STUDIES ON THE VEGETATION OF SHETLAND

A thesis submitted for the Degree of
Doctor of Philosophy
of Glasgow University

by

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Preface

The original data presented in this thesis are the results of field work carried out on Unst, Shetland, during parts of the summers of 1952, 1953 and 1955: on the Shetland Mainland during parts of the summers of 1952-1955: on Rhum, Inverness-shire in June 1954 and July 1955 and on the Coyles of Muick, Aberdeenshire, in July 1955.

Professor John Walton gave much helpful criticism during the preparation of the manuscript: Mr. A.C. Crundwell, Mr. G.D. Scott and Dr. E.F. Warburg assisted me in identifying respectively the bryophytes, lichens and specimens of Euphrasia and Rhinanthus: Dr. R.A. Robb gave statistical advice, particularly in Part IV of the thesis, and Dr. Patton and Mr. Grant Roger provided me with information about the serpentine vegetation of Meikle Kilrannoch. Mr. R.C. Voss, of the spectrographic unit, West of Scotland Agricultural College, carried out the nickel determinations, given in this thesis, of serpentine soils from Unst. Mr. Lionel Smith, of the Meteorological Division, Ministry of Agriculture, provided information, and the "cocoa-tin" shields used in the microclimatic observations. The Electrical Research Association provided data on windspeed recorded at their experimental stations in Shetland. It is a pleasure to record here my thanks to all these people for helping me in so many ways.

I must finally thank the Nature Conservancy for their award to me of a research grant during the summer of 1952, and the Principal and Deans' Committee of the Senatus Academicus of the University of Glasgow for their award to me of a grant towards travelling expenses during the summers of 1954 and 1955.

STUDIES ON THE VEGETATION OF SHETLAND

PART I.

The Shetland climate, the Unst serpentine and the flora of Unst in relation to the geology.

I. The Shetland Climate.

II. Edaphic factors in Unst with special reference to serpentine.

V. The flora of Unst in relation to the geology.

PART II

The Vegetation in relation to the serpentine debris habitat in Unst.

PART III

Serpentine and related plant communities in Scotland and the North Atlantic region.

PART IV

Field inquiry into what restricts the pioneers to the serpentine debris habitat in Unst.

INTRODUCTION

In 1908 C. H. Ostenfeld published a full account of the land-vegetation of the Faeroes. For Shetland nothing vaguely comparable exists nearly fifty years later. There is only a preliminary account of the vegetation of Unst by West (1912) and a classification of Shetland vegetation, based on Warming's system and a short visit, by Price (1927). Indeed the vegetation not only of Shetland but of the whole north of Scotland has been more or less neglected in this respect. The classic papers by Crampton (1911) on Caithness and by Crampton and MacGregor (1913) on Ben Armine in Sutherland still provide the only major account of the vegetation of this region. The descriptive part of this study, of communities in Unst and on Ronas Hill in Shetland, and the island of Rhum, is meant to help remedy this situation.*

Comparison with the Faeroes is not fortuitous. Shetland lies only 220 miles southeast of those islands. It is also equidistant between the Faeroes and Bergen in west Norway and about 105 miles from Duncansby Head in the north of Scotland. So the islands should provide a real link between the vegetation of these land masses. Floristic links have already been suggested by such authors as Bennet (1908).

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* Considerable work has been done on the <u>flora</u> of Shetland. Druce (1922) in his Flora Zetlandica incorporates all earlier work with his own. After this author's 'Additions' (1925) there have been papers by Turrill (1928) and Johnston (1927-29).

Unst, at the north of the Shetland Islands, has a varied geology. It is composed of three contrasting rock types - acid gneisses, basic greenstones and ultrabasic serpentine. It is with the vegetation of serpentine in this and other localities that this thesis is chiefly concerned.

Serpentine is a hydrated silicate of magnesium and iron derived from hydrothermal alteration of olivine. 'Serpentine' denotes both the mineral and the rock consisting largely of that mineral. Ultrabasic rocks refer mainly to serpentine but include such types as peridotite. Serpentine is used here in a botanical sense to denote the flora and vegetation of ultrabasic rocks. Serpentine 'outcrop' in Unst refers to the whole exposure, not only to the debris with sparse plant cover (see below). Occurring extensively in Unst, the other serpentine localities in Shetland are all smaller and lack debris. They are Fetlar, Fethaland, Hillswick, and Hoo Field (Fell) near Cunningsburgh. The other Scottish localities examined are on Rhum, and the Coyles of Muick in Aberdeenshire.

Serpentine is well known as a habitat which has peculiar effects on vegetation. Some description of serpentine vegetation in the Eastern Highlands (the Coyles) is given by MacGillivray (1855). But most of the published information dealing specifically with serpentine flora and vegetation and inquiries into causation seems, until recently, to have been gathered outside Great Britain. Of this work, the most important recent contribution is the paper by Rune (1953) on "Plant life on the serpentines and related rocks in the north of Sweden". This gives both new ecological data and a thorough review of earlier work. Such a review, particularly of causation, might be given at this point but it makes for a simpler account if that is deferred until Part II (p. 71 et seq.). This applies also to recent investigations, by workers at the Macaulay Institute for Soil Research, on nickel toxicity in serpentine soils.

Here it may be stated that the peculiar features exhibited by vegetation of serpentine outcrops include: extensive areas almost bare of plant cover, and vegetation which differs markedly from that of neighbouring rocks and includes species with disjunctive distributions. Crop plants may exhibit toxic symptoms.

In all but the last feature Unst is certainly no exception.* The serpentine vegetation can be seen, even from a distance, to differ markedly from that of the adjoining acid rocks. It was Edmondston (1845) who first, if briefly, noted qualitative differences in the flora of the contrasted rock types. At the same time he reported the presence of several rare species on the serpentine, such as Arenaria norvegica and Cerastium nigrescens. There are two striking features of the serpentine outcrop: one is the extensive debris with sparse plant cover which occurs in different parts of the outcrop; the other is the restriction to this debris of those rare species, and some others. Many of these plants have disjunctive distributions and arctic affinities. The debris is surfaced by small angular stones with finer particles

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* This last feature, the presence of toxic symptoms in crops, I have not investigated closely in Unst. They are certainly absent there from long-cultivated land.

mingled beneath and is scattered on level or gently sloping ground over the serpentine outcrop. Worth emphasising in relation to the habitat it provides for these restricted species are the low altitudes between which this debris occurs - from less than 50 ft (15 m.) above sea-level to 500 ft (152 m.) the maximum possible.

Such areas almost uncolonised by plants are referred to in the literature as serpentine barrens or infertile wastes (*viz.* Rune 1953, Kruckeberg 1951, Pichi-Sermoli 1948 *et al*). Why do these areas of debris remain so poorly covered by plants? Calling them infertile wastes implies edaphic limitations, that they are examples of the "serpentine effect". This infertility, even toxicity, is generally held to be the result of the unique chemical composition of serpentine. Toxicity is caused, on the most recent evidence, by nickel (see this paper: p. 71 *et seq.*).

But "barrens" is another term for fellfield (Böcher 1954 p.28). This introduces a different facet of the problem, for fellfield is open vegetation of cold, exposed habitats which often lack snow cover (Warming 1909). Since Shetland has an extreme climate in terms of exposure, one of the objects of this study is to see how far the serpentine effect is in fact due to climatic factors. This inquiry in turn helps investigate the habitat of the restricted species on which much of this study centres.

A consequence of the view that serpentine "wastes" result from toxicity is the presence of serpentine ecotypes of several species. These are ecologically and sometimes morphologically distinguished from the type-races of the species (Kruckeberg 1951). A large number of such 'serpentinophytes' has been described elsewhere. Only cultivation experiments can adequately demonstrate specific tolerances, so the value of these described taxa varies considerably. This is considered in Part II. My cultivation of possible serpentinophytes from Unst has so far been insufficient from which to draw conclusions.

Serpentine is an unusual rock. One would naturally turn for comparison to an account of 'normal' hill vegetation of the predominantly peat covered and acid rocks of Shetland. Apart from Edmondston's short list, this I have said is lacking. So, in Table I p.5a, a quantitative list is given of the floras of the serpentine, greenstone and acid rocks of Unst. That of the acid rocks may be taken as broadly representative of the normal Shetland type on poorly drained ground. From the table it is possible to say what species are characteristic in Unst on serpentine and what species, constituting the flora of the 'normal' hill land, are noticeably absent.

The study broadens from here. For this leads to the question of what floristic features are widely typical of serpentine or merely local. The same question arises with the plant communities. Originally I had intended to confine field work to the Unst serpentine communities, relying on published data for comparison. Lacking these I used a uniform method to study the serpentine vegetation in Rhum and the Coyles of Muick. Similar data were obtained from non-serpentine vegetation in Rhum and Shetland. Having Shetland's geographical position in mind, comparison was also made with published work on vegetation in the North Atlantic region. Similar communities were seen to occur in these regions but at different altitudes. With consideration of

Table I

Quantitative list of the flora of the hill-land of Unst, on serpentine (S), greenstone (G) and acid rocks (A). Figures are of % frequency on each rock; denotes frequency less than 1%. List is not exhaustive. For definition of hill-land see p. 36, method p. 36, categories p. 41.

	A:serpentine-characteristic			
(*)	A1: Exclusives	S	G	A
	Anthyllis vulneraria	1	-	-
ASA	Arenaria norvegica	4	-	-
O.N.	Armeria maritima	3	-	-
L.A.O.	Asplenium viride	+	-	-
	A. adiantum-nigrum	+	-	-
	Botrychium lunaria	+	-	-
A.A.	Cardaminopsis petraea	1	-	-
A.S.A.	Cerastium nigrescens	3	-	-
	Coeloglossum viride	+	-	-
A.S.A.	Cochlearia scotica	+	-	-
A.A.	Draba incana	+	-	-
	Euphrasia rotundifolia	3	-	-
	Gentianella campestris	+	-	-
L.A.O.	Lycopodium alpinum	1	-	-
A.S.A.	Minuartia rubella*	+	-	-
A.A.	Polygonum viviparum	1	-	-
	Rhinanthus spadiceus	1	-	-
N.M.	Rubus saxatilis	1	-	-
	Sagina nodosa	3	-	-
A.A.	S. saginoides**	+	-	-
	Schoenus nigricans	1	-	-
A.A.	Silene acaulis	+	-	-
O.N.	S. maritima	1	-	-
	Thelypteris dryopteris	+	-	-

(*) Species in Matthews' (1937,1955) geographical elements; arctic-alpine; arctic-subarctic: northern montane: oceanic northern. Also Böcher's (1954) low arctic-oceanic.

* Beeby 1887 (in Druce 1922).

** Druce 1922.

(to be contd.)

Table I (contd.)

	A2:	S	G	A
	Achillea millefolium	10	2	-
N.M.	Antennaria dioica	39	8	-
	Carex flacca (& C.panicea)	86	48	2
	C. pulicaris	42	25	-
	Linum catharticum	55	1	-
	Plantago lanceolata	25	3	-
	P. maritima	87	17	2
	Polygala vulgaris	26	3	-
	Prunella vulgaris	40	4	-
	Scilla verna	37	10	2
	Selaginella selaginoides	50	11	+
	Succisa pratensis	45	6	6
A.A.	Thalictrum alpinum	52	2	-
O.N.	Thymus drucei	86	16	3
	Viola riviniana	53	25	6
	B: serpentine-indifferent			
	Agrostis species	65	54	21
	Anthoxanthum odoratum	4	2	39
	Bellis perennis	1	+	+
	Calluna vulgaris	82	70	76
	Carex demissa	2	5	-
	C. dioica	1	+	+
	C. nigra	+	+	1
	Cerastium tetrandrum	1	+	+
	C. vulgatum	7	+	7
	Festuca rubra) F. vivipara)	69	56	19
	Holcus lanatus	2	+	3
	Jasione montana	+	+	2
	Hypericum pulchrum	8	13	1
	Leontodon autumnale	8	3	4
	Lotus corniculatus	5	+	2
	Lycopodium selago	1	+	+
	Molinia caerulea	60	50	36
	Pinguicula vulgaris	3	2	2
	Polypodium vulgare	+	+	1
	Polygala serpyllacea	-	+	+
	Potentilla erecta	88	75	66
	Ranunculus flammula	+	1	+
	R. acris	+	+	1
	Rhinanthus minor s.s.	2	+	1

(to be contd.)

Table I (contd.)

	B: (continued)	S	G	A
	Rumex acetosa	+	+	+
	Salix repens	+	+	1
	Sagina procumbens	2	+	2
	Sieglingia decumbens	44	36	12
	Trifolium repens	7	+	1
	T. pratense	1	1	+
	Viola canina	3	1	1
	C: serpentine-casuals			
	Carex binervis	2)	29	10
	C. pilulifera	1)		
	Deschampsia flexuosa	1	2	11
	Dryopteris dilatata + D.filix-mas	1	+	2
	Erica cinerea	1	38	3
	E. tetralix	5	33	11
	Luzula multiflora	8	6	30
	Nardus stricta	9	66	50
	Narthecium ossifragum	2	33	7
	Pedicularis sylvatica	+	+	1
	Rhacomitrium lanuginosum	5	63	16
	Sphagnum species	+	7	19
	Trichophorum caespitosum	+	48	34
	Vaccinium myrtillus	+	-	10
	D: acid-rock-characteristic			
	Blechnum spicant	-	+	2
	Carex stellulata	-	+	2
A.A.	C. bigelowii	-	+	+
	Comarum palustre	-	-	+
	Drosera rotundifolia	-	2	2
	Empetrum hermaphroditum	-	4	48
	Eriophorum angustifolium	-	6	70
	E. vaginatum	-	1	5
	Galium hercynicum	-	7	9
	Hydrocotyle vulgaris	-	-	1
	Juncus squarrosus	-	5	32
	Luzula sylvatica	-	-	7
	Melampyrum pratense	-	-	+
	Pteridium aquilinum	-	-	1
A.A.	Salix herbacea	-	-	+
	Solidago virgaurea	-	-	+
N.M.	Trientalis europaea	-	-	+
A.A.	Vaccinium uliginosum	-	-	4

climatic evidence, this led to an attempt to correlate climate and vegetation. It was then possible to answer fully the question put at the start of this paragraph.

Arising out of the study of the debris vegetation in Unst is the question of why the pioneer species, many of them rare, are restricted to debris where plant cover is sparse. Rare species commonly occupy pioneer habitats where climax vegetation for some reason or other has failed to develop. The Unst examples are taken to illustrate a general problem.

The thesis is presented in four parts. In part I the description of the environmental factors gives a general picture of Shetland as a plant habitat so far as climate is concerned, with a particular view of the Unst serpentine as an edaphic habitat. Some observations are made on the biotic factor. This is followed by aims and methods of quantitative analysis used in the four parts of this study. Part I concludes with a brief analysis, mentioned above, of the flora of Unst in relation to the geology. Part II is concerned entirely with the study of the interaction of the vegetation and the serpentine debris habitat in Unst. The emphasis is on the dynamic, successional aspects. The phases of the prisere on serpentine debris are described first, then the following general problems are investigated: (1) factors inhibiting the colonisation of open areas containing restricted species; (2) the cause of the serpentine effect; (3) cyclical succession and (4) origins and affinities of the debris habitat.

Part III is mainly phytosociological. It comprises a description of the communities on serpentine in Unst, the Coyles of Muick and Rhum and of related communities on non-serpentine rocks in that island and in Shetland (Ronas Hill mainly). By comparison with published data from the North Atlantic region, general and specific features are deduced of vegetation of Scottish serpentine localities I have examined. Correlation of communities and 'oceanic' and 'montane' climates is also demonstrated. Part IV is devoted to a field inquiry into the causes of the restriction of rare species to pioneer habitats, using the Unst serpentine debris as an example.

The authorities used for nomenclatuse of plants in this thesis are as follows:- (1) phanerogams and vascular cryptogams; Clapham, Tutin and Warburg (1952): (2) mosses; Richards and Wallace (Check-list, Trans. Brit. Bryol. Soc. I (1950, p. 426): (3) liverworts; Watson E.V. (British Mosses and Liverworts, 1955, Cambridge): (4) lichens; Watson W. (Census Catalogue of British Lichens (1953) London).

PART I

THE SHETLAND CLIMATE

THE UNST SERPENTINE AND THE FLORA OF UNST IN RELATION TO THE GEOLOGY

A. Temperature and general features

Temperature. Fig. I [*] (p. 9a) gives the mean monthly temperature for Baltasound, Unst, Shetland (1921-1947); it illustrates the narrow mean monthly temperature range of only 13.5 deg. F. In relation to Shetland's latitude the air temperature has high winter minima (Feb. 34.9 deg. F : Baltasound at 31 ft. (9 m.)) with snow lying on only 9 days in the year, and low summer maxima (July 59.0 deg. F : Baltasound). Both these types of narrow temperature range are features of the extreme Atlantic climate (Tansley 1939) from the Scilly Isles to the Faeroes; which is clearly illustrated for those north Atlantic islands by the mean monthly temperature for Thorshavn (25 years; in Ostenfeld 1909). By contrast a Scottish upland station is included in fig. I; Dalwhinnie (altitude 1176 ft. : 359 m.) in the Grampians. The latter is a valley station in a mountain area. It illustrates the differences between an oceanic and landward area in mean monthly temperature range and in mean monthly maximum-minimum range. Although it is based on experience of the behaviour of crop plants, I assume that a mean temperature of 42°F. can be said to indicate very broadly the start of the growing season for most plants in these regions. So, from the start of the growing season some time in April till late in September, the difference between the mean monthly maximum and minimum temperature does not exceed 10 deg. F in oceanic Shetland, while the range

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[*] The data for this and subsequent graphs in this section are given in the Appendix at the end of the thesis, p. 209-10.

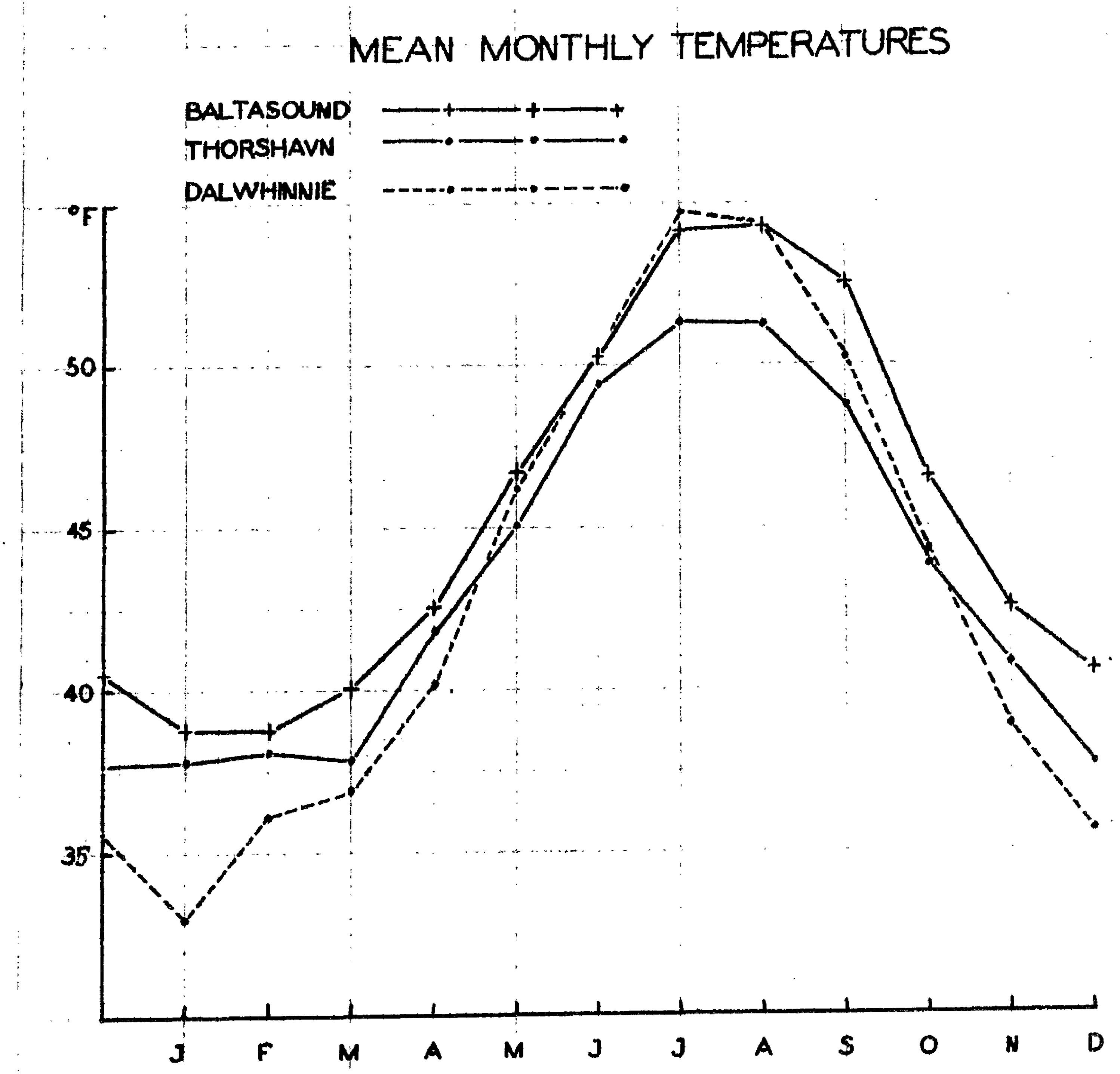

MEAN MONTHLY TEMPERATURES
BALTASOUND
THORSHAVN
DALWHINNIE
°F
50
45
40
35
J
F
M
A
M
J
J
A
S
O
N
D

FIG. 1.

in Dalwhinnie reaches 18 deg. F. During this period however the mean monthly temperatures in Baltasound are the same as those in Dalwhinnie. Shetland's mean monthly temperature near sea-level in the growing season is equivalent to that at over 1000 ft (305 m.) in the Central Highlands.

What of the temperature at higher altitudes in Shetland? Air temperature figures are available for Lerwick (altitude 269 ft : 82 m.); with Baltasound at 31 ft (9.5 m.) it is therefore possible to arrive at monthly figures for lapse rate (Appendix, p. 209 Table XXIII). A rise of 238 ft (73 m.) entails a mean monthly lapse rate of between 0.2 (November) and 1.3 deg. F. (March and April). With these lapse rates temperatures are calculated for Sandness Hill, west Mainland, at 816 ft (249 m.) and Ronas Hill at 1000 and 1480 ft (305 and 451 m.). (Table XXIII p.209). On the basis of this calculation, the mean monthly temperature on Ronas Hill never exceeds 49.5 deg. F. near the summit at 1486 ft (453 m.); even on the summit of Sandness Hill only reaching 51.6 deg. F. So the growing season is very short, while for two months of the year the mean temperature on the summit of Ronas Hill lies at or near freezing point. Unfortunately the extent of snow cover is unknown but with the high winds (see below) extreme exposure is indicated.

To find suitable comparisons is difficult. But I have already pointed out the similarities in mean monthly temperature, during the growing season, between Dalwhinnie and Baltasound. Now the lapse rate of 1 deg. F. in air temperature for every rise of 300 ft (91 m.) in altitude has been calculated from the Ben Nevis - Fort William figures. It may be assumed for my purpose to apply reasonably well to the temperature regime above Dalwhinnie in the central

Highlands. Taking an altitude of 2500 ft (762 m.), the conversion of the Dalwhinnie figures at 1176 ft (358 m.) to this altitude entails a correction of 4.4 deg. F. This is the fall in temperature, at the given lapse rate, which follows a rise in altitude of 1324 ft (404 m.). (Table XXIII p. 209).

Compared with an annual lapse rate, in Shetland, of 1 deg. F. for every increase in altitude of 238 ft (73 m.), the figure of 1 deg. F. for 300 ft (91 m.) in landward areas illustrates the higher lapse rate operating in oceanic regimes (cf. Green 1955). As the annual lapse rate is only an approximation comparisons must be viewed with caution. It is nevertheless interesting to note that, between late May and early September, the figures for Dalwhinnie at 2500 ft (762 m.) (fig. 2 p. 11a) are about the same as those for Ronas Hill at 1000 ft (305 m.); between February and May they resemble the Shetland figures at 1480 ft (451 m.). For the rest, the difference in the oceanic and more landward regime is clearly seen (and would be very apparent in the mean maximum-minimum temperature ranges in the two localities). One can therefore say that the mean monthly temperatures during the growing season (May to September) at 1000 ft (305 m.) in Shetland are equivalent to those at 2500 ft (762 m.) in the Central Highlands. It follows that for the Coyles of Muick in West Aberdeenshire, between 1600 - 1900 ft (488 - 579 m.), the summer temperatures lie within those found below 1000 ft in Shetland. For Rhum, Inverness, I have only the mean monthly temperatures, reduced to sea-level, of the Climatological Atlas (1952). For the warmest month, August, this is 57 deg. F. Assuming that on Rhum a lapse rate

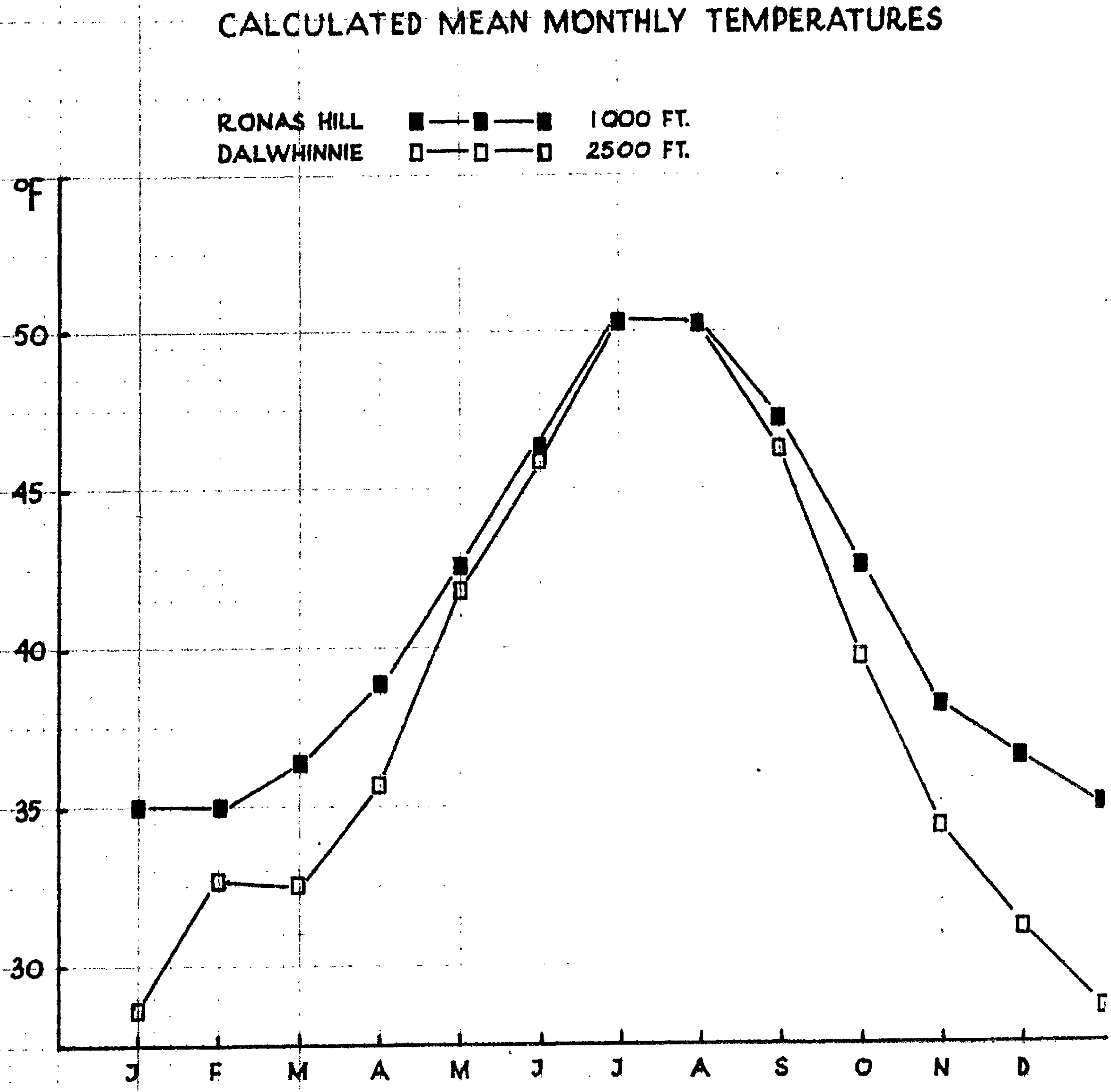

CALCULATED MEAN MONTHLY TEMPERATURES
RONAS HILL ■—■—■ 1000 FT.
DALWHINNIE □—□—□ 2500 FT.
°F
50
45
40
35
30
J
F
M
A
M
J
J
A
S
O
N
D

FIG. 2.

operates which is not greater than that in Shetland and not lower than that on Ben Nevis, the August isotherm of 50.3 deg. F. for 1000 ft (305 m.) in Shetland lies in Rhum between 1600 and 1900 ft (488 - 579 m.).

General features. Annual rainfall is moderate, 1013 mm. (43.6 ins.); but the number of raindays (precipitation 0.01" or more) at Lerwick (altitude 156 ft : 48 m.) are 260, so that a high level of humidity is characteristic. On the Index of Humidity (cf. Böcher 1954), which is the annual average precipitation in mm. divided by the mean annual temperature in deg. C. plus a constant of 10, this gives a value for Baltasound of 60. Annual hours of bright sunshine are 1039, or 24% of possible (hours of daylight); annual cloud amount (on a 0-10 scale) is 8. The picture is less gloomy if the figures for the growing season (roughly April - August) are taken. These five months have 2/3 of the annual total, or 703 hours, of the annual sunshine; an equivalent figure for central Scotland (e.g. Perth) is 825 hours. In Shetland, summer fog reduces the hours of bright sunshine and the air temperature; two-thirds of the fog-days occur in the five warmer months, as in the Faeroes (Ostenfeld 1909).

Table II

	J	F	M	A	M	J	J	A	S	O	N	D	Year
Rainfall: mm.	114	85	84	61	55	47	61	80	80	105	113	128	1013
R.H. %. (1921-35)	87	88	87	86	85	88	88	89	88	88	87	88	
Cloud 0-10	9	8	8	7	8	8	8	8	8	8	9	9	
Fog - days	4	1	1	2	4	6	7	5	3	2	1	1	

None of the general data can be applied with any accuracy to Shetland at or above 1000 ft. Rainfall, cloud amount, and humidity will obviously increase; so too, with a mean annual temperature of about 40 deg. F. (4.4°C.), will the Index of Humidity which must reach a value of at least 70.

Similarities in mean monthly temperatures during the growing season have been found with montane areas at higher elevations in the south; it may be useful therefore to compare these, and the general climatic features, with those of for instance S.W. Greenland, to which the general correspondence of the montane climate in Britain is well-known (viz. Pearsall 1951).

I use data supplied by Böcher (1954) in his paper on the vegetation of S.W. Greenland. He divides that area into five climatic regimes, three 'oceanic' and two 'continental', mainly it seems on the basis of differences in temperature range, the index of humidity and an index of oceanity (Böcher l.c. p.17). Of the three oceanic regimes, the low arctic - oceanic (A) differs from the subarctic oceanic - suboceanic (E) in its narrower (more oceanic) temperature range, its cooler summer and its slightly lower rainfall. The Shetland climate as a whole agrees with oceanic features like the high precipitation and the index of humidity in both regimes; it is closer to (A) in the matter of narrow temperature range, which at Baltasound is 7.5 deg. C. (13.5 deg. F.).

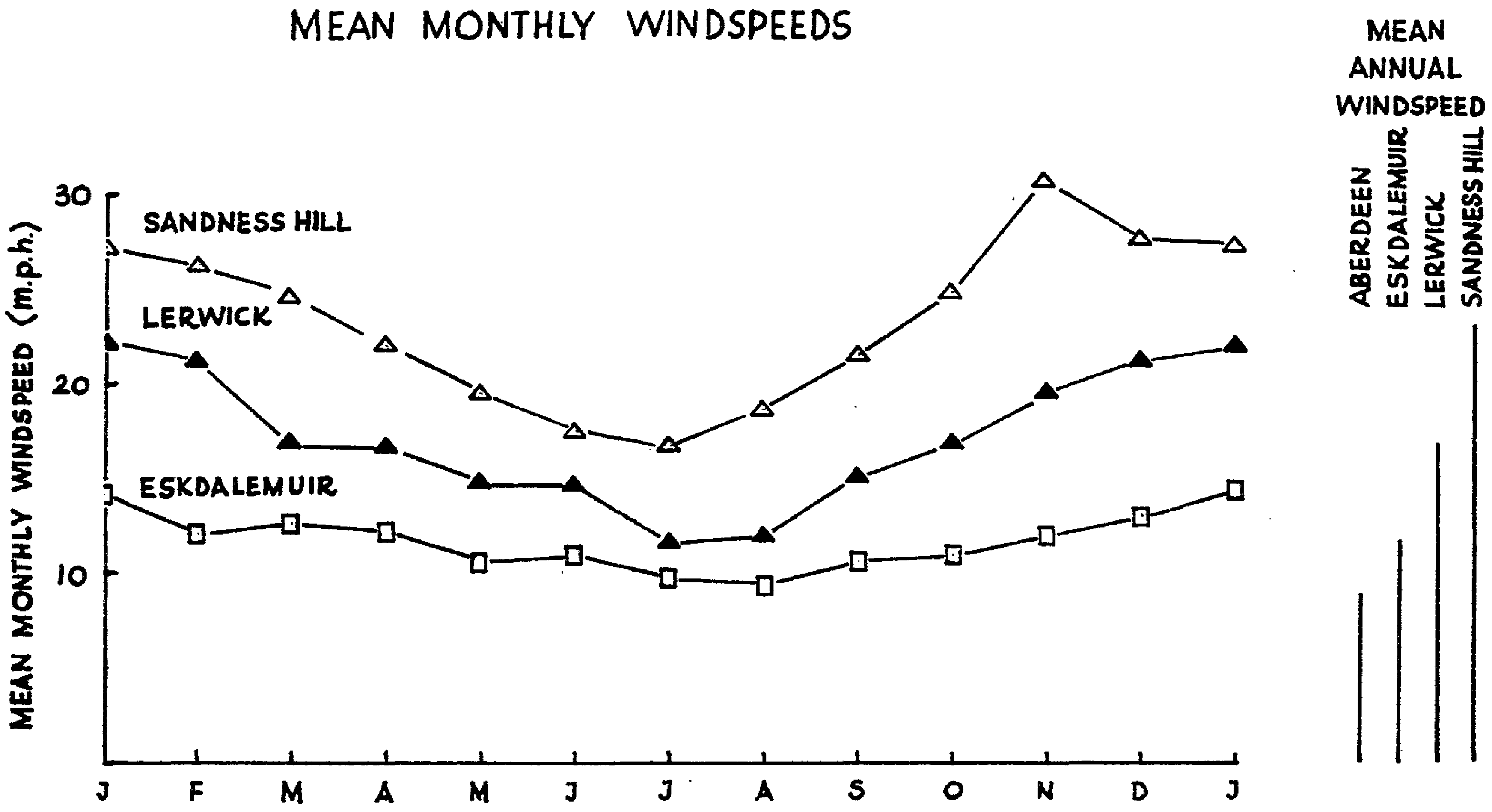
		A	E	Shetland over 1000 ft (calculated)
mean annual precipitation	mm.	500-1000	700-1400	1000(plus)
mean temperature of warmest month	°C.	6-8	9-11	c.10 (3 months over 8)
range	°C.	10-18	15-20	8
Index of humidity		60-120	60-120	over 70

Comparison thereafter can only be made with the calculated figures for Shetland's climate over 1000 ft. Now 8 deg. C. (46.5 deg. F.) is the warmest mean monthly temperature reached in the low arctic - oceanic regime (A). Exceeding this figure for three, but only three, months of the year and reaching a mean monthly temperature of 10 deg. C. (50.3 deg. F.) at 1000 ft, the Shetland climate at and above this altitude is equivalent more to the subarctic - oceanic - suboceanic regime (E). Assuming that in the Faeroes lapse rates operate which are at least as high as those in Shetland, then a mean monthly temperature of 50.3 deg. F. is not found above about 300 ft (91 m.) altitude. At 1660 ft (506 m.) the mean temperature of the warmest month, at 44.8 deg. F. (7.7 deg. C.), lies within the low arctic - oceanic summer regime (A) of S.W. Greenland.

B. Wind

The following wind data (figure 3 p.14a) are first of all taken from the Lerwick Observatory figures. The wind measurements are recorded at an altitude of 310 ft (94 m.) (at a height above the ground of 39 ft : 12 m.) on an exposed hill so they will, especially during the strongest winds, give higher values than those obtaining in much of the low lying crofting ground near the sea. There are 38 gale-days per year at Lerwick; even during the critical period of April-May when growth is being resumed, there are 2.9 gale-days.

Through the Electrical Research Association I have obtained figures for the mean monthly windspeeds on the summits of three Shetland hills. Direction is not recorded.



MEAN MONTHLY WINDSPEEDS

FIG. 3.

Only for Sandness Hill, West Mainland, altitude 816 ft (249 m.), is there a continuous 2½ year run of figures (July 1952 - December 1954). As I have not studied the vegetation of the other hills their figures are simply of interest as a check to the magnitude of the Sandness Hill ones. The short run of figures from the Ward of Scousburgh always exceed the values for windspeed from Sandness Hill. This is to be expected from the position of each hill. Sandness lies at the extreme west of the West Mainland so that the total windspeed will be lessened by many winds with an easterly component having travelled some distance overland, whereas the Ward of Scousburgh forms the top of the narrow spine of the south Mainland and is exposed, from all but a narrow northerly sector, to winds straight off the sea.

The turbulent nature of Shetland's weather is shown well enough by the Lerwick Observatory windspeed figures; but the annual average windspeed on the top of Sandness Hill is, at 23 m.p.h., almost half as high again. And the Sandness Hill anemometer was only 500 ft (152 m.) above the Lerwick one. The greatest contrast between the Sandness and Lerwick figures are during the gale periods in March and October-November, though the mean windspeed ratio still remains approximately the same. Taken as a whole the figures are very high; even during the five "calmest" months, or the growing season, the mean monthly windspeed is 18.6 m.p.h. In winter, mean monthly temperatures at 1480 ft (451 m.) lie near freezing point while snow cover is intermittent. Exposure all the year round must therefore be severe.

To appreciate fully the magnitude of these values some contrast is needed. Sandness Hill at a slightly lower altitude has about twice as much wind in any month as upland Eskdalemuir, Dumfriesshire, and sometimes more than twice as much; the annual figure is three times that at Aberdeen. A more significant comparison perhaps is with the figures for Ben Nevis. At 800 ft (244 m.) in Shetland the annual windspeed is already four-fifths that on the summit of Ben Nevis at 4406 ft (1343 m.) (30 m.p.h.: Manley, 1952, p.188). If the windspeed has increased by a third in 500 ft (152 m.), and Ronas Hill lies 600 ft (183 m.) higher than Sandness Hill, then the figures for the former may well, at 1486 ft (453 m.), approach or equal those for Ben Nevis at 4406 ft (1343 m.).

Lacking data on direction can these total figures mean anything in terms of the vegetation? The slightly lower Sandness Hill values, in comparison with those from the Ward of Scousburgh, were attributed to the former hill's lying at the western edge of a relatively broad land mass, with a consequent lessening in effect of winds with an easterly component. Assuming that wind can be responsible for bare ground, at these altitudes at least in Shetland, then the distribution of the vegetation on Sandness Hill bears out the relative importance attached in a mean total of 23 m.p.h. to winds with a westerly component. Because nearly bare ground with corresponding open vegetation occupies the broad ridges above about 700 ft (213 m.) to the summit at 816 ft (249 m.) on the westward side of the hill: while closed communities on often deep peat occur to the summit on the eastward side and in shallow gullies even on the west.

Debris with sparse plant cover occupies progressively more and more of the surface of Ronas Hill, North Mainland, above 1000 ft (305 m.), until at 1400 ft (427 m.) 90% of the ground consists of it; and closed vegetation is confined to the lea of boulders (Plate I, phot. 1) which litter the flat gravel surface, or to one or two shallow gullies which reach as far as the summit. Here again winds with a westerly component seem to be the factor which limits the spread of closed vegetation.

Salt spray is related in effect to wind. No part of Shetland lies more than 4 miles from the sea. Even in summer, spray can be carried that distance, as during a gale in August 1952 it collected on glass nearly 4 miles to leeward of the coast; vegetation was badly damaged, potato plants and tree leaves being blackened and moorland grasses scorched. I have no experimental evidence as to whether such damage is caused mechanically and/or by desiccation with salt spray, but a strong limiting effect on stature is to be anticipated, even during the growing season.

I have dealt so far with the question of the effects of exposure at higher altitudes. Combined with generally low summer temperatures and poor or no snow cover in winter, the limiting effect on stature and certain types of community is very evident at heights above about 800 ft (244 m.) in Shetland. But in view of its obvious magnitude some limitation may also be expected at far lower altitudes. While the greater part of the land surface of for instance Unst is covered in closed vegetation, serpentine debris with sparse plant cover extends down to sea level on Hamar (see p. 25); across this debris at 100 ft (30 m.) runs a dry-stone wall, from either side of which a community with 100% cover extends for only a few feet (Plate I, phot. 2). This suggests restriction of spread of a closed community associated with exposure to wind at much lower altitudes than the earlier examples I quoted. Moreover, general correlation can be noted between major debris areas in Unst and exposure to westerly winds (fig. 4, p. 21a); with, however, community restriction on both east and west sides of the wall in the example I have just given, it is obvious that local variations in topography must be considered. Further, even if some correlation is discernible at higher levels, one can go no further till something is known of the season(s) at which damage is inflicted on the plants. The final point only concerns the serpentine debris. The failure of closed vegetation to develop over this may be as much due to edaphic factors like soil toxicity as to exposure. This is the basis of the inquiry in Part II into the interaction of vegetation and habitat.

C. Climatic correlations

In Part III a description is given of the Unst serpentine and some related vegetation in Shetland and Rhum, their affinities being traced with communities in the Central Highlands, the Faeroes, S.W. Greenland etc. Some correlation is then attempted with causal climatic factors. So similarities in and differences between the climate of Shetland and these other areas have been stressed throughout this section. I conclude with a summary of them.

Irrespective of altitude Shetland's climate exemplifies those of oceanic areas in its narrow temperature range, high humidity (as expressed in the Index of Humidity) and exposure: agreeing with montane climates in the last two features. In the matter of temperature, the similarities between different areas having oceanic or montane regimes may be expressed first of all by the mean temperature of the warmest month.

Now tree growth is generally conceded to stop where the mean temperature does not exceed 50 deg. F. for at least two months in the year. This isotherm is found over much of upland Britain at about 2000 - 2200 ft (610 -671 m.) (Pearsall 1950, Manley 1952) and may be said to mark broadly the upper limit of the submontane zone: above Dalwhinnie the equivalent altitude is about 2500 ft (762 m.).

Vegetation at sea-level in Shetland is subjected during summer to mean monthly temperatures found at about 1000 ft in the Central Highlands; for 1000 ft (305 m.) in Shetland the equivalent Highland altitude is about 2500 ft (762 m.). If Dalwhinnie between 1100 - 2500 ft (335 - 762 m.) has a submontane climate, then Shetland from sea-level to about 1000 ft (305 m.) may be said to have a submontane-oceanic climate. For Rhum the figures are approximate; the upper limit is between 1650 and 1900 ft (503 - 579 m.), for the Faeroes about 300 ft (91 m.). In Rhum also it may be noted that, even with the Shetland annual lapse rate applied to the temperature of the warmest month, the division between the submontane and lowland zones cannot be under 600 ft (183 m.) above sea-level. Next, the mean monthly temperature from over 1000 ft (305 m.) in Shetland, 2500 ft (762 m.) in Dalwhinnie and about 300 ft (91 m.) in the Faeroes are equivalent during summer to those obtaining in lowland subarctic-oceanic S.W. Greenland. Shetland at higher altitudes has a subarctic-oceanic summer climate; the Faeroes reach the low arctic-oceanic summer regime. The corresponding temperatures of the warmest month at different altitudes in these areas are shown in fig. 3A, p.19a. The approximate nature of the data has already been emphasised.

