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EXPERIMENTAL TAXONOMY OF SOME MEMBERS
OF THE TEESDALE FLORA.

BY

TREVOR THOMAS ELKINGTON

B.Sc. (DUNELM)

Being a thesis presented in candidature
for the Degree of Doctor of Philosophy
in the University of Durham 1962.



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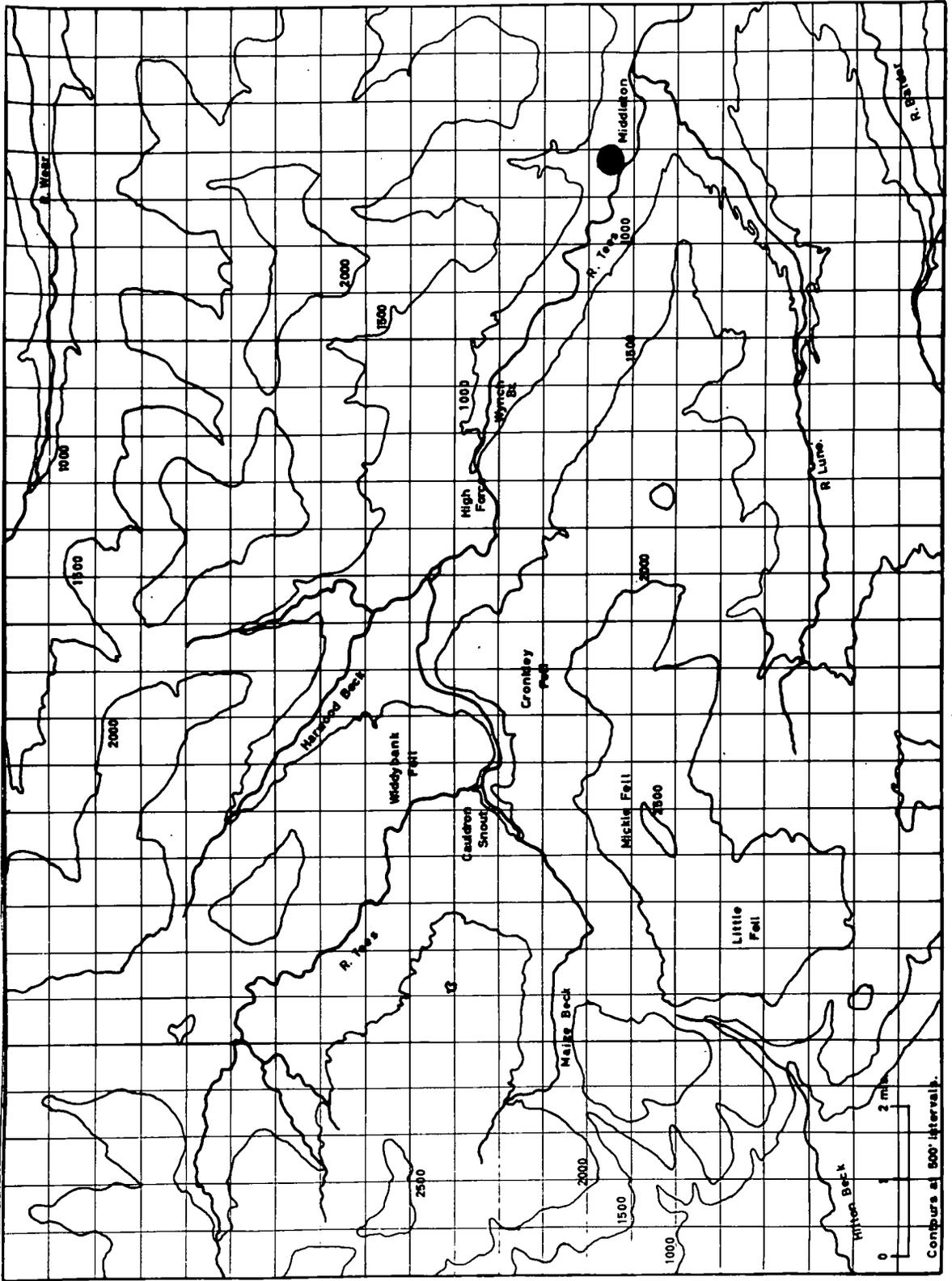
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Upper Teesdale

CHAPTER I.

Introduction

The flora of Teesdale first became known to British botanists in the first half of the nineteenth century, although some of the first records were made as early as the end of the eighteenth century by John Binks, a miner living in the area, and were communicated by the Rev. Harriman. Even earlier than this Ray (1689) knew of Potentilla fruticosa from the Tees valley. There are a number of early accounts of the area of which probably the best known are those of the Backhouses published in 1843 and 1844. From this time the valley of the upper Tees from Middleton in Teesdale to its source on Cross Fell including the surrounding hills has become famous as one of the richest botanical localities in Britain, especially renowned for the abundance of montane and rare plants, and perhaps only rivalled in Britain by Ben Lawers and Glen Clova in Scotland.

By the end of the first half of the nineteenth century the majority of the flowering plants of the area had been discovered, although this process has continued until the present day, Alopecurus alpinus only having been confirmed in the area in 1959 by Ratcliffe and Eddy. In the second half



of the century interest was aroused in the geographical distribution of the British flora and this was greatly stimulated by the publication of Watson's *Cybele Britannica* (1847) and *Topographical Botany* (1873). Interest in arctic plants was also strong at this time and the distributional types and the species present were analysed in detail by Hooker (1861). As a result of these studies it was realised that there were, in Teesdale, representatives of a wide variety of types of geographical distributions ranging from species with a southern and continental distribution such as *Helianthemum canum* to arctic-alpine species such as *Dryas octopetala*. A detailed description of some of the distributional patterns exhibited by species in Teesdale is given here in chapter II.

It was also in the middle of the last century that theories were first formed as to the origin of the British flora and here one of the best known pioneer studies was that by Forbes (1846), who put forward the idea that the British flora was a result of immigration since the Ice Age. The same idea was also developed by Darwin who expounded it in detail in the 'Origin of Species' (1859). It was gradually realised that the Teesdale flora presented somewhat special problems in relation to this theory of migration since in the area

were a large number of species with northern distribution patterns, some of which were not found in the Scottish mountains and a few nowhere else in Britain. As a result another theory was brought forward to explain this and other localities rich in such disjunct species. This is the perglacial survival theory which seeks to explain such concentrations of these species as a result of their survival, through the time of glaciation, on unglaciated areas or nunataks in situ. This is to be contrasted with the other alternative, that the total British flora is a result of immigration after the Glacial Period. The arguments are well set out in the discussion of the Royal Society in 1935 on the origin and relationship of the British flora. The views of the proponents of the perglacial survival theory are well summed up by Wilmott (1935) who writes "It seems incredible that these species could have migrated over intervening areas from their nearest stations, have settled on unglaciated Teesdale and have died out over the routes travelled. They are there because they survived glaciation there." The evidence on which a judgement may be made between these two arrival times is mainly indirect. It has been shown by Raistrick (1931) that it is probable that the summits of Cross Fell and Mickle Fell and some of the fells at the head

of Weardale were unglaciated. It is conjectural whether plants could have survived on them through the glacial maximum. Such nunataks would probably consist of shoulders of bare rock which would be extremely exposed at all times. It has been pointed out in support of the per-glacial survival theory that nunataks in Greenland at the present day sometimes bear quite a rich flora. It is therefore of interest to see how such nunataks compare with the above picture. Böcher (1956) has separated four types of refugia in East Greenland. These are (a) nunatak refugia, mountains projecting through the ice and surrounded by ice in all directions; (b) semi-nunatak refugia, mountains facing the sea on one side, but otherwise surrounded by ice; (c) cross-valley refugia, those containing cross valleys cut out during earlier glaciations, but later unglaciated due to local changes in the drainage of the ice cap; (d) parallel valley refugia, valleys with the same direction as the main valleys (or fjords) and situated between two parallel valleys which drain off the neighbouring ice cap and receive most of the local glaciers. Since in Teesdale all the surrounding areas bear evidence of glaciation it would seem that only the first type, the nunatak refugia, are valid as a comparison. The flora on these nunataks has been shown by Dahl (1946) to be very dependent

on the firn line. If this is below the foot of the nunatak, only areas where the snow is blown clear will be clear of ice and such areas bear a very poor flora. Dahl has called these antarctic nunataks. Manley (1959) has considered that in the post-Allerød recession in the Lake District, that with an annual rainfall of 70 - 80" the firn line would be in the region of 2300', and also that the annual precipitation would be similar to the present day. It is very difficult to visualise what conditions in full glacial times were like, but it seems possible that the firn line would be as low or lower than this. If this was so it seems extremely unlikely that many of the northern species now found in the dale could have survived such conditions.

New impetus has been given to the study of these problems by the development of the techniques of pollen analysis and the tracing, through this study, of the post-glacial vegetational development in Britain. The spreading of the British flora after the retreat of the ice has been considered by Godwin (1949). He envisages an open 'Park-Tundra' after the retreat of the ice, followed by the gradual afforestation of the country and subsequently, due to a climatic deterioration, the invasion of much of the upland forest by Sphagnum bog. Finally the gradual deforestation and cultivation of the

country can be traced, commencing with the activities of Neolithic man.

The studies of deposits from the late-glacial and post-glacial period when the 'Park-Tundra' type of vegetation was extant in Britain have proved of special interest in the understanding of these assemblages of disjunct species. This is because remains of many of the now relict species have been found in these deposits. Some of the discoveries (recorded in Godwin 1956) may be mentioned here. Thalictrum alpinum has been found as fruits at Hawks Tor, Cornwall, Nazeing, Essex and Barnwell, Cambridgeshire. Other species which have been found at Nazeing are Potentilla fruticosa (one unmistakable achene), Draba incana, Salix phylicifolia, and Dryas octopetala; the latter species is also known from deposits in the south of England at Barnwell, Cambridge and in the Lea valley, Herts. These, and a large number of records both of these and other species show that many of the species now restricted in Britain to upland areas, were at one time widespread over much of England. After this period, as the climate ameliorated, the open vegetation present was gradually suppressed by the invasion of closed woodland. This was first composed mainly of birch and pine, but as amelioration further proceeded a dense deciduous forest was produced.

