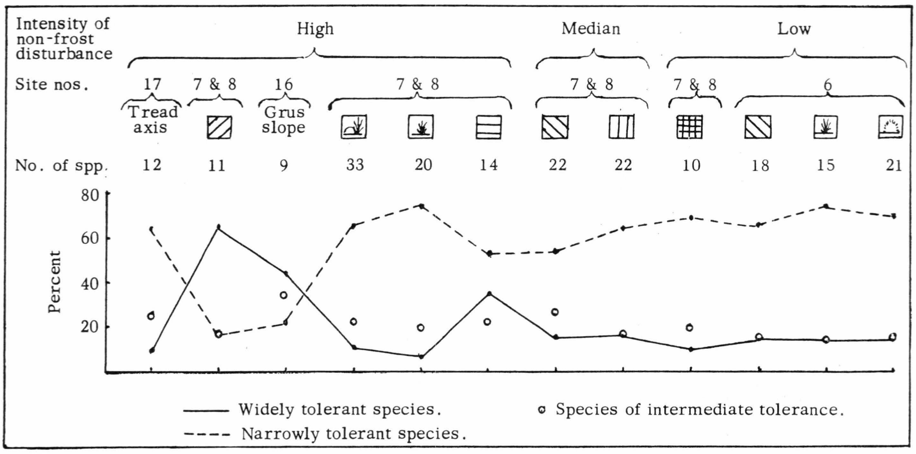

Fig. 73. Summary of the distribution of species tolerance on the nonfrost disturbance gradient in the principal habitats of ES 6, 7 & 8, 16, 17.

appear in Fig. 73 in the "dry" sectors of ES 7 and 8, and on the dry grus slope at ES 16.

It was recognized relatively early that mats of vegetation were moving downslope under the influence of gelifluction without serious disturbance of their continuity over considerable areas—often 100 or more sq. meters. Most of the plants forming these mats were, however, rooted in the moss and organic soil rather than in the underlying diamicton. They could "ride" downslope without much danger of injury. Species in the sedge and hummocky meadows of ES 7 and 8, where the gelifluction was known to be active, had high percentages of species narrowly tolerant on the nonfrost disturbance gradient and low percentages of widely tolerant ones. The same occurred to some extent in the turf hummocks and heath tundra of ES 7 and 8 where the gelifluction was median to low in intensity. But it also proved to be true for the organic crust areas of ES 6 and ES 7 and 8 where, although the rate of gelifluction was observed to be median or low, in many places the organic crust was very thin over the mineral soil. Here one might have expected more injury from gelifluction.

Gelifluction was most active in the axial part of the lobe tread at ES 17, which showed the most rapid movement measured in the Mesters Vig district. Nonetheless, the plants growing on the tread exhibited very little injury from gelifluction if the tolerance ratings for nonfrost disturbance are valid (Fig. 73). The sparse and scattered flora had about 65% of its species narrowly tolerant on this gradient, and only about 8% widely tolerant. The plants were rooted for the most part in the mineral soil and apparently could "ride" this soil downslope as safely as did plants rooted in turf. A suggested explanation is that because gelifluction does not occur except when the soil is at or above its liquid limit, the roots of the plants were merely carried along in semi-fluid mud. Under these circumstances differential movement among the soil particles was a slow and delicate process which left the root contacts essentially undisturbed, and the roots themselves unbroken. This is not to say that the process as a whole did not sometimes injure the plants, for the moving soil was often disrupted by breaks in slope or obstructions in its path.

These observations suggest that gelifluction, *per se*, was not as damaging to the plants as was previously thought, and that the high percentages of species intolerant of nonfrost disturbance seen in Fig. 73 should have been expected.

The exceptions in Fig. 73, noted above, support this suggestion, for they indicate not only the presence of species especially sensitive to nonfrost disturbance other than gelifluction, but also the contrasting selectivity of the habitats. This was most clearly shown on the grus slope at ES 16, where there was a relatively high percentage of species widely tolerant of nonfrost disturbance. Gelifluction and frost heaving being of little or no consequence on this slope, physical disturbance was primarily by dry creep. Most (2:1) of the species found there were selected from those which in general showed the widest tolerance of these kinds of disturbance.