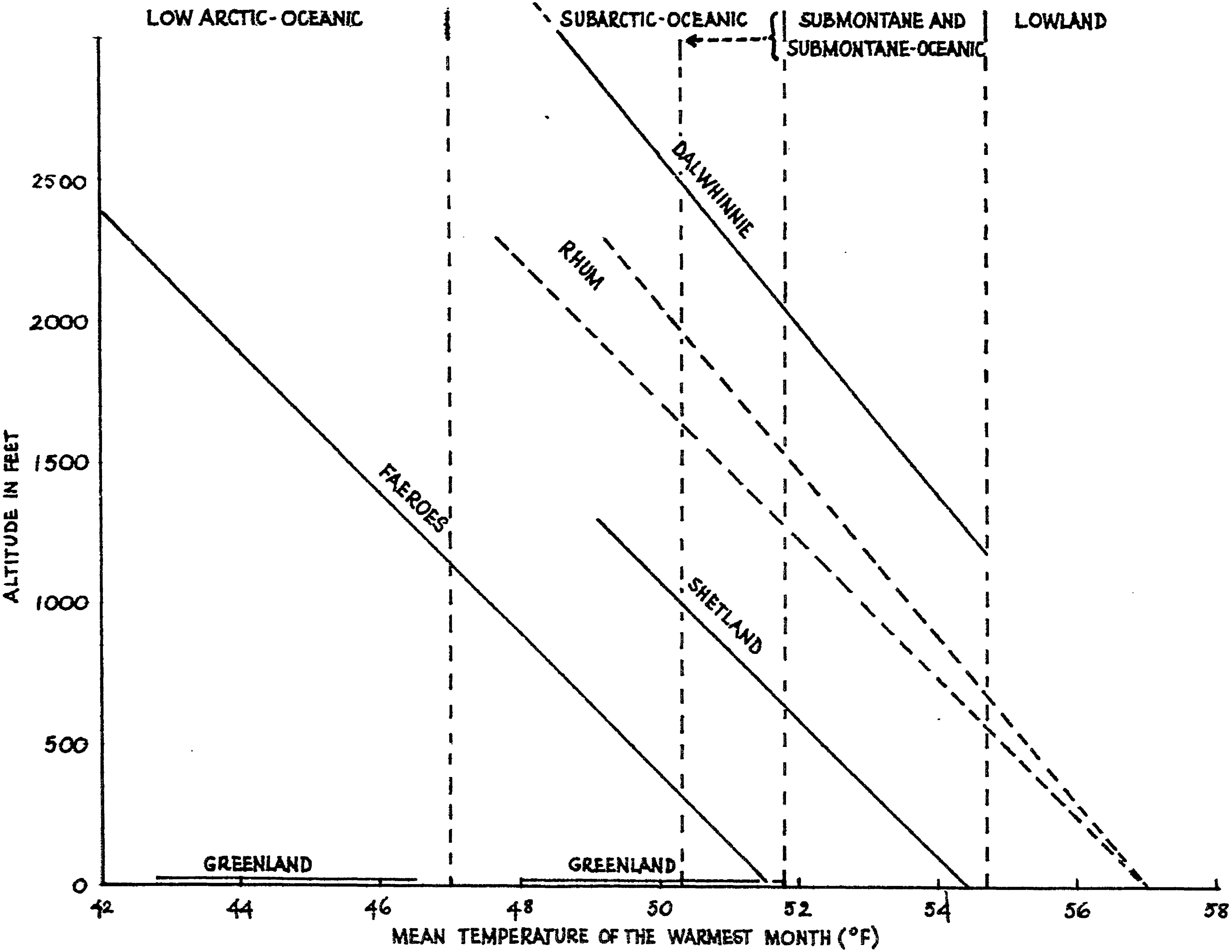

LOW ARCTIC-OCEANIC
SUBARCTIC-OCEANIC
SUBMONTANE AND SUBMONTANE-OCEANIC
LOWLAND
DALWHINNIE
RHUM
FAEROES
SHETLAND
GREENLAND
GREENLAND
ALTITUDE IN FEET
2500
2000
1500
1000
500
0
42
44
46
48
50
52
54
56
58
MEAN TEMPERATURE OF THE WARMEST MONTH (°F)

FIG. 3A.

These similarities between montane regimes in the south and oceanic regimes in the north have been exemplified by temperature; they must be increased by the presence of strong winds. Vegetation in Shetland at 300 ft (91 m.) has to contend with twice as much wind as say near Aberdeen at 100 ft (30 m.). At 800 ft (244 m.) the figure is three times; this is already four-fifths of the annual average on Ben Nevis at 4406 ft (1343 m.). Environmental similarity will be at its closest in the exposed snow-free habitats which these areas share with Shetland. It is here that vegetational similarity may be expected to be most striking. The only difference between such a habitat in an oceanic and a montane regime will be caused by the wider temperature range in the montane area: this giving lower winter temperatures.

Both in low summer temperature and in the magnitude of the windspeeds Shetland is likely at a given altitude to approach extremes for Great Britain.

II. Edaphic Factors in Unst with special reference to serpentine

Area : Unst is nearly 12 miles long and averages five miles in breadth. It has a land surface of about 50 sq.miles or 29,866 acres, including outlying islands.

The account of the geology is based on Philips (1927) and Read (1934).

A. The Acid rocks : topography, geology and soils

The block of gneisses which forms the western part of Unst is characterised topographically by the strike ridge of Vallafield (= fell) fig. 4, p. 21a. This, averaging about 500 ft (152 m.) in altitude, runs north for seven miles, to end in Hermaness. The ridge presents a steep escarpment to the west - the only major inland area of steep ground on Unst and it terminates in the steep cliffs on Tonga etc. The gneisses are bound to the east by the valley that runs from Burrafirth to Belmont.

This valley is also the western boundary of the Saxavord block of mica-schists. East of Burrafirth it reaches its highest point in the 960 ft (293 m.) Saxavord. The block persists in a thin line to the south down the valley. A belt of schists ("Muness phyllites") forms most of the south-east peninsula of the island.

Practically the whole of the gneiss and mica-schist exposure is covered in blanket-bog and associated vegetation. Exceptions are the areas of and near sea cliffs, some of the steepest slopes and eroded hill tops (Vallafield), hill pastures and areas cleared of peat by peat-cutting.

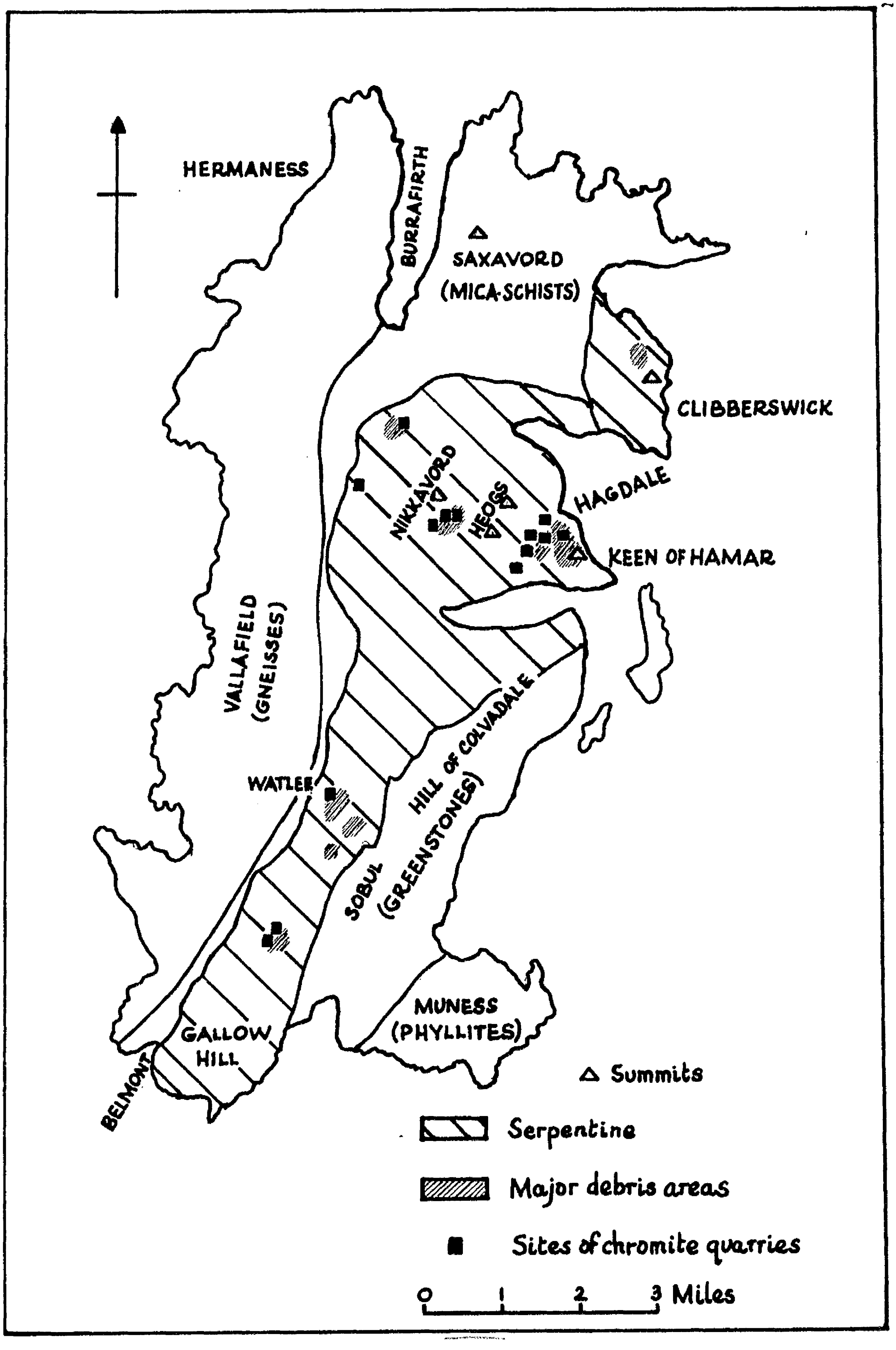


Fig.4.Sketch map of Unst,showing principal rock types and place names mentioned in the text.

B. Greenstone : topography and soils

South of the Saxavord mica-schists and east of the Burrafirth - Belmont valley lies the igneous intrusion of basic and ultrabasic rocks (see below). Gently sloping like the other rocks, the basic greenstone carries a higher proportion of water-logged soil than the serpentine. Such areas have a thin layer of peat with no tendency to blanket-bog formation (some, however, may be peat-cleared ground). On the N-S 400 ft (122 m.) summits of Colvadale and Sobul there is coarse debris covered by Rhacomitrium heath.

C. Serpentine : topography and geology

The ultrabasic or serpentine block at its broadest part forms an E - W line of 400 ft (122 m.) summits, of which the Muckle Heog has the only inland crags; the gradient otherwise being gentle. On the east, Clibberswick and Hamar form truncated headlands. The central part of the block is mainly low-lying but makes the western flank of the greenstone Hill of Colvadale and Sobul. Finally in the south the serpentine forms Gallow Hill.

The rocks of the block are well-exposed, particularly on all the higher ground, but stretches of the valleys are covered in drift which in turn carries closed vegetation. There are also extensive areas of debris with sparse vegetation (see below).

Olivine-serpentine occupies the bulk of the Main and Clibberswick ultrabasic exposures. The olivine rock weathers with an ochreous crust (Read l.c. p. 662); this characteristic colour of weathered serpentine (viz. Rune 1953 p.41) indeed predominating over the serpentine area. Chromite-serpentine is according to Philips (l.c. p.627) closely associated with this rock which he calls dunite-serpentine. Dunite rock consists essentially of olivine and chromite. Pyroxene rock occurs along the eastern margin of the main serpentine group, partly converted to an antigorite-serpentine, while a belt of antigorite-serpentine bounds the exposures to the west. It seems then that serpentinization has extended throughout the block.

Chromite has been quarried at intervals in Unst since the nineteenth century. Such workable deposits consist of what is practically a chromite rock or a serpentinized dunite (Philips l.c. p.635). Fig. 4, p. 21a, gives quarry sites. In dunite-serpentine the chromite occurs as stringers or bands of a few inches. Finally, Philips (l.c. p.629) states that, over the area of what must be Read's pyroxene rock and Clibberswick serpentine "chromite is almost constantly present as somewhat corroded-looking crystals". Chromite is widespread in the serpentine.

Philips (l.c. p.637) says that in analyses of chromite concentrate made to detect precious metals like platinum "nickel is present in some cases, as is evident from films of green hydrous nickel-carbonates found in places on the chromite". While chromium remains practically unaffected by weathering processes (e.g. carbonation) "traces of nickel, either associated with this or originally present in a nickeliferous olivine, have yielded carbonates such as zararite" (Philips l.c. p.648).

D. Serpentine soils

(1) Soils under closed vegetation. Most of the serpentine outcrop bears vegetation with 100% cover which overlies shallow drift or debris on free-draining ground and may or may not have a thin layer of mor. Drainage hollows and streamsides have characteristic soligenous mire soils which, with soil-pH of 6.0 and over, are of the mesotrophic-eutrophic type.

The section which follows however is devoted entirely to consideration of the third main soil type, debris with sparse plant cover, since it is the study of this habitat in Unst and its interaction with the vegetation which comprises Part II of this work. The free-draining soils with some profile and mire soils are described in Part III with their appropriate vegetation in and beyond Unst.

The chief point to emphasise here concerning the substrate under closed vegetation on serpentine, in contrast to the other rock types, is the complete absence of peat. Archeological evidence indicates that there has been none in the past either, because Bronze Age short-cists and cairns are found on the 400 ft (122 m.) summits such as the Heogs, while the corresponding gneiss and mica-schists are still peat covered.

(2) Debris. Debris consists in Unst of a surface layer of small angular stones with finer particles mingled beneath. This debris may be invisible from the surface, lying under vegetation with 100% cover. It may also bear very sparse plant cover. The debris is then seen clearly from considerable distances (Plate I phot. 3). It is to ground of this type, surfaced by small stones rather than by vegetation with 100%

cover, that the term "debris" refers in the subsequent account. This debris occupies about 2000 acres of the serpentine outcrop from sea-level to 500 ft (152 m.). The largest expanse is on Hamar (Plate I phot. 3).

There are various soil-movement or solifluction phenomena associated with bare or nearly-bare ground in arctic-alpine regions. On level ground of this type in such regions, soil-polygons are commonly formed (Wilson 1952). "Where the slope exceeds about 5 deg., the polygons normally elongate into stone stripes which are parallel lines, running downhill, of alternating coarse and fine debris" (Wilson l.c. p.253). There is one area in the extensive debris on the north of Hamar (Plate I, phot. 3) where formations like these stone stripes occur. Although the longest measured stripe was only 12 yds. (3.6 m.) long and the broadest striped patch about 10 yds. (3 m.) wide, the stripes as figure 5 illustrates show the essential features of the type. The altitude is only 150 ft (46 m.) above sea-level. However, the breadth and depth of these stripes and their particle-size corresponds most closely to 'stone lines' described by Taylor (1955) from Macquarie Island, 900 miles (1450 km.) north of Antarctica. The climate there is cold, wet and windy. The stone lines occur on exposed slopes of slight gradient and almost bare of vegetation. Gravel covers the surface which is thrown up in a series of waves transverse to the slope. This gravel fills the channels cut out of the underlying silt.

In spite of the fact that most of the Unst debris has a slope of less than 5 deg., soil polygons associated with such terrain were not observed. Finally, in the very few places where the debris approaches a slope of 15 - 25 deg., it is not

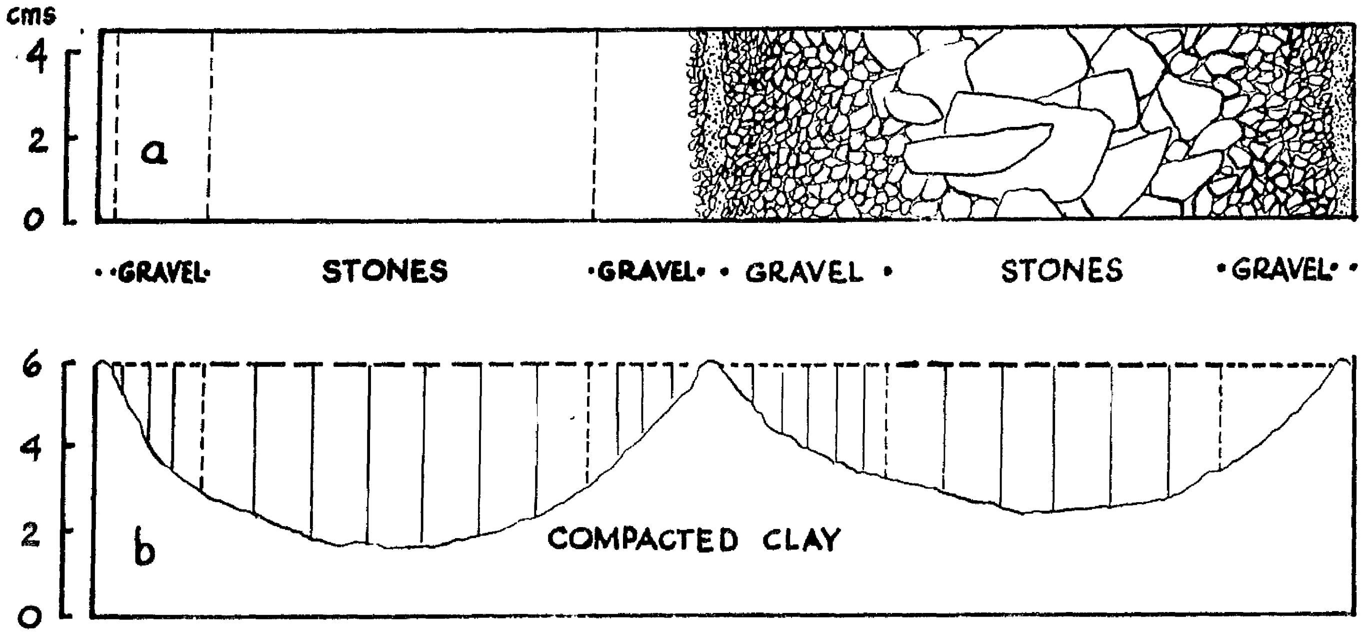


Fig.5. Scale drawing, x ½ ,of stone stripes or lines on N.W. slope of Hamar, altitude 150 ft. Loose stones (to 10 cm. diameter) and gravel (to 1.5 cm. diameter) lie in hollows in the compacted serpentine clay which forms at the surface the margins between stripes; (a) surface view, (b) profile.

continuous enough to produce the horizontal vegetation covered ridges, or terraces, associated with such slopes (Wilson 1952). (These terraces occur on Ronas Hill : see p. 121 , and Plate VII, phots. 2, 3). The few inland crags do not give rise to talus slopes.

From what has just been said it will be clear that the physical composition of the debris varies. The debris surrounds and is associated with outcrops of exposed serpentine bedrock weathering <u>in situ</u> (Plate 2, phot. 1) or else occurs as patches without such exposed bedrock, (Plate 2, phot. 2) often in areas of predominantly closed vegetation. For the purpose of this account the former is called associated debris and the latter unassociated debris. In either case its surface consists of small angular stones of up to two inches, and averaging about a half-inch, in diameter. But stones of debris near freshly weathered bedrock tend to be larger then those in presumably older debris lying at some distance from any bedrock; this has in turn a higher proportion of gravel. Where the slope varies from 0° - 10° the surface looks steam-rollered, so close-set and level are the stones.

Like its parent material, debris round exposed serpentine bedrock is ochreous in colour; so is the finely divided clay which, with varying fractions of gravel and small stones, lies directly beneath to a maximum of two feet in dug samples. Patches of debris at some distance from bedrock or lacking bedrock are red-grey or grey; and a layer of about 0·6 cm. of fine soil with some humus fraction often lies between the stone layer and the ochreous-coloured clay beneath.

It is thus possible to distinguish a patch of associated debris as one where, irrespective of area, there is available at the surface a source of freshly weathered material; ochreous near exposed bedrock, the debris surface may be greyer toward the margin of such a patch. Patches of unassociated debris lack exposed bedrock, are always grey and often, moreover, occur in small valleys or hollows. (This careful distinction of associated and unassociated debris patches has been made because of their different origins (p. 70) and because there is some correlation between debris-type and the distribution of the restricted species (see Part II, p. 69)).

The largest continuous stretches of associated debris are on Hamar (Plate 1, phot. 3); most of it is ochreous, some grey. Smaller areas of this type occur on Nikkavord, Colvadale (Plate 2, phot. 1), Sobul and Clibberswick. In many parts of the serpentine outcrop patches of unassociated debris are found, often in areas bearing predominantly closed vegetation.

(3) <u>Soil-pH</u>. As may be expected of soil derived from ultrabasic rock, the pH of soil of root horizons in mineral debris are 6.12 to 6.62. This compares well with pH 6.60 to 6.88 from the mineral debris on the peridotite summit of Ruinsival, Rhum, pH 6.70 to 7.02 from the serpentine scree on the Coyles of Muick, Aberdeenshire and pH 6.1 to 7.2 from mineral soils on the serpentine of N. Sweden (Rune 1953 p.113). (All the figures were determined electrometrically, the Unst and some of the samples from Rhum by Dr. G. Bond). It is noted that with development of humus in the grass phase (Part II, p. 55) soil-pH drops to 5.72. In the shallow mor of the serpentine heath the lowest value recorded was pH 5.12.

(4) Chemical composition of Serpentine Soil.

In their study of serpentine soils, Robinson, Edgington and Byers (1935 p.19) found that in a humid and rather cold climate (Pennsylvania, Maryland) changes in the composition of the soils are only relatively small as compared with the parent rock. Therefore, although no total chemical analyses of Unst serpentine soil have been carried out, the figures for serpentine rock in Table IVI should approximate to the composition of the serpentine debris. They certainly compare well with the figures for the composition of N. Swedish serpentine derived from a large number of localities (Rune 1953, p.113): except for nickel which Heddle does not record at all.

The debris soil can thus be described as neutral with, in contrast to neutral calcareous soils, low calcium and high magnesium content.

Chromium content in Unst serpentine varies from a trace in Haaf Gurney, 3.7% Cr_2O_3 at Hagdale ("yellow serpentine") to 45% Cr_2O_3, the richest chromite ore analysed by Heddle (Philips 1927, p.636), from a quarry above Buness. Concerning nickel, Rune (1953, p.119), states that practically all the serpentine and peridotite rocks of N. Sweden have rather similar contents of that element and Cr. - approximately 0.4% Cr_2O_3 and 0.2% NiO; they occur in the same proportions in American serpentine (Robinson et al, 1939). Chromite is widespread in Unst serpentine which has a high % content of that mineral; and nickel is present here and there associated with the chromite (cf. p.23). There was a strong inference, therefore, that quantities of nickel would occur in Unst more widely than recorded. This has been tested.

Table IV

Chemical composition of serpentine rock. Nos. 1, 2, Unst: No. 3, Shetland Mainland; Heddle, in Philips (1927). No. 4, N. Swedish serpentine: averages: Rune (1953).

	1	2	3	4
SiO_2	31.85	44.00	41.46	40.00
Al_2O_3	0.99	-	0.01	1.0
Fe_2O_3	7.46	0.11	2.42	c 0.5
FeO		6.29	1.16	c 0.5
MgO	37.09	36.72	41.76	c40.0
CaO	0.63	-	trace	trace
Na_2O	-	trace	-	trace
K_2O	-		-	trace
H_2O	17.02	13.20	12.43	
H_2O				
CO_2	1.18	-	-	
Cr_2O_3	3.07	trace	-	0.4
MnO	0.61	-	0.23	trace
NiO		not given		c 0.2
	99.90	100.32	99.47	82.6

Soil 'subsamples' were collected from widely scattered areas of debris of the pioneer phase where plant cover did not exceed 5% of a given area (p.50), and united as sample A. Subsamples were also collected from debris having plant cover up to 33% and soil with a recognisable humus fraction in the rooting layers; from, that is, the sedge phase (p.53). These formed sample B.

Spectrographic analysis for nickel was undertaken on these two bulk samples by Mr. R. C. Voss of the Spectrographic Unit, West of Scotland Agricultural College. Nickel content was determined on the dilute (0.5N) Acetic acid extracts of the soils.

A.	Mineral soil from the pioneer phase	Nickel soluble in 0.5N Acetic acid p.p.m. in soil	312
B.	Soil with recognisable humus fraction	" "	289

These are very high figures compared with those usually found in soil, where acetic-soluble nickel is less than 2 p.p.m. (Mitchell 1945). This confirms the earlier deductions about its presence on the debris in large amounts. The figures are within the range of those given by Hunter and Vergnano (1952) for serpentine soils in Aberdeenshire (49 - 403 p.p.m.).

Nickel content is unlikely to be as high on every patch of debris; distinction has already been made between patches around freshly weathering bedrock, or associated ochreous debris, and patches isolated from such bedrock, or unassociated debris (p.26). A further series of analyses was therefore carried out on samples, collected in the same manner as the previous ones, from patches of associated ochreous debris (sample C), from patches of unassociated debris (sample D) and from the rooting layers of free-draining soil under heath vegetation (sample E).

			p.p.m. in soil
C.	Associated ochreous debris	Nickel	220
		Cobalt *	9.5
D.	Unassociated debris	Nickel	90
		Cobalt	8.9
E.	Rooting layer under heath vegetation	Nickel	90
		Cobalt	12.2

The results confirm that the nickel content on the debris is very high, but by no means uniformly so: and again within the ranges reported by Hunter & Vergnano (1952). The highest nickel contents are found in ochreous patches of associated debris, in the region that is of freshly weathered bedrock. Patches of debris of the unassociated, grey, type have a nickel content which, though more than 40 times higher than normal, is actually no greater than that in free-draining soil under serpentine heath.

The chief interest of nickel and chromium lies in their possible effects as minor elements on plants, and that raises the question of their availability. Chromium occurs partly in the form of highly insoluble chromite, partly as more soluble silicates; together they normally total about 0.5% mineral content (Rune l.c. p.113). But solubility is more important to plants than total content. In this connection Sundius (1949) has shown that the silicate content of serpentine

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* Cobalt determinations are commented on in Part II p. 76 , in connection with toxicity.

increases with increasing serpentinization. Nickel behaves in the same way (Rune l.c. p.120). In Unst serpentinization has affected the whole block (p.23); so some of the chromium and nickel present may be assumed to be available to plants, in relative abundance on the chromite veins. Any patch of debris surrounding such a weathering vein would of course be of the associated ochreous type.

To test both this matter of availability and possible differences in this factor between associated ochreous and unassociated debris, herbage samples of Agrostis stolonifera were collected. This species is the most abundant in the sparse plant cover on the debris. Subsamples were gathered on either debris type in the same manner as the soil subsamples. About 3 ozs. from each collectively form sample F (ochreous associated) and sample G (grey unassociated debris).

		Nickel soluble in 0.5N Acetic acid (p.p.m. in soil)
F.	Agrostis stolonifera from associated ochreous debris	118
G.	Agrostis stolonifera from unassociated grey debris	90

The figures for nickel content in Agrostis stolonifera growing on debris compare with 3 p.p.m. in dry matter in leaves of oat plants on normal soil (Hunter & Vergnano 1952), and 0.5 - 4 p.p.m. in pasture plants (Mitchell 1945). The figures for Agrostis lie within the range reported by Hunter & Vergnano (l.c.) for that metal in fully expanded leaves of oat plants from serpentine basin soils in the Aberdeenshire localities mentioned above : namely 17 - 134 p.p.m. For oat plants on hill-slope soils the figures are 16 - 51 p.p.m.

Varying degrees of toxic symptoms are exhibited by these oat plants. It is noted that there is no spectacular difference in nickel content of material from associated or unassociated debris.

The significance of chromium and nickel in serpentine soil is discussed in Part II in relation to toxicity and the serpentine effect. For the moment it can be seen (fig. 4, p.21a) that the distribution of the major debris areas coincides broadly with the distribution of the chromite quarries; these also are the areas with the higher nickel content, of which a large amount is available, and consist largely of associated debris.

III. Biotic factors in Unst

Sheep grazing is and has been the greatest single biotic factor in Shetland. There is evidence that even the earliest inhabitants - the megalithic peoples - were sheep breeders (Childe, 1946). Hill-land accounts for 86% of the land surface of Unst. This bore one sheep to 1½ acres in 1950, but the average may be higher on the common grazings (scattalds) which also carry Shetland ponies; one to not less than ten acres. These figures will apply to most of the serpentine area. Since it is let to one farmer, grazing is lighter on the Keen of Hamar where most of the work on the debris vegetation was done. Cattle are confined to permanent pasture near the townships. Inland, rabbits are restricted to rockier parts of the serpentine area; they are more abundant on the coast or in sand-dunes.

Both grazing and exposure can affect the stature and composition of vegetation. So that eventually some assessment of these two factors may be made, 6 ft x 6 ft (1.8 x 1.8 m.) areas of sea-cliff (at Belmont) and serpentine debris and heath (on Hamar) were fenced against sheep and rabbits in July 1952. In one case the change with fencing has been spectacular.

The vegetation for 30 ft (9 m.) from the top of a small exposed sea-cliff at Belmont was a close sward dominated by Armeria maritima, with Plantago maritima and P. coronopus subdominant, and Festuca rubra, Poa pratensis and Agrostis tenuis. A plot three feet from the cliff edge was fenced off in July 1952. In September 1952 Armeria and the plantains were overshadowed by the grasses; by September 1953 Armeria and P. maritima were dead or moribund, overlaid by a dense growth of grasses; chiefly Festuca rubra, with Poa and Agrostis. Plantago coronopus still survived much enlarged, at the edge of the enclosure, plants to the inside being moribund. Festuca was 25.5 cm. high but, as the leaves were laid, their actual length was nearer 46 - 49 cm. The enclosed area in fact now resembles the tall Festuca rubra community of the adjoining "sea-banks", steep grass-covered slopes descending to the sea. F. rubra has been found to shade out Armeria maritima in rabbit-proof enclosures among the Armerieta on Skokholm (Gillham 1953, p.89).

This sea-cliff example has been mentioned primarily because it shews that, composition apart, dwarf stature in a presumably exposed area can be due to grazing. On serpentine, fenced areas of sea-bank (e.g. Clibberswick) are dominated by tall Festuca rubra or Arrhenathenum elatius and adjoin short bent-fescue turf of the hill-side. But much of the outcrop bears heath (Part III). Since grazing pressure in fact varies over the outcrop, similar conclusions on the importance of stature vis-à-vis exposure cannot be drawn for the whole serpentine area. Indeed during the same period, no change comparable with the Belmont examples has occurred in five similarly fenced heath areas on Hamar (Plate II, phot. 3); grazing, by contrast, seems subordinate to exposure or some other factors (p. 63).

Direct anthropogenic factors affecting the hill-land include heather burning, ditching, peat-cutting (for fuel) and turf-scalping. Heather burning has been little practised in Unst during the past 30 to 40 years and mainly affected areas of peat-vegetation, gneiss, mica-schists and phyllites. This applies also to ditching and peat-cutting. Turf-scalping on the other hand probably affected the serpentine vegetation most, because this ancient practice was to remove to the arable ground the turf and topsoil of the better hill-land (O'Dell 1939). Although it has ceased for more than half-a-century, turf-scalping may have left particularly near townships impoverished or at least altered grazings.

IV. Aims and methods of quantitative analysis of vegetation

Work which involved quantitative analysis of the vegetation falls into three groups, the objects of which are (A) quantitative comparison of the serpentine hill-land flora with that of acid and basic rocks in Unst: (B) study of the serpentine debris-heath prisere and inquiry into the elimination of the pioneer species: (C) description of Unst serpentine plant communities and their comparison with those of other areas in and beyond Shetland. The different methods used for each stage of this work will now be described in the above order.

A.

The vegetation of Unst can be grouped broadly as cultivated land, permanent pasture land, halophyte sand-dune and hydrophyte vegetation: and the rest which I call hill-land. The object of the first investigation was, expressed differently, to give the frequency of any species on each of the main rock-types. Samples had therefore to be limited to areas where the nature of the rock determined the soil-type rather than for example the sea, as on sea-cliff or sand-dune, or topography as in valley-bogs. So quantitative investigation was confined to hill-land; to the communities of blanket-bog of the acid rocks and the heath etc. of the serpentine.

Raunkaier's method of frequency-estimation was used with a quadrat size of 1 sq.ft. (0.1 sq.m.) (Raunkaier 1909). The vegetation was examined as a whole: each rock-type including several plant formations in Raunkaier's sense. Quadrats were thrown at paced intervals and without regard to communities over well-separated areas of vegetation of each rock-type; that is, as uniformly as possible over the area (Raunkaier 1918). 150 samples were taken on serpentine, 100 on greenstone, 200 and 100 on gneiss and mica-schist respectively. Table 1 p.5a gives the results.

The frequency of a species depends not only upon its quantity but also on its distribution. It can be argued that, by using no other quantitative measure in this analysis, accuracy has been sacrificed for speed. But, since it has been used as a means of description only, many of the other criticisms of frequency as summarised by Goodall (1952) do not apply here: I was not for instance concerned with additive functions of frequency. The object indeed was to find an approximate answer to the question "how often is species X encountered in traversing the vegetation of any rock-type?" To that limited aim this method seems precisely suited.

B.

The debris prisere was studied by means of a cover analysis. A quadrat size of 1 sq.ft. was chosen for two reasons. I thought it useful to be able to compare such frequency-figures for species on debris with their frequency in vegetation with 100% cover, the latter being obtained in analysis A. Secondly, as great a degree of accuracy as possible being required, % cover was used to estimate quantity of plant material present rather than a scale like Hult-Sernander's or Domin's (see para. C.). This meant ones using a sample size where, excluding seedlings, the smallest specimen could be said to have 1% cover. In fact 1/25 sq.ft. was found by trial to be the largest area in which this requirement was met. So the quadrat of 1 sq.ft. was divided into 25 equal squares. To increase however the spread of the samples, only 13 (alternate) squares were used in obtaining cover-values; for % frequency therefore note was always taken of the presence of any species within that area but outside the smaller area of the thirteen subsamples.

The patchy distribution of the sparse plant cover on the serpentine debris means that the sort of space-time relationship of developing sand-dune vegetation does not operate. Nor can one reliably delimit the various semi-closed cover phases and sample within each. The continuous heath round the sides of the debris was taken as the limit of the sampling area. Quadrats, placed in no particular direction, were recorded at 10 yd. intervals along several lines across the debris. These lines were placed with regard to the boundaries not the contents of the debris, to cover as wide an area as possible. 59 samples were taken. This sampling was done on Hamar, a hill with the largest number of pioneer species (p. 51) and the most extensive areas of associated debris (p. 27).

C.

The main serpentine communities were discerned subjectively then a number of quadrat analyses were taken in each, using a quadrat size of 1 sq.m. The site selected for a quadrat was always in as uniform an area of vegetation as possible. This is the simple method advocated by Böcher (1954). I used Domin's 10-point cover-abundance scale for the estimation of quantity of plant material present (Poore 1955a). This scale gives more information than a five-point scale based on cover alone, both by having more categories in the higher cover-range and by substituting a measure of dispersion for the difficult estimation of cover in its lower ranges. The five-point cover scale just mentioned, Hult-Sernander's, has been used by the majority of Scandinavian ecologists with whose

Table VII

Hult-Sernander's scale		Domin's scale		
1/1 - 1/2 area	5	cover about 100%	10	>95
		cover > 75%	9	·85
		cover 50 - 75%	8	
1/2 - 1/4 area	4	cover 33 - 50%	7	
		cover 25 - 33%	6	
1/4 - 1/8 area	3	abundant; cover c.20%	5	
1/8 - 1/16 area	2	abundant; cover c. 5%	4	
< 1/16 area	1	scattered; cover small	3	
		v.scattered; cover small	2	
present; of low cover	x	scarce; cover small	1	
		isolated; cover small	x	

results I wished directly to compare my own, namely Norway (Nordhagen 1943) and Bjørlykke (1939), Faeroes (Böcher 1937), Sweden (Rune 1951) and S.W. Greenland (Böcher 1954). The more detailed Domin's scale can however be readily converted to Hult-Sernander's (Table VII).

In each sample details were also taken of locality, altitude, slope, plant cover (% total of 1 sq.m.), height of vegetation and soil profile. Using a Pye Minimeter, soil-pH was determined in a large number of samples. The same method was employed in the Coyles of Muick (Aberdeenshire), on various hills in the Island of Rhum, and on Ronas Hill in Shetland: so results are directly comparable. 55 quadrats were taken of which 30 were in Unst.

V. The serpentine flora compared with that of the acid and basic rocks in unst

A. The species of Unst hill-land grouped according to rock-preferences

The object of the first inquiry, of which Table 1 p.5a is the result, was a comparative study of the flora in relation to the geology; sampling being limited to hill-land, to areas where the country-rock could be presumed to be the primary soil influence (see Method p.36).

The qualitative differences between the distribution of species on acid basic and ultrabasic rocks is expressed here in quantitative terms. Through them, the flora may be divided into plants which, since I am primarily interested in serpentine, are characteristic, indifferent or accidental on that rock, or absent from it. A measure to assign each species to a group is available; the ratio of that species' frequency on serpentine to its nearest frequency on another rock. This is a measure of how far that species is exclusive to serpentine. It follows that all species on serpentine having a frequency-ratio greater than unity are indicated as serpentine-characteristic. For, as one speaks of species actually confined to serpentine, it is in this sense rather than in its absolute quantity that a species is "characteristic".

With a frequency-ratio greater than unity the degree of exclusiveness is being measured. This is a clumsy term but unavoidable since the more concise Fidelity and Constancy have well-defined phytosociological uses.

When assigning species to any of the four groups shortly to be defined, frequency-ratio alone should suffice, provided the species' frequency is high on one of the rock-types. But, where neither is high, then frequency itself must be considered as well as the ratio. Consequence of error being greater at these lower levels, a frequency of at least 10% on one rock and exclusiveness to that rock of three or more have been thought necessary to assign a species to other than the indifferent group.

With this preamble the four groups may now be defined:

A. Serpentine-characteristic. Plants quite exclusive, or having an exclusiveness greater than 2-3 and frequency of more than 10%.

B. Serpentine-indifferent. Plants with exclusiveness about unity and with, therefore, no preference for serpentine or other rocks and soils ~~in Unst~~.

C. Serpentine-casual. Plants with exclusiveness to another rock and very low frequency on serpentine.

D. Acid-rock-characteristic. Plants with exclusiveness to acid rocks and absent from serpentine.

As with the degree of fidelity of a species to a community so there may be differences between a species' local and general exclusiveness to, or preference for, serpentine. Serpentine-characteristic is used here in this local sense. The wider or regional preferences of a species can only be considered after examination of other serpentine and non-serpentine areas (Part III, p. 164 et seq.).

B. Summary of communities of the blanket-bog of the acid rocks

Only a very brief summary can be given here of the major communities in the predominant blanket-bog of the acid rocks.

(1) Eriophorum angustifolium : Calluna vulgaris : Empetrum hermaphroditum; with Trichophorum caespitosum, Rhacomitrium lanuginosum etc. The number of species per 1 sq.ft. (species density) is lowest here. The community occurs on deep undisturbed peat with much cutting back.

(2) Calluna-acid grassland; any or all species of (1) with any from the following community. Its distribution is sometimes ecotonal.

(3) Nardus stricta - Juncus squarrosus (acid grassland). The dominant or subdominant species of (1) drop in quantity; while species density increases. The community occurs widely on naturally or artificially drained ground, redistributed peat etc.

(4) Vaccinium-acid grassland; differs from (2) mainly in the replacement of Calluna by Vaccinium myrtillus or V. uliginosum and an increase in Luzula sylvatica. This is a summit community of small extent, in which Trientalis europeaus occurs.

(5) Bog or mire communities; Sphagnum species, Comarum palustre etc.

C. Analysis of species distribution

Of serpentine-characteristic species most of the exclusives are confined to debris - Arenaria norvegica, Cardamonopsis petraea, Cerastium nigrescens, Cochlearia scotica, Rubus saxatilis and Sagina nodosa - or crevices, like Draba incana and Asplenium viride. There are two other species which I have not seen in Unst but which have their only recorded Shetland localities on this serpentine debris, namely Minuartia rubella in "stony places on serpentine, Wick of Hagdale" (Beeby 1887) and Sagina saginoides, recorded from the Muckle Heog by Druce (fide Lindmann) in 1922; both records are accepted by Clapham, Tutin and Warburg (1952).

Of the other exclusive species, Schoenus nigricans occurs in wet ground, Polygonum viviparum and Lycopodium alpinum on heath and Euphrasia rotundifolia on heath or debris; the rest are found on serpentine, and sea-cliffs or sand-dunes. Thus Anthyllis vulneraria, Armeria maritima, Silene maritima and Silene acaulis grow on serpentine debris, or sea-cliff of any rock type: Silene acaulis on serpentine heath also. Botrychium lunaria and Coeloglossum viride appear on serpentine debris which has passed the primary stage of colonisation (see p. 54) and in serpentine sedge-grass sociation (p. 100) or sand-dunes.

The relatively high values for soil-pH on debris suggests the flora should have a number of basicolous species. Using the more precise terms of Small (1946); of the group of highest soil-pH tolerance (alkaliphils: pH more than 7.0, to 8.4) two known members are present - Botrychium lunaria and Anthyllis vulneraria. Of the many debris species I have found a record of the soil-pH range of only one - Rubus saxatilis: this is an alkatolerant (pH4.8-7.7). In view however of the high soil-pH of the debris in this and their other stations it is probable that species like Arenaria norvegica or Silene maritima (see Part III, p. 167) will be either alkaliphils or alkatolerants.

The other serpentine-characteristic species are all widespread on serpentine; *Carex flacca*, *Thymus drucei*, *Plantago maritima*, *Linum catharticum* and *Thalictrum alpinum* being typical of the closed vegetation. Their exclusiveness varies from 2 (*Carex flacca*) to more than 50 (*Linum Catharticum*).

There is a large group of serpentine-indifferent species; nor is the list exhaustive. Most of them have low but others have high frequencies on both acid and ultrabasic rocks; some indeed like *Festuca* species or *Calluna vulgaris* dominating characteristic communities.

In the serpentine-casual group *Erica cinerea* and *Rhacomitrium lanuginosum* have their highest frequency on greenstone. Rarely present on serpentine are one or two dominants on acid rocks in Unst like *Vaccinium myrtillus* or *Trichophorum caespitosum*; and several others such as *Carex pilulifera* and *Deschampsia flexuosa* which are important in communities on these latter rocks. Quite absent from serpentine are *Empetrum hermaphroditum*, *Eripohorum vaginatum*, *Drosera rotundifulia* and *Rumex acetosella*. This again may reflect the relatively high soil-pH (5.12) recorded even on serpentine heath; for apart from *Deschampsia flexuosa* (soil-pH range 3.5 to 5.4, in Scurfield 1954), *Rhacomitrium lanuginosum* and *Erica cinerea*, all these species are known acidiphils, of soil-pH range of from less than 4.8 to 5.2 (*Vaccinium myrtillus*, *Trichophorum*:*fide* Bayard Hora 1947; the remainder, Small 1946). There are other species absent from serpentine which are widespread in raw humus habitats - *Eriophorum angustifolium*, *Luzula sylvatica* and *Juncus squarrosus*, or bog species like *Comarum palustre* and *Hydrocotyle vulgaris*. Put in another way, the rarities on or absentees from serpentine are dominant or abundant on blanket-bog or other raw humus, acid, habitats.

It is noted here for later reference (p.56) that 22 out of 104, or 21% of the species of Unst hill-land listed in Table I p.5a are arctic-alpine, arctic-subarctic, northern montane or oceanic northern species (Matthews 1937, 1955) or low arctic-oceanic (Böcher 1954). Eleven, or 50% of these plants are confined, away from sea-cliffs, to serpentine debris or rock crevices.

The ultrabasic series has either a mineral soil or one bearing thin mor. Hydromorphic peat is absent. Greenstone has some mineral soil but is covered mainly in thin mor or thin hydromorphic peat. Only the gneisses and mica-schists are practically devoid of mineral soil and mor, the latter existing on a few steep slopes; otherwise the whole exposure is covered in blanket-bog. The distribution and depth of the different types of humus indicates that the series ultrabasic, basic and acid rocks in Unst form a series showing increasingly poor drainage.

It is clear that the similarities in habitat provided by the presence of raw humus of various types accounts for the similarities in the species-lists on the three rock types. Differences in the lists can be attributed primarily to variations in depth and type of humus on the three rocks, allowing more, or less, contact with the mineral substrate. The chemical nature of the mineral substrate can substantially affect only the serpentine flora. The flora of Unst thus follows an edaphic trend from the basic mineral debris with its exclusive species, via the thin mor on serpentine, which lacks acidiphils and many species typical of raw humus; to the generally deep peat over the acid rocks with its exclusive species.

PART II

THE VEGETATION IN RELATION TO THE SERPENTINE DEBRIS HABITAT IN UNST

I. INTRODUCTION

Most of the serpentine outcrop in Unst is covered in closed vegetation. But amongst it lie areas of debris with sparse plant cover. The present part of the thesis is mainly concerned with the study of the interaction of vegetation and the serpentine debris habitat in Unst. The emphasis is on the dynamic successional aspects, the phytosociological approach comprising most of Part III.

An attempt is made to discover why, in the absence of (say) mobile talus slopes, closed vegetation has not covered the whole debris surface. Why in fact has colonisation been retarded? For all the debris, however originated, must consist of areas open because of more or less permanently retarded colonisation.

Serpentine has long been known for its peculiar effect on vegetation. The "serpentine effect" results above all in extensive waste or barren areas; relatively few species; presence of species with discontinuous distributions and (not readily determined) serpentine races, some of which are morphologically distinguished (viz. Rune 1953, p.123). In this way the sparsely covered debris is the result of the serpentine effect. Study of what retards colonisation is study of the cause of the serpentine effect.

To this end, the prisere which starts on serpentine debris is first described, together with appropriate data concerning particularly the distribution of plants typical of the pioneer stage. This failure of closed vegetation to develop over the debris must be due to serpentine features like toxicity and/or physical factors. So the physiognomy of the debris vegetation and the distribution of the debris itself is compared with earlier climatic evidence and with the probable effects of different chemicals in serpentine soil. This leads to assessment both of the factors retarding colonisation, and of the serpentine effect, in Unst itself. It also leads to consideration of cyclical succession and the origin and affinities of the debris habitat.