This process had a marked effect on many of the species common in the open communities of the early post-glacial period, with the result that they became extinct over most of England.

In Teesdale the main component of the woodland appears to have been Betula and this was extensive during the boreal period (zones V and VI) up to an altitude of approximately 2350', macroscopic remains of Betula having been found up to this level (M.E. Johnson pers. comm.). This means that in all probability the main areas where the disjunct species are found today, especially Cronkley Fell and Widdybank Fell, would have been covered by birch forest at this period. Subsequently in the Sub-atlantic period the climate became much wetter with the invasion of bog over the region so that the woodland disappeared and was replaced by blanket bog.

Since many of the species that are now relict in Teesdale were widespread during the early post-glacial period it is clear that it is unnecessary to postulate per-glacial survival in Teesdale. This does not exclude the possibility of glacial survival, but makes it irrelevant as being the cause of the presence of refugia. Godwin (1956) has given most weight to three reasons for the post-glacial diminution of range of the species involved, all three are indirect consequences of the climatic changes. These are first the dense forest which

became established, secondly the development of bog in upland areas, and thirdly the pronounced podzolisation and leaching of the soils due to the high rainfall. It is also possible that this post-glacial diminution of range has been directly effected by the climatic changes, since some boreal species may not be able to withstand high summer temperatures. This explanation has been favoured by Dahl (1951) as an explanation for distribution patterns of a number of montane species in Scandinavia.

The first of these indirect processes has probably been the most important in the south of the country and the primary cause of the southern extinction of these species. In Teesdale and other upland refugia the other two processes will also have been very significant; and in such cases it is important to consider any distinctive features which would allow such species to survive in these localities. An attempt has been made to do this by a consideration of their ecology, comparing the communities and soils to which these species are confined in their British localities. Comparisons have also been made, where possible, with the continental conditions under which these species exist.

Special mention must be made of the Burren area of Co. Clare, W. Ireland. This is another centre for disjunct plants

including some of those found in Teesdale, especially Gentiana verna, Potentilla fruticosa and Dryas octopetala. Mixed with these are a number of species with a chiefly Mediterranean distribution e.g. Adiantum capillus-veneris and Neotinea intacta. The possibility of glacial survival of plants in this region has been discussed by Jessen (1949) who comes to the conclusion that there is a distinct possibility of survival in refuges on land off the present west coast of Ireland, which is thought not to have been covered by sea in the glacial period due to the eustatic fall in sea level at this time. Further evidence has been gained for this view by the discovery by Jessen, Andersen and Farrington (1959) at Gort, Co. Galway, a few miles to the North of the Burren area, of a pollen grain of Eriocaulon septangulare, in an interglacial deposit, a record which they emphasize must be considered as absolutely reliable. This is a species which today is not found on the Continent at all, but is confined in Europe to W. Ireland and some of the Hebridean islands. Since the Irish material of this species has been shown to have $2n = 64$ while American material has $2n = 32$ (A. & D. Löve 1958), there seems little possibility of extinction after the interglacial period and reimmigration in the post-glacial period. If survival has been the case here there seems no reason why other species should not also have

survived. This does not exclude, of course, the possibility of immigration of species into the area after the final glaciation, so that the present flora may be a mixture of both glacial survivors and post-glacial immigrants. The latter possibility certainly seems more likely for the Mediterranean species, which are known to be very frost intolerant.

It is clear that the occurrence^r of any particular species in such a refugium as Teesdale is partly a matter of chance and it is interesting to consider some of the species which might possibly be expected to occur in Teesdale but which are not present there. Perhaps one of the chief of these is Saxifraga oppositifolia, which at present grows further to the south in the Pennines on Ingleborough, to the west in Wales and the Lake District and is quite a common montane species in flushed areas on Scottish mountains. Since in the Lake District (Ratcliffe 1960) S. oppositifolia is present in wet basic flushes and earthy scree it would appear that suitable habitats occur in Teesdale, so that its absence may perhaps be due to chance, especially since fossil remains have been recovered from late and post-glacial deposits in South England. The same remarks also apply to Silene acaulis, which in the Lake District, according to Ratcliffe, can grow on steep banks at the broken cliff foot, again a habitat which is present in

Teesdale especially on the sides of some of the fells in the west of the area. Another group which is altogether absent in Teesdale are the mountain willows, which today are almost entirely confined to Scotland. A number of the species have been recorded in late and post-glacial deposits in England and Salix lapponum in particular is still extant on Helvellyn in the Lake District. Finally Ratcliffe (1960) mentions Alchemilla alpina and Oxyria digyna as two common species in the Lake District which are remarkable in being completely absent from the North Pennines, and for which Teesdale certainly seems to offer suitable habitats. It is possible that some of these montane species did grow in Teesdale in the post-glacial period and have since become extinct. Although this process is known to have taken place in the last century this seems to have been more the result of overzealous collecting than of a natural extinction. As Ratcliffe points out, the explanation may lie in the fact that the migrating flora was heterogeneous in composition in N. England and some species did not reach the North Pennines when conditions for their spread were suitable. It is also possible that the climate in the North Pennines may, in some way be unfavourable for these species, although species such as Alchemilla alpina and Oxyria digyna are widely distributed in Scotland with a wide altitudinal amplitude, so that it seems unlikely that

favourable conditions should be entirely lacking in the North Pennines.

It has been widely assumed that the relict species in the well known refugia have had a continuous history there from the early post-glacial period through the period of the climatic optimum (and the greatest restriction) to the present day. Proof of this however in such a refugium was only provided in 1955 by Godwin's investigations at Cwm Idwal, N. Wales. This is a well known refugium for a number of arctic-alpine species in Wales including Dryas octopetala and Saxifraga oppositifolia. Godwin has shown that a number of species that are relict there today have a continuous record in the bottom deposits of the corrie lake from zones IV and V right through the post glacial period. These species include Plantago maritima, Armeria maritima and both Empetrum nigrum and E. hermaphroditicum, all of which are found in the area today.

It is therefore reasonable to suppose that the same situation will have held in other refugia and in particular in Teesdale. This being so, the Teesdale populations will have been isolated since woodland closed in around them, exterminating the lowland populations. This time is of the order of eight to ten thousand years according to present estimates. It is possible that in this time differentiation has taken

place between these small populations and between these and the species in their main extra-British areas, so that it is of great interest to study possible variation in and between them. Furthermore even though the explanation of the disjunction of these species has been shown to lie in the post-glacial history of British vegetation, as pointed out earlier this does not exclude per se the possibility of perglacial survival. If isolation has taken place for this length of time however the differences between the populations in the various extant localities might be larger than those produced by isolation from the immediate post-glacial period. Thus it is important in a study of this type that the size of any differences found should be accurately measured. For this reason biometrical and statistical methods have been used extensively in the study of field samples from the various populations. The use of field samples has been necessary since specimens in herbaria are not usually collected randomly and thus cannot be relied upon to give an estimate of the full range of variation within a population. This study has been supplemented by the study of cultivated plants which have given information on whether the variation observed in the field samples is environmental or genotypic. A study of the cytology of some of the species has also been made to

determine whether there is any variation in chromosome number in comparison with material of the species from elsewhere in their range.

Detailed investigations of this type have not been common. One of the most relevant is that by Proctor (1957) who has shown that Helianthemum canum is represented in Teesdale by a distinct genotype with very short glabrous or subglabrous leaves which he has named subsp. levigatum. In Scandinavia Knaben (1959) has described a situation in the Radicatum group of Scapiflora Papavers where evolution has proceeded in a number of isolated populations to produce several races which she considers to be distinct at the species level. In view of this known occurrence of variation and evolution in isolation it is clearly of importance to gain more information on this type of change, since it can throw light on both historical and evolutionary problems.

CHAPTER II.Geographical Distribution

The interest of the Teesdale flora is primarily connected with the geographical distributions of the species that grow there and nearly all of the numerous accounts of the plants of the area have stressed this feature. Within the flora of the area are plants showing a large number of different types of both British and world distributions. It is impossible to deal, in this account, with all the species involved since not only flowering plants, but ferns, mosses, liverworts and lichens all have species of phytogeographical interest in the area. Even considering flowering plants alone, in the six 10 kilometre squares which cover the upper part of the Tees valley there are, according to the B.S.B.I. maps scheme records, between 500 and 550 species.

A number of systems have been devised for arranging the plants of North Europe into phytogeographical groups and one of the most comprehensive of these is that of Hultén (1950), constructed for the vascular plants of N.W. Europe. In this he divides the flora into 48 geographical groups. In table II. 1 these are enumerated with the number of species of each group which are found in the upper Tees valley. For this

purpose the species recorded by the B.S.B.I. Maps Scheme in the six ten kilometre squares covering this area have been used. This area also covers small parts of the Eden valley to the S.W. and Weardale to the N.E., but is the most complete and up to date general plant list available for the Upper Teesdale area. It will be seen that in this way about 80 % of the species found in Teesdale can be placed in this system, showing that it is quite successful for this purpose. There are, of course, a number of species in Teesdale which are not found in the area that Hultén deals with e.g. Gentiana verna, Alopecurus alpinus. The table emphasizes the very wide phytogeographical diversity of the Teesdale flora ranging from arctic-subarctic species to boreal and continental ones.

It is clearly impossible to deal here with even one species from each of Hultén's 32 groups which are represented in the Teesdale flora. The species which have been selected all show large disjunctions in their British and world distributions and have been chosen to show the main types that are represented. They are also examples of some of the more interesting of the general phytogeographical groups distinguished by Matthews (1955).