The high percentages of widely tolerant species in the "dry" sectors of ES 7 and 8 were more difficult to account for. On the lower parts of this "dry" slope, notably in the eastern sector of ES 8 (targets 6–14) the soils remained wet for a longer time following snow-melt than those in the "dry" sector of ES 7 on the upper part of the slope. This was due to melt-water from a long southeastward extension of the principal snowdrift which fed moisture to much of the site area, and from the general snow cover on the upper part of the slope. Although this moisture in the "dry" sector of ES 8 lasted several weeks in the spring, the soils later became as dry as those on the upper slope. Nonetheless, during the weeks when they remained very wet they showed gelifluction nearly as great as that in the "wet" sectors. It is thought that the rigorous summer desiccation, inhibiting to seedlings that may have germinated in spring while the ground was wet, was a major cause of the small and scattered flora of the "dry" sectors. Species capable of withstanding such desiccation were preponderant in these sectors (Figs. 25, 71). It is suspected that the seedlings may have been sensitive also to a relatively high intensity of gelifluction coming in their early stages of development. Most of the definitive species in the "dry" sectors were widely tolerant on both the moisture and the nonfrost disturbance gradients. It is suggestive that the highest percentage of wide tolerance shown in Fig. 73 was in the *Dryas* — *Carex nardina* zone where the spring gelifluction was greatest.

The effects of dry creep, and of wind and stream action

Dry creep was most obvious and probably most effective in modifying the vegetation on the grus slope of ES 16. Here the grus was very sparsely vegetated and at least its surface materials were moving downslope at the rate of about 1 cm per year. Some individual plants of *Carex nardina* and other species, as well as mats of *Dryas*, were being undermined, while at the bottom of the slope the grus was moving out onto the adjacent vegetation. Although the grus was currently active, rendering the life of the plants in some degree hazardous, it was the driest habitat studied in any of the situations from which instrumental data were available. Consequently, it is not impossible that the extreme scarcity of plants was due more to desiccation than to creep. It is striking, however, that in the small flora growing there twice as many species were drawn from those widely tolerant of nonfrost disturbance as from the narrowly tolerant (Fig. 65). Thus the selection of species suggests that the dry creep was an effective limiting disturbance.

Dry creep was seen also on steeply sloping banks on the lateral margins of the large gelifluction lobe at ES 17. The vegetation on these banks was interrupted by areas of bare soil which increased in size toward the upper end of the lobe. Creep was evident in some of the bare areas, where the relatively fine-textured diamicton was moving downslope so as to undermine some plants and inundate others. Whether this was a prime causal factor forming interruptions in the vegetation, or secondary to vegetation breaks caused by desiccation, was uncertain.

Minor erosion and deposition by wind were seen, among the experimental sites described here, to a very small extent on the grus slope at ES 16, and somewhat more conspicuously on the convex surfaces of the trap knoll above it. In the latter place there was some evidence that materials had been blown out of the surface grus and deposited in the nearby depressions.

Erosion and deposition by water were most prominent at ES 6 where a small stream flowed in several channels through the eastern part of the target line. One of these channels was by far the largest, and appeared to have washed away one of the targets. In nearly all cases, however, the flow was relatively small, and that which demonstrated appreciable erosive power was confined in space to narrow channels, and in time to the early spring thaw period. While it was active nearly all of the ES 6 target line area was still under snow and basal ice. By the time this had disappeared, the flow had already lost most of its power. Small and highly localized erosion was found in the middle parts of the turf hummock systems in ES 7 and 8 and in ES 6, but it was not forceful enough to wash away much more than the desiccated turf of the hummock margins.

No good measures of this washing were made, but general observations suggested that it was of minor importance. The tolerance ratings of the plants graphed in Figs. 27, 39, 40 suggest that the floras of the sites in which they occurred were little affected by them.

Review of root and rhizome distribution in the experimental sites

On the assumption that the inhibiting influences of the physical factors were most effective upon the roots or rhizomes of the species, the relative proportions of species with fibrous roots, taproots, and underground rhizomes were computed for each experimental site, and for the vegetation types within each site. In the Mesters Vig district the proportions of the three groups, with the numbers adjusted for vegetative propagation capacity, and using only definitive species, showed the fibrous rooted and taprooted species to have nearly equal representation, 43.5 % and 49.6 % respectively (Fig. 74). About 15.7 % had rhizomes.

The curves in Fig. 74 indicate three major departures from the proportional arrangements of the three types of underground systems in the Mesters Vig flora as a whole. These major departures were in very wet and very dry sites. At ES 16 where a prevailing character of the site was desiccation the taprooted plants greatly increased at the expense of those with fibrous roots and rhizomes. At ES 6 which was a consistently and rather uniformly wet site the rhizomatous and fibrous rooted plants both greatly increased their percentages at the expense of the taprooted species. Whether the figures for ES 15 were realistic in this case is open to question because the total number of definitive species was extremely small. Nonetheless, most of experimental site 15 was moist to wet, and held its moisture throughout most seasons except in the nearly barren axial portion of the small gelifluction lobe.