II. The prisere on serpentine

A. The four cover-phases

Derivation of figures. Percentage cover in 59 quadrats was recorded. Percentage cover per species was noted separately but kept in groups of thirteen (total samples per 1 ft. x 1 ft. quadrat : see p. 38). This last value - cover per quadrat - is used here for both total and specific cover. C, total cover, lies between 0 and 1300; and initial study is of trends in vegetation with increasing cover. So quadrats are grouped in ascending classes where C = 0, C = 1 - 20, 21 - 40 etc. The mean cover in each class is expressed as a percentage - the average % total cover per class; this is referred to hereafter as 'total cover'. Cover values for each species are treated similarly - the average % specific cover per class; hereafter referred to as 'cover' of that species. This information is given in Table VI (p. 57a).

In considering this prisere, I wish to compare a species' performance on debris having sparse plant cover with its performance on closed, climax, vegetation. No cover analysis however is available for the latter. The frequency figures set down for this purpose in Table VI col. A come from the debris analysis (frequency being recorded simultaneously with cover): those in column B from samples got in Analysis A (p. 36) on closed vegetation over free-draining, not mire, soils; on what may be loosely termed heath. (This analysis antedated the phytosociological analysis of the pioneer and various types of closed vegetation described in Part III).

Demarcation of phases. While it is at once clear that some species are confined to this debris, it is not possible to say by inspection at what degree of total cover they disappear. This is primarily because areas of debris and heath vegetation lack a pattern discernible to the eye. Even the extremes, "open" and "closed" patches, do not necessarily bear either a spatial or temporal relationship to one another as do such phases of a sand-dune. A random method of sampling was accordingly used (p. 38).

Reconstruction of phases is based on the assumption that total cover normally increases with time. Division of phases might seem arbitrary, but inspection of the table shows there are noticeable changes in the quality of the total cover, corresponding to changes in the contribution of the dominant species or the number of species present.

The plants fall into three groups with increase in total cover and in average number of species per quadrat. These groups fit into a four-phase prisere:

(1) Pioneer phase, characterised by species exclusive on serpentine, sea-cliffs apart, to debris (serpentine exclusives, p. 42).

The next two phases are typified by species common to debris and heath:

(2) Grass phase: dominated by Agrostis stolonifera and Festuca rubra or F. vivipara

(3) Carex flacca phase and

(4) Calluna phase or heath (to ± 100 % cover: the climax vegetation) which also has some plants exclusive to heath. These phases are now examined.

(1) Pioneer phase (early open : to 5%). This phase is typified by species which, though of low cover, are exclusive on serpentine to debris or debris and sea-cliffs. Comprising more than two-thirds of the total cover even where this is at its lowest, the largest number of these species occurs where it is 5.3% and none is found where it exceeds 19.4%. This group I call the pioneers.

The other species in this phase are common to debris and heath. With low cover here as in all the other phases, and opportunists by nature, the annuals *Euphrasia rotundifolia*, *E. foulaensis*, *E. scotica*, *Linum catharticum* and *Rhinanthus spadiceus* have little significance. Low % cover also applies to *Scilla verna* and *Rumex acetosa*, while only that species and *Anthyllis vulneraria* may be said to belong rather to the lower phases of cover than to heath. The presence of one plant of *Carex flacca* at a total cover of 0.8% is probably related to secondary succession (see p. 82). While *Plantago maritima* shows no apparent relationship to total or specific cover, *Thymus drucei* does. At total cover of 8.7%, cover of *Thymus* rises but cover of pioneers and grasses drops. The cover relationship of these groups is examined in relation to secondary succession (p. 83) and competition (part IV).

Agrostis stolonifera, *Festuca rubra* and *F. vivipara* might justifiably be regarded as pioneers, but the term 'exclusive to debris' eliminates them; even at total cover of 0.8% these grasses constitute the greatest single cover value and, to their maximum at a total cover of 19.4%, they never form less than 50% of that figure where, incidentally a pioneer - *Cerastium nigrescens* - is still present. It is just the presence and increase of the grasses throughout the range of the pioneers that makes it difficult to set an upper limit, in terms of cover alone, to the pioneer phase. The pioneers do however drop in number and cover value from a peak at a total cover of 5.3% as does the average number of species per quadrat. For the present therefore I consider total cover of 5.3% as the upper limit of the pioneer phase.

The pioneers are the most important single group of species in this study and there are several features to be considered in connection with them. One question is prompted by the fact that Hamar contains the largest number of these species in Unst. What of the other Unst serpentine localities? After Hamar, Clibberswick has the greatest number, then Sobul-Watlee, while the Heogs have least. This is to some extent due to each of these localities having progressively less debris, associated or otherwise. Arenaria norvegica and three other species are found in all four places, Rubus saxatilis is confined (in Unst) to Hamar (one record each exists for Minuartia rubella and Sagina saginoides : see p. 43).

Another distribution feature is the complete absence of the pioneers from unassociated debris, on either the ochreous or grey parts of such patches. The reasonsfor this preference are examined causally in relation to the chemical nature of the soil and the pioneers' means of dispersal on pp. 69-70 .

Table VII

Distribution of the pioneers on the four main serpentine debris localities (see map, fig. 4 p. 21a).

x, observed personally; ⋇, recorded by other authors.

	Hamar	Clibbers-wick	Sobul-Watlee	Heogs
Arenaria norvegica	x	x	x	x
Cochlearia scotica	x	x	x	x
Silene maritima	x	x	x	x
Armeria maritima	x	x	x	x
Sagina nodosa	x	x	x	-
Cardaminopsis petraea	x	x	-	-
Cerastium nigrescens	x	-	⋇ (F.J.Hanbury 1894, in Druce 1922, p. 476)	-
Rubus saxatilis	x	-	-	-
Minuartia rubella	⋇ (p.43)	-	-	-
Sagina saginoides	-	-	-	⋇ (p.43)

The geographical distribution groups (arctic-alpine etc.) to which many of the pioneers belong are dealt with after the prisere has been described (p. 56); so are such biological features of the pioneers as their life-forms. The question of their means of dispersal I have just mentioned; and a remaining point, that of their adaptations to the physical features of the debris habitat in Unst, is examined on pp. 65-66 .

<u>(2) Grass phase (late open: to 19% cover).</u> This phase extends from total cover of 6.8% to 19.4% where the grasses, never contributing less than 50% of that total cover, reach

their maximum. The mean number of species per quadrat again increases with increase in total cover but is initially lower than the figure at the close of the pioneer phase; this is explained in terms of cyclical succession (p. 83).

After the grasses, *Plantago* and *Thymus* contribute most cover. Six species are first seen on the debris in this phase. They persist into heath where all but one have higher frequencies : *Antennaria dioica*, *Viola riviniana*, *Polygala vulgaris*, *Carex flacca*, *C. demissa* and *Rhacomitrium lanuginosum* - ~~the only moss on the debris~~.

Carex panicea also occurs in this and succeeding phases, growing with *Carex flacca*. There was however some difficulty in the field in distinguishing the two species. Most of the plants were heavily grazed, and material of the two species in the vegetative state alone could not with certainty be differentiated by the ligule character given in, for example, Clapham, Tutin & Warburg (1952). But by far the greater quantity of flowering material was *Carex flacca*. So, although it is impossible to give precise proportions, it is safe to say that only a small amount of the cover attributed to *Carex flacca* in, for instance, Table VI (p.57a) is in fact due to *Carex panicea*.

(3) *Carex flacca* phase (early closed : to 33.7%).

This phase occurs from beyond total cover of 19.4 to 33.7%. The drop in the cover of the grasses between total cover of 19.4 and 23.9% is countered by a sharp rise in cover of *Carex flacca*. This reversal in cover of the principal species is accompanied by other important changes in the flora. The pioneers persisted through the grass-phase; at total cover of 23.9% they are absent and *Calluna* appears. But at this stage the plants are small, prostrate and an orange-red colour, indicating the abnormal behaviour reported by Rayner (1913, 1921) in Calluna on calcareous soils where the inimical factor is chemical but of unknown nature. Calluna appears with other species (Table VI) which, like several seen for the first time in the previous phase, are typical of serpentine heath. Coeloglossum viride and Botrychium lunaria were first noted in this phase, though they did not occur in any samples.

(4) Calluna vulgaris phase - serpentine heath (late closed : to 100%). Once total cover exceeds 33.7%, cover of Carex flacca drops from its peak while that of Calluna rises. There is a gap in the readings between total cover of 33.7 and 100%. Can the final phase be said to begin once total cover exceeds 34%?

Schoenus nigricans and Carex flacca become dominants in serpentine communities where total cover exceeds 33% but which, lacking Calluna, cannot develop from this stage of the prisere. This leaves the Calluna or Erica cinerea sociations, the least affected biotically of those of the sedge-grass-heath in Unst (see Part III p.105).

With the exception of some annuals, several characteristic but subordinate heath species first appear in the grass-phase. They are augmented at the start of the sedge phase by Calluna and others. Before the arrival of Calluna the pioneers go. This suggests some habitat change in one direction, connected with the gradual accumulation of humus in the mineral debris (Table VIII) and other associated results of reaction (Clements 1916 p. 102). On increase in total cover no further species drop out; with any others that appear they persist into serpentine heath at a total cover of 100%. So the soil development must be maintained normally in one direction, as the soil-pH figures, like the % humus content, indicate (Table VIII).

Table VIII

Plant cover (max.)	to 6%	to 19%	to 33%	to 100%
Phase	pioneer	grass	sedge	heath
Soil pH range	672-612	620-577	590-530	550-512
% humus content of oven dried soil	0·42	1·27	4·82	21·54

As Calluna is established by a total cover of 33%, the final phase starts once cover of Carex flacca declines, and develops to the climax vegetation with 100% plant cover.

The pioneers are restricted to the most open phases in the plant succession; or most mineral phases in the soil succession; and they are eliminated with increase in total plant cover (and/or humus content) and the appearance of known calcifuge species such as Calluna vulgaris. This is very like the sequence described by Balme (1953) of plant and soil succession from open unstable limestone scree in the Derbyshire fells. Calcicoles occur only under the conditions of zones I and II (open and closed Festucetum), some like Anthyllis vulneraria and Helianthus chamaecistus being confined to the most open conditions of zone I on, that is, the unstable rendzinas (Balme l.c. p.341). Similarly, calcifuges (there defined as absent from the highly calcareous zone I) like Deschampsia flexousa, Nardus stricta and Vaccinium myrtillus normally invade at a later stage in the succession. It is of interest that on the serpentine of Unst (and other Scottish serpentine localities examined : Part III, Table XI p.97) these species are absent from or rare in even the closed heath. This applies also to several other species, many of them acidiphils (see p.44). (I merely wish to point out here a parallel that exists to the situation on the serpentine debris in Unst. Discussion of Balme's conclusions is held over to Part IV which I devote to a field inquiry into the general problem of the restriction of rare species to open habitats.)

Now that the succession from pioneer phase to heath has been described, two further features are noted. It was said (on p.45) that 21% of the species listed from Unst hill-land are in Matthew's (1937, 1955) arctic-alpine, arctic-subarctic, northern montane and oceanic northern elements or are low arctic-oceanic (Böcher 1954). Apart from the presence of some of them on sea-cliffs of any rock type in Unst, 50% of the species in these categories are confined there to serpentine debris or rock-crevices. The significance of this high percentage can now be examined further.

Of the 20 species listed for the pioneer phase on debris (Table VI p.57a) 9, or 45%, are in the above elements (see Table I p.5a). This compares with 5 out of 34 species or 14% in the heath (Table X p.91), the climax vegetation to which the pioneer phase is serally related. The pioneer vegetation has a far higher proportion of boreal species than the closed heath which succeeds it. This indicates that many of the pioneers are relics ("survivors of a lost flora" Ridley 1930), that the community itself has relict status. Life-forms confirm this.

The chamaephyte is the arctic life-form; the 20% Biochore (the line at and beyond which chamaephytes form at least 20% of the <u>total</u> flora of a region) corresponds to the June isotherm of 40 deg. F. (Raunkaier 1934 p. 132 <u>et seq</u>.). Shetland as a whole lies according to Raunkaier south of the 10% Biochore in the cold temperate zone. The Ch. percentage in the sedge-grass sociations in Unst (Table XI p. 97) is 20, in the heath sociations 23 (Table X p. 91), figures well above the Shetland average. But what matters here is their proportion to the figure for debris: and the Ch. percentage in the pioneer phase (Table VI p. 57a) is 45, which is twice the percentage of the communities forming the climax vegetation. ~~The presence is thus demonstrated of species with discontinuous distributions.~~ The relict status of this community is discussed in relation to climate and climax vegetation in Part III p. 150-1).

Table VI

Total cover in ascending classes		1-20	21-40	41-60	61-80	81-100	101-120	121-140	141-160	161-220	221-280	281-420	421-440	A	B
Average % total cover per class		0.83	2.56	3.34	5.34	6.79	8.74	10.24	11.34	14.71	19.37	23.94	33.69		
Number of samples per class*		5	8	7	12	3	3	3	3	3	4	3	1		
Mean number of species per sample		3	4.75	3.43	5.27	2.33	5.66	6	7	7	8	11.6	14		
Vegetation phase		PIONEER				GRASS						SEDGE		%F.	%F.
Cochlearia scotica	Ch	-	0.03	-	-	-	-	-	-	-	-	-	-	x	-
Cardaminopsis petraea	Ch	-	0.03	0.01	-	-	-	-	-	-	-	-	-	x	-
Silene maritima		0.14	-	-	0.10	-	-	-	-	-	-	-	-	1	-
Arenaria norvegica	Ch	0.12	0.06	0.04	0.11	-	-	-	0.10	-	-	-	-	2	-
Sagina nodosa	Ch	0.03	0.03	0.01	0.05	-	-	-	0.03	0.03	-	-	-	2	-
Armeria maritima	Ch	0.12	0.07	-	0.18	-	-	-	-	0.44	-	-	-	2	-
Cerastium nigrescens	Ch	0.08	0.11	0.01	0.07	0.02	-	-	0.08	-	0.09	-	-	2	-
Rubus saxatilis		-	-	-	0.02	-	-	0.54	0.85	-	-	-	-	5	-
Festuca rubra, F.vivipara: Agrostis stolonifera		0.31	2.07	2.07	3.78	5.91	4.90	4.97	7.61	8.76	11.38	8.81	9.15	F:75 A:86	65 75
Plantago maritima	Ch	-	0.09	0.94	0.65	0.77	2.31	0.80	0.41	2.48	0.69	2.25	1.72	53	75
Thymus drucei	Ch	0.01	0.02	0.21	0.33	-	1.31	1.32	0.87	0.92	2.40	2.76	1.31	46	70
Silene acaulis	Ch	-	-	-	0.01	-	0.03	2.17	-	-	-	-	-	5	2
Scilla verna		-	0.01	-	-	-	-	0.08	0.03	-	-	0.05	-	3	10
Anthyllis vulneraria		-	-	0.05	-	-	0.05	-	-	-	0.75	0.15	-	8	2
Euphrasia rotundifolia: E.scotica E. foulaensis		-	0.02	-	-	0.10	0.10	0.13	0.05	0.10	-	0.05	-	21	10
Linum catharticum		-	-	-	0.04	-	-	0.08	0.03	0.13	0.13	0.02	0.15	13	70
Rhinanthus spadiceus		0.01	-	-	-	-	-	-	-	-	0.13	0.05	-	6	-
Carex flacca (C. panicea)		0.01	-	-	-	-	-	-	0.15	0.31	2.13	8.31	17.03	18	86
Viola riviniana		-	-	-	-	-	0.05	-	-	-	0.02	0.18	0.61	8	50
Antennaria dioica		-	-	-	-	-	-	0.13	0.59	-	0.89	0.59	-	11	50
Rhacomitrium lanuginosum		-	-	-	-	-	-	-	0.10	-	0.71	0.12	-	8	30
Carex demissa		-	-	-	-	-	-	-	0.41	0.54	-	-	1.38	3	2
Polygala vulgaris		-	-	-	-	-	-	-	0.03	-	0.02	-	0.23	6	30
Calluna vulgaris		-	-	-	-	-	-	-	-	-	-	0.46	0.64	5	100
Leontodon autumnale		-	-	-	-	-	-	-	-	-	-	0.02	0.23	3	3
Selaginella selaginoides		-	-	-	-	-	-	-	-	-	-	0.08	0.23	1	40
Succisa pratensis		-	-	-	-	-	-	-	-	-	-	-	0.54	1	54
Hypericum pulchrum var. prostratum		-	-	-	-	-	-	-	-	-	-	0.05	0.15	1	14
Prunella vulgaris		-	-	-	-	-	-	-	-	-	-	-	0.31	1	25

* 4 at 0%.

B. Root-competition and the cover-phases

As soon as one plant goes short of an essential requirement due to the activities of another plant, then competition exists. Fig. 6 (p.58a) is a root-diagram of one square foot of debris. It shows a more extreme situation than that reported by Jenny-Lips (1930 : in Braun-Blanquet 1932 p.10) in a gravel-slide association, where roots intermingled when surface-cover was 5 - 15%. Here, total cover is only about 1.5%, but the roots of one plant occupy the same ground (0.7 cm. - 1.3 cm. below the surface) in the vertical and horizontal planes as those of another, well-separated on the debris surface. Thus Cardaminopsis petraea in B4 lies more than 30 cm. from Cerastium nigrescens, 20 cm. outside A4. So competition can exist even at almost the lowest cover-phases of the prisere.

Until total cover of 33% there is a broad increase in both total cover and in the mean number of species per quadrat (N). This cover increases from 33%, to 100% in grass-heath, with an increase in the total number of species in the community (22, to 36 in Calluna-sociation, p. 91). But there is no rise in the number of species per quadrat. This remains at about 12 (sedge phase, p. 53). The prisere undergoes a qualitative change between total cover of 19% and 33%. Though the plant cover has only reached 33% of the total surface yet the community has in some sense become closed and root competition, possible at the lowest total cover, is the probable explanation. Such a habitat with 2/3 of its area uncolonised would normally be regarded as open. But in view of the qualitative changes just observed

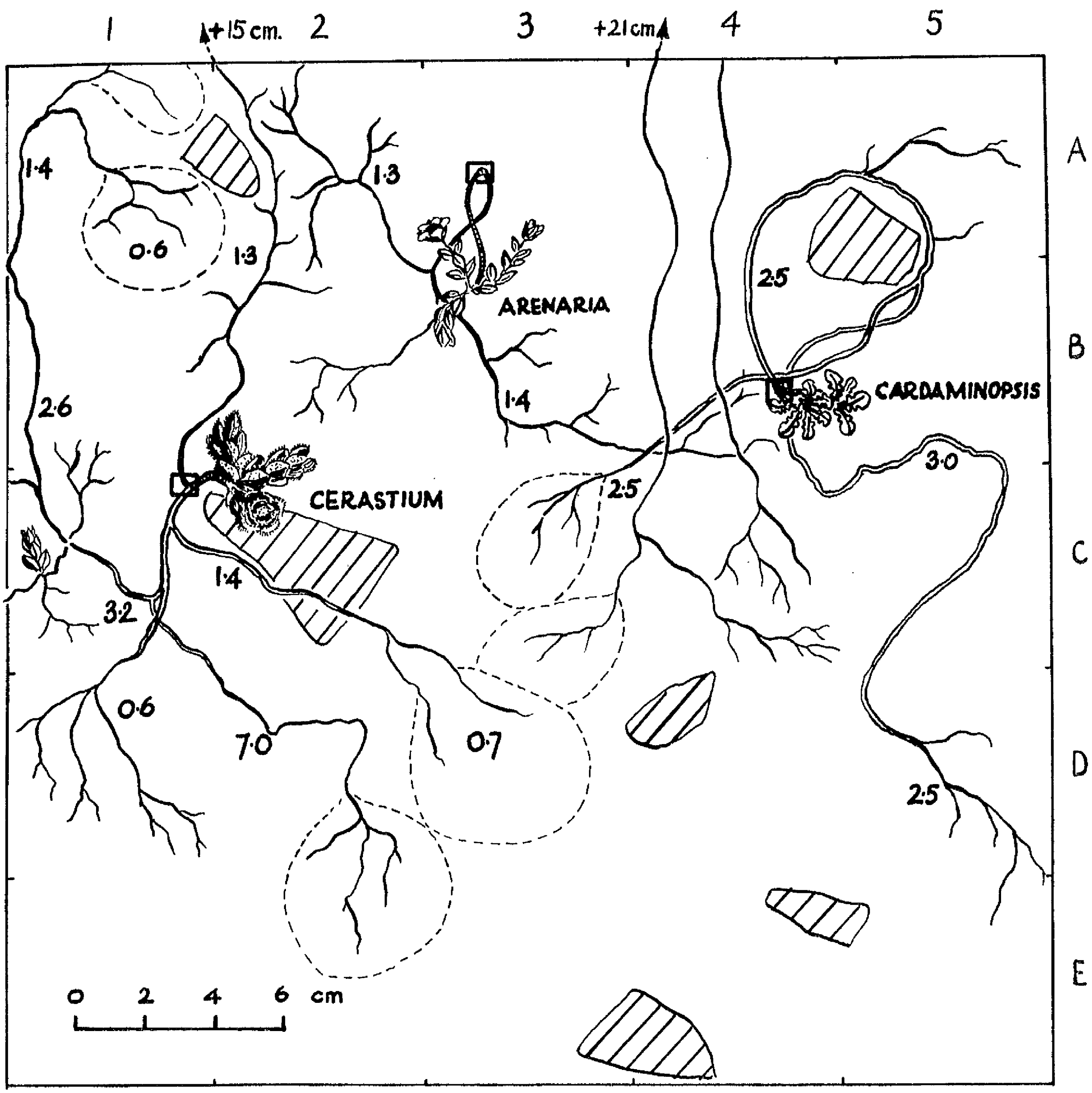

Fig. 6. Scale drawing, x ½, of roots of plants in 1 sq. ft. (15.2 x 15.2 cm.) of debris; plant cover 1.5%. ▨ = stones; □ = point of emergence of shoot from soil. A figure beside a root indicates (in cms.) the depth in the soil at which the root was found. The soil is surfaced by gravel, between 0.5 and 1.0 cms. in diameter, which forms a thin layer over about 12cms of fine earth mixed with some gravel. Beneath is bedrock.

it seems correct to refer to it rather as "early closed" phase, reserving "open" for the two earlier phases where the mean number of species per quadrat is still increasing.

The nomenclature adopted for the phases of the prisere can now be seen to be based on % cover and the probable effect of competition.

III. Interaction of habitat and vegetation

A. Plant physiognomy, wind and retarded colonisation

(1) Soil-erosion and soil-instability. Whether or not there is exposed bedrock in the centre of a patch of debris, the margins of these patches at once suggest erosion. Areas of heath alternate with the debris or bound its edges and the surface of this heath lies perhaps 15 cm. or more above it (Plate II phot. 3). The join is made by scarps of earth at the top of which the vegetation is undercut. Scarps usually lie across the slopes facing west to southwest (Plate II phot. 2). But debris patches can be seen developing in the closed mat almost anywhere on the serpentine outcrop. They often lie in slight depressions.

Let the earth-bared scarp represent a first stage in soil-erosion; then progressive removal of the earth will eventually bare the underlying layer of small stones that forms the typical debris surface. So patches of earth with sparse or no plant cover may be taken as recently eroded in comparison with areas where stones extrude. Such open patches of earth are becoming in effect areas of re-exposed debris (see p. 81). The evidence on the causes of this re-exposed debris has still to be given (p. 66), but where these patches lie in slight depressions on the hill-sides then rain-wash is clearly important.

Soil-erosion on the debris results first of all in root-baring of the scattered individual plants. Frost may assist; the soil in the early cover phases is soft to the tread, easily compressed. This may be inimical to ecesis; while I have no available figures for survival rates, I noticed that a large number of seedlings or first year plants were 'sprung' in March 1952. Exposed tap roots and laterals are usually seen in spot-bound species with lax branching systems, like Cerastium nigrescens, Arenaria, Cardaminopsis and Silene maritima (Fig. 6, p. 58a); and in Silene acaulis, Armeria maritima and Plantago maritima.

Initially low-growing as shown for the last two species by Plate III phot. 1, 2, they tend with time to develop conical tufts 5 to 8 cm. high (Plate III, phot. 3,4). These tufts may be eroded from the base (Plate IV phot. 1) like the edge of the heath patches, or die from the top; to leave in time only the bottom fringe of the tussock (Plate IV phot. 2). In this last case a semicircle of bare earth marks the missing part of the plant and must indicate recent erosion. Festuca rubra forms 7.5 to 10 cm. high tussocks which may be similarly eroded (Plate IV phot. 3) leaving young growth only at its lower edge. This would eventually produce the fringe of Fig. 7 (p. 61a), each piece of Festuca being a short length of stolon. Surrounded by a ring of nearly-dead Festuca, the circle of earth in Plate IV phot. 4 must represent the base of a tussock which has been almost completely eroded; and again more recently than the surrounding debris.

Carex flacca, and C. panicea (Fig. 8 p. 61b), shows another aspect of soil-erosion. The base of the oldest of the three rosettes must stand about 1.5 cm. above the present surface of the debris; normally (in, say, wet-flush turf) the base of the rosette of three leaves is almost level with the ground - as at the extreme left. The younger rosette is moreover about 1.5 cm. below the soil surface. This shows how rhizomatous species can resist erosion by colonising new ground vegetatively. By contrast, individuals of spot-bound species such as Arenaria

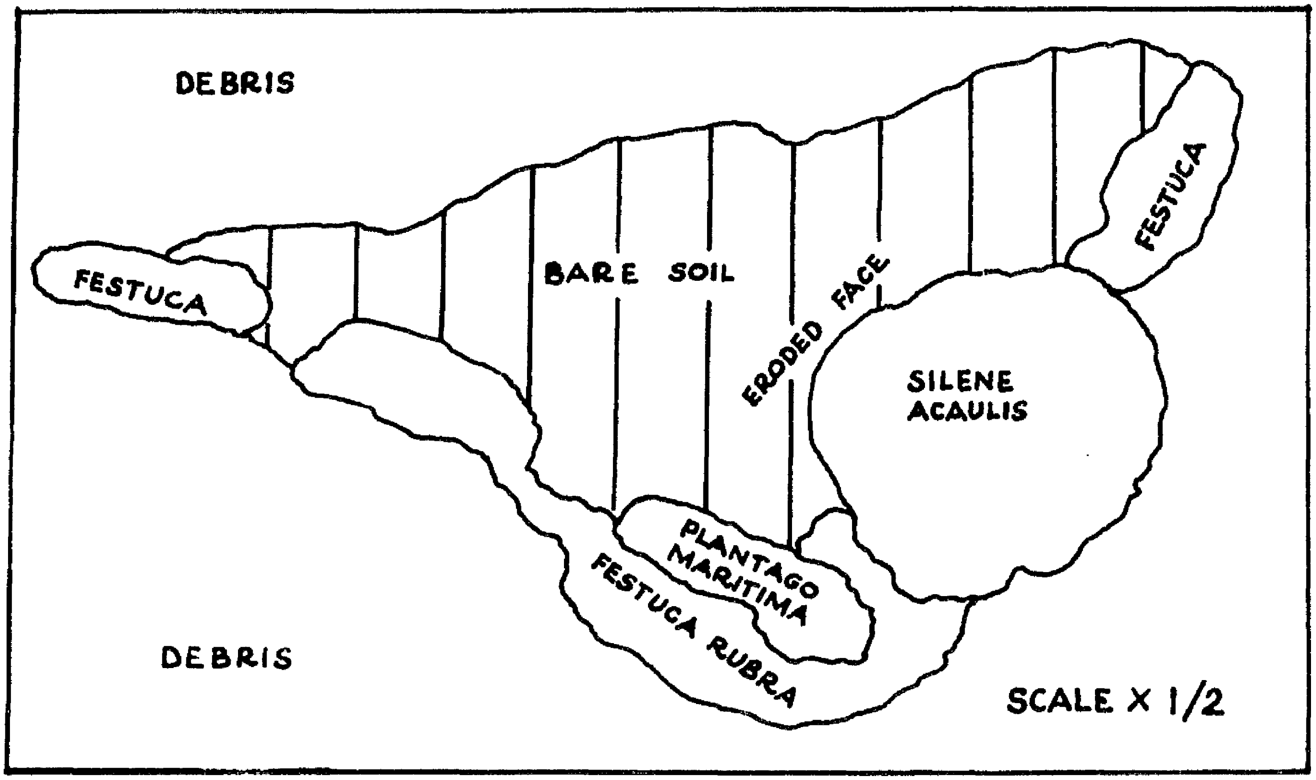

Fig.7 Diagram, x ½, showing the fringe of an eroded tussock of Festuca rubra, the bare soil indicating its probable former extent: cf. Plate IV, phot.4.

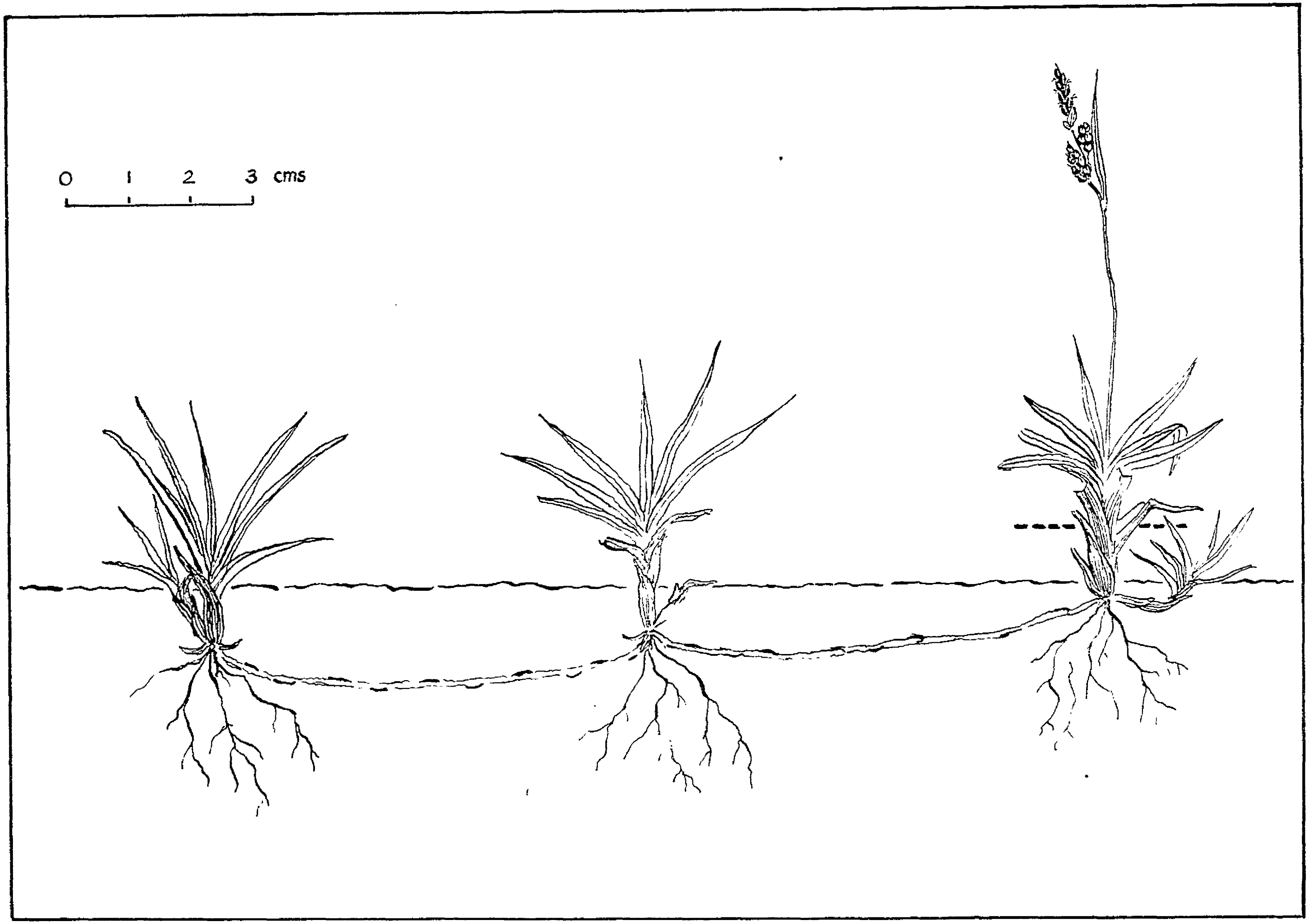

Fig.8 Elaborated field sketch, x 1, of rhizome depth in relation to soil surface, in *Carex panicea*; showing how the plant apparently resists erosion by adjusting itself to the new level of the soil. The shaded parts are dead leaves or scale leaves. The dotted line indicates probable former soil level.

or Cerastium seem to survive passively. (These different reactions are discussed on p. 65).

The evidence shows that the soil is unstable and that erosion, which in hollows is caused by drainage water, is occurring. By destroying the vegetation-mat, erosion re-exposes debris; a patch of this type is what I have called (p. 26) unassociated debris. Evidence of severe erosion among individual debris plants is also given; some species can survive by vegetative spread.

(2) Stature and community limitation. Shoots of debris specimens of Silene maritima (Pl. V phot. 1) and the peduncles of Cardaminopsis petraea (Pl. V phot. 2) are prostrate; so is the normally vertical peduncle of Rumex acetosa. A specimen of Rubus saxatilis from the open debris (Pl. V phot. 3) shows considerable dwarfing compared with one from the edge of a boulder (Pl. V phot. 4). In July 1952, two stones were set beside several specimens of Cerastium nigrescens of the usual prostrate type (Pl. VI phot. 1); by August 1953 they were all more or less erect (Pl. VI phot. 2). These examples all suggest that the typical debris plant is subject to size limitation.

Among plants found on debris and heath, debris specimens of Carex demissa average 4.5 cm. in height compared with 7.7 cm. for heath specimens (each av. 10 plants). Stature here might be attributed to edaphic differences. So measurements were made of the length and, if it differed, of the vertical height of the flower stalks - plus - inflorescences of some species common to both habitats. Readings for Agrostis stolonifera are given in Table IX. On debris the plants have a shorter flower stalk - with - inflorescence. This is also more prostrate than on heath, even more than on heath by the wall (see below) where the greatest height is achieved.

Table IX.

Length and vertical height, in inches, of flower stalk and inflorescence of Agrostis stolonifera in three stations.

station	measure	mean	range	ratio of length/ vert.ht.
heath by wall (1)	length	7.3	6 - 9	1.2
	vert.ht.	6.1	4 - 8.5	
heath (2)	length	5.0	4.5 - 6	1.6
	vert.ht.	3.2	2 - 4.5	
debris	length	3.4	2.6 - 5	2.4
	vert.ht.	1.4	0.5 - 2.6	

Stature limitation can be assumed therefore to exist over most of this serpentine area (Hamar) with a maximum on debris and a minimum or nil on the heath by the wall. The figures for Agrostis stolonifera indicate that the difference is not primarily edaphic; this is also indicated by the restriction in spread of a community with 100% cover to one metre from either side of a dry-stone wall that crosses the Hamar debris at 30 m. (Pl. I phot. 2). From the negligible change in fenced areas of Hamar over the past three years, grazing too may be discounted here (p.34).

It was earlier stated (p. 17) that wind might be important as a limiting factor; there also seemed to be broad correlation of major debris areas and west and south-west winds. With consideration of roughness height Z_0 (Hellman 1915), greater windspeed may be anticipated near the ground on the larger areas of debris than on adjoining areas of heath (Geiger 1950 p.307). The debris is smooth as if steam-rollered (cf. p.26); the heath is a low plant cover. (Windspeed will be least on heath by the wall where shelter is obvious on any suitable day.)

Microclimate readings confirm this.[*] On 13th September 1952, for example, between 12-20.00 hrs., the air temperature and relative humidity were consistently lower at 15 cm. on debris than at the same level on heath; indeed R.H. on heath at 15 cm. > R.H. on debris at 1 cm.

Stature limitation is least on heath by the wall and greatest on the debris; windspeed near the ground being the converse. So stature seems limited by wind. This relationship was studied by Whitehead (1951) who showed what he called parameter Z_o (Hellman's "roughness height") to be directly related to the height of Leontopodium nivale on Monte Maiella, Italy. Later, with selection of sample areas, he showed (1953) Z_o to be related to plant and inflorescence height of a series of communities variously exposed. ℙ Wind therefore seems to be the master factor in this habitat, dwarfing the plants and limiting their spread, and causing erosion, destruction of the vegetation mat and re-exposure of the debris.

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[*] Microclimate. Air temperature and relative humidity near the ground were measured in contrasting localities over several periods. Two maximum and two minimum thermometers were each placed in special "cocoa-tin" shields. This whitened shield has been found in practice to reduce radiation effects, giving results about 2° F. higher than standard screens (Mr. L. Smith, *in litt.*) R.H. was measured by an Assmann Hygrometer. Measurements were taken on Hamar of air temperature at 15 cm. (grass minimum at 0.5 cm.) and R.H. at several levels near the ground, in heath by wall, heath in open, and debris (Plate VI, 3,4). Vegetation heights at points of measurement were : heath (1) 13 cm., heath (2) 7.5 cm., and debris 0 cm.

(3) Scorching. Stature limitation means that, at least, growth is slowed. The day after a northerly gale in August 1952, the tops of sedge leaves and grasses on debris and heath were scorched; about 2.5 cm. in the case of the sedges. Leaves of Carex demissa had a mean (20) height of 4.5 cm. on debris. They were scorched from 2.5 cm. above the ground. In heath their leaves were nearer 7.5 cm.; these were scorched from 5 cm. above the ground. Wall specimens were unaffected. The smaller specimens of Carex were on the debris; they were scorched proportionally more (3:4) than the taller heath specimens (1:2).

Wind can limit stature directly by scorching; as expected it does this most severely on debris. This shows that colonisation is retarded on the debris and hence the vegetation tends to stay open.

(4) Adaptations exhibited by pioneers and other plants on the debris. In connection with soil-instability, the question arises whether the debris plants have any physical adaptations giving them advantages over species lacking such adaptations.

Since the pioneers, with the exception of Rubus saxatilis and Cardaminopsis petraea, lack means of vegetative spread they might seem to be passive in surviving the effect of soil-erosion, frost-heaving etc. The scale-drawings of Figs. 9 - 11, pp. 66 a,b, show that in fact, and including Cardaminopsis, they have very deep and extensive root-systems, particularly when these are compared with their aerial growth.

Pichi-Sermoli (1948) and Rune (1953 p. 57) note the great development of the root-systems as one of the morphological changes undergone by serpentinophytes. Referring to Fenno-scandia, Rune considers both nanism and greatly-developed root-systems to be "adaptive characters - xeromorphism - typical of plants in dry habitats". But I have shown stature limitation on the Unst serpentine to be largely adaptation to wind-exposure. The extensive root-systems of the pioneers I likewise consider adaptations to soil-instability that would put all but deep-rooted perennials at a disadvantage.

All the species common to Unst serpentine debris and heath vegetation and abundant on debris possess deep roots - Plantago maritima, Agrostis, Festuca, Carex flacca (C. panicea) and Thymus drucei. And all these species, except Plantago, possess means of vegetative spread by which they can evidently revive after erosion (cf. Carex panicea, Fig. 8 p.61b). This ability to resist erosion may also confer an advantage in succession, especially if ecesis is difficult (cf. p.60); certainly the grasses and later Carex flacca are dominant on the debris till cover exceeds 33%; and all persist into heath. This too can be interpreted as a direct adaptation to physical features of the environment - all these species are typical of debris and associated heath of different rock-types in Shetland and beyond (see Part III).

(5) Summary. It seems established beyond doubt that wind is the master factor in this habitat. It may be said to act directly by stature limitation (scorching) and indirectly, with rain and soil instability, by baring roots. Wind must consequently re-expose the surface of the debris; with areas re-exposed by rainwash these constitute uncolonised areas of unassociated debris. Wind must also maintain debris as an open habitat more or less permanently by retarding colonisation. Debris species have been shown to possess adaptations which suit such an interpretation. This of course bears out the supposition made (p.17) when discussing data on the Shetland climate, that wind in view of its magnitude there might well impose limitations on vegetation even at low altitudes.

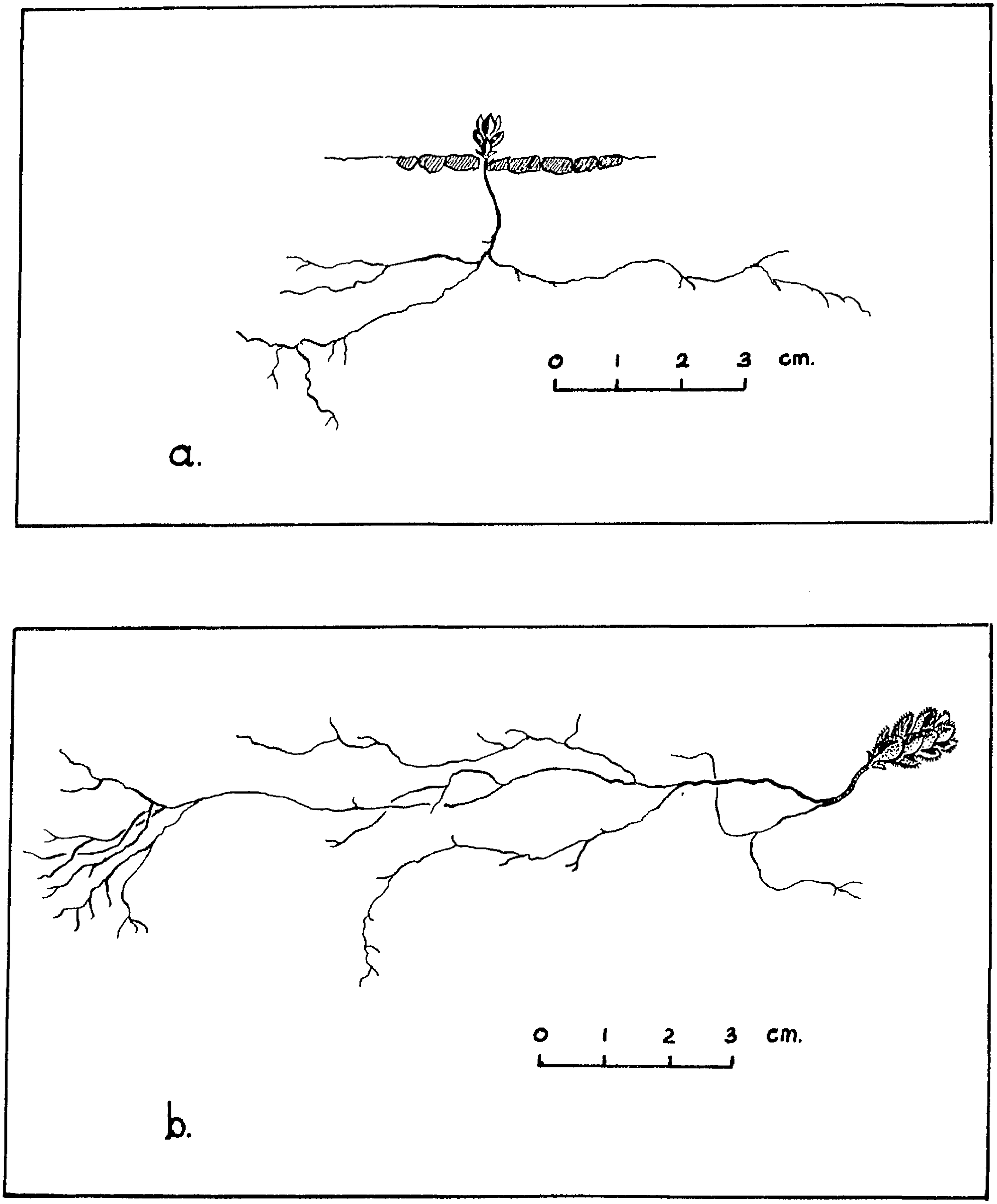

Fig.9. Scale drawing, x 1, of (a) root profile of young plant of *Arenaria norvegica* and (b) root spread of young plant of *Cerastium nigrescens*, the roots of which lie about 2.5 cms below the soil surface.