Group	Characteristics	Number of species in Teesdale
1.	Arctic circumpolar plants with continuous distribution.	-
2.	Arctic circumpolar plants with a large gap in Siberia.	-
3.	Arctic seashore plants.	-
4.	European, Arctic-montane plants.	1
5.	Eurasian, Arctic-montane plants.	1
6.	Circumpolar Arctic-montane plants lacking in the mountains of Central Europe, but with continuous distribution in Northern Siberia.	-
7.	Circumpolar, Arctic-montane plants lacking in the mountains of Central Europe and with large gaps in Siberia.	-
8.	Circumpolar, Arctic-montane plants occurring in the mountains of Central Europe and with continuous distribution in northern Siberia.	11
9.	Circumpolar, Arctic-montane plants present in the mountains of Central Europe, but with large gaps in Siberia.	5
10.	"Amphi-Atlantic", Arctic plants.	-
11.	"Amphi-Atlantic", Arctic-montane plants also present in southern mountains.	11
12.	European, boreal-montane plants with separated northern and southern areas.	3
13.	European, boreal-montane plants with northern and southern areas not clearly separated.	2

Group	Characteristics	Number of species in Teesdale
14.	North-European plants with a boreal-montane tendency.	13
15.	Eurasianic, in Europe boreal-montane plants connected with Scandinavia through the Baltic countries and Finland.	1
16.	Boreal-circumpolar plants that are boreal-montane in Europe with continuous distribution.	8
17.	Boreal-circumpolar plants that are boreal-montane in Europe but with gaps in Siberia.	1
18.	European seashore plants.	-
19.	European, Atlantic plants.	21
20.	Subatlantic plants.	52
21.	Circumpolar seashore plants.	-
22.	Circumpolar, suboceanic plants.	2
23.	Northern-Eurasianic plants lacking in Central Europe.	-
24.	Northern boreal-circumpolar plants lacking in Central Europe.	-
25.	West-European - North-Siberian plants.	23
26.	West-European - Middle-Siberian plants.	88
27.	West-European - South-Siberian plants.	33
28.	Eurasianic plants connecting with Scandinavia from both the east and the south.	14
29.	Boreal-circumpolar plants lacking large gaps in their area.	54

Group	Characteristics	Number of species in Teesdale
30.	Incompletely boreal-circumpolar plants with gaps in Asia and in the Pacific.	5
31.	Incompletely boreal-circumpolar plants with gaps in East Asia and in America.	12
32.	Incompletely boreal-circumpolar plants with a gap in West America.	4
33.	Incompletely boreal-circumpolar plants with a gap in East Siberia.	2
34.	West-European continental plants.	2
35.	East-European continental plants connecting with Scandinavia by way of the Baltic countries.	-
36.	East-European continental plants connecting with Scandinavia by way of the Baltic countries and Denmark.	-
37.	West-Siberian continental plants connecting with Scandinavia only by way of the Baltic countries and Finland.	3
38.	West-Siberian continental plants connecting with Scandinavia by both the Baltic countries and Denmark.	2
39.	Central-Asiatic continental plants.	-
40.	Southeast-European - South-Siberian plants.	-
41.	Plants with two or more widely separated areas.	9

Group	Characteristics	Number of species in Teesdale
42.	South- or Central-European plants not indigenous within the area of the Atlas, but not strongly culture-spreading.	3
43.	Southwest Asiatic plants not indigenous within the area of the Atlas, but not strongly culture-spreading.	1
44.	Central-Asiatic plants not indigenous within the area of the Atlas, but not strongly culture-spreading.	-
45.	American plants.	1
46.	Plants very strongly spread by culture.	42
47.	Plants endemic within the area of the Atlas.	-
48.	Plants with insufficiently known total areas.	2
Total		432 species.

Table II. 1. Geographical elements of the flora of N.W. Europe delimited by Hultén (1950), with the number of species of each group found in Teesdale.

Two of the species in Teesdale which show a very great contrast in their world distributions are Helianthemum canum and Alopecurus alpinus. Matthews (1955) has put Helianthemum canum into his continental southern element and diagram II. 1 shows its world distribution, the Teesdale site being one of the most northern with the species extending south to the N. African Atlas mountains and east across Turkey and the Caucasus. In the High Alps it is replaced by H. alpestre (Jacq.) Dunal. Hultén places H. canum in group 12, a group of European, boreal montane plants with separated northern and southern areas. This distribution is in complete contrast to that of Alopecurus alpinus, shown in diagram II. 2, which Matthews places in his arctic-subarctic element. Here the Teesdale locality is one of the southernmost limits of the species the main distribution area extending from Greenland across Arctic Canada and through the Eurasiatic Arctic. Since ^{are} there/a number of related taxa to the south of this area in Asia and N. America it is possible that the British material also may belong to a different biotype from the Arctic material, but no information is available on this point.

It is also of interest to examine the detailed distributions of some of the Teesdale species with respect to their distributions within the dale and also within their British

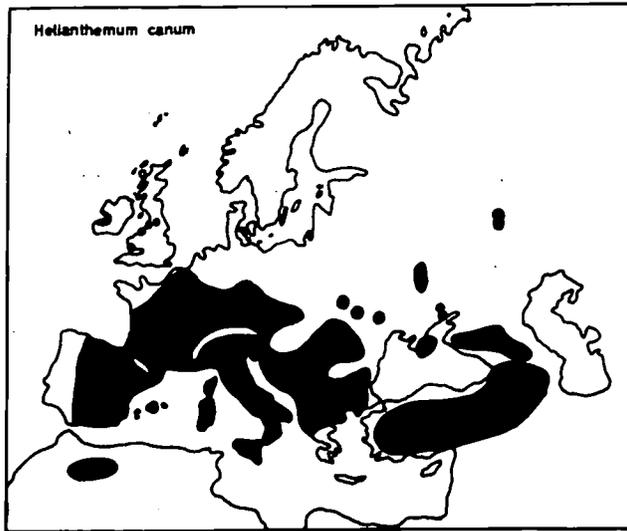


Diagram II. 1. World distribution of Helianthemum canum.
(Redrawn from Meusel 1945).

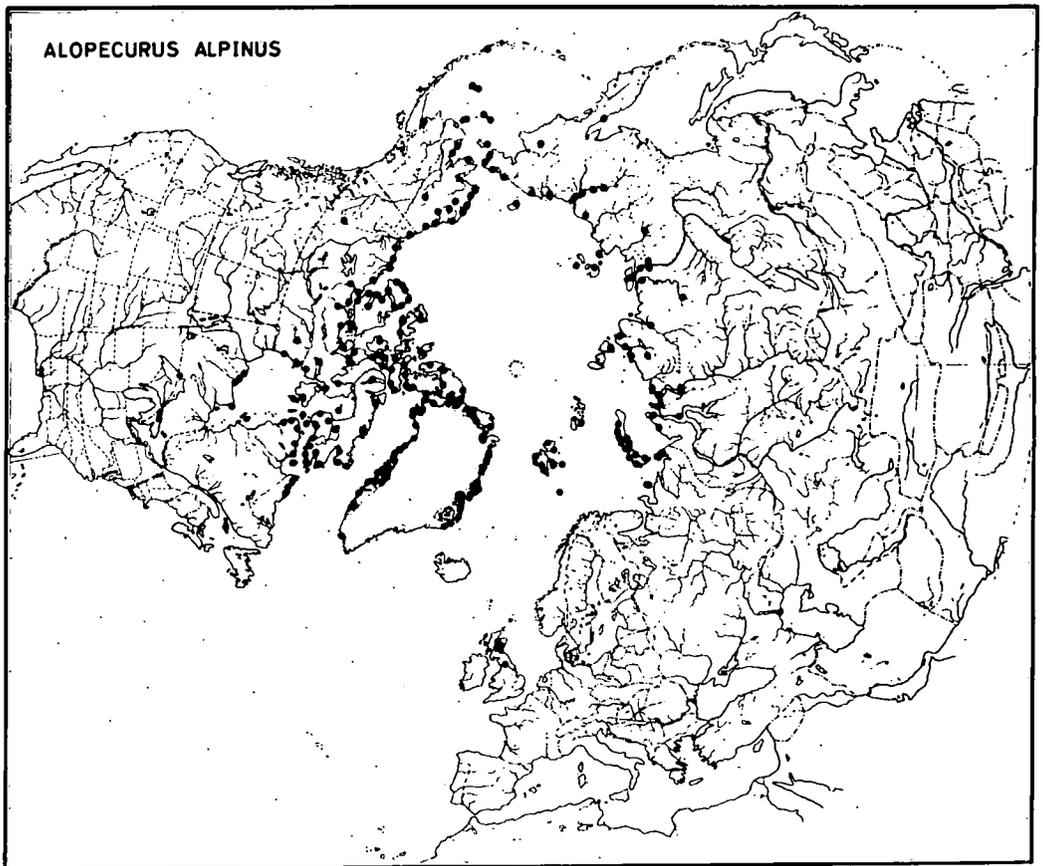


Diagram II. 2. World distribution of Alopecurus alpinus s.s.
(E.Hulten unpub.).