These observations and analyses suggest that the distribution of root and underground stem systems was closely related to moisture supply. The influences of area size and habitat differentiation upon the distribution of the three kinds of systems proved to be insignificant. There was some variation in the proportions of the three types among the major frequency classes, and although the distribution of species in the

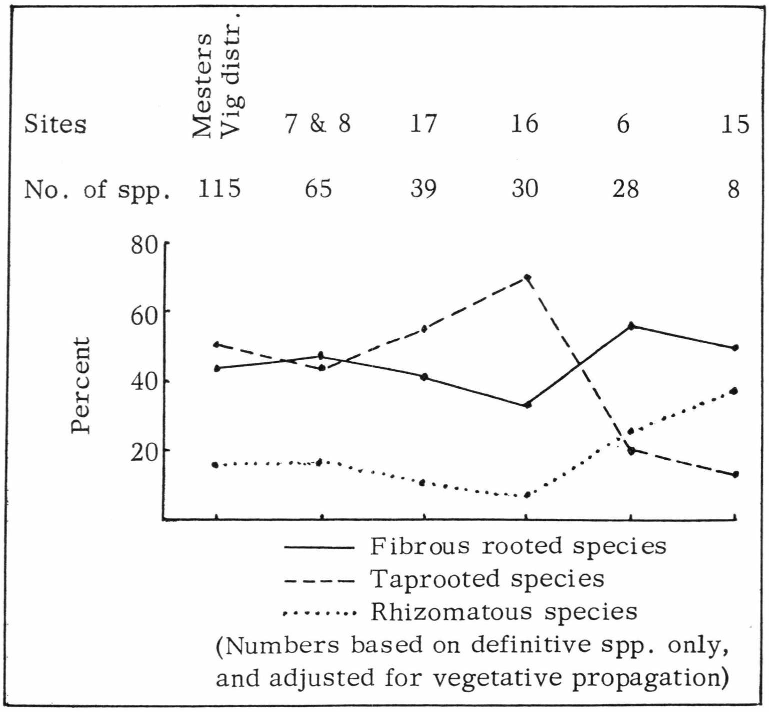

Fig. 74. General percentage distribution of fibrous rooted, taprooted, and rhizomatous species among the experimental sites, compared to their percentage distribution in the whole Mesters Vig flora.

latter was greatly influenced by area reduction, proportions of the three types within the frequency classes were altered to a minor degree by the reduction.

It was suggested in discussions of some of the sites, notably of ES 7 and 8 and ES 6, that high soil moisture persisting throughout the summer season, and possibly also a relatively low or moderate intensity of frost heaving, favored higher percentages of fibrous rooted plants. Conversely it was proposed that taprooted plants, with their greater storage capacities, probably were able to survive periods of summer desiccation and physical disturbance better than those with fibrous roots. Experience at ES 7 and 8, where sufficient contrasts were available, suggested these things and also that rhizomatous plants, though not numerous anywhere in the Mesters Vig district, were most common in such wet habitats as sedge and hummocky meadows. In order to pursue this suggestion, the proportions of underground systems were plotted on graphs having sequences of habitats similar to those in Figs. 71, 72, 73.

In these analyses the percentages of fibrous rooted species, though they commonly varied as much as 15 to 25 %, did not show notable trends toward greater or lesser proportions related to the habitat sequences. The only exception to this was at ES 16 where the dry grus slope had a low proportion of fibrous rooted plants (22.6 %) in contrast to its high percentage of taproots (77.8 %). Very little positive correlation of taproot and rhizome percentages could be found with the sequence based on seasonal variation in moisture supply (Fig. 71). There was a slight tendency for taprooted species to show higher proportions under conditions of wide variation in the supply, though the highest percentage of these plants was found on the grus slope at ES 16 where the effective seasonal variation probably was quite small. There was also a slight tendency for the rhizomatous species to be proportionately more numerous under conditions of relatively uniform seasonal moisture supply (narrow variation). No positive correlation could be seen when the underground systems were plotted against the graph in Fig. 73 showing the relation of tolerance ratings on the nonfrost disturbance gradient.

A further analysis was made by arranging an estimated sequence of habitats based on the total moisture supplies without regard to seasonal variation (Fig. 75). This provided more positive correlations than any of the analyses mentioned above. As in the case of those previously mentioned, the fibrous rooted species showed little correlation, with no upward or downward trend that could be clearly related to the habitat sequence. On the other hand the percentages of taprooted species showed a notable trend upward in the direction of the drier habitats, from 20 % in the sedge meadows of ES 6, 7 and 8 to 45–57 % in the "dry" sectors of ES 7 and 8, and to the high of about 78 % on the grus slope at ES 16. At the same time the percentages of rhizomatous plants trended downward from about 40 % in the sedge meadows of ES 6 to 7–18 % in the "dry" eastern sectors of ES 7 and 8 and the grus slope at ES 16.

Frost heaving intensity was known to be closely related to variations in the moisture supply, and it might have been expected that its sequence (Fig. 72) would show correlations with root and rhizome distribution similar to the correlations of the latter with moisture supply. The correlations here, however, were negative although they had appeared to some extent in certain individual experimental sites.