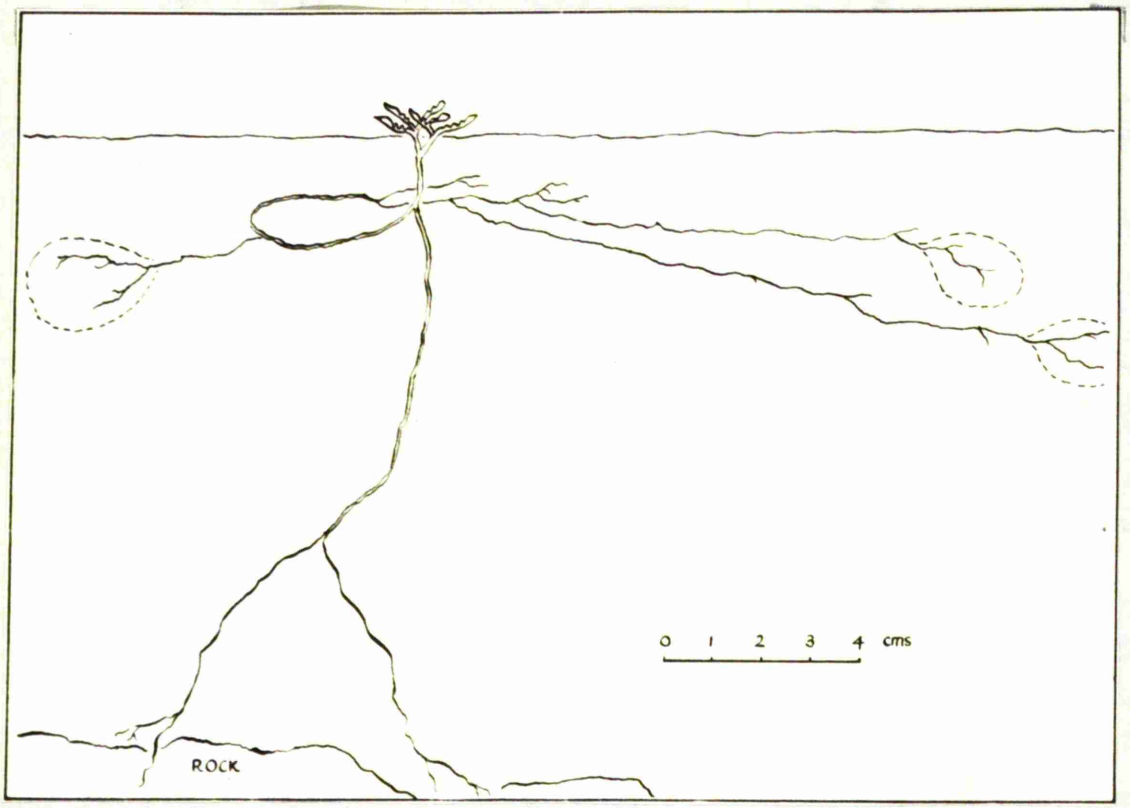

Fig.10. Root-diagram, x ½,of *Cardaminopsis petraea*. Full depth of tap root not known. Dotted line indicates extent of finer roots.

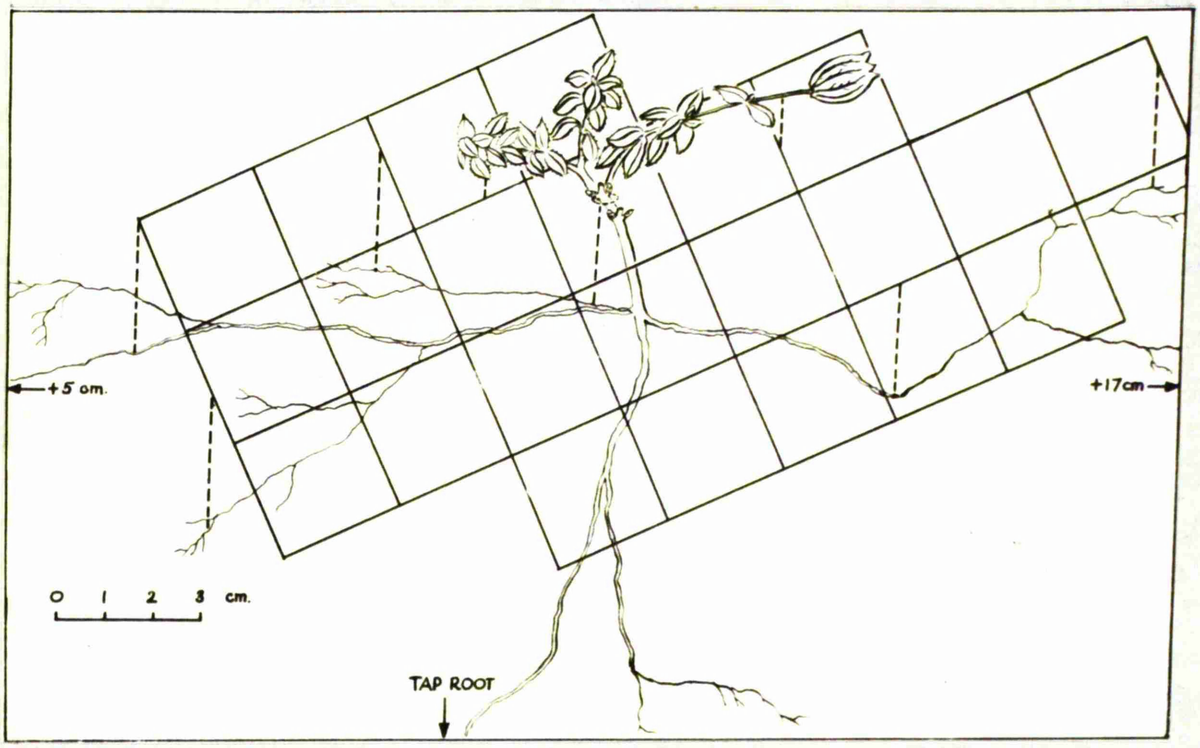

Fig.11. Root-diagram, x ½,of *Silene maritima*;also shows the prostrate stems. Dotted circle indicates point of emergence of shoot from soil.

Serpentine debris with sparse plant cover can be said to exist because the interaction of wind with an inherently unstable habitat retards colonisation. But this ignores questions arising from the chemical composition of the rock, questions which are now examined.

B. Chemical composition of serpentine soil and its effect on vegetation.

(1) Different rates of weathering and the distribution of the pioneers. There is much exposed serpentine bedrock in Unst. Some of this is immediately surrounded by heath even where, as on the Heogs, the slope is craggy. On Hamar the exposed bedrock is surrounded by expanses of associated debris. Two problems arise from the presence of different rates of weathering: the cause of these differences and their consequence for plants.

According to Rune (1953 p.101), unaltered olivine is extremely resistant to weathering and such rock is more or less destitute of soil and vegetation; in fact serpentine rocks in general weather slowly, but weathering seems to increase with increasing serpentinization.

Percentage mineral content has been determined from a large number of serpentine and other ultrabasic localities in Sweden. From these data Rune has correlated extent of weathering with degree of serpentinization. He has shown that on peridotite rock the serpentine character of the vegetation, like barrenness (this paper p. 4) increases with increase in serpentinization. This he considers the result of the consequent increase in weathering and in solubility of nickel and chromium (this paper p. 31).

Serpentinization is general over the ultrabasic rocks of Unst (p. 23) but I cannot assess difference in degree and therefore the precise effect on weathering. Rune's explanation however fits the known facts from Unst; certainly the most weathered areas, those with most extensive debris or barrens, have high Cr and Ni content (p. 31). The significance of this in producing the 'serpentine effect' is discussed on p. 76 .

The effect on colonisation is for the moment more important than the cause. Whether it is due to rate of weathering exceeding rate of colonisation or the presence of excess nickel, or both, extensive debris round bedrock means that colonisation is retarded, an open habitat constantly provided. The debris habitat as a whole illustrates the condition of ecological youth (Griggs 1940) or failure of climax vegetation to establish itself (Pigott and Walters 1954), conditions essential for the survival of relic species like the pioneers (see Part IV).

It is a distribution phenomenon of these pioneers which may be directly attributed to the rate of weathering exceeding the rate of recolonisation. How far any pioneer species is confined to one locality like Hamar, or found on all the hills, has already been noted (p. 52). Although their abundance varies greatly within these localities, the pioneers have one consistent habitat-feature; namely, that they are found only on debris associated with weathering bedrock. This debris may be of the nearby, ochreous, type or more distant, older and more fragmentary grey type (p. 27). However large the patches are, no pioneer has been found in unassociated debris. This lacks bedrock, but is otherwise similar to the grey type of associated debris; whatever else is the cause, the pioneers' consistent absence from unassociated debris cannot be due to unsuitable soil for ecesis.

A feature of some pioneers species is their limited dispersal. Adult plants are often seen surrounded by seedlings or young plants. <u>Cochlearia scotica</u> particularly occurs in clumps in the manner of foreshore plants like <u>Salsola kali</u> or <u>Crambe maritima</u>. Once, on Ruinsival in Rhum, 12 seedlings of <u>Arenaria norvegica</u> were observed growing successfully in the parent's buried capsule. Certainly these two species and Cerastium nigrescens and Cardaminopsis petraea have relatively heavy seeds in comparison with those of Euphrasia rotundifolia or Linum catharticum.

Given the pioneers' limited dispersal and poor powers of colonisation it is possible to account simply for their present distribution on the Unst debris. Patches of unassociated debris, isolated now from bedrock, have been re-exposed by secondary causes like wind or rain-wash (cf. p.66); they present more recently exposed surfaces for ecesis by the pioneers. But the pioneers themselves have limited dispersal. It is for this reason and not because the soil habitat in itself is unsuitable that the patches of debris unassociated with weathering bedrock remain more or less consistently without pioneer species. The present day survival of the pioneers must be due to the provision of permanent debris patches where the rate of weathering exceeds the rate of colonisation.

The properties possessed by the patches of associated debris are this permanent source of freshly weathered material and absence of competition, in a wide and rather loose sense; whichever may matter more to the survival of the pioneers I examine in part IV. Such associated patches can be visualised here as providing a permanent 'nursery bed' from which the pioneers can spread to associated, spatially continuous, grey debris. Now rapidly weathering bedrock is also highly serpentinised, having therefore a high nickel content. So, with time, selection must have favoured those races of pioneers adapted to this unusual factor.

(2) Opinions on the causal connection between chemical elements in serpentine and the serpentine effect.

Interpreted as a serpentine effect, features like the debris with sparse plant cover are generally presumed (vide Rune 1953 p. 115) to be due to the chemical composition of that rock. This causes toxicity, an unfavourable balance between ions or a deficiency of essential elements.

Rune reviews the literature on the effects of the presence and quantities of different elements present in natural serpentine soils. The following is a summary of this review.

Magnesium was often suspected of causing the "serpentine effect" through (1) high Mg. content or (2) Mg/Ca balance. (1) Robinson, Edgington and Byers (1935) point out that serpentine rocks of Cuba weather into a laterite soil from which nearly all Mg is lost by leaching. The vegetation of these soils nevertheless has a marked serpentine character. Again, Lammermayer (1928 in Rune 1953) noted that, in the Austrian Alps, floras of other rocks with high Mg content - magnesite, dolerite - did not show a serpentine character; Rune confirms this view from his Swedish data. (2) As to Mg/Ca ratio; the Austrian magnesite has, incidentally, almost the same Mg/Ca ratio as serpentine. Decrease in serpentine effect with presence of Ca might be considered due to decrease in Mg/Ca ratio. Kruckeberg's (1951) experiments showed that adding calcium countered the serpentine toxicity; which, however, also counters chromium toxicity (Koenig, 1910).

Apart from iron which is mentioned below there are the two minor elements, chromium and nickel, that are found in relatively large quantities in serpentine. Robinson et al cited experiments by Koenig (1910) on chromium toxicity and by Scharrer and Schropp (1933) on nickel toxicity. They assumed that the comparatively high percentages of chromium and nickel were the dominant and general causes of serpentine infertility. Rune states that all Swedish ultrabasic exhibiting the serpentine effect had chromium.

As to nickel: Rune shows that several plants typical of copper soils in Scandinavia are also typical of serpentine (Viscaria alpina is actually a nickel-ore indicator): the same applies broadly to calamine soils. This suggests a link in common effect between serpentine, copper and zinc, soils. Such a connection is provided by Ni, Cu, and Zn, 28, 29 and 30 in the Periodic System, and true minor elements. Rune concludes that his own observations support the assumption of Robinson et al. that the rather high content of chromium and nickel are the general and dominant causes of infertility. Special indications are noted with regard to nickel (Rune 1953, p.130). But Rune emphasises that the effect of these elements on sêrpentine soil depends upon many other properties of the rock like low nutrient content, mechanical composition, absence of Ca, etc.

Reviewed now are some of the findings, on nickel-toxicity, of workers at the Macaulay Institute for Soil Research. (Most of this work has been published since Rune's paper went to press). Vergnano and Hunter (1952) list the many authors besides Scharrer and Schropp, mentioned above, who have demonstrated that nickel is toxic in nutrient solutions, over a varying range, to a large number of crop plants. The same applies to cobalt (also present in serpentine soils). Similar toxic symptoms - white necrotic stripes - are produced by both metals but they are distinct from those produced by chromium (Hunter and Vergnano, 1952). They are accompanied by chlorosis caused by induced iron deficiency (Vergnano and Hunter 1952).

Vergnano and Hunter (l.c.) have shown that the toxic symptoms and anatomical changes produced in oat plants by addition of nickel and cobalt to nutrient solutions, or by iron deficiency, are similar to those occurring in oat plants on serpentine soils in Aberdeenshire (this paper p. 31). Cobalt content of sand culture plants is consistently higher than in those on natural soils; nickel content is comparable.

Nickel-toxicity is clearly demonstrated. Relationship to iron is not so certain. A further series of experiments showed that nickel toxicity symptoms were less severe when the concentrations of iron in nutrient solution was high. There appeared to be good correlation between degree of toxicity symptoms and the Ni/Fe ratio in the plant (Crooke, Hunter and Vergnano 1954) which later results do not however confirm (Crooke and Inkson 1955).

Recently Steele (1955) investigated certain aspects of the calcicole habit. He produces experimental evidence which suggests that the offspring of Arenaria verna var. gerardi from the serpentine of the Lizard, Cornwall, are adapted to high Mg supply, rather than to high Ca supply, in neutral soil. He also shows that certain known calcifuges prefer the least calcareous and most acid experimental soils. Neutrality and high calcium supply is deleterious but not sufficient to prevent growth. Magnesium content seems immaterial within wide limits. Questions of soil-toxicity are not considered by Steele.

(3) Serpentinomorphoses. If the barrens (p. 4) or open areas are assumed to exist because colonisation is more or less permanently retarded by toxicity, then the plants found in this habitat or at least in the pioneer phase, must be adapted to chemical conditions that preclude most species; "the essential factor (in such debris species) is a capacity to withstand the toxic effect of serpentine soil" (Rune 1953 p.80).

A plethora of terms like the one heading this paragraph has grown up round the vegetation of serpentine, particularly in connection with plants and their known or presumed adaptions to the serpentine substrate. Plants with the facility to withstand the presumed toxicity of serpentine soil are known as serpentinomorphoses (Pichi-Sermoli 1948, Rune 1953, Kotilainen 1950 _et al_). They form two groups, both of which are accepted features of serpentine rock (_cf_. Rune _l.c_. p.123).

On the one hand there are serpentinophytes. These are insular species (Stebbins 1942): "those which have developed on an island or an isolated ecological habitat on a continent". They are sometimes referred to as ecologically isolated neoendemics and may be morphologically differentiated from the type race of the species (Rune _l.c_. p.124). On the other hand there are depleted species (Stebbins 1942) "those which formerly were more widespread and genetically diverse but have lost many or most of their biotypes". These species have by definition disjunctive distributions. They are also known as geographically isolated serpentinicolous relics (Pichi-Sermoli 1948) or epibiotics, "the survivors of a lost flora" (Ridley 1930). To the extent that members of either group must be adapted to the toxic substrate the terms are not mutually exclusive; serpentinicolous relics are serpentinophytes _in statu nascendi_.

Serpentinicolous relics have survived because toxicity has prevented the development of closed vegetation over the debris habitat they need. Serpentinophytes may be thought of as the few successful invaders.

Some authors have raised these taxa on morphological grounds only; _viz_. Novak (1937), with the rather high total of 107 obligate serpentinophytes in C. Europe (where admittedly there has been more time compared with N. Europe for race differentiation).

Others have erected varieties after cultivation experiments; viz. Kotilainen and Seivala (1954). Rune (1953) describes four new serpentinophytes from Fennoscandia, all varieties of species in the family Caryophyllaceae. All have retained their diagnostic characters in cultivation in normal soil. While the numbers are not mentioned, cultivation in the case of Cerastium alpinum var. serpentinicola Rune nov. var., was of "one small tuft". Kotilainen and Seivala (1954) also describe a new Cerastium variety on the strength of the cultivation of a few specimens (in this case 4 pots). Doubts may indeed be cast on the value of such taxa in a highly polymorphic species like Cerastium alpinum. In extensive transplant experiments of material of Streptanthus glandulosus Hook. and Achillea borealis Bong. from the American Central Coast Range, Kruckeberg (1951) has produced the most convincing evidence of the existence of specifically serpentine races.

C. Discussion of the serpentine effect in Unst.

Both climatic and edaphic evidence has been examined. Appraisal now follows of the cause of the serpentine effect in Unst, of what retards colonisation on the debris.

Nickel is present in the soil of all parts of the hill land of the Unst serpentine outcrop examined. It is present in far larger quantities than normal. These amounts are, however, equivalent to those in certain Aberdeenshire serpentine soils where crop plants exhibit varying degrees of toxic symptoms (p. 31). As in these soils from Aberdeenshire (p. 73) cobalt content is low (p. 30). Nickel is present in *Agrostis stolonifera*, growing naturally on Unst serpentine soil, in quantities which are again far in excess of normal but comparable to figures from crops in the Aberdeen localities mentioned (p. 31). The latter plants exhibit toxic symptoms; *Agrostis stolonifera* does not.[x]

The distribution of the major debris areas is correlated with the distribution of the chromium-rich areas. These by inference are also the areas bearing the greatest amounts of nickel (p. 32). The major debris areas are expanses of associated debris having, that is, bedrock exposed on the surface. Their ochreous areas, those nearest the exposed bedrock, have in fact the highest nickel contents on the outcrop. By contrast, other areas of debris, the unassociated type, have a nickel content no greater than that under closed heath vegetation on serpentine.

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[x] A strong purple colour is characteristic of the foliage of many debris plants. This disappears with the provision of shelter in the few cases examined. While therefore exposure effects must be considered, no necrotic or chlorotic symptoms have been noted, at least in *Agrostis stolonifera*.

The quantities of nickel in the ochreous associated debris produce toxic symptoms in crop plants in other serpentine areas. Similarly the amount of available nickel, indicated by the quantities present in <u>Agrostis stolonifera</u> from this debris, is severely toxic to those crop plants. These expanses of debris may therefore be said to owe their continued existence primarily to the high available content of nickel in the soil. Colonisation will be more or less permanently retarded. Such plants as inhabit the debris must be adapted to high available nickel content. So the evidence agrees with the most recent findings that nickel-toxicity is the prime cause of serpentine barrenness.

However, high degree of available nickel also coincides with high degree of serpentinization, which in turn can cause a high rate of weathering. Irrespective of nickel content, rate of weathering might exceed any possible rate of colonisation. There are also the many smaller expanses of unassociated debris where nickel content is no higher than it is under closed vegetation and therefore unlikely to retard colonisation.

For the moment the natural consequence of soil-toxicity, the presence of serpentinophytes, is considered. I have insufficient experimental evidence of the existence of such taxa in Unst. To judge by the case of <u>Agrostis stolonifera</u>, some are likely to be present even if morphologically indistinguishable. Many of the pioneers in Unst are relics (p. 56); here they may be regarded as serpentinicolous relics, adapted to the high nickel content known to exist in the expanses of associated debris to which they are primarily restricted.

Yet here again their survival need not be due entirely to some adaptation to soil-toxicity. All the characteristic species of the pioneer phase are adapted to conditions of soil instability and similar physical factors that would exclude species lacking such adaptations (p. 65). Apart from toxicity indeed the physical nature of the habitat has been at some length shown capable of stopping the development of closed vegetation on the debris (pp. 60-67). This accords with the view of writers such as Pichi-Sermoli (1948) who considers serpentine infertility can be explained in many terms other than chemical ones, like microclimate, mechanical composition of the soil etc.

Wind is the chief <u>physical</u> factor in maintaining debris of whatever type in the open state (p. 66). But wind also re-exposes the debris by root-baring, destruction of the vegetation mat etc. With rain-wash in suitable localities, it must re-expose in this way the smaller expanses of debris; the expanses of what are called in consequence unassociated debris, lacking because of this 'origin' any exposed bedrock.

A consequence of such a dynamic habitat is cyclical succession (p. 80). The vegetation can be thought of as migratory (Crampton 1912). Since these phenomena have been shown to occur almost anywhere on the serpentine outcrop, some closed vegetation phase is therefore liable to disappear from a given patch of ground and an earlier phase appear in its place. The nearest analogy in this respect is the sand-dune habitat; inherently unstable, in any phase of the vegetation of which wind is always liable to cause blow-outs.

It seems likely then that debris can be re-exposed in any part of the serpentine outcrop, each closed area being potentially open. But each area at present surfaced by debris is not potentially closed to the same degree. All the factors will not operate equally over the whole serpentine outcrop. The slowing-up of colonisation and the existence of debris with sparse plant cover will be more, or less, permanent according to the number and degree of unfavourable factors and whether they act together or apart.

It is now possible to answer the question why colonisation has been retarded on the debris, as an explanation of the cause of the serpentine effect. The causes of the continued presence of the areas of debris lie partly in their origin and partly in what maintains them in the open state.

This is where the distinction between associated and unassociated debris is important. Retarded colonisation on associated debris is brought about by a high rate of weathering and high available nickel content, with wind-exposure and soil-instability. Major debris areas result from a combination of unfavourable factors at a maximum. Migration is correspondingly at a minimum or colonisation almost permanently retarded; the more it is, the more will the pioneer phase tend to form an edaphic climax. (Pioneer species are present only on patches of associated debris.)

On unassociated debris wind and soil-instability again play a part in retarding colonisation. But here it is a dominant role, for wind after all re-exposes the debris while weathering and soil toxicity will have only a minor part in its maintenance (the nickel soil content is no greater than it is under closed heath). Colonisation may be in consequence less permanently retarded, cyclical succession more rapid or migration greater than on comparable patches of primary debris. There are no pioneers.

D. Cyclical Succession.

Cyclical succession is the consequence of a dynamic or violent habitat. Like the generally-described pattern of cyclical succession (cf. Watt 1947) this cycle may be divided into four phases. Of these, three could be said to correspond to the four phases of the prisere, the mature phase being considered to run from where the dominance of Carex flacca is surpassed, to 100% cover. It is the breakdown phase that is considered here.

Full primary cycle		Prisere:	Total Cover
Pioneer		Pioneer	to 5%
Build-up	a	Grass phase	to 19%
	b	Sedge phase	to 33%
Mature		Heath phase (Climax)	to 100%
Breakdown			

The evidence presented so far suggests the following cyclical relationship. Excepting the first phase of the prisere each depends on its antecedent and influences its successor. For its establishment the pioneer community needs debris however this originates. In terms of cyclical succession the debris originates through the destruction of, say, the vegetation mat: With removal of the humus and finer soil-particles by soil-erosion and winnowing, the larger debris-material eventually reappears. The re-establishment of debris and the pioneer community marks the completion of a full cycle.

Any stage of a prisere is liable to destruction. Each example of such erosion, whether mat or tussock, is an example of breakdown phase. If the soil is completely eroded, debris will again appear (p. 60). The cycle will be shorter but the new succession, starting on debris, still primary (pioneers themselves will only be present if this is associated debris). Erosion or the breakdown phase may, however, stop after the destruction of the vegetation mat or tussock (e.g. Festuca "ring": p. 61a). In such a case any colonisation is of earth rather than debris. This I call secondary (cyclical) succession. Accepting that methods were not refined enough to make more than an arbitrary division - "earth" and "debris" - in what must be a series; whether the new cycle is primary or secondary depends then on the stage to which the breakdown phase (or erosion) has proceeded before recolonisation takes place.

It is to the presence of breakdown phenomena that we may look for an explanation of an anomaly in the analysis of prisere based on increase in total % cover. This is the absence of the pioneers at the start of the grass phase with simultaneous increase in cover of Thymus (cf. Table VI p. 57a).

There was a first assumption in examining the prisere - that all individual plants in the lowest cover phases were truly original. Each, that is, had arisen in that phase by ecesis or by vegetative means from such individuals. But, unless the destruction of any seral stage is complete, there is always the chance of relic plants from that stage being present in otherwise freshly-bared ground. There is also the possibility of vegetative spread by plants from patches of, for example, mature phase to pioneer patches. Of the spot-bound species found in the pioneer phase and known from the higher phases, Plantago maritima seems to be one of the few that may often be a relic (Plate IV photo. 1); for the rest, Carex panicea and

C. flacca are examples. In the diagram of C. panicea on p. 61b, the oldest rosette may be regarded as a relic of a plant from a previous sere, which has recolonised vegetatively.

Festuca rubra and F. vivipara, Agrostis stolonifera, Carex panicea and C. flacca and Thymus drucei are all capable of surviving an upheaval in their substrate by means of vegetative spread. They may therefore be considered recolonisers. Their abundance on debris and heath may indeed be interpreted as a direct result of this adaptation (cf. p. 66). Such power of recolonisation probably accounts too for the presence of isolated plants of Thymus and Carex flacca at the lowest degree of total cover (cf. p. 50). These two species are recolonisers or relics the more one considers the rest of their distribution in relation to total cover; not so, always, Festuca and Agrostis which behave as pioneers from the start (cf. p. 50).

The significance of earth surfaces. Nearly bare earth is either being recolonised or else losing the remainder of its plant cover; which is taking place can usually be determined by the appearance of the plants present. If breakdown is involved the plants are moribund like Festuca (Plate IV, photo.4) or standing free of the ground like Plantago (Plate IV, photo.1); if recolonisation is taking place the plants are close to the surface like Carex panicea (Fig.8, p. 61b).

The course of the prisere is naturally constructed on the assumption that, accompanied by concomitant soil-changes, total plant-cover increases with time. Thus the pioneer phase persists till total cover exceeds 5%, grass phase to 19% and so on. Given its total cover therefore one can assign any sample to its correct phase in the primary succession. But the presence of bare or nearly bare earth, as opposed to debris, introduces complications.

A sample with its surface consisting largely of earth may have plant cover of less than 5%: in terms of % cover alone that sample belongs to the pioneer phase. But earth indicates an eroded surface, and in terms of soil-development that sample may belong to the sedge phase. So the sample bears plant cover that is equivalent neither in composition nor extent to what it should be.

Explanation of anomalies. I will now examine the anomalies already noted in the grass phase of the prisere (p.81). Pioneers are virtually absent between total cover of 6.8% and 10.2%; at these two points, cover of Thymus increases and cover of grasses decreases. In Fig. 12 (p.83a) values of cover of grasses (from Table VI p.57a) are plotted against corresponding values for Thymus. Cover of Thymus clearly increases with cover of grasses, inferring that there is between these species no competition, where this implies the decrease in cover of one species with increase in cover of the other (see Part IV p.180). But there are two points where cover of Thymus increases abruptly. Cover of grasses must be smaller, cover of Thymus larger, than they should be at this stage of a succession based on total cover. In addition, the sum of the number of pioneer species at each value for cover of grasses gives a distinct curve with a break, again, where cover of Thymus is relatively high.

There are two problems here; (a) the cause of these abrupt changes in cover of grasses and Thymus, and (b) the significance of the lack of pioneers at high values of Thymus, in relation to their eventual disappearance at high values of total cover.

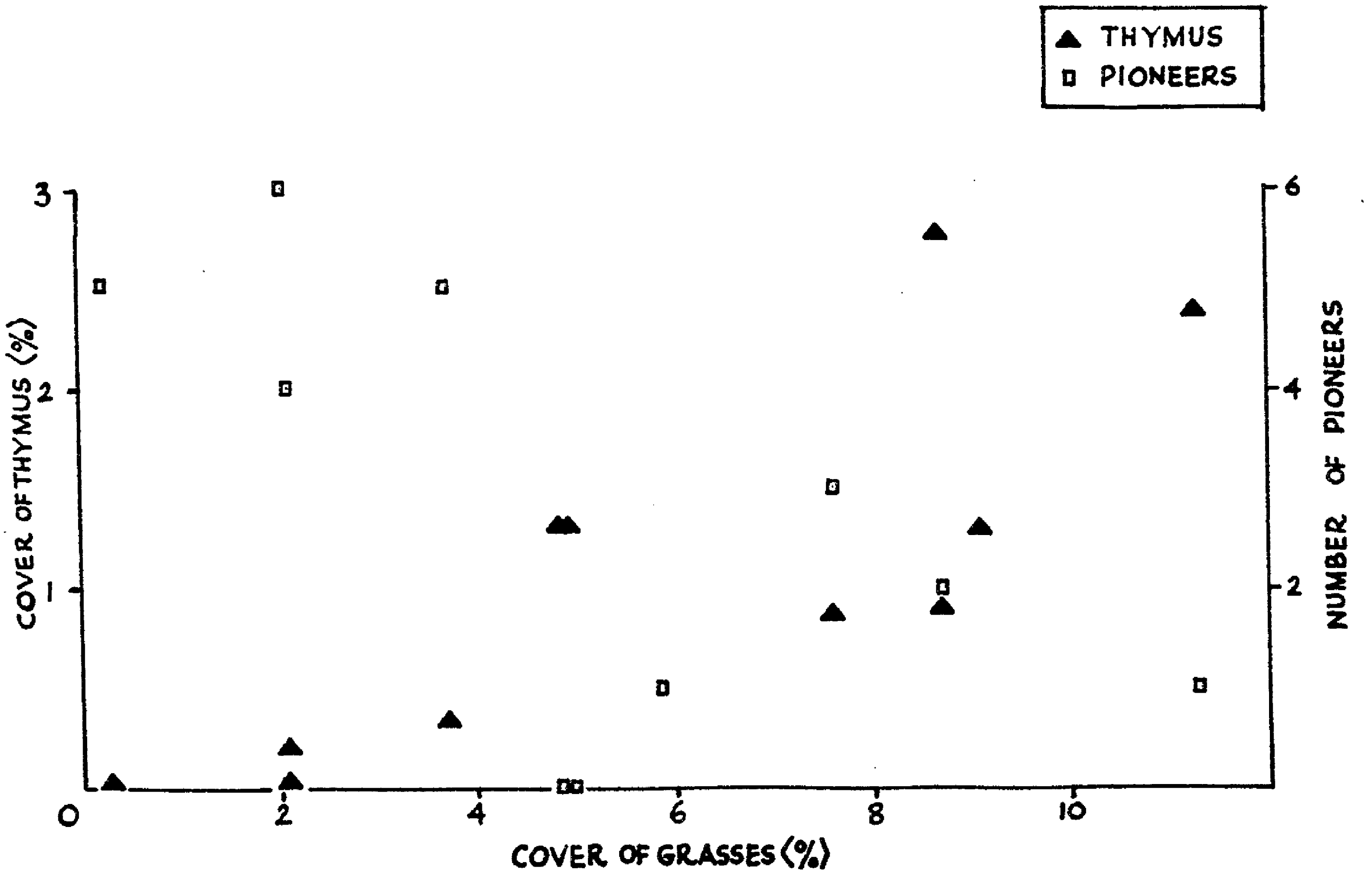

Fig.12. Cover of Thymus and number of pioneers versus cover of grasses. Cover of Thymus increases, number of pioneers decrease, with increase in cover of grasses; except where this lies near 5%. Here Thymus is unusually high, the number of pioneers unusually low.

(a) The abrupt changes between total cover of 6 and 10% in the grass phase agree precisely with the consequences of breakdown and secondary succession just postulated (so far as grasses and Thymus are concerned). The sudden decrease in cover of grasses indicates the result of breakdown, the corresponding rise in cover of Thymus illustrates recolonisation. Earth is in fact recorded on the surface of six out of eight samples showing these anomalies.

(b) I have said that samples with earth on their surface may belong edaphically to the sedge phase even if in total cover they are of the pioneer phase. Thus the absence of pioneers at the start of the grass phase is accompanied by high cover of Thymus. This perhaps represents recolonisation of a higher edaphic phase in the succession which is therefore not available to the pioneers. Since competition too may be involved, this is considered in Part IV with the general question of the elimination of the pioneer species.

IV. The origin and affinities of the debris habitat.

The over-riding influence of wind has been established in the previous sections: in the formation of secondary debris it is paramount. With rain and frost therefore it should be important in the origin of primary serpentine debris. Of the probable origin of the "frost-debris of the alpine plateaux" in climatically-similar Caithness, Crampton (1911, p.35) states that its characteristics may differ with the rock yielding the debris but depend chiefly on its having formed in situ under the influence of frost and wind ("winnowing" - Crampton l.c., p.25). He also states that where, "on the tops, disintegration is more advanced the rock is buried to some depth in fine angular debris. The surface is smooth as if rolled upon (my italics: cf. p. 26), but allows the rapid percolation of water."

Resemblances to Unst are obvious, though the particular depth of the debris in the absence of water-erosion may be regarded as a feature of the Caithness, and Sutherland (Crampton 1913), plateaux since water-erosion affects at least parts of the Unst debris. Crampton (l.c. p.35) points out that the frost debris of the alpine plateaux in Caithness is only part of a formation having a wide distribution in the Northern Highlands of Scotland and is "probably included in the Fjoeldmark of Warming and Ostenfeld" (Crampton l.c. p.25).

Similar debris, the details of which are given in Part III, was observed on Ronas Hill, Shetland, and on Rhum. On this mountainous island of the Inner Hebrides, debris occurs between 1300 ft and 2350 ft (396-716 m.) on such hills as Orval (basalt), Hallival (hallivalite and peridotite), Barkeval and Ruinsival (peridotite). In addition to the presence of solifluction phenomena such as stone lines in Unst (p. 25) and terraces on

Ronas Hill (Part III, p. 121); however limited or extensive on a particular outcrop of any rock-type, the debris always has a flat surface of small stones or gravel overlying finer material, is apparently unstable and liable to frost-heaving, and is exposed to wind.

Writing on the extensive Faeroese "rocky-flat" or Fjoeldmark formation, Ostenfeld (1909, p.909) says that "everywhere it is evident that winds are the cause of barrenness". One of the characteristics of this habitat is its freedom from snow, a freedom achieved by exposure. Another is indicated by the translation of the Icelandic Melar or Melur vegetation as gravel-*flat* (my italics) (Hansen 1930, p.178). A further characteristic is the presence of solifluction phenomena already discussed. Hansen (*l.c.* p.46) refers to Melar as an arctic vegetation type with its greatest distribution north of Iceland, though occurring at high levels in the Faeroes, Scotland and Scandinavia.

I would dispute the use of the phrase 'high levels' in describing its distribution in Scotland generally. For as the serpentine debris in Unst is essentially the same habitat as that, whether serpentine or not, normally found on mountain plateaux further south, the low altitude (0-550 ft : 168 m.) at which it occurs here is just one of its striking features. This is admittedly within a submontane-oceanic rather than a lowland regime but from its normal name of mountain-top detritus it is clearly not found at as low equivalent altitudes in say the Central Highlands. This low-level occurrence must indeed reflect the exposure, known from climatic data and supported by study of the physiognomy of the plants themselves, in this oceanic regime. This question is studied more fully in Part III with reference to similar fellfield vegetation in other areas.

PART III

SERPENTINE AND RELATED PLANT COMMUNITIES IN SCOTLAND AND THE NORTH ATLANTIC REGION

I. Introduction

The aims of this part of the thesis are to describe the Unst serpentine communities and discern their affinities both in Scotland and beyond. One can then see how far this and other serpentine vegetation is part of some general vegetation type and how far they can be said to show special serpentine features. Arising from this question of affinities is the fourth aim which is to establish some relationship between climate and vegetation.

I assumed from the outset that the closest affinities of Shetland vegetation would be with types in N. Scotland, the Faeroes, W. Norway, Iceland and S.W. Greenland. Considerable work has been done in describing the vegetation of all these places but different field-methods and methods of classifying results have been used in each.

In Iceland, Hansen (1930) and Steindorsson (1945) employed Raunkiaer's frequency method or modifications of it; broad classification is in groups analogous to Tansley's formations. The considerable volume of work undertaken by Nordhagen (1928, 1935, 1936, 1943) on the vegetation of Norway is an application of the methods of Braun-Blanquet. Crampton (1911) on Caithness vegetation, like Ostenfeld (1908) on that of the Faeroes, gives lists of dominant and subordinate species in broad habitat types. Böcher (1937) also does the same in these islands. But here and subsequently in S.W. Greenland, Böcher (1954) employs a simple field method, which I have described in Part I, and in the latter country bases his classification of the vegetation on four groups of indicator species, a blend of biological and distributional types.

It soon became apparent that, owing to the scant data available from Scotland, I would have to gather my own data beyond, as well as in, Shetland. A method of field analysis and subsequent synthesis had therefore to be chosen which, applied to the areas I myself wished to investigate, would yield results that might compare with those obtained by so many techniques. I decided to adopt Böcher's principles. In theory they make the subsequent classification of the vegetation independent within certain limits of the method of field analysis employed. Clearly however the comparative value of any results are increased by some quantitative measure of plant material present, such as cover, by a uniformly applied cover scale and some limits on sample size. So in the field I adopted like Böcher a quadrat size of 1 sq.m.. I used, mainly, Domin's 10 point scale for measuring cover and abundance (see Part I, p. 39).

Böcher develops and applies his principles of classification in his recent work on the vegetation of southwest Greenland (Böcher 1954). Applied to Scottish communities, they certainly help to fit into a broader scheme the vegetation of for instance the debris, in Unst and elsewhere, with its noticeable low and sub-arctic affinities. But several other groups of communities I describe do not have such affinities. They are therefore unrepresented in the area so far described by Böcher. Nor do they fulfil certain other requirements.

As the methods of classification could not be applied uniformly, two ways of presenting the field data here were considered. It would be possible, after uniting the data in the same basic phytosociological units as Böcher, (1) to outline Böcher's principles of classification, apply them to the grouping of the basic units just mentioned, and assess the value of the subsequent classification; or (2) arrange these units in vegetational groupings which could later be fitted into Böcher's scheme, but which at present do not involve consideration of his principles.

The first course would be instructive, particularly in view of the current interest in phytosociology; but little more. Böcher's principles seem to me to be important, and therefore in need of a more accurate assessment than is possible from their application to my relatively limited data. So the first course is deferred until more field data have been gathered.

In adopting the second course, the basic vegetation unit I use with Böcher, and earlier authors, is the sociation: a plant community with definite dominants in all strata and a related floral list (cf. Du Rietz 1930).

The next stage may not seem practicable. But, as reference to Böcher (l.c.) will show, the vegetation unit ("vegetational type") in which sociations are aggregated is defined in part by the life form of the dominant species. (Life form has here a wider meaning than Raunkiaer's). These units are intended to correspond broadly to such popular terms as 'heath' or 'copse'.

The grouping subsequently decided on, in which related sociations were to be united, had (1) to avoid terms like 'association' having established usages in or beyond Britain: (2) at the same time to correspond broadly to units, like heath, already recognised in Britain and (3) be capable of later merging into Böcher's scheme of classification.

I use therefore the term 'series' for a collection of related communities, often sociations, dominated by different species but which share both a number of species that are abundant in each community and intergrading or closely similar habitats.

Beyond the serpentine of Unst I have gathered comparable data from serpentine and non-serpentine localities in Aberdeenshire and Rhum; as well as from Ronas Hill in Shetland. I am presenting these data community by community with the Unst material. For a particular community, therefore, its composition in each of these localities is given, and its affinities.

Table X

Calluna - Erica cinerea - Juniperus nana (heath)sociations

Locality		Unst						Rhum		Unst			Rhum	
Sample number		1	2	3	4	5	6	7	8	9	10	11	12	13
Rock type (Hall-hallivatite)		serpentine							H.	serpentine				H.
Calluna vulgaris 1) 2) 3)	Ch	9	8	8	7	8	8	7	7	9	4	3	6	2
Erica cinerea	Ch	-	1	6	6	-	3	-	6	-	9	8	-	-
E. tetralix		-	-	-	-	-	-	-	-	-	-	-	4	-
Juniperus communis nana		-	-	-	-	-	-	-	1	-	-	-	6	8
Salix herbacea		-	-	-	-	-	-	(x)	-	-	-	-	-	(x)
Thymus drucei	Ch	3	3	2	3	3	2	4	2	1	3	2	3	4
Blechnum spicant		-	-	-	-	-	-	-	(x)	-	-	-	-	-
Lycopodium alpinum A.X.	Ch	-	(x)	-	-	-	-	-	-	-	-	-	-	-
L. selago	Ch	-	-	-	-	-	-	-	1	-	-	-	-	-
Selaginella selaginoides	Ch	1	-	2	-	1	1	2	2	-	-	1	3	3
Agrostis canina		-	1	-	-	3	-	-	3	-	1	-	-	1
A. stolonifera		3	3	2	3	-	3	2	-	3	1	2	3	3
Anthoxanthum odoratum		1	-	4	2	-	-	-	x	-	-	-	-	-
Deschampsia flexuosa		-	-	2	2	-	(x)	3	2	3	-	-	-	3
Festuca rubra		-	2	-	-	-	3	-	-	-	2	-	-	-
F. vivipara		2	-	1	3	3	-	3	3	-	-	2	4	6
Molinia caerulea		-	-	-	-	-	-	2	3	-	1	-	-	-
Nardus stricta		-	-	-	-	1	1	1	x	-	2	1	5	-
Sieglingia decumbens		2	-	-	-	4	3	-	-	-	-	3	-	-

1) Species in this and subsequent tables have been arranged in the following order, which is largely that used by Nordhagen (1928): dwarf shrubs (for which I take woody Chamaephytes, Chw,) : Pteridophytes, grasses, members of the Cyperaceae and Juncaceae, other monocotyledons, dicotyledonous herbs, mosses, liverworts and lichens. The species are arranged in alphabetical order within these groups. Domin's cover-abundance scale is used (see p. 39).

Species occurring as dominants, and/or in 90% or more of the samples, are underlined.

2) For authorities used in nomenclature see p.7

3) Chamaephytes (Ch) and boreal species present in the heath sociations on Unst (p. 56).

Table X (cont)

sample number	1	2	3	4	5	6	7	8	9	10	11	12	13
Carex demissa	-	-	-	-	-	-	-	-	-	-	-	1	-
C. flacca	2	-	-	-	2	1	-	-	1	-	2	-	-
C. panicea	1	1	3	3	2	2	4	1	1	3	3	2	-
C. pilulifera	-	1	-	-	1	1	1	-	-	1	1	-	x
C. pulicaris	2	3	3	3	2	3	4	2	1	3	1	2	-
Trichophorum caespitosum	-	-	2	-	-	1	4	2	1	2	-	4	-
Luzula campestris	-	-	-	-	-	-	-	-	1	-	-	-	-
Orchis ericetorum	-	-	-	3	-	-	-	1	-	-	-	-	-
Polygonum viviparum A.A.	-	-	(x)	-	-	-	-	-	-	-	-	-	-
Scilla verna	-	-	1	-	2	1	-	-	1	-	-	-	-
Alchemilla alpina	-	-	-	-	-	-	x	(x)	-	-	-	-	-
Antennaria dioica N.M. Ch	2	-	1	1	1	2	3	x	1	1	2	2	x
Euphrasia ?curta var. piccola	-	-	-	1	1	-	-	-	-	-	-	-	-
E. scotica	2	2	1	1	-	1	-	-	-	-	-	-	-
Hypericum pulchrum	2	1	2	2	1	2	(x)	1	-	-	1	-	-
Linum catharticum	1	-	x	1	-	-	-	1	-	-	x	2	-
Lotus corniculatus	-	-	-	-	-	-	-	x	-	-	-	-	-
Pinguicula vulgaris	-	-	2	-	-	-	1	-	-	-	-	-	-
Plantago maritima Hr-Ch	1	-	2	3	1	x	4	x	-	2	-	2	-
Polygala serpyllacea Ch	-	-	3	2	1	1	-	1	-	1	-	3	-
Potentilla erecta	3	3	3	3	4	3	3	2	3	2	3	2	-
Prunella vulgaris	2	-	-	-	1	-	1	-	-	-	1	-	-
Rubus saxatilis N.M.	-	-	-	-	-	-	-	-	-	-	-	-	2
Solidago virgaurea	-	-	-	-	-	-	1	-	-	-	-	-	3
Succisa pratensis	-	-	1	-	2	1	1	3	-	-	1	2	-
Taraxacum officinale	-	1	-	-	-	-	-	-	-	-	-	-	-
Thalictrum alpinum A.A.	2	-	-	-	2	-	(x)	-	-	-	2	-	-
Viola canina	-	-	-	2	-	-	-	-	-	-	-	-	-
V. riviniana	2	3	2	-	2	1	3	2	1	1	2	1	1

(to be contd.)

Table X (cont)

sample number	1	2	3	4	5	6	7	8	9	10	11	12	13
Brachythecium purum	x	-	-	-	-	-	-	-	-	-	-	-	-
Dicranum scoparium	-	-	x	x	x	x	-	-	x	-	x	-	x
Hylocomium splendens	-	x	-	-	x	x	-	x	x	-	-	-	x
Isothecium mysuroides	x	x	x	x	x	-	x	-	x	x	x	-	-
H. cupressiforme var ericetorum	x	x	x	x	x	x	x	x	-	x	x	-	x
Mnium punctatum	-	-	-	-	-	x	-	-	-	-	-	-	-
Pleurozium schreberi	-	-	-	-	-	x	-	-	-	-	-	-	-
Polytrichum formosum	-	x	-	x	x	-	-	-	-	-	-	-	-
Rhacomitrium lanuginosum	x	-	2	2	-	x	x	x	2	2	x	x	3
Rhytidiadelphus loreus	x	x	-	x	x	x	-	-	x	-	x	-	x
Thuidium tamariscinum*	x	-	-	-	-	x	-	-	x	-	-	-	-
Diplophyllum albicans	-	-	-	-	-	-	-	x	-	-	-	x	x
Frullania tamarisci	x	x	x	x	x	x	x	-	x	x	x	x	x
Lophocolea cuspidata	-	x	-	-	-	-	-	-	-	-	-	-	-
Plagiochila asplenioides	-	-	-	-	-	-	-	-	-	-	x	-	-
Cetraria aculeata	-	-	-	-	-	-	-	-	-	-	-	x	-
Cladonia rangiformis	-	-	-	x	-	-	x	-	x	x	-	-	-
Cl. subtenuis	-	-	x	x	x	-	x	-	-	x	x	-	-
Cl. uncialis	-	-	-	x	-	-	x	-	-	-	-	-	-
Peltigera canina	-	x	-	-	-	-	-	-	-	-	-	-	-

* Additional mosses : Dicranum majus, Plagiothecium undulatum and Rhytidiadelphus triquetrus.