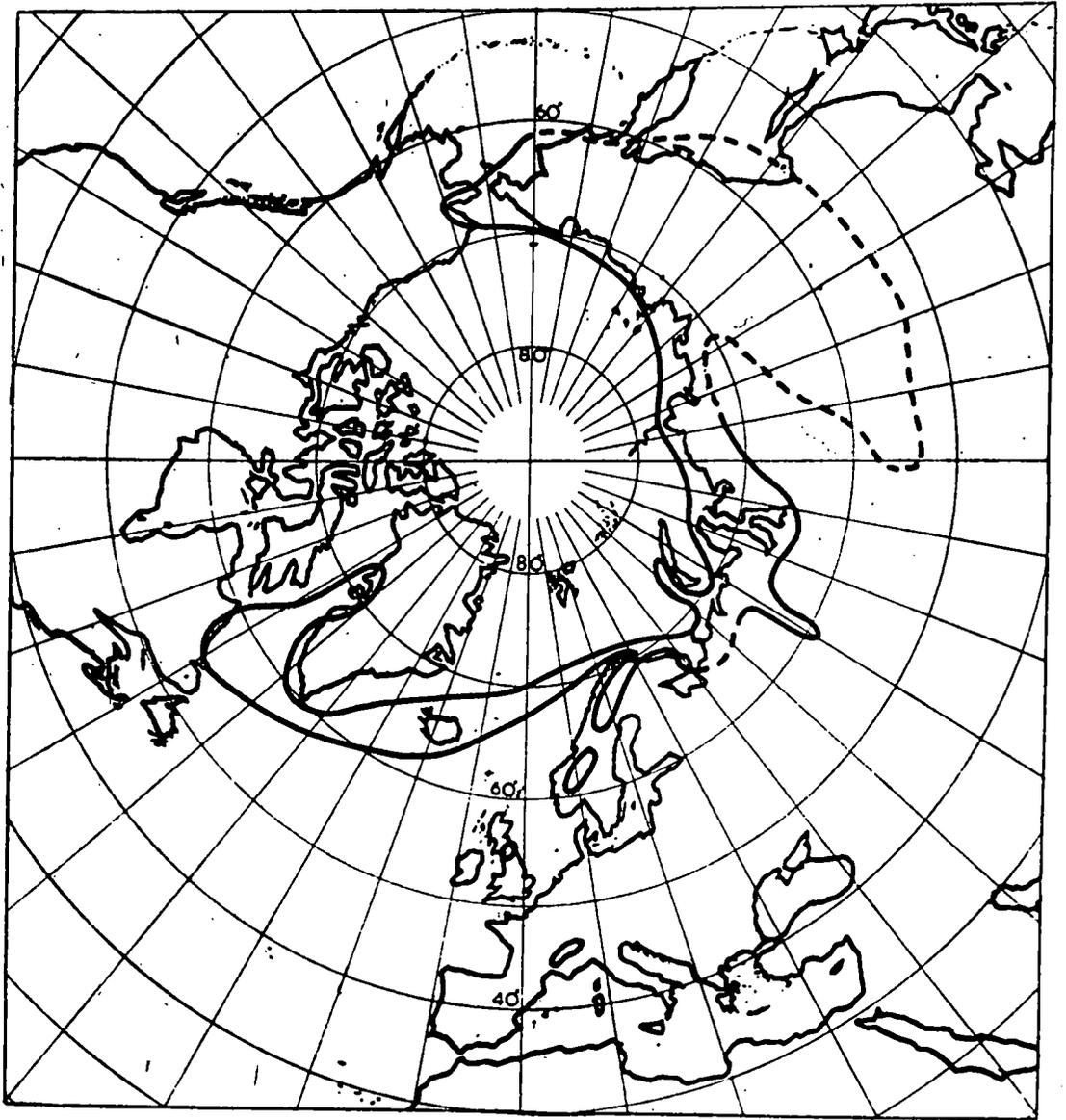
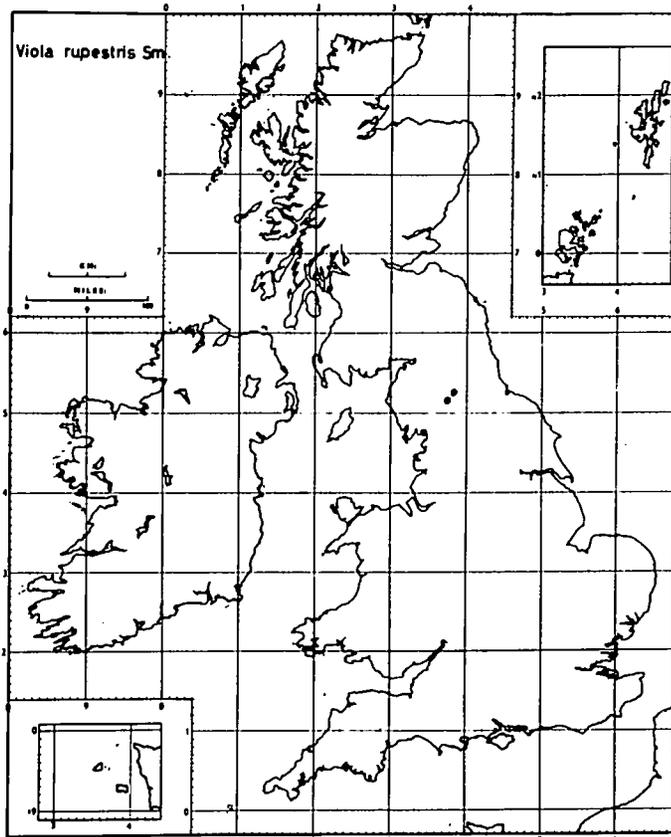


Diagram II. 3. World distribution of Minuartia stricta.

(From Raven and Walters 1956.)

areas. The most restricted species present in the ~~the~~ dale is Minuartia stricta, which is found in Britain only on Widdybank Fell; its world distribution (diagram II. 3) shows a rather unusual pattern in that it has a wide circumpolar distribution, being placed by Hultén in group 8, but in Central Europe it is confined to the Jura and Bavarian Alps, being absent from the true Alps. There are several other species which are confined to England in their British distributions. One of these, Helianthemum canum, has already been mentioned. Another, Viola rupestris, was until recently only known from Teesdale in Britain, but is now known (Valentine and Harvey 1961) from two other localities in N. England (diagram II. 4). In its world distribution, shown in diagram II. 5, it is seen to be a wide ranging eurasiatic species, but not found in N. America. This distribution is similar to that exhibited by Carex ericetorum, and both are placed by Hultén in one of his W. Siberian continental groups (no. 37). This species shows a definite continental tendency in Europe and this is reflected in its British distribution shown in diagram II. 6, where it will be seen that it has a distinct eastern tendency extending from Teesdale (its most northern locality in Britain) down through a number of localities on the Permian Magnesian limestone to the Breckland



BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

Diagram II. 4. British Distribution of *Viola rupestris*. (B.S.B.I. Maps Scheme).

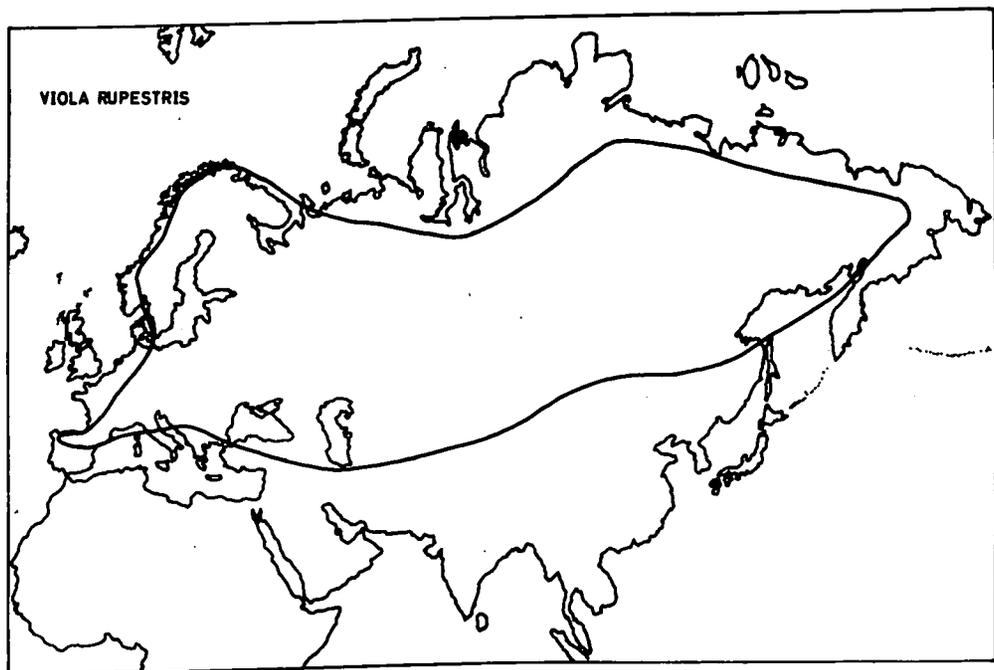


Diagram II. 5. World distribution of *Viola rupestris*. (M.J. Harvey unpub.).

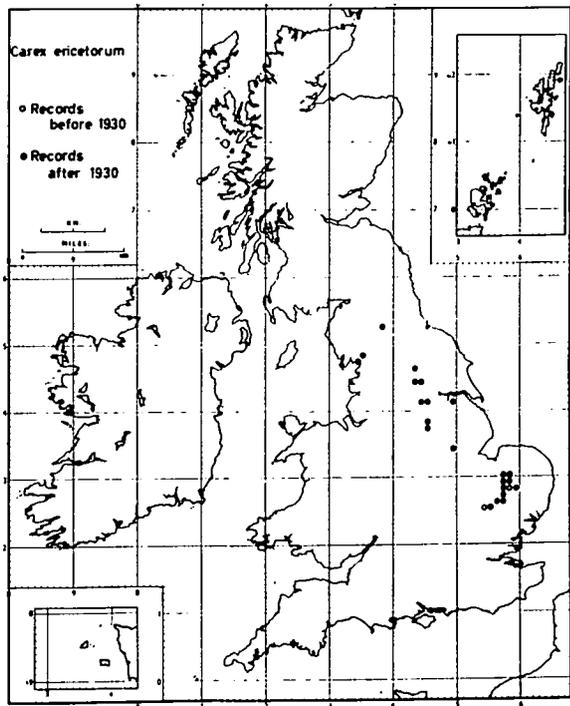


Diagram II. 6. British distribution of *Carex ericetorum*. (B.S.B.I. Maps Scheme).