These analyses lend weight to the suggestion that the moisture supply may be the most important single factor related to the distribution of root and underground stem systems. It is notable, however, that the systems were less sensitive to seasonal moisture variations than to those of total moisture supply, and that the sensitivity was restricted primarily to species with taproots and rhizomes. It is possible that the storage capacities of these two types rendered them relatively insensitive to seasonal variations, but more sensitive to the total amount of water available over periods of years. It might be expected that fibrous rooted

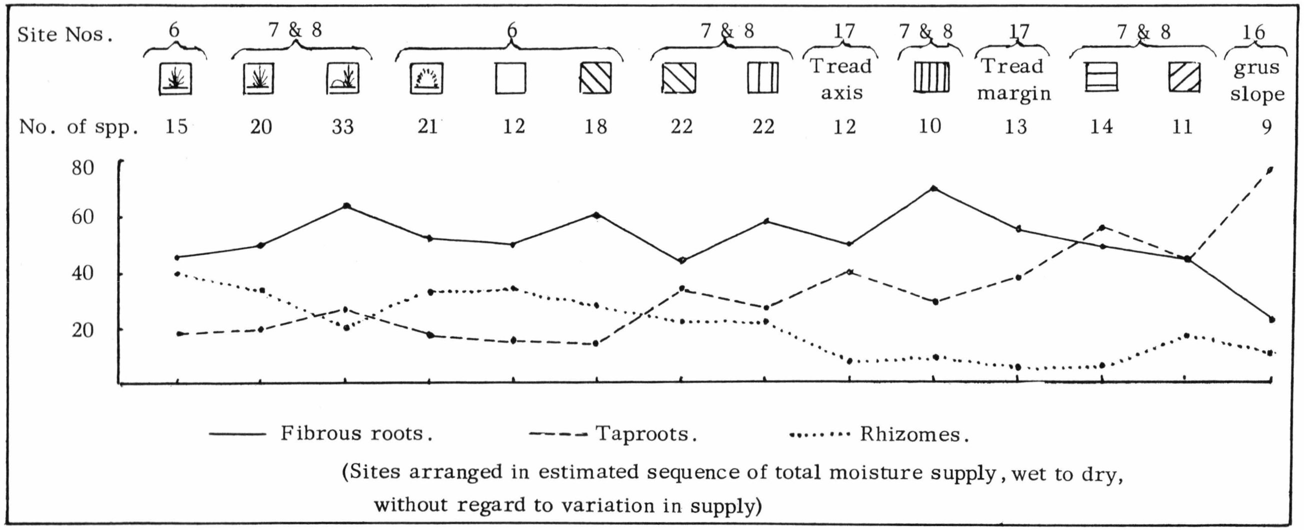

Fig. 75. Summary of the distribution of fibrous rooted, taprooted, and rhizomatous species in relation to a gradient of total available moisture, without regard to variation in the moisture supply.

plants, with more limited storage capacity, would be sensitive to seasonal variations, but this appears not to have been the case among the habitats analyzed here.

As a general conclusion it appears that the underground systems, at least in terms of the gross morphology used in defining them here, were sensitive only to differences in total water supply. This does not mean that the actual root systems in close contact with the soil were not the media through which injuries due to disturbance factors became effective. Rather it suggests that the gross structures of the systems may have been too broadly defined to show differences at the scales used in the analyses.

On the validity of the tolerance ratings of the species

It was stated in the early part of the present paper that a major issue in the study was a test of the relative precision with which the ranges of species tolerance on the selected environmental gradients could be defined. Many observations in the experimental sites were used in the ratings, and if these notes had been the sole basis for the judgments, positive correlations between the ratings and the local habitat factors would have been inevitable. But the ratings were generalized also from a large number of further observations made elsewhere in the region and added to those from the experimental sites. By this process the tolerance ranges of many species were expanded, because commonly only limited segments of the environmental gradients were found in the individual sites. The question was whether the ratings, expanded and generalized in this way, would be useful in rationalizing species distribution among micro-habitats at large map scales within the sites.

The expansion of tolerance ranges by wide observation produced a useful tool by greatly improving the segregation of the species having universally wide or narrow ranges. Removal of these from the analyses greatly clarified interpretations of distributional behavior among the more definitive species.

Imperfections in correlations of tolerance ranges with factor differences were to be expected from four main sources. First were incorrect judgments on the extent of the ranges. Second was the probable significance of factor gradients which, though not included in the observations, were playing more or less important roles in the distribution of species. Third were unknown or unmeasured interactions not only among factors not considered but also among those used. Some of these interactions were obvious and were roughly evaluated, but others were too subtle and complex to be measured. The fourth source of error was inherent in the method of analysis, which compared percentage compositions of tolerance ratings among the floras of different habitats. Numbers of species in these floras varied greatly, and were usually reduced by restricting the analyses to definitive species. Small numbers, though they usually reflected habitat differences about as well as larger numbers, tended to over-accentuate percentage differences and make comparisons uncertain.