II. Sedge-grass-heath series (Unst, Rhum and the Coyles of Muick).

A. Calluna-Erica cinerea-Juniperus nana (heath) sociations. Table X, Nos. 1 - 13. Serpentine, peridotite, greenstone and hallivalite localities, Unst and Rhum.

Calluna vulgaris sociation; Table X, Nos. 1 - 9.

This sociation is the commonest of the heath types in Unst. It occurs there and on Ruinsival on level or gently-sloping ground (0 - 10°) and on slopes of up to 20° on Hallival, Rhum. It is found chiefly on the south end of the Unst serpentine, on the flanks of Hallival and the flanks and summit of Ruinsival (alt. 1600 ft : 487 m.).

The vegetation ranges in height from 5 - 7.5 cms. (summit of Ruinsival) to 25.5 cms. (at 50 ft : 15 m. on Unst). In all the sociations of this group the bryophytes excluding Rhacomitrium lanuginosum are almost confined to the ground beneath the suffruticose bushes and consequently contribute little surface cover. Lichens too are unimportant in this respect.

Erica cinerea sociation; Table X, Nos. 10, 11.

Erica cinerea contributes some cover in five out of nine of the first samples, becoming subdominant in three - Nos. 3, 4 and 8. These show the transition to the full dominance of Erica in Nos. 10, 11; Calluna however is still present. The sociation covers little ground compared with the previous one, in or beyond Unst.

Juniperus communis nana sociation; Table X, Nos. 12, 13.

Juniper is absent from Unst, though scattered between the same altitudinal limits on the free-draining granite-diorite of North Roe, Shetland Mainland. It was seen once on the Coyles of Muick; forms sociations on Ruinsival from isolated occurrences at 500 ft (152 m.) to small areas on the summit plateau of Ruinsival at 1500 ft (457 m.). Present already on Hallival at 1200 ft (365 m.), (No.8), the juniper forms patches 5 - 7.5 cms. high on the summit of that mountain at 2350 ft (716 m.). *Calluna vulgaris* is present in both cases, co-dominant in No. 12. *Rubus saxatilis* was noted in the Hallival samples, in *Calluna* sociations on the peridotite Barkeval and Ruinsival, and in debris on these hills and in Unst.

Soils are considered below in conjunction with the sedge-grass group.

Inter-sociation relationships. *Calluna* is present throughout, sharing dominance with *Erica cinerea* or *Juniperus communis nana*, or giving way to them. In addition the sociations as represented in these samples all share *Agrostis stolonifera*, *Antennaria dioica*, *Festuca rubra* or *F. vivipara*, *Potentilla erecta*, *Thymus drucei*, *Viola riviniana* and (except No.12) *Carex panicea* and *C. pulicaris*. Lacking sufficient data to account causally for the distribution of these three sociations, I am not excluding this sample. It still has the other six species and the three constantly occurring bryophytes *Hypnum cupressiforme* var. *ericetorum*, *Rhacomitrium lanuginosum* and *Frullania tamarisci*.

This group of heath sociations is clearly related to the sedge-grass sociations, from which *Trichophorum caespitosum*, *Deschampsia flexuosa* and *Erica cinerea* seem to be its only species that are quite lacking; I consider its wider affinities then.

B. Carex flacca-C. pulicaris-Festuca species (sedge-grass) sociations.

Table XI, Nos. 1 - 9. Serpentine and peridotite localities, Unst, Rhum and the Coyles of Muick.

Carex flacca - Plantago maritima - Carex pulicaris sociations; Table XI, Nos. 1 - 5, 7.

Carex flacca is the usual dominant in the sedge-grass communities in Unst, but Plantago maritima (No. 1), Festuca rubra (No. 2) or Carex pulicaris (No. 3) may be co-dominant. This last species is dominant in No. 7.

The Carex flacca sociation is widespread in Unst, occurring on level or gently sloping ground (0 - 5°) mainly in the north of the serpentine outcrop. The Carex pulicaris sociation is found on 10 - 20° slopes on the Coyles of Muick (± 1800 ft).

With leaves from 1.3 to 7.7 cm. (rarely 10 cm.) this community forms a close-cropped turf and is, like the following sociation, one-layered. Soil is often visible between the plants, the bryophytes contributing little cover. Lichens are only important in the East Highland samples (Nos. 6, 7, 8).

Festuca ovina-F. vivipara sociations (Table XI, Nos. 6, 8, 9, 10).

Festuca vivipara being absent, F. ovina dominates in a short turf on the Coyles of Muick. Anthoxanthum odoratum is co-dominant in one sample. F. vivipara dominates in short turf on the steeper slopes of Ruinsival (No. 6). Carex pulicaris is of little account or absent in this sociation. No. 10 is pasture improved by the guano of Manx shearwaters,

Table XI

Carex flacca - C. pulicaris - Festuca (sedge-grass) sociations

locality		Unst					Coyles			Rhum	
sample number		1	2	3	4	5	6	7	8	9	10
Calluna vulgaris	Ch	4	4	3	4	-	-	1	-	-	-
Empetrum hermaphroditum	Ch	-	-	-	-	-	5	1	1	-	-
Thymus drucei	Ch	3	3	2	2	4	2	1	1	3	4
Vaccinium myrtillus		-	-	-	-	-	-	-	-	3	2
V. vitis-idaea		-	-	-	-	-	4	3	3	-	-
Botrychium lunaria		(x)	-	-	-	-	-	1	-	1	-
Selaginella selaginoides	Ch	3	2	2	3	1	2	1	1	1	-
Agrostis canina		-	-	1	-	1	-	1	3	-	1
A. stolonifera		5	5	4	3	4	1	-	2	4	-
Anthoxanthum odoratum		-	-	-	-	2	6	-	2	3	4
Deschampsia flexuosa		-	-	-	-	-	-	-	-	-	3
Festuca rubra		5	6	4	5	2	-	-	-	-	1
F. ovina		-	-	-	-	-	7	5	6	-	-
F. vivipara		-	-	-	-	3	-	-	-	6	7
Koeleria gracilis		-	-	-	-	-	1	-	-	-	-
Molinia caerulea		5	2	5	5	-	-	-	-	-	-
Nardus stricta		-	-	-	-	-	3	-	1	1	-
Sieglingia decumbens		-	3	-	-	2	-	-	-	-	-
Carex caryophyllea		-	-	-	-	-	1	-	-	-	-
C. demissa		-	-	-	-	-	1	1	-	-	-
C. flacca		5	7	4	6	5	-	-	-	-	-
C. panicea		1	-	2	1	1	2	2	2	1	-
C. pilulifera		-	-	-	-	-	-	-	1	2	-
C. pulicaris		2	5	6	3	4	1	6	1	-	-

(to be contd.)

Table XI (contd.)

sample number		1	2	3	4	5	6	7	8	9	10
Luzula campestris		-	-	-	1	-	-	-	-	-	-
L. multiflora		-	-	-	-	1	-	-	-	-	x
Coeloglossum viride		x	1	-	-	3	(x)	-	-	2	-
Polygonum viviparum		-	-	-	-	-	x	-	-	-	-
Scilla verna		2	3	1	-	-	-	-	-	-	-
Alchemilla alpina		-	-	-	-	-	-	-	-	-	1
Antennaria dioica	Ch	3	1	1	2	5	3	-	1	3	-
Anthyllis vulneraria		-	-	-	1	-	-	-	-	-	-
Armeria maritima	Hr-Ch	(x)	-	-	-	-	-	-	-	-	-
Campanula rotundifolia		-	-	-	-	-	2	2	1	-	-
Euphrasia scotica		1	3	-	-	2	-	-	-	1	-
E. curta		-	-	-	-	-	1	-	-	-	-
E. rotundifolia		1	-	-	-	-	-	-	-	-	-
Galium hercynicum		-	-	-	-	-	-	-	1	1	-
G. verum		-	-	-	-	-	2	-	2	-	-
Gentiana campestris		-	-	-	-	(x)	-	-	(x)	-	-
Hypericum pulchrum		2	-	1	1	1	-	-	-	-	-
Leontodon autumnale		1	1	1	1	-	-	-	-	-	-
Linum catharticum		3	2	2	2	2	2	1	-	(x)	-
Plantago maritima	Hr-Ch	6	2	2	3	5	-	-	-	5	-
P. lanceolata		-	2	2	-	1	-	-	-	-	-
Polygala oxyptera		-	-	-	-	-	-	-	1	-	-
P. vulgaris	Ch	-	1	-	-	-	-	-	-	-	x
Potentilla erecta		3	4	3	3	3	3	1	1	4	1
Prunella vulgaris		2	1	1	3	2	-	x	-	-	-
Rhinanthus spadiceus		1	-	-	-	-	-	-	-	-	-
Silene acaulis	Ch	1	-	-	-	-	-	-	-	-	-
Succisa pratensis		-	-	2	2	-	-	-	-	3	-
Thalictrum alpinum		2	2	3	-	3	-	-	-	x	(x)
Viola riviniana		2	1	1	2	2	2	1	1	2	2

(to be contd.)

Table XI (contd.)

sample number	1	2	3	4	5	6	7	8	9	10
Bryum *cf* pallens	-	-		x		-	-	-	-	-
Campylopus atrovirens	-	x		-		-	-	-	-	-
Dicranum scoparium	-	x		x		x	-	x	x	x
Drepanocladus revolvens	-	-		x		-	-	-	-	-
Fissidens osmundioides	-	-		x		-	-	-	-	-
Hylocomium splendens	-	-		x		x	x	x	x	x
Isothecium mysuroides	x	-		x		-	-	-	x	-
H. cupressiforme var. ericetorum	-	x		x		-	x	x	x	-
Mnium undulatum	-	-		-		x	-	-	-	-
Plagiothecium undulatum	-	-		-		-	-	-	-	x
Pleurozium schreberi	-	-		-		x	x	x	x	-
Polytrichum piliferum	-	-		-		-	-	-	x	x
Rhacomitrium lanuginosum	x	-		x		x	-	-	x	x
Rhytidiadelphus loreus	-	-		-		-	x	x	x	3
R. triquetrus	-	-		-		x	-	x	-	-
Thuidium tamariscinum	-	-		-		-	-	-	x	-
Weissia microstoma	-	x		-		-	-	-	-	-
Diplophyllum albicans	-	x		-		-	-	-	-	-
Frullania tamarisci	-	x		x		x	x	-	x	-
Alectoria nigricans	-	-	-	-		-	x	x	-	-
Cetraria aculeata	-	-	-	x		x	x	-	-	-
C. islandica	-	-	-	-		1	-	1	-	-
Cladonia cariosa	-	-	-	-		-	-	x	-	-
Cl. rangiformis	-	-	-	x		x	-	x	-	-
Cl. cervicornis var. subcervicornis	-	-	x	-		-	-	-	-	-
Cl. sylvatica	-	-	-	-		3	4	4	-	-
Parmelia omphalodes	-	x	-	-		-	-	-	-	-
Peltigera canina	-	-	x	-		-	-	x	-	-
Thamnolia vermicularis *	-	-	-	-		-	x	-	x	-

* Additional lichens (Coyles of Muick): Anaptychia leucomelaea, Cladonia pyxidata and Parmelia saxatilis.

vast numbers of whose burrows riddle the boulder clad mountainside of Hallival from about 1800 to the summit at 2300 ft (459 - 716 m.). I include this example here because the normal closed vegetation, which is so changed in the vicinity of these burrows, seems to be the Juniperus communis nana sociation.

Inter-sociation relationships. The sociations share eight species more or less constantly: Agrostis stolonifera, Antennaria dioica, Carex panicea, Linum catharticum, Potentilla erecta, Selaginella selaginoides, Thymus drucei and Viola riviniana. The bryophytes Hypnum cupressiforme var. ericetorum, Rhacomitrium lanuginosum and Frullania tamarisci occur fairly regularly (though two samples are unfortunately missing). Present also, even if sparingly, are Botrychium lunaria and Coeloglossum viride.

There are however differences in floristic composition in these samples from such widely separated localities. Of the dominant species, Carex pulicaris is the only one found, within the communities in question, in all three localities; it also occurs constantly as a subordinate species. Festuca ovina is confined to the Coyles, F. rubra, F. vivipara and Plantago maritima to the oceanic samples, and Carex flacca as a dominant and, almost, as a subordinate species, to Unst. The Coyles samples alone contain Empetrum hermaphroditum, Vaccinium vitis-idaea and Campanula rotundifolia. They also have a denser and more varied lichen cover, including Alectoria nigricans, Cetraria islandica, Cladonia sylvatica and Thamnolia vermicularis.

The causes of these differences are important in deciding whether the latter outweigh the similarities. Concerning dominants, for example, *F. vivipara* can reasonably be regarded as replacing *F. ovina* in the oceanic samples. Likewise the absence of *Plantago maritima* from the Coyles in contrast to its presence in most of the oceanic samples may be regarded in part as a reflection of geographical position.

The predominance of *Carex flacca* in the Unst sedge-grass community may, by contrast, have a different significance, particularly in view of the widespread mire sociations in which that species is co-dominant in Unst (see p. 110). As, however, with the question of the affinity of the Coyles samples with the rest, it is arguable whether, on the strength of the small number of samples available, final conclusions may be drawn. For the present they are regarded as related sociations, united by a large number of regularly occurring species, in which the dominants replace each other both within and between different localities.

Soils. These are considered with the heath-group samples because of their obvious similarities.

Three soil types underlie the various heath and sedge-grass sociations.

Type A. Heath (Table 1, Nos. 1, 2, 3, 4, 8); on ± level ground in Unst: Hallival, 20° slope.
Sedge-grass (Table 2, Nos. 3, 4, 7); on ± level ground in Unst: Ruinsival, 25° slope.

		Heath	Sedge-grass
1.	little or no litter: no raw humus	0 - ½cm.	0
2.	fine loam ('burnt sienna')	15 - 26cm.	2(R'val) -5-7cm.
3.	white,ochreous or red clay(drift) or sand (*cf.*Böcher 1954:Fig.36, p.141)	30 - 60cm. - (> 2m. H'val)	30cm.

Type B. Heath (Table 1, Nos. 9, 10, 12, 13); 0-15° slope. Sedge-grass (Table 2, No. 5) 5° slope.

		Heath	Sedge-grass
1.	raw humus and litter	1 cm.	0
2.	fine soil (?stained) with humus	2-4 cm.	5-7 cm.
3.	debris and gravel (rocks often protrude).		

Type C. Heath (Table 1, Nos. 5, 7, 11); 0-15° slope. Sedge-grass (Table 2, Nos. 1, 2, 6, 7, 8); 0-5° slope in Unst: Coyles of Muick, 20°.

		Heath	Sedge-grass
1.	fibrous root-mat with raw humus and some mineral soil	3-4 cm.	2½-4 cm.
2.	soil (? stained) with humus	3-5 cm.	6-8 cm.
3.	black humus pan	3 mm.	3 mm.
4.	clay: white, ochreous or red-grey (stained black for 15 cm. and lacking layer 3, in Nos. 6, 7)	25-30 cm.	to 30 cm.

Type A is clearly immature: the striking feature being its possession on level ground of characters, like lack of humus accumulation and profile, normally associated with soils of steep slopes. Type B is again immature, developed on debris. Type C has a slightly developed profile, with some raw humus and a humus pan, but it is still shallow.

It is only this type which shows any tendency to even seasonally impeded drainage. The larger number of sedge-grass samples fall into this category: this suggesting a trend towards the mire soils which, in drainage hollows in Unst, underlie the Carex flacca-C. demissa sociation (p. 110). (The widespread occurrence of this habitat in Unst may account in part for the predominance of Carex flacca in samples of the sedge-grass-heath series from that island). But it is only a trend, and in general it is clear that no particular feature of the vegetation can be correlated with a particular soil-type. All the soils share immaturity and generally good drainage despite the presence or absence of drift, and variation in slope and geology.

C. Affinities of the series.

Inter-series relationships. Not only do the heath and sedge-grass sociations occupy the same soil series; floristic resemblances are also close. Of the dominants in the sedge-grass sociations, Carex pulicaris, Festuca rubra or F. vivipafa are invariably present in the heath sociations (except Table 1, No. 13), while Calluna occurs in most of the sedge-grass examples. Six species, Agrostis stolonifera, Antennaria dioica, Carex panicea, Thymus drucei, Potentilla erecta and Viola riviniana, occur in almost every sample of both groups. In addition, Linum catharticum and Selaginella selaginoides which are fairly constant in the heath group become quite constant in the sedge-grass group, Plantago maritima in the oceanic examples.

Grazing must be one of the variable factors here. Evidence of grazing pressure is given by the short turf adjoining tall, fenced, grasses on Clibberswick, Unst (p. 34), and probably by the high incidence of Plantago maritima in the sedge-grass sociations; I have shown how in Unst this plant disappears, even if dominant, on the cessation of grazing and the development of tall plant cover (p. 33), this agreeing with Gillham's (1954) findings on Skokholm. Then there is direct evidence of the conversion of Calluna-patches into grassland:- the zone of small, dense, isolated Calluna bushes, themselves biotically induced forms (Gimingham, 1949), in the short turf surrounding such patches and the presence of dead heather rooted in the turf. (A special case of this conversion is the 'improvement', noted on p. 96 , of Juniperus communis nana sociations on Hallival by the guano of Manx Shearwaters.)

The sociations of the heath type are those which, on well drained moderately acid soil that shows little tendency to humus accumulation, are converted to sedge-grass sociations under increased grazing pressure. This is the same as the heath:bent-fescue conversion described by Farrow (1916) and Gillham (1955).

The presence of Coeloglossum viride and Botrychium lunaria only in the sedge-grass type is interesting because these species, with Lycopodium alpinum and Gentiana campestris, are in my experience typical of relatively short vegetation: so they must to some extent depend here on the maintenance of short turf by grazing. So far as Coeloglossum viride is concerned, Summerhayes (1951, p.212) says that comparatively short turf is a common feature of most of the habitats in which the plant is found in Britain.

Apart from the dominants, the heath communities are distinguished from the sedge-grass sociations by their possession of Trichophorum caespitosum, Deschampsia flexuosa and Erica cinerea which are absent from, and Carex pilulifera which is rare in, the latter communities. The sedge-grass communities in turn have Coeloglossum viride and Botrychium lunaria, absent from the heath, while Linum catharticum and to a lesser extent Selaginella become less frequent in heath.

Without going further afield it is obvious that, with the possible exception of the Carex flacca sociation in Unst, the sedge-grass-heath series on serpentine is indistinguishable from that on non-serpentine rocks examined.

Other affinities. With published accounts of heath or grass-heath communities in Britain I am unable to make any comparisons.

Beyond Britain, Rune (1953, p.50) notes their dry nature as one of the features of the serpentine outcrops in N. Sweden and accordingly the closed vegetation, like that of much of the Scottish serpentine examined, is heath. On the most exposed parts of the outcrops this heath is a version of the Loiseleuria-Arctostaphylion alliance[*] of Kalliola (Nordhagen 1943) or Empetrion of Du Rietz (1950); these are low-alpine heaths on acid soils, especially on parts not protected by snow during the winter. Empetrum nigrum, one of the most xerophytic plants, with abundant Rhacomitrium lanuginosum and Calluna vulgaris, are the chief features of what Rune considers a specialized or serpentine facies of the Empetrion alliance. (The lichen-rich samples from the less oceanic Aberdeenshire serpentine may be related to the Cladonia sylvatica-Cl. rangiferina-rich Calluna sociation of Nordhagen. This author includes that sociation in his Phyllodoco-Myrtillion (Nordhagen 1943, p.124) a dwarf shrub heath alliance having moderate snow cover.)

In the Faeroes Böcher (1937) refers to but does not describe the Calluna-Erica cinerea Atlantic heath of the 0 - 200 m. "Atlantic" zone; but Ostenfeld (1909, p.947) says that dry Calluna heath does not exist, the nearest representative being Calluna-Erica cinerea heather-moor, which he differentiates from the moist Danish heath containing Erica tetralix.

Two of the seven lists given by Ostenfeld are from communities resembling my sedge-grass-heath series. Of species

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[*] Associations, in the sense of Braun-Blanquet, which are nearly related ecologically are grouped into Alliances (termination -ion). For definition of Association and Alliance see Poore (1955, pp.233, 241).

conspicuous in my examples, Ostenfeld's two lists share the dominant Calluna and the subdominant Empetrum hermaphroditum and Erica cinerea: and Anthoxanthum odoratum, Festuca ovina, Leontodon autumnale, Polygala serpyllacea, Potentilla erecta, Prunella vulgaris and Thymus drucei. One or other list also contains Agrostis stolonifera, Carex panicea, Hypericum pulchrum, Plantago maritima and Selaginella selaginoides. In all, 22 out of 25 phanerogams occur in my samples. Taking the heath formation as a whole Ostenfeld describes the first three species as above, and states that the following are subordinate but characteristic: Vaccinium myrtillus, V. uliginosum (not common), Thymus drucei and Juniperus communis nana (very rare). Lichens as in my oceanic examples are unimportant.

This heather moor is however uncommon in the Faeroes; according to Ostenfeld (l.c. p.959), "it picks and chooses its stations"; it needs a rather dry substratum and sunshine (both rare there). Ostenfeld considers this community part of the moor formation of the subalpine (0-300 m.) zone, in which Nardus-Juncus squarrosus grass-moor is the predominant type. He gives no detail of soil beyond saying that it is humous, but examination of his lists indicates that communities which are distinct in Shetland are less obviously separated in the Faeroes. In all my sedge-grass-heath samples, Nardus stricta, Juncus squarrosus and Trichophorum caespitosum are absent or very rare. In Shetland at least they are characteristic of deep peat or thin wet peat - in Unst on the gneisses, mica-schists or greenstones (see Part I, Table I, p.5a). In the Faeroes by contrast these species are present even in the two examples which bear some resemblance to my own.

Even at its lower limit as in Unst, the presence of such arctic-alpine species as Lycopodium alpinum, Silene acaulis, Polygonum viviparum and Thalictrum alpinum (Matthews 1955) indicates that, wherever else it may lie, the general affinity of the series is not with lowland heaths. Yet neither is it montane as inspection of the list readily shows. I therefore designate this series submontane sedge-grass-heath.

Table XII

(a) Carex flacca-C. demissa sociation

Locality sample number	UNST				
	1	2	3	4	5
Calluna vulgaris	-	-	1	-	-
Thymus drucei	-	-	3	-	-
Selaginella selaginoides	-	-	1	-	-
Agrostis stolonifera	3	2	2	4	2
Festuca rubra	2	-	3	-	-
Molinia caerulea	-	-	-	4	3
Sieglingia decumbens	3	-	3	-	-
Carex demissa	5	6	6	5	6
C. flacca	7	1	6	6	6
C. nigra	-	3	-	-	-
C. panicea	-	-	1	2	-
C. pulicaris	2	-	3	-	-
Eleocharis pauciflora	-	3	-	-	4
Juncus articulatus	2	1	1	2	3
J. bulbosus	-	3	-	-	3
Scilla verna	-	-	1	-	-
Euphrasia micrantha	2	-	2	4	-
Plantago maritima	6	-	5	4	2
Polygala vulgaris	-	-	1	-	-
Potentilla erecta	2	-	-	-	-
Prunella vulgaris	1	-	2	1	-
Ranunculus flammula	2	2	3	2	5
Thalictrum alpinum	3	-	-	-	-
Viola riviniana	-	-	1	-	-
Bryum cf. pallens	-	-	-	-	1
Drepanocladus revolvens	x	x	x	x	x
Fissidens osmundioides	-	-	-	-	1
Scorpidium scorpioides	x	1	x	x	x

Table XII (contd.)

(b) *Schoenus nigricans*-*Molinia caerulea* sociation

Locality	UNST				
sample number	6	7	8	9	10
Selaginella selaginoides	-	1	-	-	-
Agrostis stolonifera	1	1	1	1	2
Festuca rubra	-	-	-	1	1
Molinia caerulea	2	3	2	1	5
Carex dioica	1	-	-	-	-
C. demissa	1	1	2	1	3
C. flacca	1	3	4	1	4
C. panicea	-	1	1	-	-
Eleocharis pauciflora	1	1	-	-	-
Schoenus nigricans	4	8	8	9	8
Juncus articulatus	1	4	-	-	-
Triglochin palustre	1	-	-	-	-
Armeria maritima	x	-	1	x	-
Leontodon autumnale	-	-	-	-	1
Pinguicula vulgaris	1	2	-	-	-
Plantago maritima	1	3	3	1	4
Polygala vulgaris	-	-	1	-	-
Ranunculus flammula	1	-	-	-	-
Bryum sp.	x	-	-	-	-
Dicranum bonjeani	-	x	-	-	-
Drepanocladus revolvens	x	x	-	x	x
Scorpidium scorpioides	x	x	x	x	x

III. Mire sociations (Unst).

Table XII, Nos. 1 - 10 Serpentine localities, Unst.

A series of soligenous mire communities occurs on serpentine in flat-bottomed drainage hollows or alongside streams, where the drainage water rises close to the soil surface. Observed also on the Coyles of Muick, two of the communities from Unst are described here.

A. Carex flacca-C. demissa sociation

With a total plant cover of from 50 - 90%, Carex flacca and C. demissa dominate in a short heavily grazed turf with leaves from 1.3 to, exceptionally, 5 cms. long; Ranunculus flammula and Euphrasia micrantha flower at these heights. Brown mosses (Scorpidium scorpioides and Drepanocladus revolvens) are scattered sparsely over the black mud. The sociation often merges in the field into the Carex flacca-C. pulicaris-Festuca group with which it shares many species. It is distinguished, however, from these sociations by its possession of Ranunculus flammula, Juncus articulatus and Scorpidium scorpioides, while Eleocharis pauciflora is sometimes present too. The sociation is distinguished from the following one only by the absence of Schoenus nigricans, there being no species exclusive to this sedge sociation at least as I have discerned it. Soil I describe below.

B. Schoenus nigricans-Molinia caerulea sociation

This community again is subjected to very heavy grazing, the leaves of Schoenus itself varying from about 1.3 up to a maximum of 10 cms., the inflorescences, which under these circumstances are rare, from 7.6 to 12.5 cms. Within a 6 ft x 6 ft (1.8 x 1.8 m.) rabbit- and sheep-proofed area, erected in summer 1952, these dimensions were increased by summer 1953 to 31 cms. for leaves and 35 cms. for inflorescences. In the community in general, plant cover varies from as little as 5%, up to 100%. The lower degree of plant cover is a reflection of the fact that here the leaves of Schoenus are grazed down to the base, leaving spaces between each tussock which in the ungrazed state are not visible. Mosses are rare in grazed and ungrazed samples. The fenced area has not been enclosed long enough to show any changes other than an increase in the size of Schoenus; but one nevertheless gains the impression that this is an unnaturally impoverished community - it contains fewer species than even the related sedge sociation.

The following observation confirms this view. Below the north of Colvadale lie a series of open areas of deep waterlogged clay in which, during a normal year, grazing animals would sink. In one such patch, at an altitude of 50 ft (15 m.), there was in July 1951 a small 'island' of not more than 30 sq.ft (9 sq.m.) in extent. This island was formed by hugh tufts of Schoenus nigricans, nearly 40 cms. high and in full flower; Armeria maritima was subdominant and nearly as large. There were in addition the following species: Molinia caerulea, Euphrasia micrantha, Plantago maritima, Carex flacca or Carex panicea, Erica tetralix, Selaginella selaginoides, Pinguicula vulgaris, Carex dioica, Juncus articulatus and Sphagnum species. When, in late July 1955, the area was revisited the community was no longer distinguishable; the mud had dried out during the prolonged drought and had presumably allowed access to grazing animals.

Soils

With a flat surface, the soil under the Carex flacca-C. demissa sociation showed the irregular stratification associated with areas of deposition. Thus a black surface layer of fibrous roots, humus and many mineral fragments (1.5 to 10 cms. deep) was often underlain by a layer of white clay 2.5 to 15 cms. deep; this is turn overlaid black sulphide-smelling peat. At other times the predominantly organic soil was continuous, the root mat overlying blue-grey humus stained clay. Soil-pH (first 7 cms.) 6.1 to 7.4. In the dry summer of 1955, the surface layers were quite dried out, crumbling in the hand.

Under Schoenus nigricans the soil surface was uneven and showed little layering beneath. Lying in drainage hollows, it consisted of alluvial soil in a gravel or stone matrix, the stones being up to 15 to 30 cms. in diameter. Samples were examined at the same time as the preceding ones and, even during this drought, several had standing water at the surface. When the stones were extracted the drier samples had soil like a dark brown loam; but the prevailing conditions could have produced an atypical appearance in what is usually, to judge by preceding years, a waterlogged soil. Soil-pH (first 7 cms.) 6.9 to 8.1.

Relationships

There is a gradient in both soil-pH and the height of the water table which may be correlated factors. At most these communities may reflect two relatively level stretches in a gradient of variation connected with these factors. Not enough is known to say more.

From soil-pH it is apparent that both communities are eutrophic-mesotrophic mires or fens. They resemble wet flush (*sensu* Pearsall 1950) communities of high soil-pH described by Holdgate (1955) from Westmorland. Particularly does this apply to what Holdgate (*l.c.* p.85) calls the vegetation of the open surface, having a similarly high soil-pH and many species in common. Closer comparison is not possible as species-lists only are given. The *Carex flacca*-*C. demissa* sociation is also related to the *Carex demissa*-*C. panicea* nodum of Poore (1954) on mesotrophic mires in Breadalbane.

IV. The fellfield series.

Table XIII. Unst and Ronas Hill, Shetland:
Rhum and the Coyles of Muick.

From the start of my study of the prisere on serpentine in Unst (Part II, p. 49) it was obvious that certain plants, the pioneers, were confined to open debris but it was not possible to say at what degree of total plant cover these pioneers disappeared. Patches of debris alternated with patches of heath in no discernible fashion (Part II, p. 38). With the subsequent investigations however it was established that the pioneer phase can be said to persist till total plant cover exceeds 5%. As this figure is reached the maximum number of pioneer species are present. Later I came to study this pioneer vegetation of the serpentine debris as a community in itself and without reference to succession. So I adopted a total plant cover of 5% as its approximate limit. The same limit was applied in the other debris areas I investigated. As a check, however, a few samples with higher cover were taken in various places: these are indicated in Table XIII. My criterion of uniformity was that the 1 sq.m. site selected should lack patches of vegetation of obviously higher stages in the succession; patches for instance of Calluna growing in humus and fine-particled earth where, otherwise, the substrate was predominantly mineral and composed of debris.

A. Arenaria norvegica-Cardaminopsis petraea sociations
Table XIII, Nos. 1 - 13(-17); serpentine and peridotite:
Unst, Rhum and the Coyles of Muick.

The Arenaria norvegica sociation has a floristic

Table XIII

The fellfield series

(a) Arenaria norvegica-Cardaminopsis petraea sociations (b) J. trifidus-D. flexuosa-A. alpina open sociations

*	locality	Unst (U)								Ruinsival		Coyles(C)			R	C	U	C	Orval	Hallival		Ronas Hill			Orval
	sample number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	degree of cover (%)	5	1	5	5	5	5	5	5	5	5	5	5	5	19	20	10	50	5	5	5	7	5	25	50
	rock type (b = basalt) (h = hallivalite)	Serpentine													Serpentine				b	h	h	granite-diorite			b
x	Arenaria norvegica **	2	2	2	1	-	x	1	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
x	Cardaminopsis petraea	-	-	-	-	1	1	2	-	1	-	1	1	2	-	-	-	-	-	-	-	-	-	-	-
	Silene maritima	-	-	-	x	2	-	1	x	x	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
x	Alchemilla alpina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	2	1	1	-	2
	Juncus trifidus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	1	1	-
	Deschampsia flexuosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	3	1	1	1	-
	Calluna vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	-	1	x	-	-	-	-	-	-	-	-	4
x	Salix herbacea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-
x	Thymus drucei	x	-	x	-	1	1	1	1	1	-	-	1	-	2	2	1	1	2	2	2	1	1	1	3
x	Vaccinium myrtillus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
	V. vitis-ideae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
	Lycopodium alpinum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
x	L. selago	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	1	1	-
	Selaginella selaginoides	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
	Agrostis canina	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	1	3
	A. stolonifera	1	-	2	x	-	1	1	2	1	-	1	1	1	-	3	4	1	-	1	1	1	1	-	-
	Festuca rubra	1	2	2	-	-	x	-	1	2	1	-	-	-	-	-	2	-	-	1	1	-	-	-	-
	F. ovina	-	-	-	-	-	-	-	-	-	-	3	1	3	-	4	-	4	-	-	-	-	-	-	-
	F. vivipara	-	-	-	1	-	-	1	-	-	1	-	-	-	4	-	-	-	3	1	2	2	1	2	3
	Koeleria gracilis	-	-	-	-	-	-	-	-	-	-	1	-	1	-	2	-	3	-	-	-	-	-	-	-

* Chamaephytes present where plant cover does not exceed 5%.

** The six species which respectively distinguish the sociations on acid and basic debris are placed first in this table, irrespective of life-form.

(to be contd.)

	sample number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	Carex bigelowii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
	C. demissa	-	-	-	-	-	-	-	-	x	1	-	-	-	-	-	-	-	x	-	-	-	-	-	-
	C. flacca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	4	-	-	-	-	-	-	-
	C. panicea	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	1	1	-	-	-	-	-	-	1
	Luzula spicata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
	Juncus triglumis	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Scilla verna	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Polygonum viviparum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
	Tofieldia pusilla	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Achillea millefolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
x	Antennaria dioica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	4
	Anthyllis vulneraria	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
x	Armeria maritima	-	-	-	-	1	1	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
	Campanula rotundifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
x	Cerastium alpinum	-	-	-	-	-	-	-	-	-	-	1	2	1	-	-	-	-	-	-	-	-	-	-	-
x	C. nigrescens	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
x	C. vulgatum	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
x	Cherleria sedoides	-	-	-	-	-	-	-	-	-	(x)	-	-	-	-	-	-	-	-	-	(x)	-	-	-	-
x	Cochlearia scotica	1	1	1	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Euphrasia rotundifolia	-	-	2	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-
	E. scotica	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	E. foulaensis	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-
	Galium verum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
	Leontodon autumnale	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
	Linum catharticum	-	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
x	Plantago maritima	x	-	1	x	-	1	-	2	3	2	-	-	-	1	-	3	1	2	1	x	-	1	1	2
	Potentilla erecta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-
	Rhinanthus spadiceus	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Rubus saxatilis	-	-	-	-	-	-	-	2	x	-	-	-	-	-	-	-	-	-	-	1	-	-	(x)	-
	Rumex acetosa	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
x	Sagina nodosa	1	1	2	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Saussurea alpina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
x	Saxifraga hypnoides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
x	S. oppositifolia	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
x	Silene acaulis	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Solidago virgaurea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	Viola canina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-
	V. riviniana	x	-	1	-	-	-	-	-	-	-	-	1	x	x	1	2	1	-	-	-	-	-	-	-

2

(to be contd.)

Sample number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Bryum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	x	-	-	-
Campylopus atrovirens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
C. flexuosus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x	-
Dichonodontium pellucidum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Dicranum scoparium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Grimmia decipiens var. robusta	-	-	-	-	-	-	-	-	-	x	-	-	-	-	x	-	-	x	-	-	-	-	-	-
Hypnum cupressiforme var. ericetorum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Polytrichum alpinum	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-
P. piliferum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Rhacomitrium lanuginosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	x	-	x	-
Rhytidiadelphus loreus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Ceratodon purpureum	-	-	-	-	-	-	-	-	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-
Rhacomitrium ellipticum	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Diplophyllum albicans	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Frullania tamarisci	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Lejeunia cavifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Cetraria aculeata	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	x	-	-	-	-	-	-	-
Cladonia cariosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	x	-	x	-
Cl. cervicornis var. subcervicornis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	x	x	-
Cl. rangiformis	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	x	-	-	-	-	-	-	-
Cl. subtenuis	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Cl. sylvatica	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Cl. uncialis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-

composition in Unst indicated by the samples in Table VI, Nos. 1 - 8; its debris habitat has already been described in detail (Part I pp. 24-7). Distribution of the sociations is (Part I p. 24) the distribution of this debris habitat itself. For Rhum and the Coyles of Muick these are therefore described together.

The Arenaria norvegica sociation has its maximum, on the debris areas of peridotite Ruinsival, between 1300 - 1600 ft (396 - 488 m.) but small patches also occur on the gravelly shores of Loch Fiachinis at 75 ft (229 m.). On Ruinsival there are broken cliffs and short scree slopes (with, as on the Coyles, Cardaminopsis petraea sociations) to N.W., W. and S.W. Eastwards the hill presents a slope of not more than 20 deg. overall, flatter near the col with Sgurr nan Gillean and level on the summit. Where the slope is at its maximum small level terraces about 3 m. broad alternate with steeper rock and boulder slopes formed from peridotite blocks disintegrating in situ. While larger areas of debris occur near the summit and the col, both these and the flat terraces consist of gravel and fine dark earth, which may form 80% of the surface and is up to 30 cm. deep. The soil is very soft to the tread and easily compressed, indicating frost-heaving. The essential similarity of the Unst and Rhum habitats is striking.

Cardaminopsis petraea sociation occupies, on the serpentine Coyles of Muick, short, steep talus slides in which the stones average 1 cm. diameter but are frequently larger and conversely approach gravel in size. Plants are often partly covered by stones sliding down from above. These talus slides lie at the base of a series of short crags chiefly to the southwest of the hill and between 1600 ft (488 m.)

and the summit at 1900 ft (579 m.). They resemble those beneath the broken cliffs on Ruinsival in which too *Cardaminopsis* is abundant. More or less flat patches of debris are rare on the Coyles; but the less steep a talus slide becomes the more it may resemble debris as a habitat, particularly where as here the talus itself is of comparable size to much of the debris under consideration. This is borne out by the similar communities in the two habitats. (Where by contrast the talus consists of larger stones, as happens in isolated localities on the Coyles, Ruinsival and Unst, then the communities consist mainly of ferns such as *Dryopteris filix-mas*, *D. dilatata*: see p. 147).

Soil-pH of this most open debris varies from between 6.12 to 6.62 in Unst, 6.60 to 6.88 on Ruinsival and 6.70 to 7.02 on the Coyles of Muick.

There is some variation between the sociations in the three localities. *Arenaria norvegica* (Plate VII, phot.1) and *Plantago maritima* are absent from the Coyles: *Cerastium nigrescens* is replaced here by *C. alpinum*. *Koeleria gracilis* (absent from Shetland) is confined to the Coyles, *Tofieldia pusilla* to Rhum, *Sagina nodosa* to Unst and so on. But there is basic similarity between these communities in such widely separated localities: in the presence of *Cardaminopsis*, *Silene maritima*, *Armeria maritima*, *Festuca rubra* or *F. vivipara*, *Agrostis stolonifera* and *Thymus drucei*.

On Unst the sociations with their name species and other pioneers (Part II p. 69) are only found on associated debris. On unassociated debris an impoverished form occurs. This lacks the pioneers but still has at least one of the fescues, bent, thyme and sea plantain.

B. Juncus trifidus-Festuca vivipara-Alchemilla alpina open sociations. Table XIII, Nos. 18, 24 basalt, Orval: Nos. 19, 20 hallivalite, Hallival: Nos. 21-23 granite-diorite, Ronas Hill.

F. vivipara-Alchemilla alpina open sociation occurs in the debris which is scarce on the predominantly peat covered basalt summit ridge, the only one examined, on the north of Orval at about 1300 ft (396 m.). Even if scarce the debris is still similar in appearance to the ultra-basic type. With some stones up to 20 cm. across, gravel forms a flat easily compressed surface over fine black earth.

Juncus trifidus-Alchemilla alpina open sociation is fairly common above about 1800 ft (549 m.) on Hallival, on debris terraces around 3.0 m. wide with 5 deg. slope. On these terraces gravel with some small stones overlies fine black earth, the surface sinking to the tread. The terraces alternate with 50 - 100 ft (15.2 - 30.5 m.) high dykes of hallivalite which traverse the mountain. Both from the appearance of the chips and the soil-pH (5.2) the debris seems derived from this hallivalite, not the abundant underlying peridotite of which the mountain is mainly formed. With these dykes, the overall slope of Hallival above about 1800 ft (549 m.) is nearly 30 deg. Much of this steep ground as far as the summit at 2300 ft (701 m.) is occupied by a closed 'improved' pasture associated with a vast number of burrows of the Manx Shearwater (Table XI, No.10, p.97).

Ronas Hill with an altitude of 1486 ft (453 m.) is the highest land mass in Shetland. Rising as a gently sloping hill in the south of the Shetland Mainland it is, like that district, composed of granite-diorite. Its summit plateau extends north-south for about half a mile at over 1400 ft (427 m.) and debris occupies more than 90% of the surface, extending to below 1000 ft (305 m.) on the westward side of the hill. The debris consists of a surface layer, about 1.3 cms. deep, of granite chips (1.3 - 2.6 cms. dia.) over very fine dark earth (indicating some humus fraction) in every sample taken. Many boulders strew the ground at this altitude; closed vegetation is confined to the lea of these (Plate I, phot.1) or to shallow gullies (see p. 136). Much of this debris covers ground with 0 - 5 deg. slope. On steeper 10 - 15 deg. slopes solifluction phenomena are visible (Plate VII, phots.2, 3), the debris being crossed by horizontal lines of closed vegetation. These are similar to the terraces on such slopes (or up to 25 deg.) in arctic-alpine regions (Wilson 1952) described by that author (l.c.) from Jan Mayen; from Iceland by Hansen (1930: Plate VIII, figs. 16-17) and from the Cairngorms by Watt and Jones (1948). Festuca vivipara, like Deschampsia flexuosa on Hallival, actually covers more ground than Juncus trifidus but the latter species and Alchemilla alpina differentiate these communities from those on basic debris. All the plants are very short, the leaves of the sedges and grasses rarely attaining more than 2.6 cms. in height, the herbs less. The flowering shoots of Leontodon autumnale and Deschampsia flexuosa lie along the ground. Luzula spicata (not in samples) and Saussurea alpina, which was barren and grazed (1952, 1955) are confined to the open sociations and, moreover, to altitudes above 1000 ft (305 m.). Juncus trifidus is also confined to the top 400 ft (122 m.) of the hill but occurs, if rarely, in the closed mat. Polygonum viviparum and Salix herbacea are also encountered in the most open conditions and in the closed mat. Mat-forming lichens which colonise the bare chips do not cover much ground and consist chiefly of Cladonia cariosa and Cladonia cervicornis var. subcervicornis. In all these cases from non-serpentine localities the debris is acid - varying between 4.05 on Orval and 5.2 on Hallival and 4.4 - 5.3 on Ronas Hill.

These examples from acid debris show similarities in the dominance or presence of Alchemilla alpina as a debris plant, of Juncus trifidus and Deschampsia flexuosa and Festuca vivipara, with Agrostis stolonifera, Plantago maritima and Thymus drucei. These last five species represent, on seaward parts of Sandness Hill between 700 ft (213 m.) and the summit at 816 ft (249 m.), an impoverished form of these sociations from which the differential species are lacking.

Red or viviparous fescue, bent, thyme and sea plantain are typical of debris areas lacking pioneers in Unst: areas that is of unassociated debris. With the general paucity of mosses and lichens these four or five species therefore provide a link between the sociations on basic and acid substrates.

The physical features of the habitat indeed seem similar - whatever its rock type and however limited or extensive on a particular outcrop, the debris always has a flat surface of small stones or gravel overlying finer material: is apparently unstable, liable to frost heaving and exposed to wind. These are the features of the classical fellfield (see Part II, p. 86). Sharing these physical features and a number of species are two groups of sociations, one on acid, the other on ultrabasic, debris. These sociations are distinguished by two mutually exclusive sets of species, some of which are used in naming the sociations. On the ultrabasic debris there are *Arenaria norvegica*, *Silene maritima* and *Cardaminopsis petraea*; on the acid debris *Juncus trifidus*, *Luzula spicata*, *Alchemilla alpina* and *Deschampsia flexuosa*.

Out of 45 species occurring in all samples in Table XIII (p. 115) where total plant cover does not exceed 5% (see p. 114): 19, or 42% are chamaephytes.

C. Affinities of the *Arenaria norvegica*-*Cardaminopsis petraea* sociations.

Whether the distinction between sociations on acid and basic debris can be maintained in other areas will be seen shortly. In seeking affinities however I am regarding the distinction for the present as valid. I take the group on serpentine first.

Another serpentine locality in Scotland, Meikle Kilrannoch of 2850 ft (869 m.) altitude, in Angus (V.C.90) harbours *Viscaria alpina* which is so characteristic of Fennoscandian serpentine (Rune 1953, p.56 and this paper p. 167). The species occurs here in open ground (Patton *in litt.*) subject to solifluction, the accompanying grasses showing signs of wind-erosion. Other species in the open community include *Armeria maritima*, *Cochlearia micacea*, *Cerastium semidecandrum*, *Cerastium vulgatum*, *Carex rigida* and *Festuca ovina*. To theseRoger (*in litt.*) adds *Cherleria sedoides*.