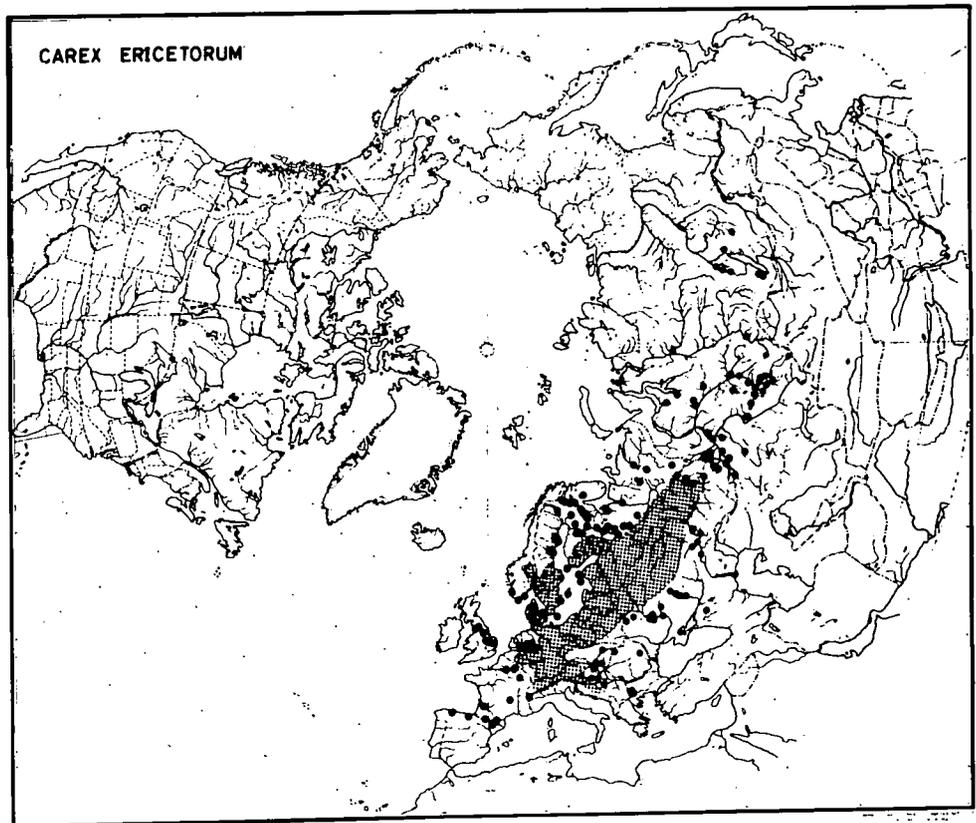


Diagram II. 7. World distribution of *Carex ericetorum*. (E. Hulten unpub.).

of Suffolk and Norfolk and into adjoining Cambridgeshire. The continuous Eurasiatic distribution is clearly seen in the map of its world distribution (diagram II. 7).

Two of the most interesting species found in Teesdale are confined in Britain to localities in England and W. Ireland. Gentiana verna is a species which shows a fairly wide distribution area in Teesdale as shown in diagram II. 8, extending over a distance of approximately 12 miles, from a number of localities near head of the R. Tees in Cumberland south east to localities in Lunedale in N. Yorks, all the outlying localities in the area being on limestone grassland. The only other area in Britain where G. verna is known is in W. Ireland, as will be seen from diagram II. 10. Here its headquarters are the limestone areas of the Burren in Co. Clare, although it extends round the head of Galway Bay on to the limestone and calcareous drift of Co. Galway. In its wider distribution area Gentiana verna is one of the few British species which is present in the Alps, but not in the Arctic. As will be seen from diagram II. 11 the British localities are the most northern, the main area of the species extending from the Pyrenees and Sierra Nevada, across the Alps and Balkans to the Caucasus. Beyond this it extends across Asia to the Altai and Mongolia. A subspecies, ssp. Peneti is also known from

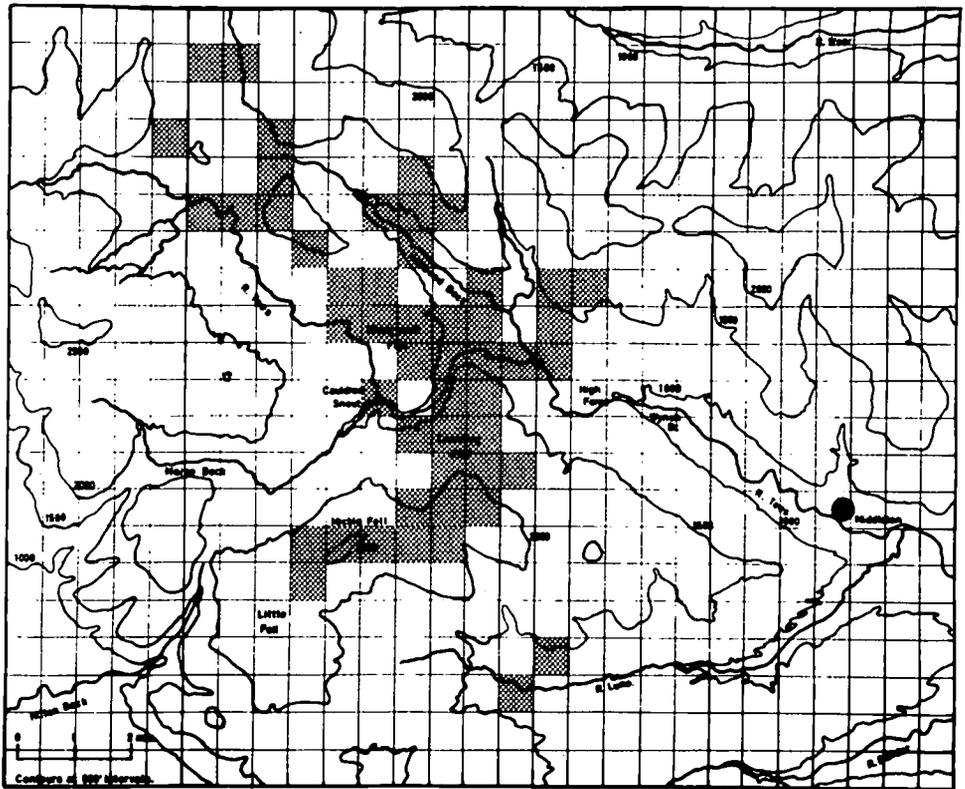


Diagram II. 8. Distribution in Teesdale of *Gentiana verna*,
 each square representing one square kilometre.
 (Personal and E.C.M. Haes' data.)

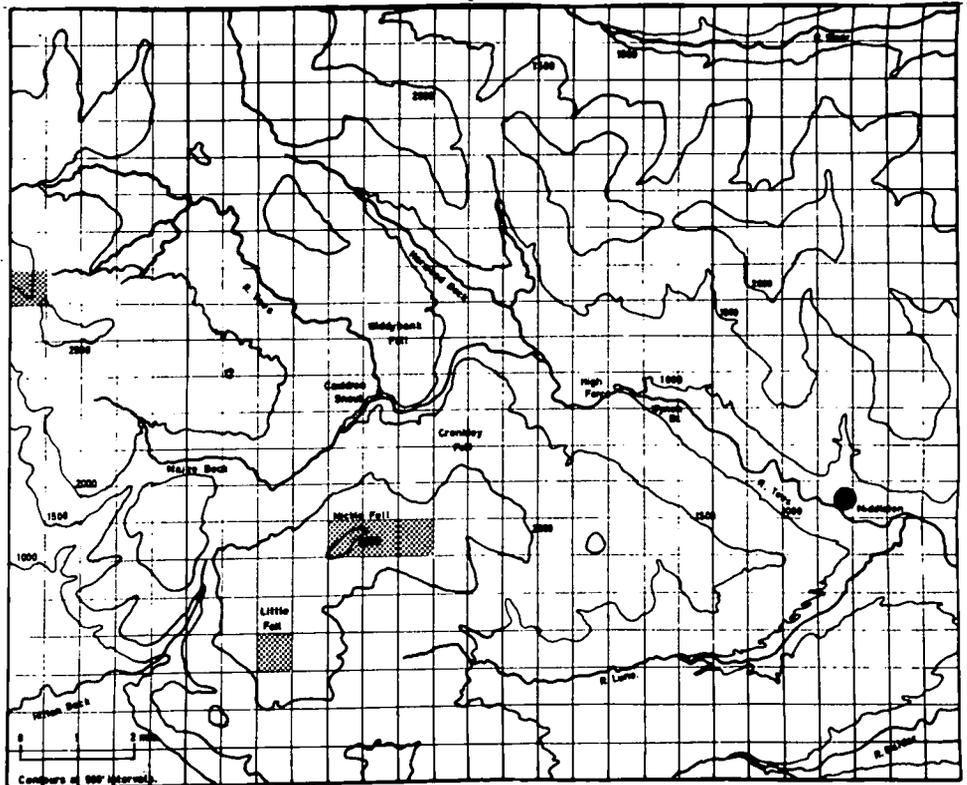
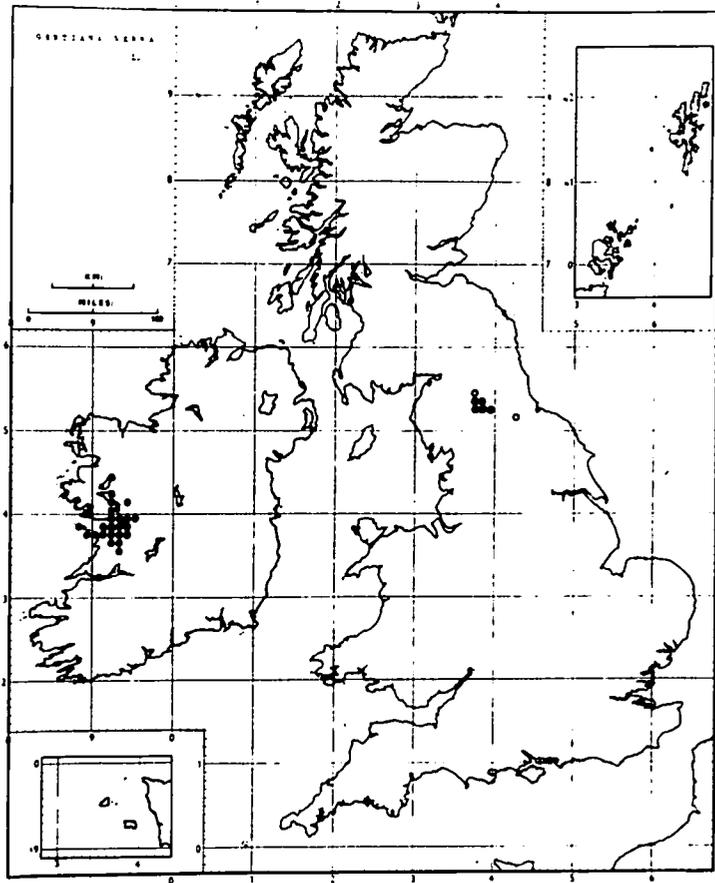


Diagram II. 9. Distribution in Teesdale of *Myosotis alpestris*,
 each square representing one square kilometre.
 (personal data.)



BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

Diagram II. 10. British distribution of *Gentiana verna*.
(B.S.B.I. Maps Scheme.)