Review of the analyses for individual experimental sites, as well as review of those comparing habitats drawn from differing sites, indicated that in spite of the imperfections noted above the tolerance ratings were accurate enough to show positive correlations between the survival capacities of the species and the factoral variations known to occur in the sites. It also indicated that the ratings, though generalized from wide observations, were still effective at the large map scales used in defining the micro-habitats in the sites. In most of the analyses plants having wide tolerance on a given factor gradient predominated in vegetations where this factor was active and limiting enough to demand wide tolerance of variation in it for survival. If the factor was much less active and injurious, the plants present showed relatively higher proportions of species more sensitive to variations (narrowly tolerant).

Experience with the nonfrost disturbance gradient provided an unexpected check upon the usefulness of the ratings. As previously noted most of the judgments on tolerance ranges for this gradient, with the possible exception of species reaction to gelifluction, were made in habitats other than those represented in the five mass-wasting sites. Although gelifluction was evaluated as a nonfrost process in the ratings, application of the ratings to the mass-wasting sites showed that the species were in reality not very sensitive to it and manifested wide tolerance of its effects. The striking exception at ES 16 (Fig. 73), where gelifluction was absent but other nonfrost disturbances occurred, showed that species actually were being sorted into differing habitats on the nonfrost gradient.

The extent to which the tolerance ratings made for the Mesters Vig district can be applied beyond its limits is unknown. Comparative studies by the present writer of species-habitat relationships which were described for different parts of the fjord region by GELTING (1934, 1937) and SØRENSEN (1933, 1937) have suggested that many species differ in their capacities to survive habitat variation within distances of 300–400 kilometers. The findings of JOHNSON and PACKER (1965) in northwestern Alaska suggest that widespread species occurring in Northeast Greenland and Alaska differ markedly in the two areas with respect to tolerance ratings. They also found evidence of differences among populations in the same general vicinity. It is probable, therefore, that the Mesters Vig ratings are directly applicable within a radius of something less than 300–400 kilometers, and perhaps within an area much smaller than this.

Vegetational change in the experimental sites

Evidence from studies of the origin and development of turf hummocks in the Mesters Vig district (Raup, 1965 B) indicated that vegetational change had occurred in the turf hummock systems below large snowdrifts in past years and probably was continuing. It was possible to interpret some of the changes as biological successions within vegetation types such as moss-sedge meadows and in the hummocks themselves. However, these biological changes proved to be fragmentary and indeterminate when viewed in the larger perspective of changes due to factors exogenous to the vegetation.

These factors appeared to be primarily climatic, and had resulted in a general desiccation of the district as a whole. The progress of the desiccation was marked by the retreat of the snowdrifts and by "migration" in their wake of whole "turf hummock systems". Rates of changes in the systems were computed from the growth rings of arctic willows (*Salix arctica*) which had lived through a system from its incipient stages to final disintegration. From these data and from information on recent climatic change in the North Atlantic area, it was proposed that the general desiccation had occurred within the last 60–75 years, and that single hummock systems had in some cases completed their whole terms of existence in less than 40 years.

Such short periods were less than the life spans of many of the more abundant plants growing in the systems, and precluded long-term development of the plant cover *in situ* by biological processes within specific habitats and types of vegetation. They did not preclude all biological successions in these habitats, but rendered them fragmentary and indeterminate in time, space and content.

Modifications of the "typical" turf hummock system described by the present writer (*l. c.*, p. 63–76) were found at ES 7 and 8 and at ES 6. Fragments of them were also present in the turf hummock area at the foot of the grus slope at ES 16. The tundra immediately adjacent to the small gelifluction lobe at ES 15 had many of the characteristics of stages in the deterioration of turf hummocks. The fragments seen near ES 15 and 16 were not studied in detail.

The diamicton slope at ES 7 and 8 was watered from a snowdrift which did not melt back up the slope in a direction at right angles to the contours, but rather in a northwesterly direction diagonally across the map area. This produced a skewing of vegetational boundaries so that the moss and sedge meadows were toward the northwest and west margins of the slope, and the area of deteriorating hummocks was toward the east and southeast. The progressive desiccation of the soils eastward on the slope made for further modification. Living "perched" willows in the vicinity of the "dry" sectors of ES 7 and 8 suggested that these areas formerly had been "wet", and now represented hummock deterioration resulting from the recent period of desiccation. At ES 6 two major sources of moisture, coming from different directions, had altered the "typical" hummock system. The principal elements of this system appeared along the line of ES 6 targets, with the extreme snow bed at the western end, and widely spaced deteriorating hummocks toward the east. However, the later (desiccation) stages in the deterioration of the hummocks had been prevented by moisture from the broad valley to the northward. The relatively thick accumulation of organic soil at this site, and the appearance of a certain amount of gleying in the mineral horizon beneath it (UGOLINI, personal communication) suggested that the whole system had been shifting its position due to progressive desiccation much more slowly than the rate proposed for the "typical" system.