The two other British stations for *Arenaria norvegica* are both found off serpentine. The only published information on one, its Morven, Argyll, locality is given in a short note by MacLeay (1952, p.82). This colony of *Arenaria norvegica*, of about 100 plants, is on rocky detritus, a very unstable rich loam on a steep northwest slope with occasional *Cardaminopsis petraea* as an associate. Rock-type is not mentioned; to judge from the distribution of *Arenaria norvegica* it is probably basic (Nordhagen 1936, Rune 1953).

In Scandinavia, Nordhagen in several publications (1935, 1936, 1943) deals with the peculiar vegetation of talus slopes ('Rasmarkenes Plantesamfunn', Nordhagen 1943) in the low alpine sub-alpine regions. Of that occurring on unstable calcareous scree (limestone, dolomite and mica-schists) he distinguishes (1935, 1936) a particular widespread northern group: the Arenarion norvegicae subarcticum.

Of species found in the Scottish serpentine examples (Table XIII), this alliance on calcareous scree in Salten, Norway, has as constants: *Arenaria norvegica*, *Campanula rotundifolia*, *Cerastium alpinum* and *Saxifraga oppositifolia* (and six others); samples from north Norway have *Arenaria norvegica*, *Polygonum viviparum*, *Silene acaulis*, *Thalictrum alpinum*, *Tofieldia pusilla*, *Carex bigelowii* and *Festuca ovina* plus four species not in my samples.

Rune (*l.c.*, p.47) considers the abundance of *Arenaria norvegica* on Scandinavian serpentine debris to be sufficient justification for including that pioneer vegetation in Nordhagen's Arenarion for, apart from the name species, only one of the character-species of the alliance is apparently found on serpentine - *Cardaminopsis petraea*. But several of the constants such as *Silene acaulis*, *Campanula rotundifolia*, *Cerastium alpinum* and *Festuca ovina* are found even on pure serpentine. To these may be added *Minuartia rubella*.

In Rune's vegetation analyses (Rune *l.c.*, Table 3 p.48), by 1 sq.m. quadrats, of the Arenarion communities in N. Sweden, the open nature of the vegetation as in my examples is very apparent. Similarities in habitat are also shown by soil-pH

6.5 - 7.5, by the level nature of the ground (Rune, l.c., p.44) and by the remark (p.47) that, in contrast to calcareous ground where unstable soil is more or less restricted to scree at the base of cliffs, instability on serpentine is caused by frost-action or deflation. As to the serpentinicolous* species: Cardaminopsis, Cerastium alpinum and Luzula spicata (serpentinicolous in north Sweden: Rune l.c., p.51) are actually missing. Of the twenty species listed, fifteen, including Viscaria alpina and Juncus trifidus, are found in Britain and eight of these in my Scottish samples. Agreement is therefore moderate; but apart from geographical position itself, Rune's examples come from sub-alpine and low alpine regions.

In his study of the vegetation of the olivine of Sunmöre in south west Norway, Bjørlykke (1939, p.64) gives a vegetational analysis, in ten 1 sq.m. samples, of what I take to be a Cardaminopsis petraea sociation on a serpentine gravel slope at 175 m. above sea-level. Once again bare ground occupies 50 - 90% of the surface of every sample and cover of any species does not exceed 2 (Hult-Sernander's scale), being generally 1. There are 18 species, all but Agrostis capillaris occurring in Scotland and in some community or other on serpentine. But only 8 of these species are found on Scottish serpentine debris - Cardaminopsis itself, Festuca rubra, Viscaria alpina, Cerastium alpinum, Juniperus communis (as ssp. nana, on debris at Loch Fiachinis, Rhum), Rumex acetosa, Campanula rotundifolia and Silene acaulis. Silene vulgaris is represented in all my samples by S. maritima, while Asplenium viride is found in crevices, Deschampsia flexuosa and Lycopodium selago on acid debris (basalt etc., Table XIII, p. 115) and Calluna atypically on serpentine where total cover is 20% (see Table XIII, Nos. 14, 15, p. 115). Rubus saxatilis, a plant so

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* For Rune's definition of serpentinicolous see thesis p.164.

characteristic of oceanic debris (in Rhum, Ronas Hill and Unst) Bjørlykke says (l.c., p.120) is constantly found in crevices on the olivine crags.

There are some species characteristic of the Scottish serpentine debris examples which are not recorded by Bjørlykke from any of the Sunmöre serpentine localities: Arenaria norvegica, Sagina nodosa, Thymus drucei and, surprisingly in an oceanic climate, Armeria maritima and Plantago maritima. Since the relationship of the Scottish serpentine examples to the west Norwegian area might be expected to be closer than this, it is of interest that Rune (1953, p.125) records these last two species (A. maritima and P. maritima) with Sagina nodosa, Silene maritima and (p.87) Agrostis stolonifera as occurring abundantly in the serpentine of the Norwegian coastal districts "even comparatively far from the sea" (e.g. Isle of Rödön, latitude 66 deg. N. : Rune l.c.,p.90).

The Arenaria norvegica-Cardaminopsis petraea sociations on the Scottish serpentine are seen to be matched by counterparts on scree in Scandinavia, particularly in the oceanic regions. Where particle size is much the same and particularly where angle of slope approaches nil, then debris and scree intergrade as on the Coyles (p. 119). So it is possible to include these Scottish representatives in an oceanic serpentine facies of Nordhagen's Arenarion norvegicae subarcticum of communities on basic scree in Fennoscandian low alpine and sub-alpine regions.

D. Affinities of the Juncus trifidus-Festuca vivipara-Alchemilla alpina-Luzula spicata open sociations.

Within Britain good comparison can be made with the eroded Calluna - Loiseleuria facies in the Cairngorms between c.2600 - 2800 ft (793 - 854 m.) (Metcalfe 1950). Poore (1954) mentions small patches of an open Juncus trifidus community on coarse sand (soil-pH (A) 5.3, (B) 6.0) over quartzite on the top of the S.E. spur of Ben Lawers. The flora of these patches consists of Festuca vivipara, Juncus trifidus, Rhacomitrium lanuginosum, Polytrichum piliferum, P. alpinum, Cetraria islandica and Cornicularia aculeata (cf p.117).

Beyond Britain the calcifuge tendency of these sociations is not without foundation. The three differential species J. trifidus, Alchemilla alpina, and Luzula spicata are all facultative chasmophytes in the Saxifrágion cotyledonis subarcticum alliance of Nordhagen (1936, p.12), of communities of crevice plants on acid rocks in Scandinavian sub- and low alpine regions.

The sociations can be related floristically to the Juncion trifidi scandinavicum alliance of Nordhagen (1943) of dry grassland on acid mountains, for which Luzula spicata is a differential species; in particular to the F. vivipara-Rhacomitrium lanuginosum sociation (1943, p.205); of its 29 phanerogams 16, including J. trifidus and Saussurea alpina, occur in my examples which have however fewer lichens. Indeed the comparison is poor ecologically for these are predominantly closed grassland communities.

With the Juncus trifidus - Minuartia groenlandica grassland and fellfield vegetation type in S.W. Greenland (Böcher 1954) the Scottish examples share 11 out of the 21 phanerogams, including _J. trifidus_ itself, _Luzula spicata_, _F. vivipara_, _Carex bigelowii_, _Salix herbacea_ and _Polygonum viviparum_. Like the Scottish examples the soil is acid, from pH 4.3 - 5 in the _Luzula_ and _J. trifidus_ sociations. With the examples of open sociations the agreement with my Scottish samples is good. The moss and lichen flora, and cover, is far richer in the Greenland cases but the essentially very open nature of my samples must be set against this (see p.114).

E. Affinities of the debris sociations considered as fellfield.

The affinities so far suggested for the examples of sociations on acid and basic debris have been largely with closed vegetation, scree or at least where open vegetation is the exception not the rule. Only once has a sociation, in this case on acid debris, been shown to resemble fellfield which is typically open vegetation. No such affinity has so far been noted for the sociations on ultrabasic debris. The relationships have indeed tended to uphold the distinction drawn earlier between the basic and acid sociations without emphasising their many similarities. Both share several species regularly and, of factors assessed, only in soil-pH does there seem to be a significant habitat difference - and it is quite possible that even this distinction breaks down in other areas. So I deal briefly now with the Faeroes and Iceland where fellfield is a predominant type and the soil richer; in the latter, Hansen (1930, p.160) gives values for soil-pH between 6.2 and 6.9.

Icelandic fellfield ('melar'). Fellfield or melar (Hansen 1930, Steindorsson 1945) is an exceedingly sparse and mainly phanerogamic vegetation type in which bare ground is the chief physiognomic feature. It occupies most of the Icelandic Highland and parts of the Lowland. Its habitat is typically exposed and usually snow-free.

The most frequent phanerogams (Steindorsson 1945, p.462) are Silene acaulis, Armeria vulgaris, Cardaminopsis petraea, Saxifraga oppositifolia, Cerastium alpinum, Salix herbacea (Poa glauca) and, where the melar is more sandy, Arenaria norvegica, Festuca rubra, Silene maritima (and Carex incurva). In the relatively more fertile oases there are such additional species as Polygonum viviparum, Festuca ovina and F. vivipara, Luzula spicata (L. arcuata and Dryas octopetala). Chamaephytes are the predominant life-form, comprising 47% of the biological spectrum of melar. This compares with 15% for the flora of Iceland as a whole (Hansen 1930, pp.33, 178).

In the given samples, 600-720 m. in altitude, there is no Juncus trifidus or Alchemilla alpina but, as on Swedish serpentine debris, Luzula spicata occurs with Cardaminopsis petraea and Salix herbacea. Again, in Hansen's (1930, p.44) Table of melar vegetation at 250 m. altitude on Lyngdalsheiði, Cardaminopsis, Silene maritima and Silene acaulis grow in the same 0.1 sq.m. as Juncus trifidus and Luzula spicata. One only knows that the soil is non-serpentine but with a soil-pH range comparable to that on serpentine debris. So it would be pointless to speculate on the causes of the intermingling of species which are indicators, in the areas I have investigated, of acid or ultrabasic substrates.

It is unfortunately not possible to compare either author's associations with my sociations as their information was acquired by Raunkiaer's frequency method and no indication of cover, individual or total, is given. The general similarity however to my debris samples considered collectively is good. Of the 17 abundant Icelandic melar species in Steindorsson's table, 13 are found in my Scottish examples, many being very common there; for Hansen's table the figures are 16 and 14. It is also noted that the chamaephytes percentage for melar, of 47, compares closely with the chamaephyte percentage of 42 for all the samples of the debris sociations taken together (p. 123).

<u>Faeroese fellfield</u>. On the basaltic Fareoes, fjeldmark or fellfield and <u>Rhacomitrium lanuginosum</u>-rich vegetation are the two characteristic groups of communities from c.500 - 800 m. above sea-level. (Of the fellfield Ostenfeld notes that wind is the chief cause of barrenness.) Both communities may occur in suitable localities lower than the altitudes just given. In fact the examples of fellfield which Böcher (1937, p.160) gives in his table 1 are from below 500 m. One from 270 m. (5 - 15 deg. slope) and two from 400 m. (flat ground) are given in this paper Table XIV, p. 131. Total cover is very low; <u>Festuca vivipara</u>, <u>Agrostis</u> varieties, <u>Thymus drucei</u> and <u>Plantago maritima</u> are all there as in the Rhum and Shetland examples.

Also listed are <u>Cardaminopsis petraea</u>, <u>Silene acaulis</u>, <u>Cerastium nigrescens</u>, <u>Viola riviniana</u> and <u>Polygonum viviparum</u>. Unfortunately soil-pH is not indicated; but the gravel will be basaltic (Ostenfeld 1909) and, in view of its slow weathering may be weakly acid even if nutrient-rich (Nordhagen 1943, p.544) (the Orval, Rhum, basalt debris is distinctly acid - pH 4.03; p. 122). Certainly <u>Alchemilla alpina</u> and <u>Luzula spicata</u> and <u>Deschampsia flexuosa</u> of the 'calcifuge'

Table XIV

Vegetational analyses of Faeroese fellfield; Hult-Sernander's 5 point cover scale (see Part I, p. 39) (from Böcher 1936, p.160).

Altitude : metres	270	414	414
Slope : degrees	5-10	0	5
Aspect	east		west
Sample size : sq.m.	4	1	1
Silene acaulis	1	2	
Alchemilla alpina		2	2
Festuca vivipara	1-2	1	1
Thymus drucei	1	1	
Saxifraga caespitosa		1	1
Oxyria digyna	1		1
Luzula spicata	1	1	
Cerastium nigrescens			1
Viola riviniana	1		1
Sedum villosum	1		
Agrostis canina (var.)	1		
A. tenuis (var.)	1		
Polygonum viviparum		1	
Salix herbacea		1	1
Empetrum hermaphroditum	1		
Plantago maritima (var.)	1		
Saxifraga oppositifolia			1
Ranunculus acer var. pumila			1
Deschampsia flexuosa var. montana			
Selaginella selaginoides	1		
Euphrasia borealis and scotica	1		
Taraxacum faeroense	1		
Cerastium caespitosum	1		
Rhacomitrium lanuginosum	1	2	
Stereocaulon denudatum	1		

Ostenfeld (1909) also lists *Juncus triglumis*, *Cochlearia officinalis* (forma), *Saxifraga nivalis* and *S. stellaris* (*pygmaea*) and *Thalictrum alpinum*.

sociations are all there, the latter in an adjoining sample, while J. trifidus is recorded in open vegetation for boulder-strewn hillsides (Geröllhalden) at 600 - 660 m., Luzula spicata and Cardaminopsis petraea are also recorded together at 730 m.

Once again the distinction between basicole and basifuge sociations breaks down. But the general similarity to my fellfield, taken together, is striking - 16 out of 24 species in the Faeroese list for fellfield alone (and excluding Geröllhalden and Fliessererdeboden) are common to my Scottish lists.

The serpentine debris vegetation can be related to the Arenarion norvegicae subarcticum of basic scree and that on acid debris to communities on acid substrates, including rock crevices, in Britain and beyond. But the species which distinguish the acid and ultrabasic sociations in Scotland grow together on fellfield in Iceland and the Faeroes; where accordingly the distinction between such sociations, as defined, breaks down. Collectively however they have marked affinities, floristically, in life-form and in habitat, with exposed snowfree fellfield vegetation of the Faeroes and Iceland in particular. They can therefore with justice be considered sociations of the same vegetation type.

Table XV

Rhacomitrium-rich dwarf shrub heath series

	Locality (S=Sandness Hill)	Ronas Hill								S	Orval	
	Sample number	1	2	3	4	5	6	7	8	9	10	11
	Cover scale: HS, Hult-Sernander: D, Domin.						HS	HS			D	D
x	Arctostaphylos uva-ursi	-	-	cd	d	-	-	-	-	-	-	-
x	Arctous alpina	-	-	-	-	-	-	-	cd	-	-	-
	Calluna vulgaris	d	d	cd	x	x	-	1	x	cd	4	-
x	Empetrum hermaphroditum	sd	x	x	-	x	-	1	x	x	-	-
	Erica cinerea	sd	-	x	-	-	-	-	-	-	-	-
x	Loiseleuria procumbens	-	-	-	-	d	5	-	-	-	-	-
x	Salix herbacea	x	-	-	x	x	-	-	-	x	4	-
	Thymus drucei	x	x	x	-	x	-	-	x	x	(x)	-
	Vaccinium myrtillus	-	x	x	x	x	1	1	x	x	3	2
x	V. uliginosum	-	-	-	x	-	-	5	x	-	-	-
x	V. vitis-idaea	-	x	-	x	-	1	1	x	-	-	-
	Lycopodium alpinum	x	x	x	x	x	2	-	x	x	4	-
	L. selago	x	x	x	x	x	1	1	x	x	(x)	2
	Hymenophyllum wilsoni	-	-	-	-	-	-	-	-	x	-	-
	Agrostis canina	x	-	-	-	-	x	-	-	x	4	3
	A. tenuis	-	x	x	-	x	-	2	x	-	x	-
	Anthoxanthum odoratum	-	-	-	-	-	-	-	-	-	1	-
	Deschampsia flexuosa	-	x	x	-	-	2	1	-	x	3	2
	Festuca rubra	-	-	-	-	-	-	-	-	x	-	-
	F. vivipara	x	x	x	x	x	1	x	x	x	6	4
	Molinia caerulea	-	-	x	-	-	-	-	-	-	-	-
	Nardus stricta	-	-	x	-	-	3	-	x	-	1	-
	Sieglingia decumbens	-	-	x	-	-	-	-	-	-	-	-

(to be contd.)

Table XV (contd.)

	sample number	1	2	3	4	5	6	7	8	9	10	11
x	Carex bigelowii	x	x	x	x	x	3	1	x	x	-	7
	C. binervis	-	-	x	-	-	-	-	-	-	3	-
	C. panicea	-	-	x	-	-	-	3	-	-	4	-
	C. pilulifera	x	x	x	-	x	1	-	x	-	5	3
x	Juncus trifidus	-	x	-	-	x	-	-	-	-	-	-
x	Polygonum viviparum	-	-	-	-	x	-	-	-	-	-	-
x	Alchemilla alpina	-	x	-	-	x	-	-	x	-	-	-
	Antennaria dioica	x	x	x	-	x	-	-	-	x	-	-
	Euphrasia foulaensis var. maritima	-	-	-	-	-	-	x	-	x	-	-
	E. rotundifolia	-	-	-	-	-	x	-	-	-	-	-
	E. scotica	-	-	-	x	-	-	-	-	-	-	-
	Galium hercynicum	-	-	-	-	-	-	-	x	x	1	-
	Hypericum pulchrum	x	x	-	-	-	-	-	-	-	-	-
	Jasione montana	-	-	-	-	-	-	-	-	x	-	-
	Leontodon autumnale	-	x	-	-	x	-	-	-	-	-	-
	Luzula multiflora	-	-	-	-	-	-	-	-	-	1	-
	Plantago maritima	-	-	-	-	x	-	-	-	-	-	-
	Polygala serpyllacea	-	-	-	-	-	-	-	-	-	1	1
	Potentilla erecta	x	x	x	-	-	1	3	x	x	3	2
	Rhinanthus minor	-	-	x	-	-	-	-	-	-	-	-
	Taraxacum officinale	x	-	-	-	-	-	-	-	-	-	-
	Viola canina	x	x	-	x	x	-	x	-	x	-	-
	V. riviniana	-	-	x	-	-	-	-	-	-	-	-
	Campylopus atrovirens				-	x	1	-	-	-	-	-
	C. flexuosus				x	-	-	-	-	x	-	-
	Dicranum bonjeani				-	-	-	-	-	x	-	-
	D. scoparium				-	x	x	-	-	-	x	-
	D. falcatum				-	-	-	-	-	x	-	-
	Hylocomium splendens				x	x	-	-	-	x	x	-
	Isothecium mysuroides				x	-	x	-	-	x	x	-
	H. cupressiforme var. ericetorum				x	x	-	x	x	x	x	x
	Polytrichum piliferum				-	-	x	x	-	x	x	x
	Plagiothecium undulatum				-	-	x	-	-	x	-	-
	Rhacomitrium lanuginosum	cd	cd	cd	cd	cd	4	5	cd	cd	6	6
	Rhytidiadelphus loreus				-	-	-	x	-	-	-	x

(to be contd.)

Table XV (contd.)

sample number	1	2	3	4	5	6	7	8	9	10	11
Diplophyllum albicans				-	-	x	-	-	x	x	-
Frullania tamarisci				x	-	-	-	x	-	-	-
Cetraria aculeata				-	-	-	-	x	-	-	-
C. islandica				x	-	-	x	-	-	-	-
Cladonia cervicornis var. subcervicornis				-	x	x	-	x	-	-	-
Cl. subtenuis				-	-	-	-	-	-	x	x
Cl. uncialis				x	-	x	x	-	x	x	x

V. Rhacomitrium-rich dwarf shrub heath series

Table XV. Shetland Mainland and Unst, Rhum.

A. Rhacomitrium-rich Loiseleuria-Calluna heath.

Table XV, Nos. 1 - 8; Ronas Hill, Shetland.

The preceding fellfield vegetation is successionally related in all my samples to the grass-heath series already described, except on Ronas Hill. There the fellfield is succeeded in suitable localities by a Rhacomitrium-rich Loiseleuria-Calluna Heath. This is described here because its presence in Shetland has a distinct bearing on the ecological status of the fellfield vegetation in Unst and, by extension, in the other localities examined. This description is a preliminary one.

Lowland and submontane communities. There are three groups of closed community on Ronas Hill corresponding to three main intergrading habitats. The first two are mentioned briefly.

Deep peat is distributed on and is most typical of lower ground wherever drainage is impeded, but persists to the summit of Ronas Hill in a very shallow but apparently sheltered gully. Trichophorum caespitosum - Eriophorum - Empetrum - Rhacomitrium communities occupy the greater part of the low-lying peat both on Ronas Hill and in North Roe. It is replaced at higher levels - from c.1100 ft upwards - by a Nardus-Juncus squarrosus community with an underlayer of Vaccinium vitis-idaea, V. myrtillus and V. uliginosum. The vegetation here is 23 cms. high compared with 1.2 - 3.8 cms. on the adjoining open debris.

Better drained peat occurs at lower levels along stream sides or edging the steeper granite knolls with which so much of North Roe is covered. A Calluna-Listera cordata-

Pleurozium schreberi community occupies such ground, Calluna itself reaching 61 cms. in height in sheltered localities. Poore (1954) records a similar lowland sociation in the Breadalbanes in Perthshire. The community in Shetland merges at lower altitudes into the Trichophorum-Eriophorum group on poorly drained ground and at higher levels into some of the following series.

Rhacomitrium* -rich Loiseleuria-Calluna series. The soil is analogous to the more stony, not drift, types under the Calluna-Juniperus nana-Carex pulicaris series in Unst, Rhum etc. Exceptionally as deep as 20.4 cms. the black humus is thin, usually admixed with granite chips, typically well drained and overlying debris or the knolls of granite bedrock; in the latter cases the closed communities usually alternate with patches of open debris. This well drained habitat occurs from as low as 500 ft (152 m.) in North Roe and not below about 800 ft (244 m.) on the southwest, most exposed, flank of Ronas Hill itself. Apart from some local occurrences of the preceding communities, the Rhacomitrium-rich Loiseleuria-Calluna series (Rhacomitrium heath hereafter) forms the only closed vegetation above about 1000 ft (305 m.) on that hill.

The heath consists of a series of communities, dominated by alternative suffruticose species, in all of which Rhacomitrium is present, co-dominant or dominant. These dwarf shrubs form a flat mat level with the Rhacomitrium, from 1.3 - 7.6 cms. deep, the inflorescences and leaves of the grasses and sedges protruding beyond that (Pl.VIII phot. 4). The community is grazed by

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* Rhacomitrium lanuginosum

sheep. Though the methods of getting results varied, the Table shows that there is an underlying similarity in the usual co-dominance of *Rhacomitrium* itself and in the invariable presence of *Carex bigelowii*, *Festuca vivipara*, *Vaccinium myrtillus*, *Lycopodium alpinum* and *L. selago*.

From 500 ft (152 m.) upwards the suffruticose co-dominants may be *Calluna*, *Empetrum hermaphroditum*, *Arctostaphylos uva-ursi*, *Arctous alpina* and *Erica cinerea*. Above 900 to 1000 ft (274 - 305 m.) areas of heath may have as alternative dominants or co-dominants *Loiseleuria*, *Salix herbacea* or *Vaccinium uliginosum*.

Considerable work has still to be done before any causation, on the lines of Crampton's work (1911) in Caithness and Metcalfe's (1951) in the Cairngorms, can be discerned between the various communities in this *Rhacomitrium* heath. It is obvious that exposure is the master factor and that gradations in this factor and in drainage, both resulting from micro-relief, must largely affect the interrelationship. It is evident for example on the last 200 - 300 ft (61 - 91 m.) on the south and southwest of the hill that such closed vegetation as there is is entirely confined to wind shadows in the lea of boulders and largely consists of prostrate *Calluna*-mat in which *Rhacomitrium* itself is subordinate.

Eleven arctic-alpine species (Matthews 1955) and one low arctic-oceanic species (*Lycopodium alpinum* : Böcher 1954) comprise 29% of the flora of the *Rhacomitrium* heath on Ronas Hill (Table XV, p. 133). The dwarf shrub species and *Lycopodium alpinum*, *L. selago*, *Antennaria dioica* and *Polygala serpyllacea* together total 15. Of 42 species, therefore, 36% are chamaephytes. These figures compare with an arctic-alpine total of 30% for fellfield on Ronas Hill and a Ch [illegible] percentage also of 30. (*Salix herbacea*, *Alchemilla alpina*, *Juncus trifidus*, *Luzula spicata*, *Polygonum viviparum* and *Saussurea alpina* are all arctic-alpines; *S. herbacea*, *Thymus*, *L. selago*, *Antennaria dioica*, *Plantago maritima* and *Armeria maritima* are all chamaephytes).

B. *Rhacomitrium*-rich *Calluna* communities.

Table XV, Nos. 10-11. Sandness Hill, Shetland; Orval, Rhum.

On sandstone Sandness Hill, West Mainland, from 700 ft (213 m.) to the summit at 817 ft (249 m.) open sociations on debris and *Rhacomitrium* heath occupy the tops and seaward faces of the ridges, while blanket-bog occurs in the hollows and up to the summit on the east side. The *Rhacomitrium* heath has *Salix herbacea*, *Carex bigelowii*, *Lycopodium alpinum*, *L. selago*, *Vaccinium myrtillus* and *Calluna*. In Unst, a *Rhacomitrium*-*Empetrum hermaphroditum* community, with *Carex bigelowii* and *Calluna* but lacking *Salix herbacea* (on gneiss rocks at 500 ft : 153 m.) occurs on very coarse greenstone debris from 300 - 400 ft (91-122 m.).

In Rhum one sample was taken on basalt debris, of small compacted stones, at the summit of the col between Orval and Fionchra; the other was also in an exposed situation, this time near the edge of the west facing cliffs of Orval, at 1350 ft (412 m.); the plateau behind consisted largely of *Nardus*-*Juncus squarrosus* communities on thick peat.

C. Affinities in and beyond Britain.

Within Britain, *Rhacomitrium* heath was first recognised by Robert Smith (1900) as a community on mountain top detritus above 3000 ft (914 m.) in Perthshire. There are 20 species of vascular plants given, in W. G. Smith's (1911) list amended by Tansley (1939), as characteristic of the Rhacomitrium heath. Of these, 15 occur in the Ronas Hill Heath; three of the remainder are absent from Shetland. But Loiseleuria, so typical of the Caithness examples (see below) and locally co-dominant in the heath on Ronas Hill, is not mentioned.

The Rhacomitrium-heath on the plateau of Cader Idris (2700 ft : 820 m.) includes no species of vascular plant not found on Ronas Hill (except Campanula rotundifolia which has one doubtful station in Shetland). Lacking for example many of the dwarf shrubs like Calluna or Loiseleuria, it seems an impoverished version of most of that heath and equivalent more to a Rhacomitrium-Carex bigelowii nodum (for definition of 'nodum' see Poore 1955 a) described by that author from the Breadalbanes at 2700 - 3100 ft (823 - 945 m.) on exposed ridges, usually swept bare of snow in winter or late spring.

Beyond Britain, Ronas Hill Rhacomitrium heath shows poor correspondence with Icelandic Rhacomitrium-heath as described by Hansen (1930) and Steindorsson (1945). Once, from S.Iceland, Steindorsson (l.c., p.455) records an "unusual variant of Grimmia-heath" - one rich in Vaccinium uliginosum. Otherwise its affinities lie far more with the dwarf shrub heath (Icelandic mo) of well drained lowland ground with moderate snow cover.

The Icelandic Rhacomitrium-heath, with Carex bigelowii, Salix herbacea and Polygonum viviparum as the most frequent phanerogams, is more like the species-poor Rhacomitrium-heath of the highest and most exposed altitudes in Britain; so is Böcher's Rhacomitrium-heath, rich in Empetrum or some other species, from southwest Greenland (which he places in the

Loiseleuria-Salix uva-ursi type of dwarf shrub heath with inconstant snow cover). Here too may belong the *Rhacomitrium*-heath recorded by Du Rietz (1925, in Böcher 1937 p.166) from flat ground at 550 m. altitude above Bergen, west Norway. The vegetation (Hult-Sernander's scale) consists of *Rhacomitrium hypnoides* 5 : *Carex rigida* 2-3 : *Salix herbacea* 1 : *Juncus trifidus* 1 : *Festuca vivipara* 1. Further inland in Scandinavia *Rhacomitrium* only forms small cushions, not a carpet. I return to this point shortly; meanwhile the absence of *Calluna* from all these *Rhacomitrium* heath samples is noted. This applies also to the *Rhacomitrium*-rich vegetation in the Faeroes which occurs most typically from 500 - 800 m. but is found down to 300 m.; *Calluna* is mentioned by Ostenfeld (this paper p. 107) as scarce even in the lower parts of the Faeroes. Otherwise the correspondence of the Faeroese *Rhacomitrium* heath, at least to 500 m., is the closest so far to the Ronas Hill type; among the 33 vascular plants found there, 26 occur in the 36 on Ronas Hill.

The lack of *Rhacomitrium* as a mat former in landward Scandinavia is in line with the paucity of this species in the Loiseleuria-Arctostaphylion (Kalliola 1939) alliance, in the Braun-Blanquet classificatory system, of communities presumed able to do without good snow cover (Nordhagen 1943) and therefore corresponding to one of the chief features in the habitat of *Rhacomitrium* heath. Its sociations as described by Nordhagen (*l.c.*) from the Sikkilsdalen are conspicuously lacking in that moss as they are, indeed, abundant in lichens. This applies to more continental parts of Iceland also (Steindorsson 1936 in Böcher 1937 p.166).

Three points emerge from this survey : (1) the North Atlantic distribution of *Rhacomitrium* heath with its absence from, for instance, continental Norway, (2) the lack of equivalence of the Ronas Hill and most of my other examples with this Rhacomitrium heath which (3) normally lacks Calluna and in Britain, anyway, is found at the higher levels.

Returning now to comparisons within Britain, I note that all the species found in the Ronas Hill series except Salix herbacéa, Polygonum viviparum and Juncus trifidus are listed by Crampton (1911) in the same sort of communities, the "Plant formations of the alpine plateaux" in Caithness (e.g. Morven, altitude 2313 ft : 705 m.); the same dwarf shrub species at any rate act as alternative dominants. As on Ronas Hill lichens are scarce. Ignoring for the present the prominence of Rhacomitrium in the Ronas Hill samples, most of them can, with Crampton's Calluna-mat, be related to the sub-alpine Calluna sociation described by Poore (1954) from the Breadalbane mountains. This is in the most exposed localities, regularly blown free of snow in winter, between 2600 - 2850 ft (792 - 869 m.), lower by all but 1000 ft (305 m.) than the Rhacomitrium-Carex bigelowii nodum (see p. 139). All the phanerogams in Poore's list, except Gnaphalium supinum are found in the Ronas Hill examples above 1000 ft (305 m.).

The alignment of most of this Rhacomitrium-rich series with high-level Calluna vegetation seems further justified from the reported behaviour of that species in the Cairngorms (Watt and Jones 1948, Metcalfe 1950). Mountain Callunetum according to the latter author occurs there from 220 - 3200 ft (671 - 976 m.) on well-drained exposed slopes. In sheltered localities its maximum altitude is much less; this is attributed to its intolerance of snow-lie. Arctostaphylos uva-ursi is typical of the lower parts of the zone - up to 2600 ft; Loiseleuria from 2600 - 3000 ft (790 - 915 m.), descending lower on the ridges than in the valleys: in exposed places *Loiseleuria* may reach as low as 2200 - 2000 ft (671 - 610 m.). All the vascular plants present in Metcalfe's *Calluna*-*Loiseleuria* facies occur in the Ronas Hill heath; the most notable difference lying in the high percentage cover (25 - 30%) of lichens in the Cairngorms. This relationship is confirmed by the fact that, on Ronas Hill, the open *Juncus trifidus*-*Luzula spicata*-*Alchemilla alpina* sociation is serally related to the *Rhacomitrium* heath series and is equivalent (p. 127) to the eroded *Calluna*-*Loiseleuria* facies in the Cairngorms.

In Norway the Ronas Hill *Rhacomitrium* heath resembles the *Cladonia sylvatica*-*Cl. rangiferina*-rich *Calluna* sociation (Nordhagen, 1928) from Sylene, which has, again, little *Rhacomitrium*. Linked to the sub-alpine *Calluna* sociation from Breadalbane, this lichen-rich sociation is placed by Nordhagen in a dwarf shrub heath alliance (Phyllodoco-Myrtillion : Nordhagen 1943) having moderate snow cover. In Iceland too the Ronas Hill heath resembles more closely the dwarf shrub heath (Icelandic mo) of well drained lowland habitats having moderate snow cover. In these, *Calluna* is present and *Rhacomitrium* according to Hansen (1930) is of local occurrence. (Correspondence is good with examples from the oceanic south country - *Arctostaphylos uva-ursi* and *Loiseleuria* communities : Hansen, *l.c.*, p.48, Table 11A, Nos. 8, 9).

The paradox incidentally arises that this *Rhacomitrium*-rich dwarf shrub heath belongs to an alliance typified in terms of habitat by little or no snow cover, but actually has its greatest affinity with communities characterised in continental regions by moderate snow cover. (This of course illustrates the difficulty of applying a classification of vegetation to an area far from that for which it was originally invented.)

Nevertheless the alignment of the Ronas Hill Rhacomitrium heath with a Calluna zone in which Rhacomitrium is normally inconspicuous, at once explains its lack of correspondance with the usual Rhacomitrium heath. Although an Empetrum-Vaccinium zone is interpolated in the Cairngorms, in more sheltered areas which have some snow lie, the Rhacomitrietum lies on exposed slopes directly above the Calluna-Loiseleuria zone (Watt and Jones 1948). This Rhacomitrietum is related in turn to the Rhacomitrium heaths of Iceland, the Faeroes, S.W. Greenland etc. So both these facts confirm the importance attached earlier to the absence of Calluna from these heaths.

Not only has Rhacomitrium greatly increased, in Shetland, in a community in which it is beyond Shetland normally inconspicuous; it even descends there on certain hilltops as low as 300 ft (91 m.) above the sea. This question is discussed later in relation to climate (p. 159).

VI. Asplenium viride sociation (Basic rock crevice series).

The crevice habitat is merely an extension of a more or less horizontal talus slide, which in turn grades into debris. So species lists for crevices from various localities may overlap similar lists for debris. Only presence or absence of a species was recorded from the crevices. Lists were made in serpentine and, for comparison, on basalt, hallivalite and granite-diorite localities in Shetland, Rhum and Aberdeenshire.

In the localities examined, two species are confined to the ultrabasic crevices - Asplenium viride and A. adiantum-nigrum; Silene maritima is confined to ultrabasic debris, scree or crevices. Cardaminopsis petraea which is so characteristic of ultrabasic debris or scree is confined, on rocks of which the debris at least is acidic, to crevices.

These 4 species are found in each of the three areas examined. Asplenium adiantum-nigrum also occurs on very small serpentine outcrops on Hoo Fell, Shetland Mainland. Asplenium viride is the one plant among them confined in Britain to crevices on basic rock (C.T.W.1952). This plant is also typical of crevices on basic rocks in Scandinavia where it is widespread enough to have been used to characterise the plant communities in that habitat (see below). In N. Sweden, Asplenium viride occurs in nearly every serpentine area, but here the fern "forms tufts etc. on plain bare soil patches" (Rune 1953, p.45), suggesting that it characterises sociations without parallel in Scotland, whether on serpentine or not. There is indeed little or no correspondence between my lists and Rune's serpentine examples of the Asplenion viride subarcticum. Nordhagen (1936, p.12), however, originally described this alliance as crevice communities of basic rocks

Table XVI

Communities of rock crevices

Rock type	serp.	serp.	serp.	basalt	halli-valite	granite-diorite
Locality	Unst	Coyles	Ruin-sival	Orval	Halli-val	Ronas Hill & N. Roe
Asplenium viride	x	x	x (scree)	-	-	-
A.adiantum-nigrum	x	x	x	-	-	?
Cardaminopsis petraea	x mainly debris	x mainly scree	x mainly debris	x	x	-
Silene maritima	x mainly debris	x	x	-	-	-
Draba incana	x	-	x	-	-	x
Avena pratensis	-	x	-	-	-	-
Sedum roseum	x	-	x	x	x	x
Oxyria digyna	-	-	x	x	x	-
Cystopteris fragilis	-	x	?	-	x	x
Polypodium vulgare	x	x	x	x	x	x
Saussurea alpina	-	-	-	x	-	debris
Luzula sylvatica	-	-	-	x	-	x
Thelypteris dryopteris	x	x	-	-	-	x
Lastraea montana	-	-	x	-	-	-
Dryopteris dilatata	x	x	x	?	x	x
D. filix-mas	x	-	x	?	-	x
Cryptogramma crispa	-	-	-	x	-	-

in Scandinavian sub-alpine and low alpine regions. In this paper, Nordhagen points out that the crevice communities of basic rocks on the west coast of Norway contain *Asplenium viride*, *A. adiantum-nigrum*, *A. marinum*, *Phyllitis scolopendrium* etc. *A. marinum* in Shetland, and that species and *Phyllitis scolopendrium* (doubtfully recorded for Shetland) in Rhum, are restricted to seacliffs. *A. viride* is typical of crevices on the serpentine of Sunmöre, S.W. Norway, occurring (Bjørlykke 1939, p.85) on 28 out of 30 outcrops. *A. adulterinum*, *A. adiantum-nigrum*, *Viscaria alpina*, *Silene vulgaris*, *Silene maritima* and *Cardaminopsis petraea* also occur, though the last four are most typical of the serpentine scree. From similar evidence Nordhagen (1943, p.568) concludes that the crevice communities of the Norwegian west coast belong to a particularly oceanic alliance. Containing the four species found constantly in the 3 Scottish serpentine crevice localities examined, from 100-1800 ft. (30 - 549 m.), the Sunmöre examples certainly correspond with them far better than the Swedish examples. (The corresponding sociation of acid rock crevices is not described here, though some examples are given.)

Footnote

Luzula sylvatica is quite absent from the serpentine localities, even from the stable boulder scree which occurs sparsely on Ruinsival and the Coyles. Among such boulders however are some of the larger ferns which accompany that species in the ledge vegetation of which it is so characteristic: *Dryopteris dilatata*, *D. filix-mas*, *Lastraea montana* and, surprisingly in view of its calcifuge tendencies (C.T.W.1952), *Thelypteris dryopteris* found among boulders of both the Coyles and Unst, one of its few Shetland stations.

VII. Climate and vegetation.

A. Vegetation zones and climatic affinity.

Both fellfield and Rhacomitrium heath as represented in the Scottish examples have been shown to be related to vegetation with a north Atlantic distribution; the fellfield resembling most closely those of the Faeroes and Iceland. An attempt will now be made to see whether the occurrence of these communities, and submontane heath, at different altitudes in different regions can be connected with some causal climatic factor; such as the mean temperature of the warmest month. Since fellfield and Rhacomitrium heath in particular are typical throughout their range of a well drained, humid, exposed and usually snow free environment, this is presumed initially to provide a reasonably uniform background against which variation in temperature can be assessed.

The existence has long been known of apparent anomalies in the altitudinal distribution of certain species in Scotland. Montane in the east or central Highlands, they descend to sea-level in the west and north and occur in many of the islands. The correlations traced here elucidate this so-called problem.

Fellfield and Rhacomitrium heath are characteristic of all the more exposed, usually snowfree areas in low and subarctic - oceanic regimes in S.W. Greenland (from 900 m.) (Böcher 1954) and Iceland (Steindorsson 1945 and Hansen 1930). They form the characteristic vegetation in the Faeroes from 500 m. (Böcher 1937), where the calculated mean temperature of the warmest month must be at least 7.7 deg. C. (45.9 deg. F.*) or already low arctic- oceanic, to 800 m. above sea-level; but occur in suitable localities down to 240 m., in the subarctic - oceanic summer climate.

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* Throughout Chapter VII the temperature data used in this and subsequent cases are taken from Fig.3A (p. 19a) and Appendix Table XXIII, p. 209.

Rhacomitrium heath is limited in the Highland areas noted to exposed snowfree localities above 2700 ft (823 m.) (Breadalbanes) or 3100 ft (945 m.) (Cairngorms: this paper, pp. 140.144); below that is a mean temperature of the warmest month of about 48 - 49 deg. F. or well within the subarctic-oceanic summer regime, and probably also at its upper limits in a low arctic - oceanic summer regime. In Shetland however Rhacomitrium has become prominent in a Calluna-Loiseleuria heath; and its analogous Highland community in similar exposed snowfree localities occurs from 2600 - 2850 ft : 743 - 869 m. (Breadalbane) or 2600 - 3000 ft : 793 - 915 m. (Cairngorms) (this paper, p.142); not that is above a mean temperature of about 50 - 51 deg. F. and not below about 49 deg. F. (Its narrow range lies entirely within the subarctic-oceanic summer regime.) The same lower altitude applies to the related fellfield vegetation on Ronas Hill and in the Highland areas noted.

So far two fairly definite zones have been established. While the possible correlation of their lower limits with a given mean summer temperature of the warmest month is new, one would expect the low arctic and subarctic affinities demonstrated here - from the high percentage of chamaephytes (30 - 36) and the fact that the important species in both communities have predominantly low arctic or subarctic distributions (p. 138). Above the temperatures of 50 - 51 deg. F. (or below the equivalent altitude) the picture is less clear; for they may extend well above this temperature.

In Shetland, Rhacomitrium-rich Calluna heath occurs on exposed parts of Sandness Hill at 700 - 816 ft (213 - 249 m.). It is found down to 300 ft (91 m.), and fellfield from 500 ft (152 m.) to sea level, in suitable localities in Unst. This is up to an isotherm of 53 - 54 deg. F., or within the submontane-oceanic regime. In the Coyles the analogous scree community, at 1600 - 1900 ft (488 - 579 m.) occurs within the submontane regime. Correlation must be regarded as very tentative in Rhum where fellfield extends from 2300 - 1200 ft (701 - 366 m.) down in a few places to 750 ft (229 m.). The lower limit can be said with reasonable certainty to lie not below an isotherm of about 54.3 deg. F. - the arbitrary lower limit of the submontane (oceanic) regime which lies at sea-level in Shetland, 1176 ft (359 m.) at Dalwhinnie. To that extent neither community may be said to exist in lowland regimes.

Consideration of upper altitudinal limits in Rhum I leave for the moment, beyond noting that these cannot lie much below the 50 - 51 deg. isotherm. One important point however is that the closed vegetation which is successionally related to this fellfield is submontane grass-heath. This applies even at the highest altitude, 2300 ft (701 m.), examined.

This leads to the question of climax vegetation. Low and subarctic - oceanic fellfield is succeeded on Ronas Hill (or the Cairngorms) by low arctic - oceanic dwarf shrub heath. At higher levels - over 1000 ft (305 m.) - on that hill the communities forms a mosaic and the predominant vegetation. This mosaic on Ronas Hill is therefore the climatic climax in what has been shown independently to be a subarctic-oceanic summer climate. In Unst and Rhum the fellfield (or scree on the Coyles) is succeeded by a sub-montane sedge-grass-heath which with other, peat, communities is the predominant vegetation. Fellfield there is an edaphic climax. The same could be said of the <u>Rhacomitrium</u>-heath on Unst and Sandness Hill. (In this way, incidentally, the serpentine fellfield in Unst can be seen to persist through the failure of submontane climax vegetation to develop over its surface. Its relict nature, indicated by the high proportion of arctic and boreal species and high Ch percentage (p. 57) is very clear.) Finally the analogous submontane heath is uncommon in the Faeroes where it picks and chooses its stations, needing the habitat, rare in these islands, of dry substrate and sunshine (Ostenfeld 1909). It is subordinate to the <u>Nardus-Juncus squarrosus</u> grass-moor. Persisting up to 200 m. (Böcher 1937) this heath community may well be an edaphic climax over most of its range.

In Shetland and the Highland areas noted, then, this suggested isotherm of 50 - 51 deg. F. for the usual lower altitudinal limit of the low and subarctic communities also seems to coincide with the upper altitudinal limit for the submontane heath community. (To this extent it is fortunate, if fortuitous, that "submontane" is usually accepted as approaching an isotherm of 50 deg. F.). In Rhum the figure for the upper limit of the submontane heath community is unlikely to be less than 49 deg. F. I therefore feel reasonably justified in regarding temperature, expressed by the mean temperature of the warmest month, as controlling the limits of certain communities in well drained, humid, exposed and usually snow free habitats.

In summarising the findings it may be said that <u>Rhacomitrium</u> heath and fellfield are characteristic of and predominant in low arctic - oceanic climates in S.W. Greenland, Iceland and the Faeroes and extend there into subarctic - oceanic regimes or, as <u>Calluna-Loiseleuria</u> and fellfield, into subarctic - oceanic summer regimes on Ronas Hill, the Cairngorms and Breadalbane. With an isotherm between 49 - 50 deg. F. marking the transition, Rhacomitrium-heath and fellfield extend as edaphic climaxes into submontane - oceanic regimes in Rhum and Shetland (or as scree in the Coyles), where submontane heath predominates. None occurs in lowland regimes.