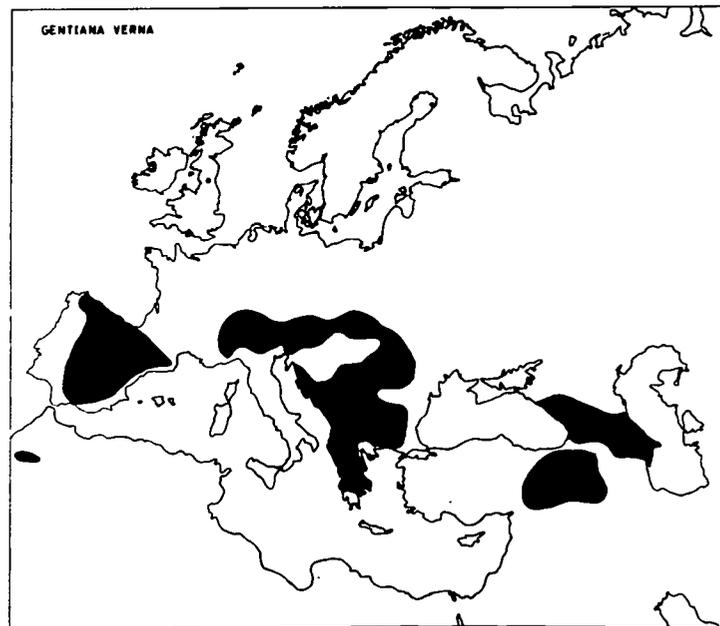
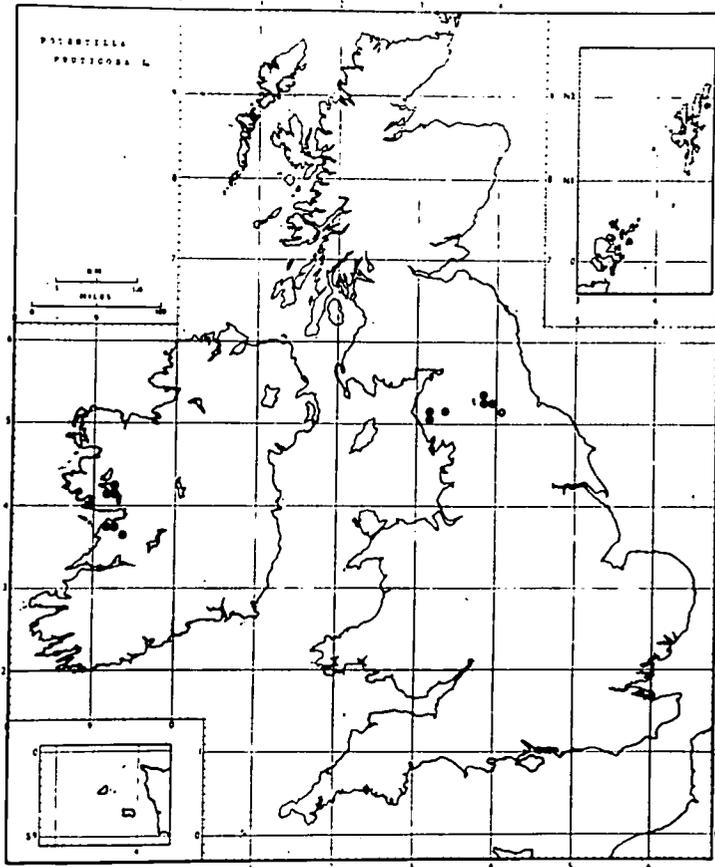


Diagram II. 11. European distribution of *Gentiana verna*.
(Personal data.)

the High Atlas mountains in Morocco. Potentilla fruticosa is also a species which is found in both Teesdale and W. Ireland, but it also has localities in the Lake District as is shown in diagram II. 12. In Teesdale it is confined to the banks of the River Tees occurring⁺ intermittently from the base of Cronkley Fell down to just below the town of Middleton in Teesdale, its greatest abundance being from High Force to Wynch Bridge. In the Lake District the species is known from Ennerdale and Wasdale and it was formerly also found on Helvellyn, although it has not been found in this locality for a number of years. In the west of Ireland this species is also centred on the Burren area, characteristically forming a zone round the edges of the turloughs or temporary winter lakes of the area. It also extends north to Lough Corrib and localities round the edge of the lake in both Co. Galway and E. Mayo are known. This disjunct British distribution is reflected in the European distribution shown in diagram II. 13. One of the most striking features of this is that P. fruticosa is not found in the Alps. It is present in the Pyrenees and Alpes Maritimes and according to Hegi (1931) a number of localities in Germany. It is also present in a number of localities around the Baltic, from Oland and Gotland to localities in Estonia and Latvia; from here there is a disjunction to the Urals. The species is, according to



BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

Diagram II. 12. British distribution of *Potentilla fruticosa*.
(B.S.B.I. Maps Scheme.)

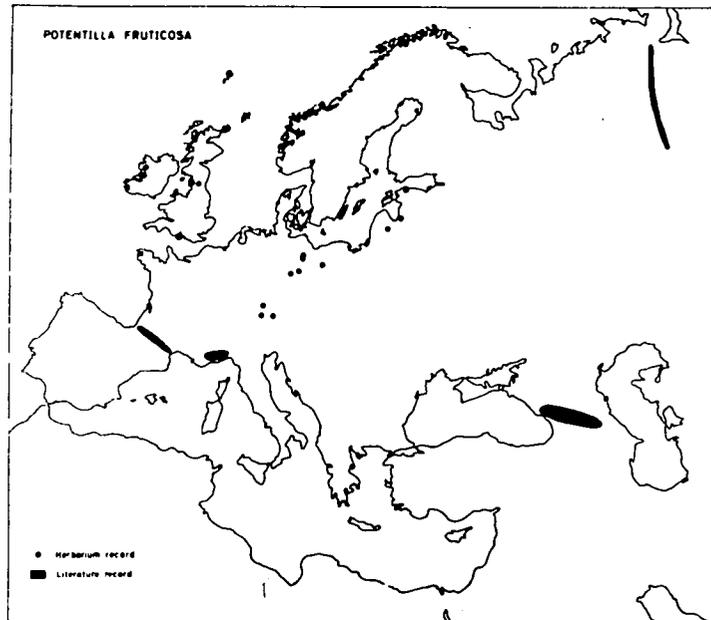
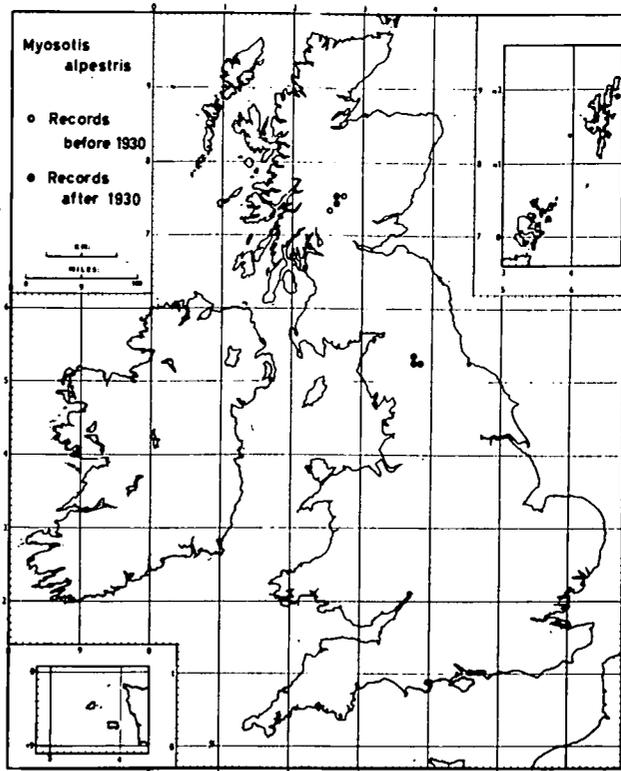


Diagram II. 13. European distribution of *Potentilla fruticosa*.
(Personal data.)

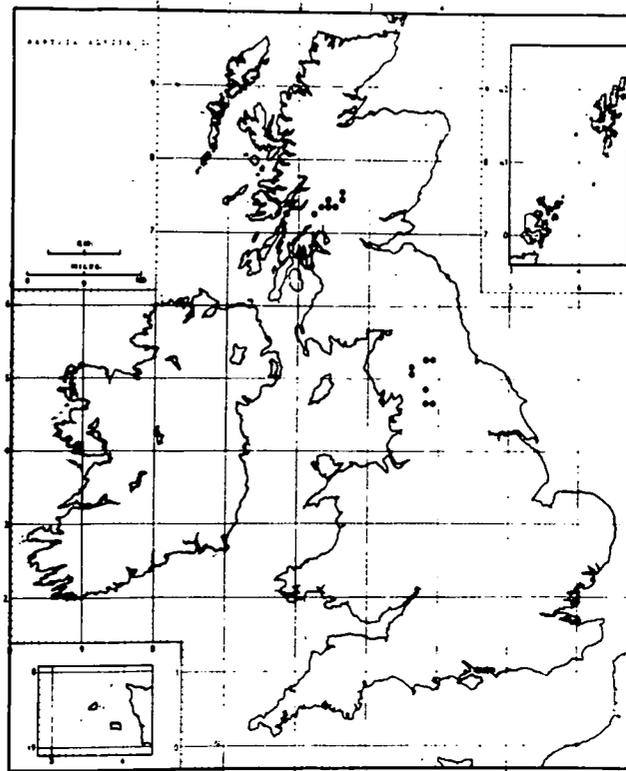
Gorchakovsky (1960), widely distributed in Asia. As pointed out later (p. 45) the British and Oland material is known to be tetraploid. In N. America, where P. fruticosa is widespread, it appears to be uniformly diploid. The species is placed by Hultén in group 16, a boreal circumpolar group, but because of the differing chromosome numbers this is not a very good designation from a biological point of view.

The majority of disjunct species found in Teesdale are also present in Scotland and there is a wide range, from species which are restricted to those which are widely distributed there. One of the most restricted species in this sense is Myosotis alpestris. In Teesdale this shows a scattered distribution on three of the high fells in the west of the area (diagram II. 9). In Scotland the species is confined, in a natural state, to a small region of the Central Scottish mica schist belt in Perthshire as will be seen from diagram II. 14. This species has also been collected in Caenlochan Glen, Angus, but according to Buchanan White (in Raven and Walters 1956) this is an introduction. In its world distribution M. alpestris is an arctic-alpine species present in the European mountains and in both Asia and N. America. A species which shows a somewhat wider range in Britain than this is Bartsia alpina. This is also confined



BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

Diagram II. 14. British distribution of *Myosotis alpestris*.
(B.S.B.I. Maps Scheme.)



BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

Diagram II. 15. British distribution of *Bartisia alpina*.
(B.S.B.I. Maps Scheme.)

to the mica schist belt, but extends from Glen Lyon in central Perthshire to Argyllshire in the west as shown in diagram II. 15. The diagram also shows that this species has a number of other localities in the north of England, the most southern being at Malham in the Craven district of Yorkshire which is another centre, although not so rich as Teesdale, for a number of species with disjunct distributions including several of the species found in Teesdale e.g. Carex capillaris and Dryas octopetala. Helianthemum canum has also been recorded in the past at Malham Cove. In its world distribution (diagram II. 16) B. alpina is seen to be an arctic-alpine species, but not circumpolar, being placed by Hultén in group 11, an amphi-atlantic distribution group. This distribution may be compared with that of Thalictrum alpinum (diagram II. 17), a Teesdale species common in Scottish mountains, which in its world distribution is placed by Hultén in group 8 being completely circumpolar and also present in the central European mountains.

One of the very restricted species in Teesdale is Dryas octopetala which has, as shown in diagram II. 18, only one locality in the dale and present here only in a very restricted area. It is in Britain, however, quite a wide ranging species present in Wales, several areas in the north

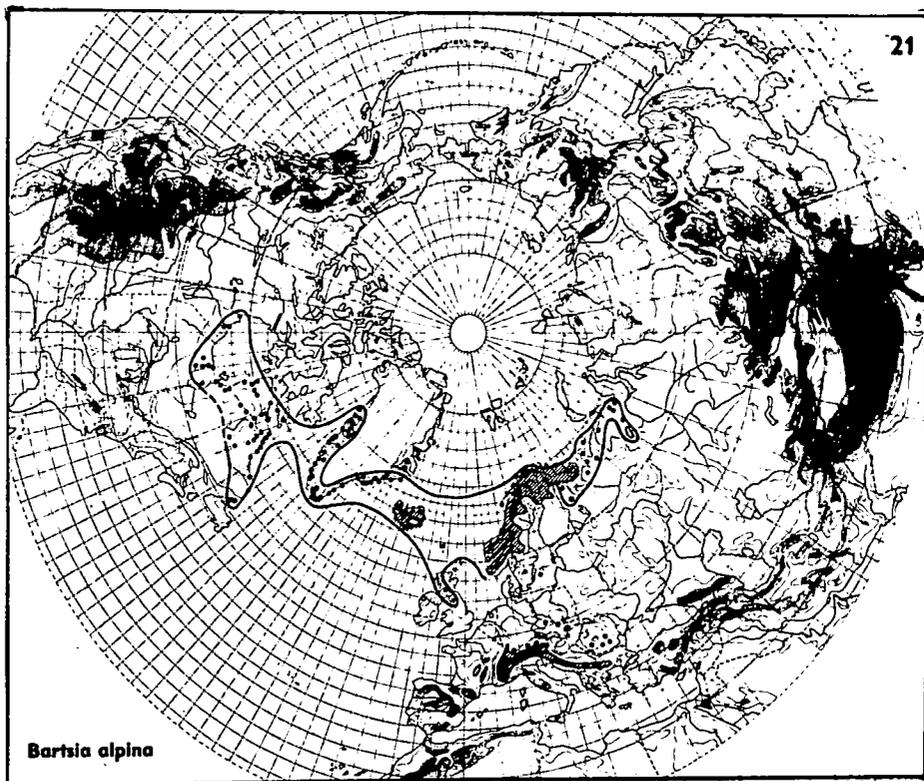


Diagram II. 16. World distribution of Bartsia alpina. (E. Hultén 1958.)

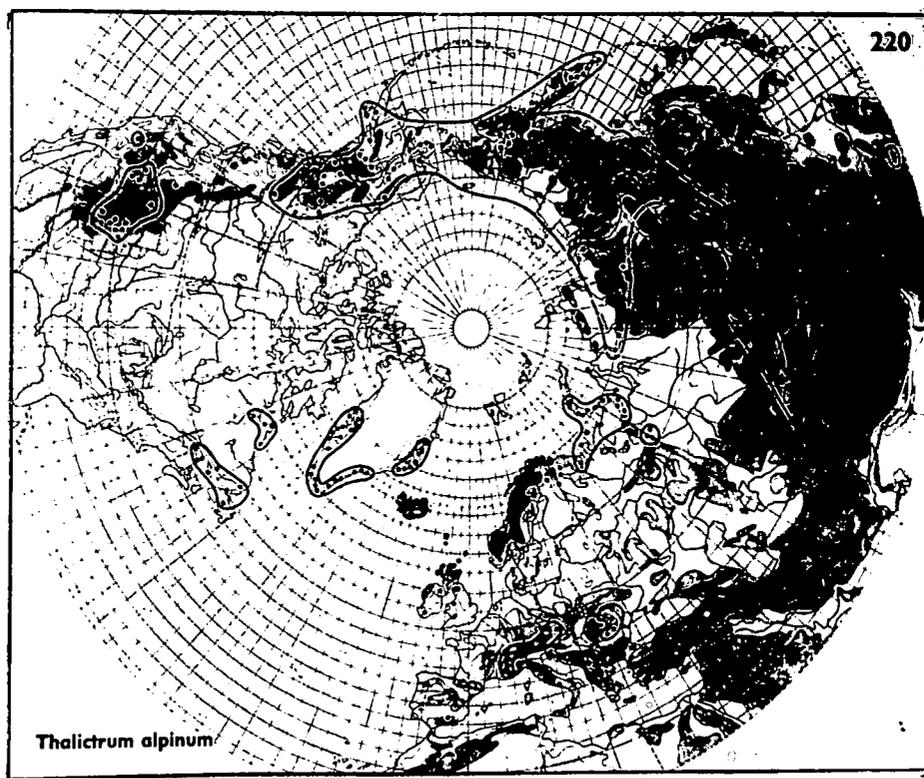


Diagram II. 17. World distribution of Thalictrum alpinum. (E. Hultén 1958.)

of England, including two localities in the Lake District (Ratcliffe 1960) and in Scotland. Here it is fairly widely distributed in Central and Northern Scotland where there are suitable basic rocks present, as will be seen from diagram II. 19. This map also shows that D. octopetala is abundant in the Burren area of Co. Clare and also has a number of localities in the west and north of Ireland. The species has an arctic-alpine distribution, but it is impossible to give an accurate map of its world distribution because of the complex variation shown by the genus which is, as yet, not understood. This is especially true of the material from Asia, Arctic America and Greenland. It is interesting that Carex capillaris has a very similar British distribution to that of Dryas octopetala, in the pattern in England and Scotland, but is not found in Ireland.

It is impossible to analyse the distributions of the disjunct cryptogams found in Teesdale, but some of the distributional types are very similar to those of the angiosperms described. Thus the British map of the moss Pseudoleskea catenulata given by Proctor (1960) shows a distribution very similar to that of Dryas octopetala with a number of localities in the north of England (including Malham), and in Scotland scattered across the Central Scottish mica schist

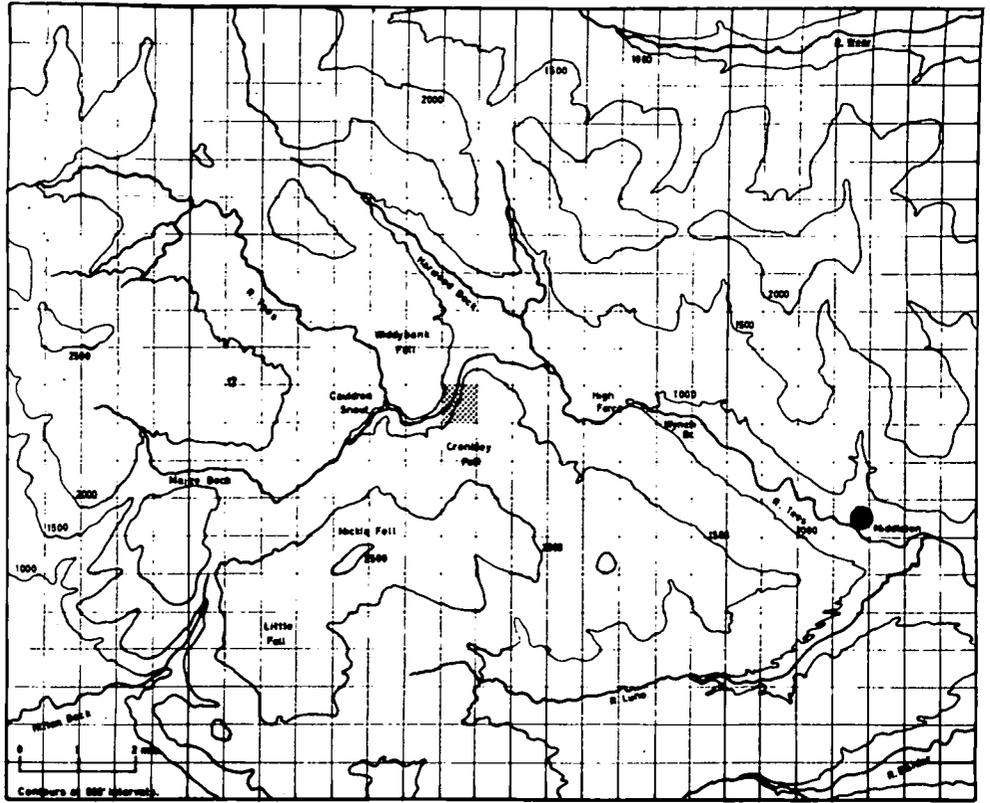
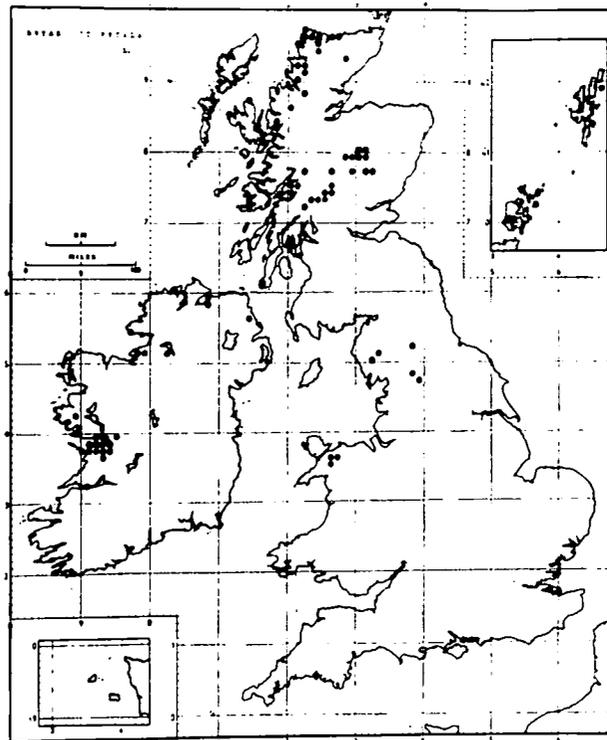


Diagram II. 18. Distribution in Teesdale of *Dryas octopetala*, each square representing one square kilometre. (Personal data.)