It seemed clear that vegetational change on the gelifluction lobes was at the mercy of the geomorphic processes by which the lobes were being formed. Whatever vegetation was present when rapid gelifluction began was inundated by the moving soil. On the tread, plant cover soon became restricted to scattered plants of species capable of withstanding the intense frost heaving, partial desiccation, and probably to some extent the gelifluction movement. Thicker vegetative cover became possible on the partially stabilized fronts, and as the latter grew larger, firmer, and farther away from the activating water supply still denser tundra appeared on them. This was later reduced by further desiccation.

Little evidence of vegetational development was seen on the creeping grus slope at ES 16. A suggestion of it might be inferred from the slightly less scattered plants on the rock outcrops that were present in the midst of the grus. On these the slopes were a little less steep and the grus was moving more slowly. Further accumulation of grus from the weathering cliffs above, however, tended to bury the outcrops, making the somewhat denser vegetation on them relatively ephemeral.

Evidence from all of the mass-wasting sites treated here bears out the conclusion with respect to vegetational change reached from studies of turf hummock systems. It is that biological successional change was of relatively small consequence compared to changes caused by the exogenous interacting physical factors of site. A primary factor among these in the recent past appeared to be progressive desiccation. Existing patterns of vegetation in the Mesters Vig landscape appeared, therefore, to be much more closely related to differing combinations among the physical factors than to processes of biological change within the vegetation.

Some causes of sparse vegetation

Barren or very sparsely vegetated soils were found in all of the sites. In the ES 7 and 8 map area they predominated in the "dry" sectors, in the organic crust areas of the "wet" sectors, and on the cliffs and talus along the western border. At ES 6 they were represented mainly in the organic crusts, but also were present to limited extent in shallow stream channels. On the gelifluction lobes at ES 17 and 15 they were found primarily on the treads. The most open vegetation studied was on the grus slope at ES 16.

Sparse "fjaeld-mark" vegetation in the experimental sites appeared to have been caused, at least in large measure, by variations in moisture supply interacting with physical disturbance factors in the soils. Although desiccation may be placed first among these causes, it by no means accounted for all of this vegetation. The presence of an adequate water supply was, in itself, not sufficient to increase the density of the plant cover or enlarge its flora. Many diamicton habitats, though well supplied with moisture, yet had sparse vegetation. Many of the moist habitats were characterized by differing intensities of physical disturbance in the soils, due largely to frost heaving and gelifluction. Consequently these geomorphic processes were invoked to explain the paucity of plants in such habitats.

Desiccation

In several habitats summer desiccation seemed adequate to account for their sparse flora and vegetation. The dry sectors and talus of ES 7 and 8, the lateral margins of the gelifluction lobe tread at ES 17, the grus slope at ES 16, and to some extent the tread of the small lobe at ES 15 were all characterized by water supplies that were limited to spring and early summer snow-melt. Most of their surface soils (10–15 cm) became nearly dry in mid- or late summer. Vascular plants that may have germinated in them while they were wet in spring suffered excessively from the summer droughts. What little atmospheric moisture that came to them in the summer and autumn probably would save only a small fraction. The species found in their scattered vegetations were mainly those with wide tolerance of wide variation in moisture supply. Probably this tolerance applied to all phases of their life histories, and permitted more of their seedlings to survive the summer desiccation than was possible for those of less tolerant species.

Differences in the extent of desiccation appeared due primarily to differences in soil texture and in the lengths of time during the spring when some moisture remained available. The extreme of quick drying was seen at ES 16 where the soil was very well-drained grus and was moist for only a few days after snow-melt or rain. The "dry" sector of ES 7 lost its water supply almost as quickly, but its finer textured diamicton held the moisture available for a few days longer. The lateral tread margins of large active gelifluction lobes probably had moisture regimes similar to this. The "dry" sector of ES 8 remained moist longer than that of ES 7 because of the larger supply of snow-melt which watered it. The small lobe at ES 15 was moist throughout the summer in some years, but dry at the surface in others. Although treated as a "wet" site, its occasional dryness made it somewhat marginal. In general, species tolerance ratings in this sequence of "dry" to "wet" habitats reflected the moisture differences.