B. Vegetation, temperature and the oceanic climate

It has been possible to correlate climatic zones, based on the mean temperature of the warmest month, with vegetation zones in exposed habitats at different altitudes in north Atlantic oceanic areas and several Scottish montane areas. Changes between limits of zones it would seem one may correlate with gradations in this factor. Exceptions are dealt with below (p. 158).

First, current evidence on the relationship between temperature and plant growth is briefly examined. By controlled experiment it has been found that certain plants only grow where day and night temperatures are kept within certain limits (Went 1945). Conditions for flowering and fruiting are usually narrower than they are for vegetative growth. This has been demonstrated empirically in the field by Pearsall (1950). Using Juncus squarrosus this author shows that with increase in altitude there is a decrease in the yield of flowers and mature capsules of this species. He notes for instance (Pearsall l.c., p.51) that "a point is reached generally about an altitude of 2500 - 2700 ft (762 - 823 m.) above which fertile fruits are not usually produced though plants may form inflorescences of considerable size and in other ways be capable of making satisfactory vegetative growth." He concludes from further evidence that the effect is mainly due to the retardation of the development of flowers and fruit. Until 1947 for example, viable seeds had not been collected from above 2700 ft (823 m.) but the exceptionally warm summer of that year led to abundant seed production - viable seeds were actually collected on Ben Wyvis at 3400 ft (1037 m.). This indeed may explain the common experience of finding only barren plants of many species at high altitudes.

Went (1950) has summed up the findings of a series of his experiments with cultivated vascular plants in controlled day and night temperature conditions. He points out that a revision is necessary of our ideas on the temperature limits within which plants can exist. Freezing for example has been thought to be the lower temperature limit which most plants can endure; the explanation being the damage inflicted through the formation of ice crystals. Yet the African Violet dies if subjected for long periods to night temperatures of 50 deg. F. (10 deg. C.), far above any possible frost injury. Similarly Bellis perennis dies when kept for long enough at night temperature of 66 deg. F. (20 deg. C.) or over - hardly a high enough temperature for the infliction of heat damage. Went (l.c., p.493) concludes that "the distribution of plants is not just a question of heat coagulation or frost damage but is correlated with very specific temperature requirements only met with in certain climates". One obvious remark in connection with frost damage is this: it is an arbitrary point, and any plants growing beyond for instance the firn line are likely, and indeed known (like Salix herbacea) to continue growth where soil temperature is below freezing point. Just as other arctic species, for instance Oxyria digyna (Russell 1940), have been demonstrated to have high sugar concentrations which may both confer frost immunity and promote the rapid growth and early flowering observed in arctic climates.

It seems that one may postulate for a plant a temperature range within which it gives its best vegetative or, in a narrower range, reproductive performance and an upper and lower limit beyond which it will die. This is no less reasonable than assuming a specific soil-pH range for a plant, or indeed a range in any other factor.

Correlation has been shown in my own examples to exist between certain veg zones and the mean temperature of the warmest month. This mean would seem from first principles to be as convenient a way as any of indicating broadly the amount of warmth available to a plant during the growing season. Similarly, as a lower (summer) temperature limit (or upper altitudinal limit), it could mark the minimum total requirement for growth. This is of course the basis of the 'tree-line'. It is usually accepted that trees (however these are defined!) cease to grow where the mean temperature does not exceed 50 deg. F. for at least two months in the year. Lowering temperature may progressively lengthen a plant's life-cycle, or prevent its completion and thereby eventually produce a limit for that species at a given altitude in a particular region.

It is possible however that extreme temperatures may also create such a barrier to spread. Salisbury's dictum that extremes are more important than means in determining plant distribution was substantiated by that author (Salisbury 1939) by ample evidence, mainly with reference to lower temperature limits. More recently Dahl (1951) in a paper on the relationship between summer temperature and the distribution of alpine vascular plants in Fennoscandia, has produced evidence, quite independently, in support of this view but, this time, of upper temperature limits. Dahl, using a standard lapse rate, calculated a series of isotherms based on the mean annual maximum temperature (for 15 years) in upland stations throughout Fennoscandia. He then shows the distribution of a large number of alpine species in Fennoscandia can be correlated with particular isotherms. It seems quite reasonable to assume such a relationship, but surely the length of the period during which the plant is subjected to such temperatures is of some importance. While one may agree that extremes may be more important than means, the assumption being made here(as with frost injury)is that less than a day, perhaps a few hours, of a maximum temperature in a year are fatal to a perennial plant. It would be interesting to know the relationship of maximum temperature to mean temperature of the warmest month. The isotherm for maximum temperature could correspond, on the ground, to that for a related temperature (see p. 157).

Examples of Dahl's findings are examined shortly. Meanwhile, having in mind the experimental evidence of temperature effect, some examples of my own data are now examined to see whether the limit of any species can be correlated with a particular mean isotherm of the warmest month. *Calluna vulgaris* persists to 984 ft (300 m.) in the oceanic Faeroes (Ostenfeld 1909); as a dominant there it reaches 656 ft (200 m.): and it reaches 3200 ft (976 m.) (Watt and Jones 1948) as a dominant in the analogous Cairngorm community. The calculated mean temperature of the warmest month at that altitude in the Faeroes is 47.2 deg. F. and 49 deg. F., and for the Cairngorms about 47 deg. F. (*Calluna* persists to the top of Ronas Hill at 1486 ft (453 m.) as a very prostrate plant, even below this altitude mainly in the lea of boulders (Plate I, phot.1), which suggests that the approximate limit of tolerance is being reached. Here the equivalent (calculated) temperature is 49.5 deg. F.) These figures are only approximate (see Part I p.11 and Appendix, Table XXIII). They nevertheless suggest that a figure for the mean temperature of the warmest month, in this case about

47 deg. F., does indicate a limit for *Calluna* in exposed humid habitats.

Loiseleuria procumbens and *Juncus trifidus* are species for which upper mean temperature limits may be set. They are restricted to higher ground in Britain (C.T.W.1952). So far as I am aware, on Ronas Hill they reach their lowest altitude and in this respect an extreme in Britain. The species do not descend below 1000 ft (305 m.) there, where the mean temperature of the warmest month is calculated to be about 51 deg. F. *Loiseleuria* descends to 2200 ft (671 m.) in the Cairngorms, *Juncus trifidus* to 2400 ft (732 m.) (Watt and Jones 1948) in the analogous community and habitat, where the calculated temperature is between 51.8 and 50.6 deg. F. In Caithness, 1349 ft (411 m.) is the lowest altitude for *Loiseleuria* mentioned by Crampton (1911). *Juncus trifidus* descends in Rhum to about 1900 ft (579 m.) where, on the basis of a lapse rate not lower than that operating at Dalwhinnie, the equivalent temperature cannot be in excess of 51.6 deg. F. Now *Saussurea alpina*, *Alchemilla alpina* and *Luzula spicata* are also all confined to altitudes over 1000 ft (305 m.) in Shetland, below that is the temperature of 51 deg. F. *Luzula spicata* is like *Loiseleuria* absent from Rhum and is confined to high ground in Sutherland (Crampton and McGregor 1913). Both *Saussurea* and *Alchemilla alpina* by contrast occur in Rhum at considerably lower altitudes - *Saussurea* on Orval scree at about 1000 ft (305 m.) (well within that is the submontane oceanic regime) which suggests a tolerance of higher summer temperature. These observations on the altitudinal distribution of *Luzula spicata*, *Saussurea* and *Alchemilla alpina* agree with the data given by Clapham, Tutin and Warburg (1952) for their altitudinal distribution in Britain; both *Saussurea* and *Alchemilla* descend nearly to sea level in Scotland

(*Alchemilla* in Skye). *Luzula spicata*, like *Loiseleuria* and *Juncus trifidus*, is confined to higher ground. For these three species then, in exposed humid habitats, a lower altitudinal limit is indicated by a mean isotherm of about 51 deg. F. This temperature is not greater than that found in subarctic-oceanic summers.

Occurring down to sea level in Unst (54.3 deg. F.) *Arenaria norvegica* in Rhum does not occur below 750 ft (229 m.) where the analogous temperature, again on the basis of a lapse rate no lower than that at Dalwhinnie (p.11), cannot be more than 55 deg. F. From these few examples it may be said therefore that correlation does exist between the lower altitudinal limits of some species, the upper limits of others and the mean temperature of the warmest month.

There remains to be considered the data given by Dahl (1951) for some of the species I have mentioned. For *Arenaria norvegica*, Dahl gives a mean annual maximum temperature of 23 deg. C. (73.4 deg. F.) which fits the facts from Unst; at Baltasound, altitude 31 ft (9.5 m.), the recorded extreme between 1917 and 1947 is 73 deg. F. *Juncus trifidus*, *Loiseleuria* and *Luzula spicata* are montane in Britain and confined on Ronas Hill to a mean temperature of the warmest month below about 51 deg. F. The limit of penetration of all three low-arctic species into north temperate regimes of Fennoscandia is indicated broadly by the 27 deg. C. (80.6 deg. F.) isotherm. If there is any doubt as to the actual limiting temperature involved, it is apparently of the same order for all three species. And, though I have insufficient evidence to judge properly the importance of this maximum temperature factor, certain observations make some of the figures Dahl quotes unlikely to be of general application. *Juncus trifidus* cannot endure a maximum temperature of more than 27 deg. C., *Arenaria norvegica* of 23 deg. C. Yet the former is montane in Britain generally and occurs in both Rhum and Shetland well above *Arenaria norvegica* (where in Unst the maximum temperature for that species has been recorded). *Juncus trifidus* in Scotland does not apparently penetrate as far up the maximum temperature gradient (or down in altitude) as it does in Fennoscandia.

In other words while it is reasonable to postulate a maximum temperature above which a species cannot for any length of time grow, it does not follow that that line is always reached in nature; its distribution may stop short of the maximum value possible where some other factor or group of factors modify or become more important than the temperature effect.

Similarly, while the evidence on the relationship, between the limits of certain species in this habitat and the mean temperature of the warmest month, has confirmed the significance attached to this measure; there are still certain exceptions to the actual zonations particularly in oceanic areas which suggest that temperature, at least for the specific values given to each zone, is not always a limiting factor.

There is the overlapping of certain communities such as fellfield or *Rhacomitrium* heath in Unst into what are atypical climatic zones - where they form, it was noted, edaphic climaxes. There is also the general increase in prominence of *Rhacomitrium* in oceanic areas. What factors common to the oceanic and montane climates under discussion could so vary as to modify the postulated limiting effect of temperature?

High humidity and strong winds are two such features. Any case of the limiting effect of temperature has always been qualified by reference to exposure. For this factor with the total or almost total lack of winter snow cover is particularly characteristic, throughout their distribution range, of fellfield and Rhacomitrium heath. And it is moreover a factor which is independent within limits, of altitude, being determined as often by topography. In these communities above all the oceanic and montane environments must be most alike.

Given of course particular edaphic conditions, the importance attached to variations in exposure (in this case an extreme) therefore fits in exactly with the conclusions reached from study of the debris vegetation in Unst (Part II). That is to say, exposure controlled in large measure the presence of the open habitat itself. These findings in turn bore out the original evidence of the magnitude of the winds blowing in Shetland compared with similar altitudes in 'exposed' upland, landward, areas (viz. Sandness Hill and Eskdalemuir ; Appendix Table XXIV). Again, while it is on well drained ground, the Rhacomitrium heath in Unst and all its Shetland localities occupies hilltops where it too may be subjected to exposure and, with the prevalent cloud, a particularly high degree of atmospheric humidity.

Atmospheric humidity, like exposure, is likely to increase with altitude in the climates in question; and in comparing oceanic and montane climates, one cannot go further than assuming that humidity will be consistently high in all oceanic regions, and generally high in montane regions with equivalent summer temperatures. So the general increase in dominance of Rhacomitrium in oceanic areas must be due to an increase in humidity and/or exposure relative to landward montane areas with the same summer temperature.

Lack of winter snow cover has been mentioned as a point of environmemtal similarity (from low arctic - oceanic areas downwards): it also indicates a difference between oceanic and montane climates which will be most marked at the extremes. For, owing to narrow temperature range of the former, winter temperature will be one factor not shared by zones with some temperature equivalence in summer. This difference will become particularly apparent in snowfree habitats. This too might affect the spread of Rhacomitrium.

Another instance of this is perhaps the closer similarity of most of the Rhacomitrium heath on Ronas Hill, not to Rhacomitrium heath itself, but to communities having negligible Rhacomitrium and no snow cover in the Cairngorms, or moderate snow cover in Norway and Iceland. Equally may the higher winter temperature allow certain species like Salix herbacea to persist in exposed ground where in colder regions they are normally covered by snow.

Existence of some correlation between climatic zones, based on the mean temperature of the warmest month, and vegetation zones in exposed humid habitats has been demonstrated empirically. Further observations on the distribution of individual species in these habitats has strengthened this correlation. Exceptions in oceanic areas to the suggested limits of certain zones has been explained by reference to the increased exposure and, possibly, humidity operating in these areas relative to landward montane areas with the same summer temperature.

Mention was made, at the start of this chapter, of 'anomalies' in the altitudinal distribution of certain species in the Scottish Highlands; Saussurea alpina and Alchemilla alpina may be quoted as examples (p. 156). The evidence presented above offers a reasonable explanation of this so-called problem. But the correlations traced here have not, so far as is known, been attempted before. Experimental evidence and large amounts of comparable data on species distribution are also lacking. So the causal connections suggested for particular cases must be regarded as tentative.

VIII. General and specific features of serpentine vegetation shown by the Scottish examples examined.

A. The affinities of serpentine vegetation.

It is now possible to assess how far the vegetation of the serpentine areas I have examined can be said to exhibit general features and how far specifically serpentine features.

The heath sociation-group is not restricted to serpentine but is typical rather of well drained soil (like the north Swedish serpentine heath). It has some affinity with the Faeroes Calluna-Erica cinerea heather moor of dry substrates. Though all the samples of the sedge-grass sociation-group were confined to serpentine, this group nevertheless is closely related to the heath, of which it seems largely to be a grazed variant. The series as a whole has a small proportion of arctic-alpine species and its climatic affinity is indicated by referring to it as submontane-oceanic sedge-grass-heath (the Coyles samples lacking Plantago maritima and having more lichens); it may well prove to have a far wider distribution.

The mire sociations, only examined in Unst, are related to eutrophic-mesotrophic types on non-serpentine substrates.

Looked at from a basicolous point of view the debris community in general, and the Coyles scree in particular, resemble the Arenarion norvegicae subarcticum, a northern alliance of communities described by Nordhagen on basic scree in subalpine and low alpine regions of Fennoscandia. In particular it resembles the communities of serpentine debris of that region in Scandinavia. The closest floristic relationship is however with the vegetation of the serpentine screes of oceanic south-west Norway.

The serpentine debris sociations in the areas investigated share a habitat, essentially the same apart from its soil-pH and chemical composition, with sociations on various types of acid debris in Scotland. They also share a number of species with these sociations. Considered collectively indeed the debris communities are seen, in their exposed snowfree habitats and oceanic climates, to be part of a predominantly north Atlantic vegetation type. Their closest affinity lies with fellfield of the Faeroes and Iceland. Fellfield itself is a low arctic-oceanic and subarctic-oceanic community, the serpentine sociations in Unst and those on serpentine and non-serpentine debris in Rhum forming edaphic climaxes in a submontane-oceanic climate. This fellfield is absent from lowland regimes.

Always having Asplenium viride and A. adiantum-nigrum in the three localities examined, the crevice community is related to the Asplenion viridis subarcticum of Nordhagen, of crevices in basic rocks in sub- and low-alpine regions of Fennoscandia. It shows no correspondence with the north Swedish Asplenium viride sociation on serpentine debris but rather, again, with the examples, this time of crevice communities, from S.W. Norway: which Nordhagen has suggested might be part of an oceanic alliance.

Where closed vegetation is present and contact with the underlying rock to some extent lessened by humus and a developed soil profile, there is as expected nothing to distinguish such communities on serpentine from others on non-basic substrates. Debris and crevices of course allow such contact; so, through flush effect, do soligenous mires. Wider affinities apart, the communities there are seen to resemble those in similar habitats on basic rocks or subjected to basic flush effect. There are still no specifically serpentine features.

B. Serpentinicolous species.

Neutral calcareous soils have high calcium supply, but the neutral substrates of serpentine debris and rock crevices differ from these in their low calcium and high magnesium supply and, frequently, high nickel supply. Vegetation of these serpentine habitats should be best distinguished by any species which may be said from their distribution to have a preference for serpentine in the sense just given. Observations on this point now follow. The relationship to the calcicole habit I discuss on p. 168 .

It was noted in Part I that, as with the degree of fidelity of a species to a community, so will there be differences between local and general preference for (or exclusiveness to) serpentine.

Now Rune (1953) uses serpentine-characteristic and serpentinicolous synonymously, defining such plants (Rune l.c., p.50) as occurring more frequently or abundantly on serpentine than on other rocks or soils in the vicinity. (My frequency-ratio expresses these differences quantitatively in Unst: Part I, p. 41). Rune is inconsistent here. Although he defines the term in a local sense he uses it in a wide sense - of species with a preference over their distribution range for serpentine. That indeed seems a proper use of serpentinicolous in the way that basicolous indicates a regional preference for base-rich substrates. As it is, the definition leads one to class as serpentinicolous both a species which might prefer, let us say, a dry habitat and is therefore found locally on serpentine, and one preferring serpentine itself. Wider as well as local distribution must be known and the terms included in any definition. This can be illustrated by example.

Rubus saxatilis is only found, in Unst, on serpentine debris. There it is serpentine-characteristic. On the Shetland mainland however it occurs in several stations, among them granite-diorite debris (Ronas Hill) and sandstone boulders by Loch Clousta. It is absent from the Coyles of Muick but widespread, particularly in the debris, on hallivalite Hallival, or peridotite Barkeval and Ruinsival, Rhum. There it is not even serpentine-characteristic in the sense of being locally exclusive to serpentine (or peridotite).

On the other hand Asplenium viride, in Britain a plant of basic crevices, is noticeably confined in my samples to serpentine. Although there is an appreciable amount of exposed limestone in Shetland the species is actually restricted in these islands to one rocky locality on Unst serpentine. The situation is paralleled in Rhum where, although limestone is present, this fern is confined to scree on the north side of the peridotite Ruinsival; this and Pabbay are its only stations in VC 104 (Heslop Harrison 1939). This plant is very rare in Rhum and Shetland and confined in both places to small areas of extensive serpentine.

So I reserve serpentine-characteristic, as in the analysis of the flora of Unst in Part I, for local use. There are 24 species of that type in Unst (Part I, Table I, p.5a). I define a serpentinicolous species as one found more often on serpentine than on other rocks or soils in the vicinity (local preference) and usually, within the limits of its own range, where serpentine occurs (regional preference).

Confining attention to the Scottish examples, four species in Table XVI (p. 146) occur in all three localities, three fulfilling the second requirement of the definition. A fifth, Arenaria norvegica, has two of its four British stations on serpentine. As to local preference, Arenaria norvegica only occurs in Shetland and Rhum on serpentine, and Silene maritima in the samples in question prefers ultrabasic rock to other local types. The serpentinicolous nature of Asplenium viride has already been noted. Asplenium adiantum-nigrum is the fourth species found only on serpentine within the samples given and on Hoo Fell (p. 145). Being more widespread, it may not at least in Rhum have such a marked local preference as Asplenium viride.

Cardaminopsis petraea is found in the three serpentine examples. Exclusive to that rock in Shetland, this species occurs in Rhum on other rock types also but still has a local preference for serpentine, in that it is far more abundant on that rock. Cardaminopsis is found in Rhum on serpentine debris, scree or crevices; on hallivalite (Hallival), basalt (Orval) and mugearite (Fionchra) it is confined to rock crevices.

(Finally there is Viscaria alpina ,outwith my serpentine examples. The species is however confined in Scotland to serpentine at 2850 ft (869 m.) on the Angus hills: Asplenium viride, A. adiantum-nigrum, Silene maritima and Cardaminopsis petraea are absent (fide Roger in litt.) from this montane region.)

Of the 24 serpentine-characteristic species in Unst (Part I, p. 5a) these five (and Viscaria alpina) can be judged serpentinicolous in Scotland.

Comparison is now made with what have been judged serpentinicolous species in N. Sweden (Rune 1953) and W. Norway (Bjørlykke 1939).

Rune lists 17 species and varieties of vascular plants as serpentinicolous in N. Sweden. Six (4 species with 2 varieties of one) of these are absent from Britain; of the remaining 11, 3 are serpentine varieties of Cerastium alpinum, C. vulgatum and Viscaria alpina, undescribed from this country;

the presence on Scottish serpentine of the Cerastium varieties might however be demonstrated by experiment. That applies also to Rumex acetosa, present on Unst debris; it is a so far undescribed serpentine race of the species which Rune (l.c., p.52) lists as a serpentinicolous plant in N. Sweden. The remaining 7 are Agrostis stolonifera, Asplenium viride, Arenaria norvegica, Luzula spicata, Molinia caerulea, Silene acaulis and Viscaria alpina (s.s.).

Molinia caerulea and Agrostis stolonifera in Scotland at least, show no preference for serpentine and Luzula spicata is quite absent from the serpentine localities examined, though present on heath on the Kilrannoch serpentine. In the same way Juncus trifidus in my Scottish examples favours non-basic substrates; in Scandinavia it occurs commonly on serpentine debris (Rune and Bjørlykke). Silene acaulis, away from sea-cliffs, is serpentine-characteristic in Unst and Hoo Field (Fell) on the Shetland Mainland but is also on a number of other well-drained rocks like granite-diorite etc. Absent from the Coyles, and in Rhum behaving rather as in Shetland, it is not therefore serpentinicolous in Scotland. This leaves Asplenium viride, Arenaria norvegica and Viscaria alpina.

Bjørlykke (1939) lists Asplenium adulterinum and its hybrid with A. viride as exclusive in Sunmöre to serpentine. Cardaminopsis petraea, Asplenium adiantum-nigrum, A. viride, Cerastium alpinum, Silene maritima, S. vulgaris and Viscaria alpina are serpentine-characteristic on that W. Norwegian island. Apart from Silene vulgaris and Cerastium alpinum, this is the list of serpentinicolous species from Scotland.

In common with their behaviour in Fennoscandia, Asplenium viride and Arenaria norvegica are serpentinicolous in submontane and submontane-oceanic regions of Scotland. With oceanic west

Norway, these regions share the serpentinicolous species *Silene maritima*, *Cardaminopsis petraea* and *Asplenium adiantum-nigrum*. *Viscaria alpina*, another Fennoscandian serpentinicolous species, is found on east Scottish serpentine at 2850 ft (869 m.); but *Cardaminopsis*, the two *Asplenia* and *Silene maritima* are lacking in this montane region.

None of the serpentinicolous species common to Scotland and Fennoscandia or west Norway is confined to serpentine or in some cases even to basic rock. This applies both within these regions and beyond (in say Iceland or the Faeroes). The relationship of the serpentinicolous to the calcicolous habit is therefore briefly mentioned. Some recent findings by Steele (1955) are pertinent here.

From field observations and by experiment Steele shows calcicoles are of at least two types. The exacting types grow successfully on experimental neutral soil with high calcium supply; in the field they are confined to limestone. The less exacting types occur in the field also on soils with low calcium supply. These may be more acid, or neutral (serpentine), soils. On experimental soils these types showed a wider range of tolerance.

Of the serpentinicolous species listed above, *Asplenium viride* is the only one for which Steele has data. As expected, it is a less exacting calcicole. If this species conforms, *Cystopteris fragilis* does not. That other fern of basic rocks is listed by Steele, from field-observation, as an exacting calcicole. Yet in the regions examined in the present study, *Cystopteris fragilis* has been observed in basic rock crevices on serpentine (the Coyles), on hallivalite (in Rhum) and on granite-diorite (North Roe, Shetland).

This illustrates the difficulty always encountered in any attempt to establish some definite soil preference of a species throughout its range, as opposed to the preferences of races of that species. Steele notes for example the difference in soil preference of inland chalk-down and maritime cliff populations of Anthyllis vulneraria. The same question was illustrated in a general way by noting the marked acid and basic preferences, in the Scottish fellfield, of two mutually exclusive groups of species (e.g. Juncus trifidus and Arenaria norvegica). On circumneutral soils in Icelandic fellfield they intermingle in the same 0.1 square metre.

One can list the serpentinicolous species common to Scotland and Fennoscandia, (as one could the calcicoles). This does not however deepen our understanding of the problem. It merely indicates which species it would be most profitable to study. For, in dealing with isolated occurrences of certain species, particularly where as in the Scottish examples some of these are at or near the limit of their range, it is by study of these individual populations that some answer will be found.

PART IV.

FIELD INQUIRY INTO WHAT RESTRICTS THE PIONEERS TO THE SERPENTINE DEBRIS HABITAT IN UNST.

I. Introduction and review of problem

What I have called the pioneers are by definition (p. 50) confined on serpentine in Unst to debris, or debris and sea-cliffs. Some species like Armeria maritima occur in and beyond Shetland on a wide variety of rock-types. Others are restricted to debris or scree throughout their range, like Arenaria norvegica, which is confined to debris in all its Scottish localities (Part III), Iceland (Hansen 1930, p.83), Sweden (Rune 1953) or scree in Norway. Likewise Cardaminopsis petraea is confined in Scotland to debris (Part III), scree or rock crevices, in Iceland to melar (Hansen, l.c., p.83), in Sweden to river gravels, scree etc. (Rune l.c., p.30). Species such as Armeria maritima occur on sea-cliffs in short pasture; Rubus saxatilis is found, in the Scottish localities examined, in closed vegetation (see p. 95). Most of the species however share more or less open habitats. Some causes of this restriction are now examined.

The problem becomes indeed the general one of species that are rare and have discontinuous distributions in some or all parts of their range. The commonest feature of their habitat - whether debris, gravel-bank or sand-dune - is its ecological youth; they are pioneer habitats (Griggs 1940). The rare species have survived because, for some reason or other, climax vegetation has failed to develop over the surface (Pigott and Walters 1954). These conditions are of course fulfilled precisely in Unst, both in the ochreous associated patches of debris (Part II, p. 69) providing the conditions of ecological youth and retarding colonisation, and in the relict nature of the pioneer community itself (Part III, p.150-1). This is an Arenaria norvegica or Cardaminopsis petraea sociation in a submontane-oceanic climatic regime in which submontane sedge-grass-heath forms the predominant vegetation.

There are two approaches to this general problem which may or may not be mutually exclusive. Plants are restricted to habitats like debris because they are positively adapted only to the chemical and/or physical conditions of such soils and could survive under natural conditions in no other, disappearing with increasing plant cover; or they are restricted because they are adapted to open conditions per se and are therefore eliminated by increasing plant cover.

The absence in Unst of pioneers from unassociated grey debris was discussed in Part II (p. 69). The soil itself was not regarded as unsuitable, for pioneers grow in grey patches of associated debris. This absence was in fact attributed to the limited powers of dispersal of the pioneers and the lack, through the secondary origin of the unassociated debris, of a source of supply of these species.

The present restriction to associated debris has deeper implications. The pioneers form a relict community. With their undisputed need for highly mineral soil and/or open ground, the progressive advance of the heath vegetation will have meant the pioneers' becoming more and more dependent on areas where either the fresh supply of mineral soil or the retarding of colonisation was more or less continuous. Rapidly weathering areas are only found in highly serpentinized rock which inevitably, and as demonstrated, gives soil with a very high nickel content. Such soil also has neutral pH and high magnesium content. Toxic symptoms similar to those occurring in oat plants on serpentine soils in Aberdeenshire have been induced experimentally by several workers, on oat plants in nutrient solutions, through the addition of nickel (see Part II, p. 73). And experimental evidence suggests that offspring of Arenaria verna var. gerardi from the Lizard serpentine are adapted to high Mg. supply in soil of neutral pH (Steele 1955). Positive adaptation to the specialised chemical conditions of associated debris is therefore very likely. (This is not of course axiomatic in the case of serpentinicolous species so far as that definition goes (Part III, p. 149)).

I have already (Part II, p. 55) drawn attention to the parallel between the plant and soil succession starting on serpentine debris in Unst and that on the limestone scree in Derbyshire described by Balme (1953). Although this authoress was writing mainly with a view to elucidating the calcicole-calcifuge problem, her general conclusions are pertinent here. Balme (l.c., p.342) notes that the development of the soil from rendzina to podsol is essentially a process of chemical differentiation, and it seems probable that the chemical composition of the soil plays the most important part in determining the major floristic differences in the succession. "Whereas the lack of severe competition and the good drainage and aeration of the shallow rendzinas may help to produce a favourable environment for the calcicoles, the sudden disappearance of exclusive species, reduced frequency of calcicoles and simultaneous invasion of calcifuges suggests an essential chemical change occurs in zone II" (the transitional Festuceto-Agrostidetum). (Balme's exclusive species can in the present context be considered 'rare'.) Preliminary experiments conducted by Balme, of which details are not given, suggest that the calcicole habit may be a positive adaptation to the specialized conditions of calcareous soils such as high soil-pH and calcium-ion concentration.*

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* Since Balme's paper appeared, Steele (1955) has elucidated the relationships of calcicoles to some of these conditions; see this paper, Part III, p. 168.

These are, however, only suggestions and by far the larger volume of literature inclines to the view (suggestion too!) that rare species are restricted to open habitats because of this very openness; they cannot compete successfully with the commoner plants. Images of corresponding aggressiveness and weakness are sometimes employed (viz. Fernald 1940). Griggs (1940) says that "the main conditions for the survival of epibiotics", such as constitute a relict community (Part II, p. 74), "seems to be the rather low competition in their habitats; their disrupted ranges support this view". Rune (1953, p.125) says "Arabis petraea, in Scandinavia, grows exclusively in localities with low competition - shores, or river gravels and screes"; and Rune (l.c., p.80): "As only a limited part of the surrounding flora seems to have the capacity to withstand the toxic effects of serpentine soils (by which I presume Rune means debris), serpentine areas are always more or less barren and they are seldom invaded by closed communities. Thus plants thriving in serpentine (debris) live almost without any actual competition". Rare species are confined to open habitats largely because these are areas of low competition. In a prisere they must be eliminated by increasing competition. As an explanation of their restriction to open habitats, that is the question mainly examined in this part of the thesis.

Competition and related terms are now examined. Most of the previous examples must be taken to imply competition as "the whole struggle for existence so far as this is conditioned by biotic factors" (Griggs 1940). Competition exists as soon as one plant goes short of an essential requirement due to the activities of another plant.

'Low' competition has already been mentioned. This, and 'severe' competition, seem to be concepts derived primarily from spacing. Spacing leads to open or crowded conditions. Crowding implies shortage of space, and therefore of nutrients, water and light, and hence severe competition. (This seems reasonable so long as one distinguishes between actual space occupied in air or ground as opposed to nutrients and water taken up and shade cast.) If crowding implies severe competition, openness implies the converse. But in the climax vegetation of (say) desert, open spacing does not necessarily mean low competition. Competition on the contrary is severe for the little available water. The great extent is well known of the root systems of desert shrubs in relation to their aerial growth. Clements, Weaver and Hanson (1929) point out that herbs and grasses are quite absent around or in the large spaces between such shrubs. They suddenly appear in great quantity when the shrubs are cleared. Similarly, on an extensive rock face, competition must be severe for the few places which can support plant growth. So it is invalid necessarily to equate at least open spacing with low competition.

A further difficulty connected with competition arises from its relationship to reaction - the effect a plant or community exerts on its habitat (Clements 1916, p.79). Clements, Weaver and Hanson (1929, p.316) regard competition as the cardinal function of the community. Yet they also state that competition is inseparably connected with all the reactions that have to do with the supply of energy and raw materials in the habitat. One may well ask how, if competition is expressed by reaction, they are ever to be separated in effect. (This question is examined again shortly.)

For the present, Gleason's view of what eliminates species with succession, or indeed of the whole process of succession, must be considered. Gleason (1926) introduced the concept of environmental selection. A plant is limited to a particular complex of environmental conditions which may be correlated with location or controlled, modified or supplied by vegetation. Ecesis occurs in a suitable environment (Gleason *l.c.*, p.27). In the course of plant succession, plants disappear due to the uni-directional change in environment having passed their physiological demands, because, in other words, of environmental selection.

Pertinent to the question of these terms competition, reaction and environmental sifting is a recent paper by Philips (1954) on rhizome performance of *Eriophorum angustifolium* in relation to this species' elimination from certain communities. The authoress illustrates mathematically three different causes of elimination with examples from three types of community.

There is first of all space competition: *E. angustifolium* is eliminated by space competition from *E. vaginatum* communities, its rhizomes being unable to penetrate the latter plant's thick tussocks. Then in some communities "the species are sensitive only to the environmental sifting suggested by Gleason: e.g. *E. angustifolium* in the *Vaccinium myrtillus* - *Empetrum nigrum* community" (Philips *l.c.*, p.207); moisture deficiency is mentioned as a possible factor. Finally Philips holds that there may sometimes be a combination of the two effects; "for example, there is probably no space competition between *E. angustifolium* and *Sphagnum* spp., but the latter creates an environmental condition (i.e. deficiency of mineral nutrients) which eliminates *E. angustifolium*, so that the total effect is one of competition."

This last seems to me to be a clear case of Clements' reaction; reaction amounts here in effect to competition: so does Gleason's environmental sifting in the second example. Finally Philip's space competition is equivalent to the mechanical competition of Clements, Weaver and Hanson (1929, p.317), the rhizomes providing a "purely mechanical" barrier. So all these terms seem to some extent to overlap.

The difficulty of separating reaction in effect from competition has been noted. It was recognised even by the author of the term (Clements 1916, p.102). This only adds to the doubts about competition as the prime factor in succession, doubts already raised by Gleason's views and Philips' findings. There is also an important general case where the effect is obviously caused by reaction as opposed to competition. Competition from a plant ceases with its death. But it is clear that the reaction, accumulated during the life of a plant, on a soil habitat continues after its death. It is reaction after all that determines whether a succession which starts on bare ground will be primary or secondary.

On the other hand, 'reaction' covers all the effects by a plant on its habitat that result from its uptake of nutrients and water and from the shade and litter it casts. So 'competition' as a term must be limited to effects arising from the space the plant occupies in ground or air. This is Philips' space-competition.

In the following field-inquiry into why the pioneers are restricted to open habitats, it is therefore the concept of competition in the wide sense which, within the limits imposed by such a study, is tested first.

II. The Evidence

A. Pioneers, and competition from increasing plant cover

The initial argument is based on the type of evidence given by Robertson (1947). Growing twenty forage species under three intensities of competition (or spacing) with sage-brush (*Artemisia tridentata* Nutt.), this author found that, despite beneficial reactions on wind and evaporation, brush competition significantly reduced plant size, earliness, seed yield and succulence.

The pioneers must disappear, either as adults or at ecesis, because of the increase in total plant cover or cover of an individual species. These increases in cover exert that is to say a direct competition effect.*

Examined first is the possibility of the pioneers' being eliminated, as adults, by increases in total plant cover. In these and subsequent examples I use, as a measure of plant material present, the results of the original cover analysis of the prisere; few seedlings were present (August 1952) and their cover contribution was not included (see p. 37).

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* Distinct from competition and reaction, as causes of the eventual disappearance of species with succession, are parasites and old age (Clements 1916, p.102). Disappearance due to parasites may be discounted here; I have observed no insect or fungal attack (e.g. Rusts) on the pioneers and none is listed by Dennis and Gray (1954) in their paper on Shetland fungi. I cannot see that Clements' fourth category is, in succession of populations, more than a corollary of (1) and/or (2). Surely to attribute the disappearance of a species, upon increase in total plant cover, to old age in its individuals merely implies that the younger generation has been eliminated by competition or reaction before ecesis is completed?

None of the pioneers cited in Table XVII occurs in less than ten samples. Each is represented by one plant per sample. In each case these quadrats have been arranged in the ascending order of percentage cover of the accompanying species, the quadrats meaned in groups and the appropriate percentage cover of the pioneers given beneath.

Table XVII

Percentage cover of certain pioneer species in relation to percentage cover of the accompanying species

							No. of samples
Arenaria	$C - C_{\underline{A}}$	0.35	1.76	2.23	5.00	8.61	14
norvegica	$C_{\underline{A}}$	0.18	0.18	0.12	0.31	0.31	
Cerastium	$C - C_{\underline{C}}$	1.46	4.53	6.23	9.69		11
nigrescens	$C_{\underline{C}}$	0.41	0.23	0.10	0.31		
Armeria	$C - C_{\underline{A}}$	1.92	3.69	4.76	10.23		11
maritima	$C_{\underline{A}}$	0.33	0.58	0.12	0.65		

There is no decrease in pioneer cover, so increase in total plant cover cannot be held responsible for the eventual elimination, as adults, of these species from the prisere. Elimination as adults might still however be caused by the increase in cover of a particular species.

B. Pioneers, and Competition from Thymus drucei

At the start of the grass phase, pioneers and grasses decrease in cover while Thymus rises (Fig. 13, p. 179a). It was concluded (Part II, p. 84) that cyclical succession was the cause of this abrupt change, the resulting figures being due to breakdown of the grasses and recolonisation by Thymus. I am concerned here with the Thymus - pioneer relationship.

Table XVIII

% frequency and mean % cover of pioneers
in quadrats with and without Thymus

Pioneer	without Thymus % F.	without Thymus % C.	with Thymus % F.	with Thymus % C.
Silene maritima	12	0.31	0	0.00
Cochlearia scotica	4	0.11	0	0.00
Cardaminopsis petraea	4	0.11	2	0.08
Arenaria norvegica	24	0.18	4	0.35
Cerastium nigrescens	18	0.25	4	0.26
Sagina nodosa	18	0.25	4	0.19
Armeria maritima	14	0.11	8	0.51
Rubus saxatilis	0	0.00	6	1.41

In Table XVIII are all the pioneers as originally defined (p. 50), their frequency and mean cover in the presence, and absence, of Thymus. All the species are found without, or more often without, Thymus; except Rubus saxatilis which I exclude from this analysis. (This conforms to the distribution pattern of Rubus saxatilis in Rhum. On Hallival, Barkeval and Ruinsival it was growing in open debris and closed heath; see Part III, p. 95).

This tendency of the pioneers to occur more often without Thymus is further examined in Table XIX. The pioneers are treated as a group, and this table gives the distribution of quadrats containing pioneers and Thymus, and pioneers or

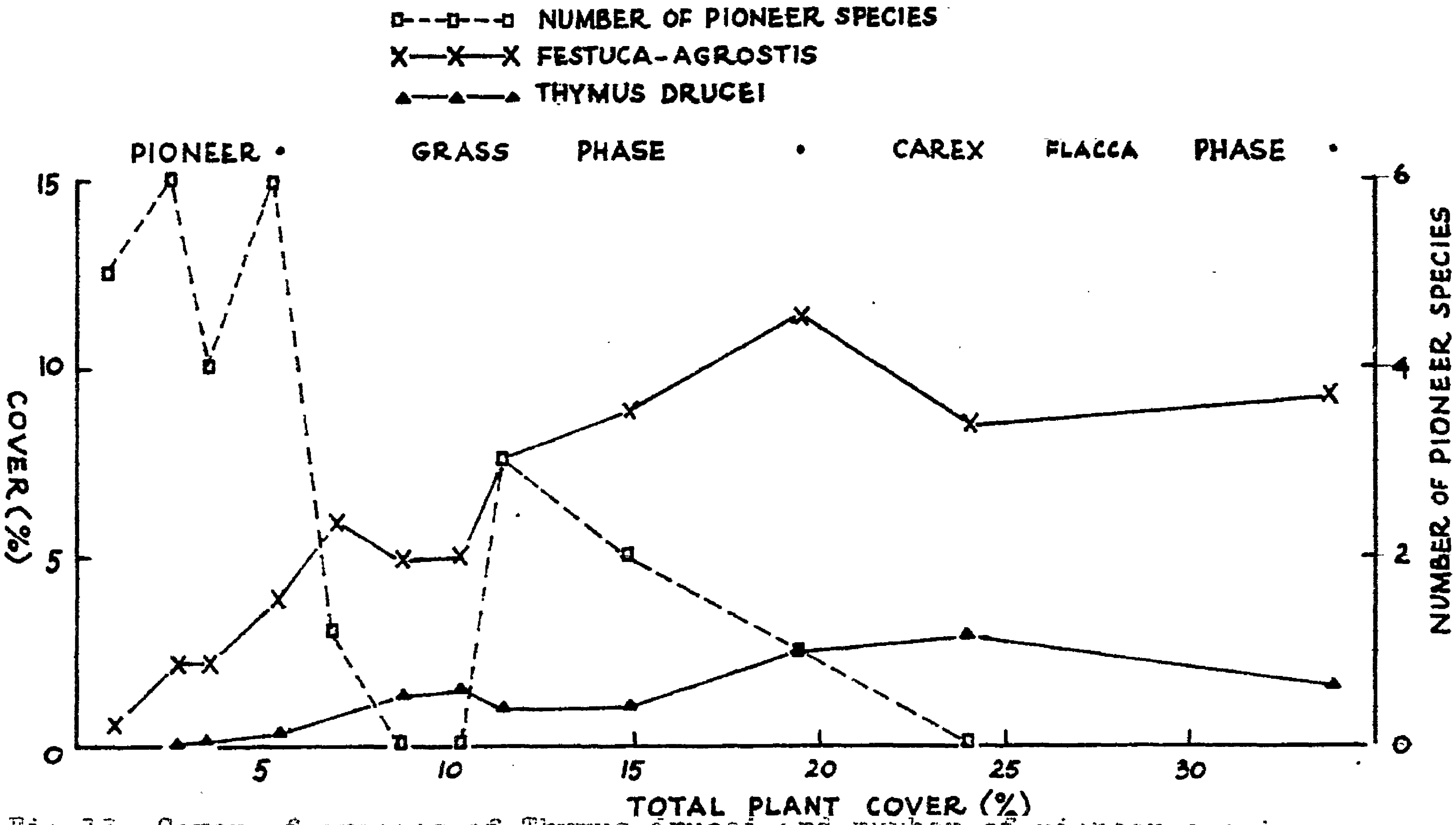

Fig.13. Cover of grasses, of *Thymus drucei* and number of pioneer species *versus* total plant cover; cover of *Carex flacca* is not shown. This figure shows the limits of the first three phases and the drop in cover of grasses, in number of pioneers and rise in cover of *Thymus* at a total plant cover of 8 - 10%.

Thymus alone (other species apart), in the 51 quadrats of the pioneer and grass phase.

Table XIX

Distribution of quadrats with pioneers *or* *Thymus*, or pioneers *and* *Thymus* in the pioneer and grass phases

	without *Thymus*		with *Thymus*		
without pioneers	6	(a_1)	16	(a_2)	22
with pioneers	21	(a_3)	8	(a_4)	29
	27		24		51

Substituting in the formula: $\chi^2 = \frac{(a_1 a_4 - a_2 a_3 - \frac{n}{2})^2}{(a_1+a_2)(a_1+a_3)(a_2+a_4)(a_3+a_4)}$

$\chi^2 = 8{\cdot}5$ with 1 degree of freedom, $p = < 0{\cdot}01$.

This negative association is significant and is due either to competition between *Thymus* or (section C) their belonging *from the start* to different stages in the prisere, (in a way that the pioneers and *Festuca-Agrostis* do not); this is obvious in later stages in the succession, in that *Thymus* persists to where total plant cover is 100% while the pioneers go after it exceeds 20%.

This distribution in fact suggests competition as a factor, as does the possibility of root-competition even where total cover is about 1.5% (p. 58). Such competition should be expressed by a decrease in cover of the pioneers in the presence of *Thymus*.

Table XX

Mean %cover-values of pioneers in quadrats with Thymus, of Thymus with pioneers, and these two when apart, in the pioneer- and grass-phases: of grasses: and of total cover in these quadrats.

	Mean percentage cover values					
	Pioneer phase			Grass phase		
Quadrats containing:	Pioneers	Grasses	Total	Pioneers	Grasses	Total
Pioneers in absence of Thymus	0.51	2.57	3.25	0.47	10.59	12.38
Pioneers in presence of Thymus	0.54	2.20	5.12	0.57	9.38	16.00
	Thymus			Thymus		
Thymus in presence of pioneers	0.75	2.20	5.12	1.46	9.38	16.00
Thymus in absence of pioneers	0.26	2.33	3.09	1.38	6.05	11.98

Table XX shows there is no change in cover of the pioneers whether with or without Thymus. The pioneers cannot be said to be eliminated by direct competition with Thymus.

C. Pioneers, Thymus drucei and different successional stages

To see if pioneers and Thymus drucei might belong to different stages in the succession as far as a total plant cover of 20%, all the quadrats in the pioneer and grass phases were next grouped into those with, and those without, Thymus. Within each group, the quadrats were arranged in ascending cover of the grasses (C_g), mean values being obtained per four quadrats. Equivalent values for total cover (C), cover of pioneers (C_p) and, in one group cover of Thymus (C_t), were found. 'Residual cover', which is total cover less cover of grasses, is plotted against C_g for samples without Thymus (Fig. 14, p. 182a). For samples with that species I have plotted $C - C_g - C_t$. In Fig. 15, cover of pioneers, as a percentage of residual cover in samples with and samples without Thymus, is plotted against cover of grasses.

Fig. 14 shows that (1) in samples with Thymus the residual cover is always greater than in samples lacking that species; (2) in these latter samples too the residual cover is as high where grasses contribute no cover as where they give their maximum. Fig. 15 shows that the pioneers contribute from between one-fifth and five-sixths of the residual cover in samples lacking Thymus: and always more than in samples with Thymus.

From all this it is clear that samples with Thymus are at a higher stage in the succession than those without; Thymus drucei and the pioneers belong from the start to different stages in the prisere.

The pioneers are not eliminated by direct competition as adults. They must be eliminated at ecesis.

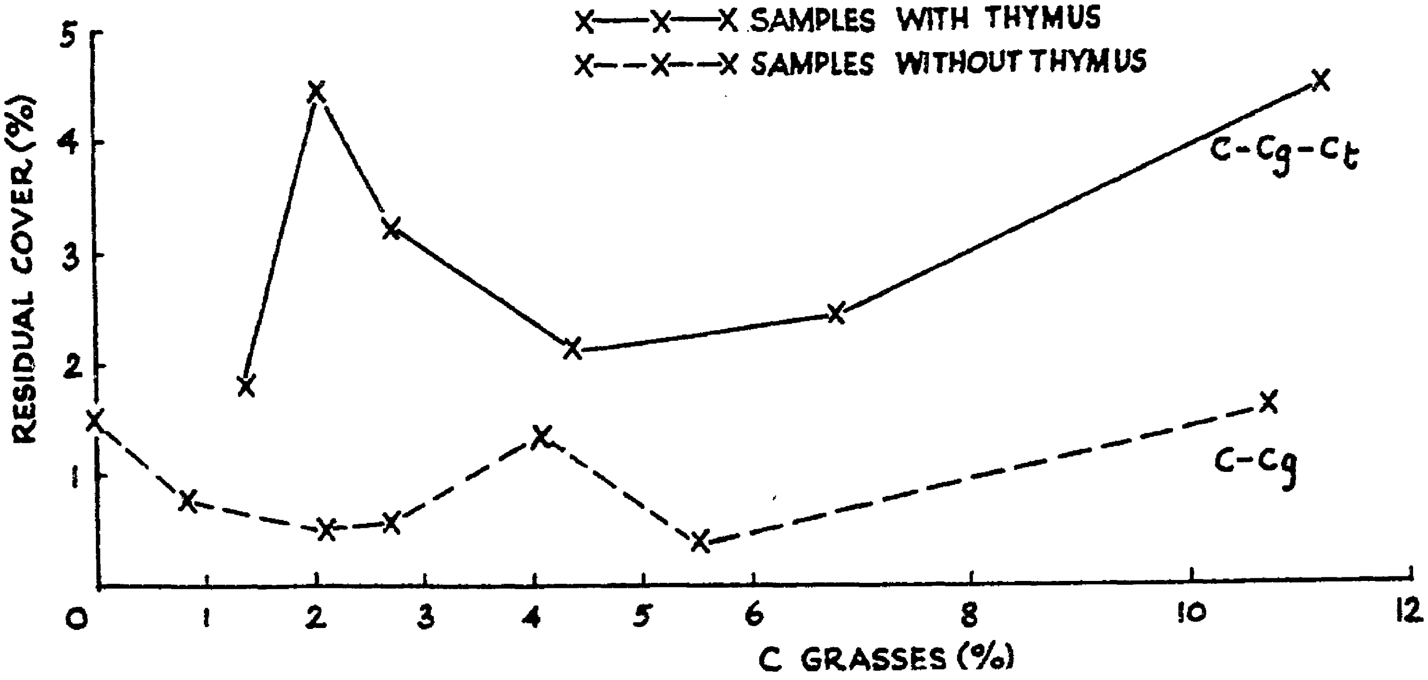

Fig.14. Cover of grasses *versus* residual cover, showing that samples with *Thymus* belong in terms of plant cover to a higher stage in the succession than samples without *Thymus*.

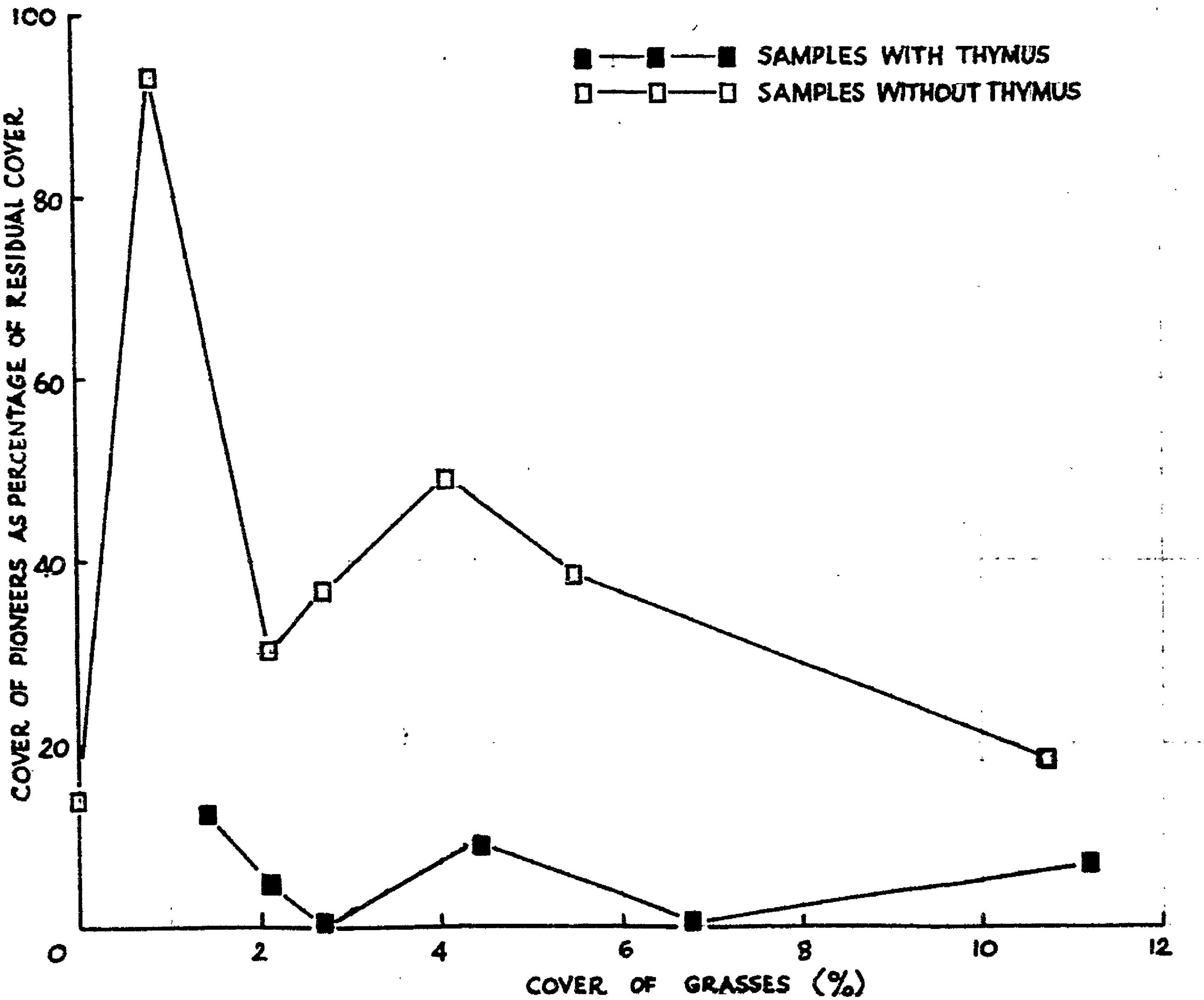

Fig.15. Cover of pioneers,as a percentage of residual cover, versus cover of grasses;showing that the pioneers contribute far more cover in samples lacking *Thymus* than they do in samples with that species.

D. Edaphic limitation of the pioneers at ecesis

The fact that Thymus and the pioneers belong to different stages in the prisere must also be connected with the absence of pioneers from samples with low total plant cover and high cover values of Thymus (Fig.13, p. 179a). Can these samples in fact be at a different stage in the succession than their total cover would indicate?

This is where cyclical succession enters. In a sample within a normal prisere a given degree of cover indicates an equivalent stage of soil-development. All samples with total plant cover between 6 - 19% are put in the grass phase. Such would also be the case with a sample which belonged in terms of soil-development to the sedge phase but which has lost plant cover due to soil-erosion and other breakdown phenomena. On debris a layer of small stones overlies finer material. Bare earth overlying debris indicates recent breakdown (Part II, p.60). This recording of bare earth is the only evidence I have of the occurrence of breakdown in these quadrats which were taken at random over the debris; and bare earth occurs in 6 out of 8 of those with no pioneers, low total cover and high cover values for Thymus.

So there is combined evidence that, despite the open surface, some edaphic limitation is imposed on the pioneers, at ecesis, by bare earth compared with debris. Absent from closed vegetation, the pioneers are also missing from certain types of open ground. This suggests they are not restricted by competition in the wide sense.

E. Further evidence of the edaphic limitation of the pioneers

It may well be argued that the number of bare soil samples was insufficient and that anyway there is no direct evidence of seedling distribution to indicate the effects on ecesis. To test the possible significance of bare earth, further patches of debris were examined in a subsequent year (1955). All contained pioneer species and were associated with bedrock _in situ_. They all had a zone of ochreous fragments in the centre with one of greyish gravel between this and the zone of gravel and earth at the margin which adjoined the eroding scarp (p. 60 and Plate II, phot. 2) of the surrounding heath.

These gravel-earth margins were examined carefully for the presence of seedling or adult pioneers. Very few were found particularly in comparison with their abundance in most equivalent areas of ochreous or grey debris. Since the whole debris habitat is by definition (p. 24) largely bare of plant cover, one would expect on the margins as on the debris itself to have some samples with no pioneers, even with no cover. Yet this virtual absence from the margins was consistent.

The absence of pioneer seedlings from these margins could be counted the result of a poor year were it not for the lack of adults also. This confirms the significance attached earlier to the absence of adult pioneers from bare earth patches on the debris itself.

To illustrate this centre-to-margin change numerically, a 3 x 1 m. transect was taken from an ochreous area to the earth margin where it abutted on but excluded a scarp topped by closed heath vegetation. My choice of site was determined by the presence of a few pioneers on typical ochreous debris a few metres in from an equally typical margin. The ground was searched carefully for the all adult and seedling plants and the results are given in Table XXI, p. 186 .

Not only are pioneers more or less absent from the earth-gravel margin; there is also an abrupt fall from samples Nos. 1 and 2 to No. 3 in number of pioneer adults, namely 20 and 34 to 3; and seedlings, 13 and 24 to 0.

Table XXI

Belt transect 3 x 1 sq.m., from centre of a patch of ochreous serpentine debris to earth margin where it abutted on but excluded a scarp topped by heath vegetation: Sobul; Unst, 250ft. 24/7/55. Indicates total plant cover, approximate soil-particle size (at surface) and the number of flowering, non-flowering and seedling plants present per quadrat.

fl: flowering or fruiting specimens; n-fl: non-flowering specimens with some dead leaves, and cotyledons no longer present; s: seedling, cotyledons present.

	Total plant cover	±1% bedrock visible ochreous fragments 1/2 cm.up av. 2cm. dia.			5% no bedrock: red-grey gravel 1/2 - 1cm.			>10% almost abuts on scarp: gravel and earth <1/4 cm.		
		fl.	n-fl.	s	fl.	n-fl.	s	fl.	n-fl.	s
PIONEERS	Arenaria norvegica	12	5	6	14	8	10		1	
	Cochlearia scotica	1	1	7	1	1	8			
	Sagina nodosa		1		1	9	6		2	
	Festuca rubra	3	1	3	8	6		numerous: cover 4%		
	Cerastium vulgatum				1	1	2			
	Thymus drucei						1	4		
	Linum catharticum						1	5		
	Euphrasia rotundifolia					17			30	
	Viola riviniana						1		6	
	Scilla verna				1	14		3	14	
	Agrostis stolonifera					16		numerous: cover 3%		
	Plantago maritima				3			8	2	1
	Carex flacca							numerous: cover 2%		

III. Discussion

Why do the pioneers fail to establish themselves in bare earth? Lack of openness I discount. Pioneers persist well beyond this total cover of 9%; and the resulting space competition seems in any case unlikely to inhibit ecesis. From some evidence given earlier (p. 69) of how very poor might be the carriage of some pioneers' seed, limited dispersal is a possible cause. If so, it is odd that the limitation should be so abrupt and only to one side. Again it seems the soil itself is responsible.

Soil-instability is considerable near an eroding scarp but it is improbable that instability in these particular patches would inhibit ecesis of the pioneer plants. They are after all restricted almost always to essentially unstable habitats like debris, subject to soil-erosion, frost-heaving etc. (Part III, p. 122). Concerning particle-size; Pigott (1955, p.378) sowed seeds of Thymus drucei on several types of soil and exposed them all winter. Seedlings only survived on short turf, rock gravel or chalk rubble; on bare sieved soil for example the seedlings were continually disturbed by rain, lay on the surface and finally died from desiccation. But most of the Unst pioneers occur on Ruinsival, Rhum, where 80% of the debris surface is composed of fine earth. Finally, ecesis still takes place - Euphrasia rotundifolia actually has more adults (non-flowering at 24 July 1955) in No. 3 than in No. 2 (Table XXI, p. 186).

The characteristic of any debris-margin like sample No. 3 is that, possessing bare earth and adjoining an eroding scarp, it belongs to a higher edaphic stage in the succession; (p.); incidentally the absence of pioneers at low total cover with corresponding presence of Thymus is corroborative evidence (p. 183). This supposition is made even more credible by figures for humus content. The mean humus content, expressed as a percentage of oven dried soil, of three samples of the first 5 cms. of soil from the pioneer phase, was 0.42 (from p. 55). Total plant cover here was less than 5%, and the ground was surfaced by gravel. In three samples of the first 5 cms. of soil from the earth margins under consideration, where total plant cover is similarly less than 5%, mean humus content was 5.43% of oven dried soil.

The edaphic limitation which may cause failure in ecesis of the pioneers must result from the former presence on these areas, or continued presence nearby, of more developed plant-cover. This limitation could result from the demonstrated accumulation of humus or consequent decrease in mineral content. Either cause would be attributable to Clements' reaction or Gleason's environmental sorting. Final conclusions must of course await detailed germination tests.* Those that follow are therefore to be regarded as tentative.

The bare earth areas it can be said are a special case and my purpose has been to see why the pioneers are eliminated when the total plant cover increases. That however is the point I want to emphasise, for here the pioneers are lacking in spite of low plant cover and possible seed-parents nearby. The pioneers are absent from areas in which competition is not operating, but in which reaction may be. All these facts suggest that they are restricted at ecesis not to open ground

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* Several of the pioneers have germinated successfully in normal garden soil. This of course only shows they can do this. It has no bearing on their germination behaviour in nature; and I stress this because of the obviously important part played in this habitat by exposure, soil-instability etc.

per se, but rather to the chemical conditions found only in certain types of open ground and that they can survive under natural conditions in no other.

It follows that the pioneers are eliminated not by but with increasing total plant cover. This supports my earlier inference that, by their inevitable dependence on soil with for instance a high nickel content or neutral pH and high Mg content, the pioneers have become at least within their normal environment positively adapted to or dependent on such conditions. (The pioneers were incidentally earlier shown (Part II, p. 65) to be adapted to the physical conditions of soil instability.) Arrived at by different means, this hypothesis is in agreement with Balme's suggestions (this paper, p. 172) as to the nature of the calcicolous habit.

I suggest in conclusion that to speak of rare species as being restricted to areas of low competition gives the wrong impression of the probable causes of this restriction.

SUMMARY OF EVIDENCE AND CONCLUSIONS

The order, in which the data are given and the problems investigated in this thesis, is noted at the end of the introduction (p. 6). A summary is presented here of the main evidence, and conclusions derived from that evidence, in the four parts of the thesis.

PART I.

1. (1) Shetland has a submontane-oceanic climate up to 1000 ft (305 m.); above that altitude, in summer at least, the climate is subarctic-oceanic.

(2) Wind is strong. Approaching at 1480 ft (451 m.) the average annual windspeed on Ben Nevis at 4406 ft (1343 m.), its effects on vegetation there are noted; so is the possibility of its affecting vegetation at far lower altitudes. Correlation is noted between the major areas of serpentine debris in Unst and winds with a westerly component.

2. (1) Unst is composed of gneisses and mica-schists, greenstones and serpentine. On the latter outcrop the debris with sparse plant cover is described in detail. Solifluction phenomena are noted. Associated and unassociated areas of debris are defined.

(2) In high magnesium content and neutral soil-pH, this debris is similar to those in other serpentine localities. Very high nickel content, inferred from known high chromium content, is shown. This is greatest on associated debris. Nickel content in <u>Agrostis stolonifera</u> from debris is as high as that known to produce toxic symptoms in crop plants on other serpentine areas.

Correlation is noted of major (associated) debris areas with chromium- and hence nickel-rich areas.

3. Grazing is shown by fencing experiments to be in places more important than exposure; in other places, particularly on serpentine, it is less important than exposure or other factors.

4. The species of Unst hill-land are divided into four groups. (1) Serpentine-characteristic species, including several exclusive to serpentine; (2) serpentine-indifferent and (3) serpentine-casual species, and (4) a group of species absent from serpentine; many of these are acidiphils and dominant in adjoining blanket-bog.

Similarities in habitat provided by the presence of raw humus accounts for the similarities in species lists on the three rock types. Differences are attributed primarily to variations in types of humus and in its depth. From acid rocks with deep peat, to the extreme case presented by the mineral serpentine debris with sparse plant cover, there is increasingly shallower humus, better drainage and higher basicity.

PART II.

5. (1) The four phase prisere on Unst serpentine is described. Increase in soil acidity and humus content accompanies the development of plant cover. Root competition is possible at very low total plant cover. Distinction between open and closed phases is based on qualitative changes in the plant cover as this cover increases.

(2) Pioneers are species limited to the lowest cover phases. Their restriction to associated debris is noted. The percentage of boreal species and of chamaephytes is far higher in the pioneer phase than in the climax vegetation. The pioneers are classed as relics.

6. (1) Study of why closed vegetation has not covered the whole debris surface, or why colonisation has been retarded, is study of the cause of the serpentine effect.

(2) Colonisation of the debris may be retarded more or less permanently by wind. Soil instability also is involved. This is shown by study of the physiognomy of the vegetation in this habitat. Wind also re-exposes the surface of the debris. Debris species have adaptations which suit such an interpretation. These conclusions bear out the supposition, based on climatic data, of para.I (2)[*] above.

(3) Rate of weathering may exceed rate of colonisation. Colonisation may be more or less permanently retarded near exposed bedrock. The restriction of pioneers to associated debris is attributed to this fact and their poor powers of dispersal.

(4) A review of current literature reveals that nickel toxicity is the prime chemical cause of serpentine barrenness. Serpentinophytes and serpentinicolous relics adapted to high nickel soil content are discussed.

(5) From evidence given in para.2 (2) above, the presence of serpentinophytes in Unst debris is likely. Restricted to associated debris where available nickel content is high, the pioneers are serpentinicolous relics.

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[*] Cross-references refer to paragraphs in this summary.

(6) Retarding of colonisation by nickel toxicity is probable on Unst serpentine debris. But (1) high nickel content is correlated with high rate of weathering and (2) it will not operate equally over all debris areas, for nickel content is known to vary.

(7) It is concluded that the serpentine effect in Unst is expressed first of all by areas of debris with sparse plant cover. These exist because colonisation is retarded by wind-exposure and soil instability, the prime factors on unassociated debris. On associated debris, constituting the major debris areas, these factors may be exceeded in importance both by a high rate of weathering, and by nickel toxicity, the result of high available nickel content.

7. (1) Cyclical succession of four phases is outlined. Breakdown may re-expose the gravel surface of the debris. It may only re-expose earth. Distinction is drawn between a new cycle starting on debris and one starting on earth. "Recolonisers" and "relics" are plants able to withstand erosion in ground where this has removed all other plant cover. So they may occur "out of phase".

(2) It is assumed that a degree of plant cover is an indication of seral position. A sample may belong in terms of cover to the pioneer phase. But if it has earth rather than debris on its surface, it may belong in terms of soil development to the sedge phase.

(3) Anomalies noted in the course of the prisere are seen to agree with the results of breakdown and cyclical succession postulated.

8. The Unst serpentine debris is similar to non-serpentine frost debris of Caithness, of which the origin is described by Crampton. Like other serpentine and non-serpentine debris examined, it provides the same habitat as fellfield, Icelandic gravel-flat, or mountain-top detritus in the Scottish Highlands. Even allowing for the submontane-oceanic climate at sea-level, it is not found at as low equivalent altitudes in the Central Highlands. This again reflects the severe exposure and special edaphic factors operating at this low altitude in Shetland.

PART III.

With the field method used in this part of the study, it has been possible to describe related communities on serpentine and non-serpentine substrates in widely separated localities, and to trace their affinities, through published data, to communities in and beyond Britain.

9. The sedge-grass-heath series comprises two related groups of sociations, in one of which grazing is important. They occur on well-drained soil, usually with an immature profile. The samples from the less oceanic Coyles may be related to dry heath on Swedish serpentine. Some general affinity is noted to 'heather-moor' on dry substrates in the Faeroes. From its floristic composition the series is designated submontane sedge-grass-heath.

10. Two mire sociations in drainage hollows on Unst serpentine are described. Both are heavily grazed; one is shown by fencing experiments and other observations to be much altered by this factor. On normally waterlogged soils, they

are related to eutrophic-mesotrophic mire communities on non-serpentine substrates.

11. (1) Sampling technique in the open (fellfield) community is described. Plant cover, for reasons given, does not normally exceed 5%.

(2) Two groups of sociations share, in the area investigated, the physical features of fellfield and a number of species. One of these groups is on acid, the other on ultrabasic, debris (and scree). The groups are distinguished by two mutually exclusive sets of species, some of which are used in naming the sociations. Chamaephytes comprise 42% of species occurring in samples where cover does not exceed 5%.

(3) Floristically the sociations on ultrabasic substrates are related to the Arenarion norvegicae subarcticum of Nordhagen; most closely to the sociations on basic scree in oceanic southwest Norway. The sociations on acid debris can be related to open communities on acid substrates, in Britain and beyond.

(4) The species which distinguish the acid and ultrabasic sociations in Scotland grow together in the fellfield of Iceland and the Faeroes. Collectively, however, the vegetation examined has its most marked affinity floristically, in life form and in habitat, with the fellfield of these regions.

12. (1) A preliminary account is given of _Rhacomitrium_-heath on exposed parts of Ronas Hill. Related communities are described from hill-tops in other areas.

(2) A survey is made of Rhacomitrium-heath in and beyond Britain. This shows (1) the North Atlantic distribution of Rhacomitrium-heath and its absence from continental areas (2) the lack of equivalence of the Ronas Hill heath, and other examples examined, to this heath. Rhacomitrium-heath normally lacks Calluna and, in Britain anyway, is only found at higher levels.

(3) The Ronas Hill heath is related to high-level Calluna-Loiseleuria vegetation in exposed snowfree localities in the Central and East Highlands, or to communities having moderate snow cover in continental areas (Norway, Iceland). Rhacomitrium itself is inconspicuous in all these communities, but this alignment is confirmed by reference to fellfield vegetation.

(4) Correlation with Calluna vegetation explains the lack of correspondence of the Ronas Hill and other examples with normal Rhacomitrium heath. In the Cairngorms this lies in exposed localities directly above the Calluna zone.

13. There is no affinity of the Asplenium viride sociation with those on serpentine debris in the north of Sweden, but there is no doubt that the examples examined are part of the Asplenion viridis subarcticum, of Nordhagen, of crevice communities on basic rock. Closest correspondence lies with samples from the serpentine of Sunmöre, southwest Norway.

14. (1) Using climatic zones based on the mean temperature of the warmest month, and data on climatic and edaphic climaxes, it is shown that: Rhacomitrium-heath and fellfield are characteristic of and predominant in low and subarctic-oceanic climates in S.W. Greenland, Iceland and the Faeroes. Calluna-Loiseleuria and fellfield vegetation occur in

subarctic-oceanic summer regimes on Ronas Hill (with dominance of Rhacomitrium in the heath there), the Cairngorms and Breadalbane. An isotherm between 49-50 deg. F. marks the transition. Thereafter, Rhacomitrium-heath and fellfield extend as edaphic climaxes into submontane-oceanic regimes in Rhum and Shetland (or as scree in the submontane regime of the Coyles): where submontane heath predominates.

(2) Distribution of plants is seen, from a brief review of the subject, to be correlated with specific temperature requirements. (a) The mean temperature of the warmest month, and (b) extremes, are examined as ways of indicating broadly upper and lower limits. There is, from data presented in the thesis, correlation between the altitudinal limits of some species, and (a): but not (b).

(3) It is stressed that the postulated limiting effect of temperature operates within the humid, exposed and snowfree habitats typical, throughout their range of fellfield and Rhacomitrium-heath. Given suitable edaphic conditions, the general presence of fellfield as an edaphic climax in maritime areas must be due to increase in exposure in these areas, already shown for Unst in para. 8; for Rhacomitrium-heath, the main factors may be exposure and high humidity, found in the hill-top localities it favours.

(4) The correlations traced here offer a reasonable explanation of the so-called problem of those species which, montane in the east and central Highlands, descend to sea-level in the west. In the absence, however, of experiment and large amounts of comparable data, this first attempt at correlation should be regarded in particular cases as tentative.

15. (1) Summarised in the corresponding section of the thesis are the relationships of all the communities described from the Scottish serpentine localities examined. These findings have been given in the present summary under the appropriate communities. Even the debris, scree, and crevice sociations are not distinctively serpentine.

(2) Any such feature will be shown by individual species having an apparent preference for serpentine. Distinction is made between serpentine-characteristic and serpentinicolous species. From a review of species found in the three localities examined, it is shown that, of 24 serpentine-characteristic species in Unst, five are serpentinicolous in Scotland.

(3) By comparison with species judged serpentinicolous in Fennoscandia, it appears that, in common with their behaviour there, Asplenium viride and Arenaria norvegica are serpentinicolous in submontane and/or submontane-oceanic regions of Scotland. With these latter regions, oceanic west Norway shares as serpentinicolous species Silene maritima, Cardaminopsis petraea and Asplenium adiantum-nigrum. Viscaria alpina, another Fennoscandian serpentinicolous species, is found on east Scottish serpentine at 2850 ft ; but the other species are lacking in this montane region.

(4) Relationship to the calcicole habit is discussed.

PART IV.

16. (1) Rare species commonly occupy pioneer habitats where climax vegetation for some reason or other has failed to develop. These conditions are fulfilled precisely in

Unst, so the pioneers' restriction to the serpentine debris there illustrates a general problem.

(2) There are two approaches to this problem which may or may not be mutually exclusive. (a) The pioneers form a relict community. Their eventual restriction to associated debris will have meant a progressive adaptation to the specialised conditions of such soil (para. 2 (2) above). As has been suggested for calcicoles in calcareous soils with sparse plant cover, this adaptation might in time become positive. (b) In most of the literature, rare species are regarded as confined to open habitats because these are areas of low competition. It follows that in a prisere they must be eliminated by increasing total cover.

(3) The term 'competition' is examined, and discussed in relation to 'reaction' and 'environmental sifting'. Doubts are cast on the validity of the concept of competition, in the accepted sense of (2) (b) above, as the prime factor in succession.

17. The concept is tested by using the data of the % cover analysis, from which the prisere was constructed (Part II): to see whether pioneers disappear (either as adults or at ecesis) because increase in cover exerts a direct competition effect.

18. (1) On the evidence presented, the pioneers are restricted to serpentine debris in Unst at ecesis. They are eliminated as total cover increases, not by competition due to plant cover itself, but by factors akin to reaction or environmental sorting.

(2) Final conclusions on this and the following points must await detailed germination tests. From further evidence one may infer meanwhile that the pioneers are positively adapted to the chemical conditions, probably related to the high nickel content, of associated debris.

(3) It is suggested that to speak of these rare species as being restricted to areas of low competition gives the wrong impression of the probable causes of this restriction.

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APPENDIX

Table XXIII

Mean monthly temperatures at Baltasound, Lerwick, Thorshavn and Dalwhinnie, and calculated figures for Sandness Hill, Ronas Hill and Dalwhinnie at 2500 ft.

	Alt.	J	F	M	A	M	J	J	A	S	O	N	D	Year
Baltasound : 1921-1947	31 ft	39.0	39.0	40.3	42.8	46.6	50.4	54.3	54.3	51.3	46.6	42.2	40.6	45.7
Lerwick : 1921-1950	269 ft	38.2	37.2	39.0	41.5	45.6	49.5	53.3	53.5	50.6	45.9	42.0	39.8	44.7
Ht. difference and mean monthly lapse rate	238 ft	0.8	1.1	1.3	1.3	1.0	0.9	0.8	0.8	0.7	0.7	0.2	0.8	1.0
Thorshavn		37.7	38.1	37.7	41.9	45.0	49.4	51.4	51.2	48.7	43.8	40.6	38.1	
Dalwhinnie	1176 ft	33.0	39.1	36.9	40.1	46.3	50.2	54.7	54.3	50.1	44.1	38.7	35.6	
Sandness Hill (calculated)	816 ft	36.4	35.4	36.0	38.8	43.3	47.4	51.6	51.6	49.0	44.3	41.6	38.0	42.4
Ronas Hill (calculated)	1000 ft	35.8	34.6	34.1	36.6	42.6	46.8	51.1	51.1	48.5	43.8	41.4	37.4	41.7
Ronas Hill (calculated)	1480 ft	34.2	32.4	32.5	35.0	40.6	45.0	49.5	49.5	47.1	42.4	41.0	35.8	39.7
Ronas Hill (calculated with mean <u>annual</u> lapse rate)	1000 ft	35.0	35.0	36.3	38.8	42.6	46.4	50.3	50.3	47.3	42.6	38.2	36.6	41.7
Dalwhinnie (calculated with mean annual lapse rate) (1324 ft : - 4.4°F.)	2500 ft	28.6	32.7	32.5	35.7	41.9	45.8	50.3	50.2	46.2	39.7	34.3	31.2	

Table XXIV

(a) mean monthly windspeeds in m.p.h., and (b) number of gale-days

(a)

	Height above m.s.l. ft.	Effective height ft.	J	F	M	A	M	J	J	A	S	O	N	D	Year	
Sandness Hill	816	30	27.0	26.3	24.7	22.0	19.5	17.4	16.7	18.3	21.4	24.8	30.9	27.7	23.1	1953-54
Lerwick	310	39	22.2	21.0	16.5	16.5	14.8	14.5	11.4	11.8	15.0	16.8	19.2	21.0	16.6	1921-50
Eskdalemuir	825	35	14.0	12.1	12.6	12.0	10.5	10.7	9.5	9.2	10.3	10.8	11.9	12.9	11.4	Bilham
King's College, Aberdeen	120	32													8.8	Bilham

(b)

	J	F	M	A	M	J	J	A	S	O	N	D	Year
Lerwick	9	6	2	2	0.9	0.5	0	0.2	0.5	1	5	7	38

Table XXV

sample number in Table:field		Date	Locality	Alt. (ft)	Asp-ect	Slope (deg)	Cover (%)	Ht. of veg.[x] (cms)	Rock type
Table X		July 1955							
1	U4	16	Unst:Colvadale	250	–	0	100	4	Serpentine
2	U7	17	" Brecksie	50	–	0	100	(10)	"
3	U8	17	" Sobul	150	W	5	100	6	"
4	U13	17	" Watlee	150	–	0	100	(5)	"
5	U17	18	" Heog	300	E	10	100	(5)	"
6	U32	19	" Belmont	150	E	5	100	(4)	"
7	RR4	5	Rhum Ruinsival	1600	–	0	100	6 (3)	"
8	H1	8	" Hallival	1200	E	20	100	10(6)	Hallivalite
9	U3	16	Unst:Colvadale	200	N	5	100	(6)	Greenstone
10	U5	16	" "	250	–	0	100	(6)	Serp.
11	U18	18	" Heog	300	E	15	100	4 (3)	"
12	RR2	5	Rhum Ruinsival	1500	SE	5	100	–	"
13	H4	8	" Hallival	2350	W	5	100	8 (3)	Hall.
Table XI									
1	U15	18	UNst:Nikkavord	200	S	0	100	5 (1)	Serp.
2	U16	18	" Muckle Heog		E	5	100	3 (2)	"
3	U25	18	" Hamar	150	W	0	100	7 (4)	"
4	U26	18	" "	100	–	0	100	4 (3)	"
5	U34	19	" Gallow Hill	200	E	5	100	4 (2)	"
6	C.7	1	Coyles of Muick	1800	W	20	100	–	"
7	C.5	1	" "	1900	W	10	100	–	"
8	C.3	1	" "	1800	N	20	100	–	"
9	RR6	5	Ruinsival	1400	N	30	100	8 (5)	Peridotite
10	H5	8	Hallival	2340	W	0	100	9 (3)	Hallivalite
Table XII									
1	U27	19	Unst: Dam loch	50	E	0	90	2 (2)	Serp.
2	U28	19	" Coutt's Dam	100	–	0	50	–	"
3	U30	19	" Sobul quarry	100	W	5	80	2 (2)	"
4	U31	19	" " "	150	S	0	80	–	"
5	U33	19	" Gallow Hill	200	E	0	80	3 (2)	"

[x] hts. of inflorescences; hts. of leaves in brackets.

(to be contd.)

Table XXV (contd.)

sample number in Table	field	Date	Locality	Alt. (ft)	Aspect	Slope (deg)	Cover (%)	Ht. of veg. (cms)	Rock type
Table XII		July 1955							
6	U1	16	Unst: Colvadale	250	W	20	5	3 (½)	Serp.
7	U6	17	" Dam loch	50	W	0	70	3 (1)	"
8	U14	18	" Nikkavord	200	S	0	100	(½)	"
9	U19	18	" Hamar	100	N	0	100	14 (12)	"
10	U20	18	" "	100	N	0	95	5 (4)	"
Table XIII									
1	U9	17	" Sobul	300	W	0	5	5	"
2	U10	17	" "	250	W	0	1	5	"
3	U10A	17	" "	250	-	-	5	5	"
4	U11	17	" Watlee	150	S	0	5	5	"
5	U21	18	" Hamar	150	W	5	5	5	"
6	U22	18	" "		N	5	5	5	"
7	U23	18	" "	50	NE	0	5	5	"
8	U24	18	" "	100	W	0	5	8	"
9	RR1	5	Rhum Ruinsival	1440	SE	0	5	5	"
10	RR5	5	" "	1600	S	0	5	5	"
11	C4	1	Coyles of Muick	1900	E	40	5	-	"
12	C2	1	" "	1750	W	40	5	5	"
13	C8	1	" "	1650	S	30	5	-	"
14	RR3	5	Rhum Ruinsival	1520	E	0	19	6	"
15	C1	1	Coyles of Muick	1700	SW	30	20	5	"
16	U10B	17	Unst: Sobul	250	W	-	10	5	"
17	C6	1	Coyles of Muick	1800	SE	15	50	-	"
18	O2	7	Rhum: Orval	1300	SW	0	5	5	Basalt
19	H2	8	" Hallival	1800	NE	10	5	8	Hallivalite
20	H3	8	" "	2350	-	0	5	8 (5)	"
21	Ro3	5	Ronas Hill	1350	S	0	7	-	Granite diorite
22	Ro2	5	" "	1350	S	0	5	-	"
23	Ro5	5	" "	1400	NSW	0	25	-	"
24	O4	7	Rhum: Orval	1200	-	0	50	8 (5)	Basalt

(to be contd.)

Table XXV (contd.)

sample number in Table:	field	Date	Locality	Alt. (ft)	Aspect	Slope (deg)	Cover (%)	Ht. of veg. (cms)	Rock type
Table XV		1952							
1	521	25/7	Ronas Hill	1200	–	–	100	–	Granite diorite
2	522	18/8	" "	1200	–	–	100	–	"
		1954							
3	540	–/8	" "	500	–	–	100	–	"
4	523	1952							
		25/7	" "	1000	–	–	100	–	"
5	524	18/8	" "	1350	–	–	100	–	"
6	Ro1	1955							
		24/8	" "	1280	S	0	100	8	"
7	Ro4	24/8	" "	1400	SW	5	100	6	"
		1952							
8	525	18/8	" "	1000	–	–	100	–	"
9	Sa2	22/7	Sandness Hill	800	SW	5	100	–	"
10	O1	1955							
		7/7	Rhum: Orval	1100	W	5	100	20(5)	Basalt
11	O3	7/7	" "	1350	W	5	100	8(5)	"

Plate I

Phot.1 Granite-diorite debris on south shoulder of Ronas Hill, altitude 1400 ft.; showing closed vegetation of ericoids and *Rhacomitrium lanuginosum* confined to the lea of a boulder. 18/8/52.

Phot.2 Looking north along a dry-stone wall which crosses serpentine debris on the Keen of Hamar, altitude 100 ft.; showing that closed vegetation here extends outwards for only a few feet from either side of the wall. 31/8/52.

Phot.3 View, looking southeast, of the Keen of Hamar showing as a lighter coloured area the extensive debris on the north west shoulder of the hill. In the middle distance, at the right, the spoil heaps of chromite quarrying are seen. 9/9/52.

PLATE I

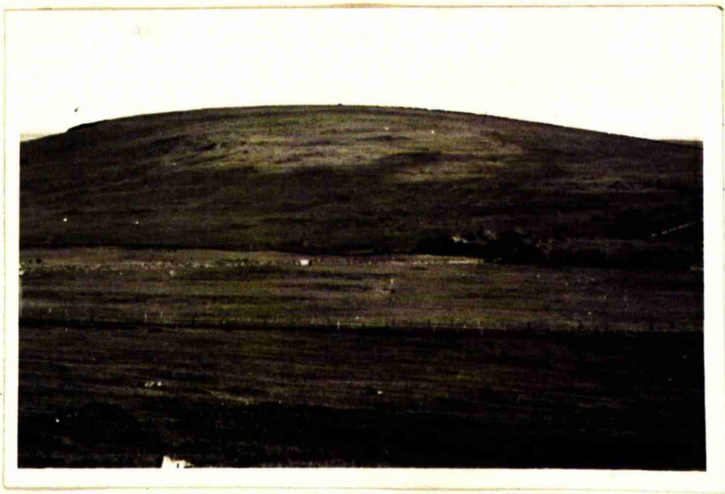


Plate II

Phot.1 Patch of associated debris on Sobul, altitude 200 ft., showing exposed serpentine bedrock and small areas of closed vegetation in the foreground, continuous closed vegetation in the background. 9/9/52.

Phot.2 Patch of unassociated debris on Sobul, altitude 300 ft. Loose stones at left foreground but no bedrock is visible in the patches of debris. Note the scarps of eroded heath vegetation, here facing west and southwest. 9/9/52.

Phot.3 Type of hurdle used in excluding grazing animals from an area of 36 sq.ft. of, in this case, heath vegetation on Hamar; altitude 100 ft. Also shows heath vegetation, with eroded edges, lying about 15 cm. above the debris. 9/9/52.

Plate III

Phot.1 Young plant of Plantago maritima, scale as phot.3. Hamar, altitude 100 ft. 8/7/52.

Phot.2 Young plant of Armeria maritima (and tufts of Festuca rubra). Hamar, altitude 100 ft. 8/7/52.

Phot.3 Slightly older plant of Armeria maritima, showing more pronounced cushion habit; 2.5 ins. (6.3 cms.) high. Hamar, altitude 100 ft. 7/9/52.

Phot.4 Cushion of Silene acaulis, 3 ins. (7.6 cms.) high (with Festuca rubra). Hamar, altitude 100 ft. 7/9/52.

PLATE III

Plate IV

Phot.1 Old plant of *Plantago maritima*,3.5 ins. (8.9 cms.) high,showing severe erosion. The plant is undercut. Note how small stones form the soil surface,except in the eroded region of the plant, where earth predominates. Hamar,altitude 150 ft. 7/9/52.

Phot.2 Old plant of *Armeria maritima*,scale as phot.1,with only part of the base of the cushion remaining. Bare earth on the surface,as opposed to gravel,must indicate roughly the missing part of the plant. Hamar,altitude 100 ft. 7/9/52.

Phot.3 Old tussock of *Festuca rubra*,scale as phot.1,and about 10 cms. high,with its left side eroded. Hamar,altitude 100 ft. 9/9/52.

Phot.4 This circle of bare earth,with little gravel,contrasts with the surrounding debris. Fringed by a ring of nearly dead *Festuca rubra*, it must represent the base of a tussock which has been almost completely eroded. Hamar,altitude 75 ft. 7/9/52.

PLATE IV

Plate V

Phot.1 *Silene maritima*, showing prostrate habit. Hamar, altitude 200 ft. 8/7/52.

Phot.2 *Cardaminopsis petraea*, showing prostrate habit. Hamar, altitude 250 ft. 8/7/52.

Phot.3 *Rubus saxatilis*, scale as phot.1, in open debris. Hamar, altitude 100 ft. 6/9/52.

Phot.4 *Rubus saxatilis*, scale as phot.1, in lea of boulder. Hamar, altitude 100 ft. 6/9/52.

PLATE V

Plate VI

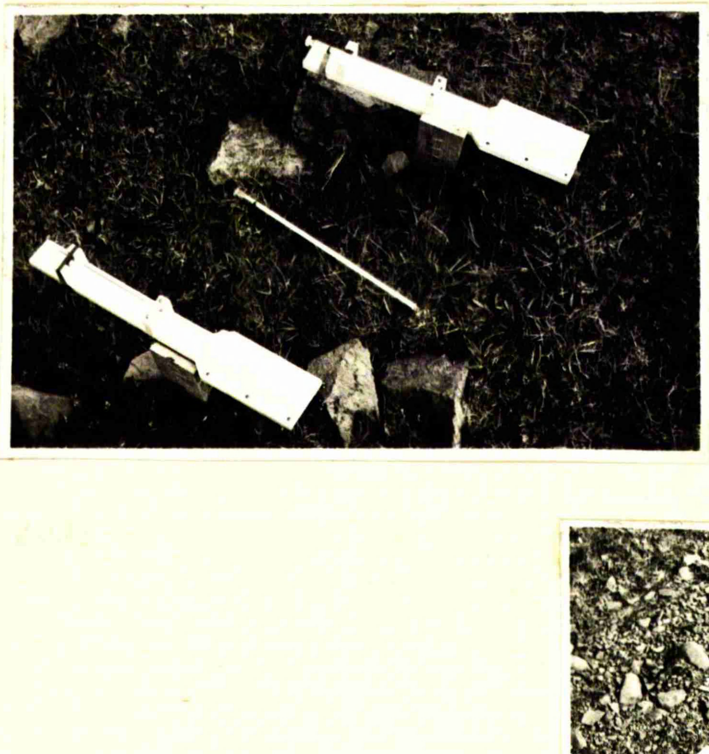
Phot.1 *Cerastium nigrescens* in open debris. Hamar, altitude 100 ft. 9/9/52.

Phot.2 *Cerastium nigrescens*; specimen of the usual prostrate type, after a year in the protection of two boulders. Hamar, altitude 100 ft. 7/9/53.

Phot.3 Maximum and minimum thermometers at 15 cms. above the ground in "Cocoa-tin" shields; grass minimum thermometer on the ground. On the heath by the Wall. Hamar, altitude 100 ft. 31/8/52.

Phot.4 The thermometers in the debris site. Hamar, altitude 100 ft. 31/8/52.

PLATE VI



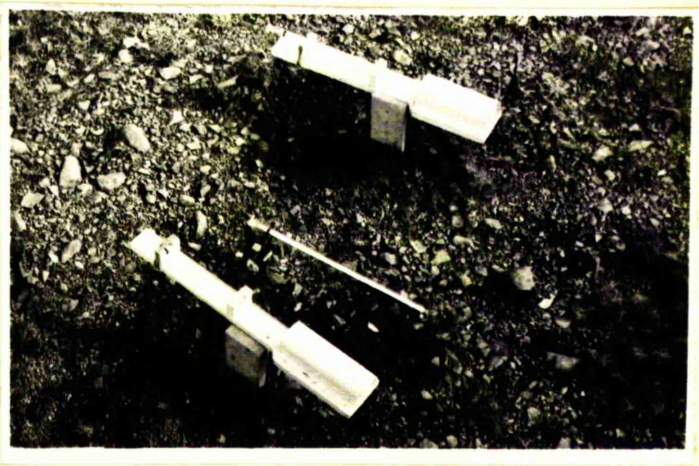


Plate VII

Phot.1 *Arenaria norvegica*, x 1, on serpentine debris of Namar, altitude 150 ft. 9/9/52.

Phot.2 View southwards down a 10-15 deg. slope of Ronas Hill at 1300 ft. Showing the horizontal stripes of closed vegetation crossing the granite-diorite debris. 18/8/52.

Phot.3 View across the slope of phot.2 on Ronas Hill, showing how the horizontal stripes, under the influence of solifluction, form steep terraces alternating with the flatter stretches of debris. The closed vegetation here consists here of *Loiseleuria procumbens*, *Calluna*, *Salix herbacea*, *Lycopodium alpinum*, *Thymus drucei* etc. The open debris contains *Luzula spicata*, *Juncus trifidus* etc. 18/8/52.

Phot.4 Rhacomitrium-rich dwarf shrub heath on the southwest flank of Ronas Hill, altitude 1200 ft. Showing the low mat of *Arctous alpina*, *Calluna*, *Vaccinium vitis-idaea* and *Rhacomitrium lanuginosum*. 18/8/52.

PLATE VII