Physical disturbance

Where the moisture supply persisted into the autumn it set the stage for frost heaving at that season, culminating in the major heave activity at the time of freeze-up. The thin veneer of organic crusts over the mineral soil, which characterized many of these places, sometimes covered large areas in nearly unbroken sheets, with or without scattered vascular plants, moss polsters and occasional turf hummocks. Elsewhere they were interdigitated with turf hummock and heath tundra vegetation. High mortality among the vascular plants was common in the crust areas.

The frost heave data accumulated by WASHBURN in the mass-wasting sites indicated that the most intense heave was in bare, moist diamictons, and in similar soils covered with the thin organic crusts. The nature and condition of the vascular plants in the crust areas, together with their scarcity and high mortality, indicated that the heaving was injurious to the plants, and commonly lethal.

Moisture supplies sufficiently large and concentrated to form gelifluction lobes produced topography and soil moisture conditions conducive to intense frost heaving. Exposure of the lobe treads while the surrounding terrain was still snow covered made them more susceptible to frost heaving. The concentrations of fines and moisture on the treads also made them especially favorable sites for frost action. Absence of plants from many spots in the axial parts of gelifluction lobe treads, coupled with heave data available for these areas, suggested that the intensity of frost disturbance in these spots was great enough to be completely lethal. Barren areas in ES 6 may have been similarly caused.

Gelifluction, *per se*, appears to have been only moderately effective as a direct cause of sparse vegetation. It may have inhibited the early development of seedlings, and if very active it fractured and disintegrated mats of dense vegetation; but well-established individual root systems seemed not to be seriously injured by it. It was probably most effective as an agent inhibiting to plants on the gelifluction lobe tread at ES 17, to a considerable extent on the small lobe tread at ES 15, and in the early season movement recorded in the "dry" sector of ES 8. It is probable that spring heaving was also effective to some extent in these habitats, which tended to be exposed from the snow and had adequate moisture in the period when spring thaw cycles occurred.

The experimental sites, therefore, indicated that frost heaving probably was in some places nearly or quite as effective as desiccation in causing sparse cover by vascular plants. In this case the species able to survive were mainly those of wide tolerance to frost induced disturbance.

Observations of temperature have indicated a general warming of the Arctic beginning late in the 19th century, with a reversal of this trend in the past two decades (Fristrup, 1952; Ahlmann, 1941, p. 198–207; 1948, p. 72–73; Koch, 1945; Willett, 1950; Mitchell, 1961, 1963). Geomorphic and botanical observations in the Mesters Vig district probably reflect the warming trend in the retreat of snowdrifts and presumably in the resulting desiccation of the soils (Raup, 1965 B, p. 96–99). Under these circumstances it is also probable that prior to the warming period freeze-thaw cycles were more prevalent during the growing seasons and were thus more injurious to plants than today.

Development of the dense vegetations

If frost disturbance had the inhibiting effects assigned to it, then it became necessary to account for the heavier vegetations in the "wet" areas of ES 7 and 8, ES 6, and on the downslope edges and the frontal crests of gelifluction lobes. These vegetations consisted mainly of the sedge and hummocky meadows and/or turf hummocks. Comparison of these habitats with many others like them in the Mesters Vig district suggested, as noted earlier, that they were modifications of the vegetational sequence of development found in turf hummock systems. It is probable that the relatively heavy vegetation produced in these systems was made possible by protection from frost heaving in the early stages of their development. In these early stages their soils were bathed by sheet flow during most of the thaw season and into the autumn, and thus were insulated from most short-term freeze-thaw cycles. Also they were sometimes protected by late-lying snow in spring. Under these conditions wet mossy meadows and subsequently a thicker cover formed further insulation.

Frost heaving seems to have been partially checked on new gelifluction lobe fronts both by free water flowing over them from above, and by better internal drainage than on the treads. The better drainage was due in part to the steepening of slope on their crests and in part to somewhat coarser textured soils commonly found in the fronts.

Thus frost disturbance as a major cause for sparse vegetation probably should be limited to intermediately "wet" habitats which were not bathed with running water throughout the thaw season but retained enough moisture in their soils to activate frost heaving whenever temperature conditions were suitable for it. All of these conditions were characteristic of the organic crust and moist bare soil areas in the experimental sites here considered.

The heavy vegetations proved to be relatively short-lived because of the reduction or displacement of the water sources resulting from gradual desiccation in the region as a whole. In the processes of desiccation and deterioration in these vegetations frost disturbance was a highly significant cause as long as some moisture persisted in the soils through the open season. When this was no longer the case, desiccation probably became the more important cause for the sparse plant cover. There was evidence in the ES 7 and 8 map area that the "dry" sectors of the diamicton slope had gone through approximately this series of changes. Probably the primary cause for the contrasting vegetations of the "dry" and "wet" sectors lay in the more abundant and persistent moisture in the latter.

In the prevailing trend toward general desiccation there seems to have been gradual lessening of heaving and downslope movement on the gelifluction lobes with the advent of more dense vegetation on the treads. The tread vegetation underwent gradual reduction due to further drying, but apparently at a slower rate than was seen in the turf hummock systems. Comparative observations on the densely vegetated lobe fronts and lateral banks suggested that these were temporary, truncated and condensed versions of turf hummock-like systems. They maintained thick cover only as long as abundant water from above flowed over and through them. As this tapered off they became increasingly xerophytic.

Later vegetational change on the large gelifluction lobes can only be surmised. Those on the lower slopes of the mountains appeared essentially stable, with both treads and fronts covered by tundra. Old lobes at low altitudes had vegetation resembling in part that of the "dry" sectors of ES 7 and 8 and in part the scanty cover of gravelly talus slopes. Partially stabilized ones probably had become so during the recent period of desiccation, but older ones appeared to have had their present form and vegetation for a much longer time.

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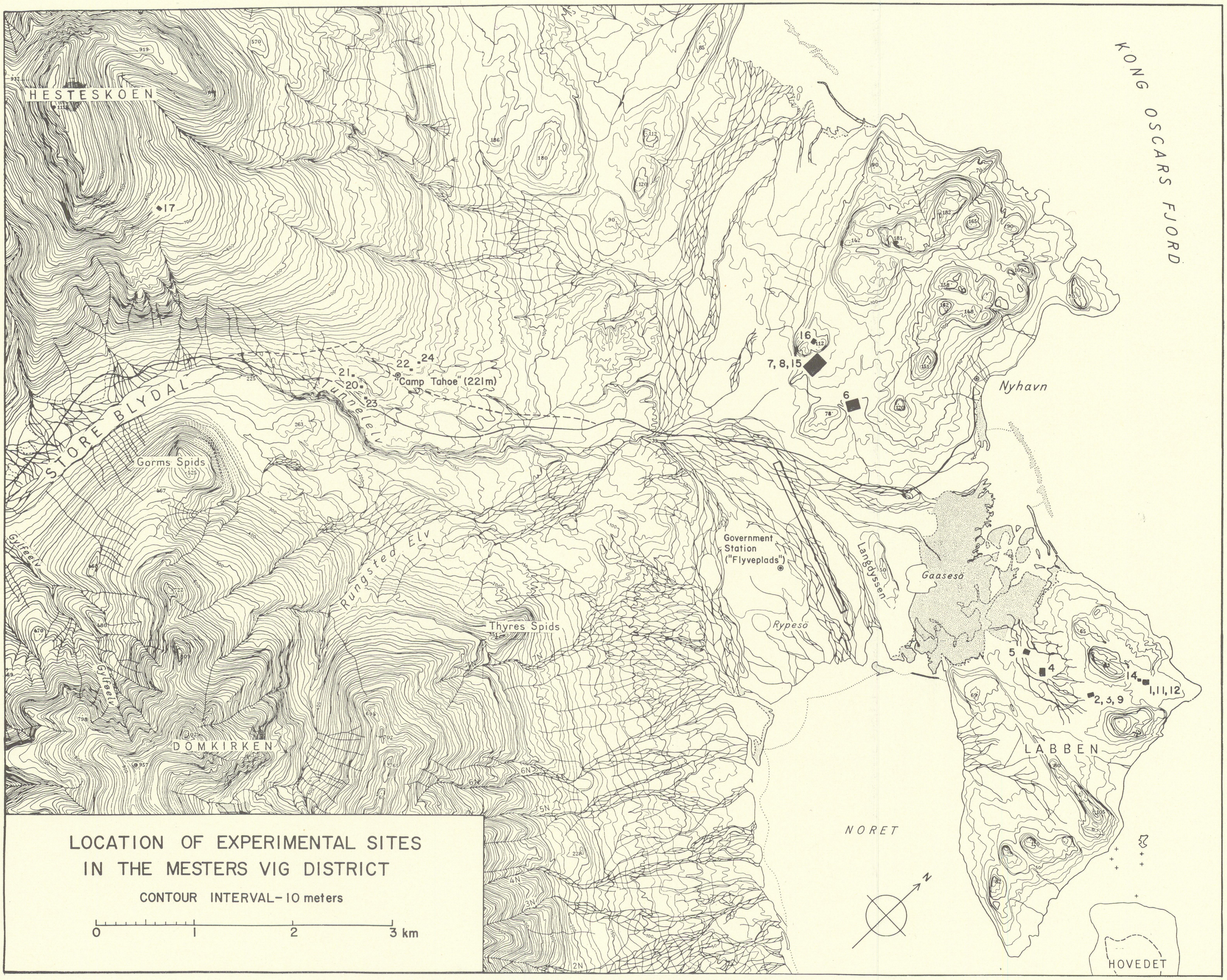

Map of Mesters Vig district, showing location of experimental sites.