BOTANICAL SOCIETY OF THE BRITISH ISLES DISTRIBUTION MAPS SCHEME

Diagram II. 19. British distribution of *Dryas octopetala*. (B.S.B.I. Maps Scheme.)

belt and with localities in the extreme north of Scotland. Unlike D. octopetala, but like Carex capillaris, it is not found in Ireland. In its wider distribution it is found north to Iceland and Arctic Norway and south to Italy and Spain, extending east through the Caucasus to China. It is also found in N. America in New York State and in the Rocky Mountains. Pigott (1956) also quotes Catascopium nigritum and Meesia uliginosa as having similar distributions in Britain. Both these species have a wide distribution area from the Arctic to Central Europe and east through Asia; they are also both present in N. America.

Information on lichens is even more scanty than that for mosses, but Swinscow (1958) has recorded Hypogymnia alpicola (Th. Fr.) Wats. on Little Dun Fell in the west of the Teesdale area. This species has previously been recorded in Britain from the Grampian Mountains in Scotland and there is also one doubtful record from W. Mayo, Ireland. In its wider distribution H. alpicola is known from mountain summits in the Pyrenees, Alps, Central Europe, Scandinavia and N. America.

The Teesdale flora is thus extremely diverse in the geographical relationships shown by its members, with a high proportion of species showing large disjunctions in their

areas. Of special interest is the occurrence in Teesdale of ~~both~~ species with arctic and with temperate affinities. Chief among these latter are Helianthemum canum, Carex ericetorum and Viola rupestris. Helianthemum canum, in particular, is discussed by Proctor (1958) who gives a number of examples of continental communities in which this species grows and in many cases these are open xeric grasslands on south facing slopes with chalk or limestone substrates. Another example of this group is Hippocrepis comosa, a species which is known to have occurred in Teesdale in the past, but which now appears to be extinct in the area.

These are to be contrasted with the large number of species which have arctic and alpine affinities, and whose distributional types have been detailed in the previous pages. The possible explanations for the presence of this mixture of elements will be discussed in detail in chapter VI.

CHAPTER III.CYTOLOGY.Introduction

In considering the relict species of the Teesdale flora it is interesting to consider changes that may occur in isolated populations. Some types of change will be detectable by the study of chromosomes; thus local polyploid populations might arise, or populations in which the chromosomes have undergone structural change (e.g. as found in Californian populations of Clarkia by Lewis (1953)). Again, if a particular species complex is known to be cytologically heterogeneous (e.g. Bartsia alpina) it is important to determine which particular cytotype is represented in Teesdale.

The following account gives data for a number of species and lists the counts made on them over the whole of their range. The detection of the nature of polyploidy and of structural chromosome change is usually only possible by examining hybrids between plants from different populations, and though some hybrids have been made (e.g. between $2n$ and $4n$ Potentilla fruticosa) results from the hybrids are not yet available.

Methods.

Meiosis has been studied in pollen mother-cells (P.M.C.). Buds were fixed in a mixture of 3 parts absolute alcohol : 1 part glacial acetic acid, and a few drops of ferric acetate solution in 45 % acetic acid added as a pre-mordant. Belling's modification of acetocarmine stain (adding a few drops of ferric acetate solution in 45 % acetic acid) was used in making squash preparations, so that no further addition of iron was needed. Slides were made permanent with Euparal.

Mitosis was studied in root tips and developing ovaries. Root tips were pretreated with .002 M 8-hydroxyquinoline for three hours at approximately 15°C. (temperature of running tap-water), and then fixed in the same mixture as before. Staining and maceration were combined, using the method developed by Proctor (1955a) the roots being boiled in ferric acetocarmine for several minutes. The root tips were then tapped out and squashed on a slide in a little acetocarmine, (R.T.S.); slides were made permanent with Euparal. Mitosis was also examined in dividing ovary wall tissue (O.S.). Buds fixed for meiotic examination were used for this when meiosis could not be found. The entire ovary, if small, or part of it, was placed on a slide with a drop of ferric acetocarmine,

tapped out, warmed, and squashed. No maceration was found to be necessary. In many instances cells from the ovary wall were in an active state of mitotic division.

Results.

The species are listed alphabetically. Personal counts are given first and then compared with those given by other workers.

Bartsia alpina L. ($2n = 12, 24, 28, 36$).

Cetry Bank, Teesdale, Co. Durham	$n = 12$	P.M.C.
Great Close Mire, Malham, N. Yorks	$2n = 24$	O.S.
Lanche du Pra, near Sallanches	(a) $2n = 24$	O.S.
Haute Savoie, France	(b) $n = 12$	P.M.C.
Chermignon, near Leukerbad Valais, Switzerland.	$2n = 24$	O.S.

Both the English and Alpine material counted had $2n = 24$; and regular meiosis was observed in plants from Cetry Bank and Lanche du Pra. All the plants studied were of similar stature except those from which count (b) (Lanche du Pra) was made. These were much smaller in all parts, but proved however also to have $2n = 24$. Similar counts have also been made from other European material. Thus Witsch (1932) from Austria, Favarger (1953) from Emasson, Switzerland, Skalinska,

Czapik and Piotrowicz (1959) from four localities in the Western and High Tatra, Poland, and Sokolovskaya and Strelkova (1960) from Khibini Mt., Kola, U.S.S.R. all record $2n = 24$. A. & D. Löve (1956) also record this number from Iceland. Mattick (in Tischler 1950) however found $2n = 12$ from Austrian material and Doulat (1946) found $2n = 36$ in plants from the Col du Lauteret, France. It is interesting that Böcher and Larsen (1950) have counted, in plants from the Nugssuaq peninsula, W. Greenland, a number of $2n = 28$, and they specifically state that the plates could not possibly interpreted as having $2n = 24$. If, as they suggest, there is an arctic race with a basic number of $x = 7$ and a European race with $x = 6$, then British material would belong to the latter.

An attempt has been made to try and recognise plants of differing chromosome numbers from herbarium specimens by measuring their pollen diameters. The results are given in table III. 1.

Locality	No. of plants	Mean lf. length	Pollen diameter
Kodnitztal, Lienz prov., S. Austria	3	1.3 cm.	32 μ
Near Murnau, Bavaria, Germany	6	1.3	33
Louron Valley, Haute Pyrenees, France	2	1.4	32
Gtl. Lojsta Tamklint, Sweden	7	1.3	31
Kongsvold, Dovrefjell, Norway	5	1.9	33
Mt. Åreskutan, Jämtland, Sweden	2	2.3	30
Hafnarfjardhurbraun, Iceland	1	1.9	32

Table III. 1. Mean leaf lengths and pollen diameters of specimens of Bartsia alpina from Cambridge University herbarium.

Leaf length is given as an indication of plant size and the mean of twenty measurements of polar views of pollen grains has been given as the pollen diameter. There is very little difference between the mean pollen diameters even with a quite a large variation in leaf (and plant) size. Thus if the specimens contained material of differing chromosome number this was not revealed by the pollen diameter measurements.

Carex capillaris L. ($2n = 54$).

Creag an Lochan, Perth. $2n = c. 54$ O.S.

A large number of plants has been counted by Löve, Löve and Raymond (1957) from Sweden, Iceland, Greenland, Canada and N. Russia and all these had $2n = 54$, which is the number also recorded by Heilborn (1924) and Levan (in A. & D. Löve 1942) in Swedish material. Although an accurate count could not be obtained the number was certainly close to $2n = 54$.

Draba incana L. ($2n = 32$).

Great Dun Fell, Westmorland. $n = 16$ P.M.C.

This number is the same as has been recorded in the counts previously made. Thus in Scandinavia Heilborn (1927) has recorded this number in plants from Jebrenjock, Lapland; Tofte, Dovre, Norway; and Funasdalen, Sweden. Elsewhere it has been recorded by Jørgensen, Sørensen & Westergaard (1958) from Denmark, by Böcher & Larsen (1950) from Arsukfjord, S.W. Greenland, and by A. & D. Löve (1956) from Iceland.

Dryas octopetala L. ($2n = 18, 36$).

Le Leutellet, near Megeve, Haute Savoie, France	$2n = 18$	O.S.
Gemmi Pass, near Leukerbad, Valais, Switzerland.	$2n = 18$	O.S.

It has, unfortunately, not been possible to obtain counts from British material of this species. The localities were visited too late in the year to obtain buds for meiosis studies or for ovary squashes and the plants in cultivation grow slowly and vigorously growing roots are difficult to find. Böcher & Larsen (1955) have, however, made a count of Teesdale material and this has $2n = 18$. The Alpine counts made agree with this and with all other counts made in the genus, except one. D. octopetala has been counted over a wide range; Jørgensen, Sørensen & Westergaard (1958) have examined material from Clavering Is., N.E. Greenland and from E. Greenland, Flovik (1940) from Spitzbergen, A. & D. Löve (1956) from Iceland and also (1944b) from Laktatjakko, Sweden. In Central Europe counts have been made by Mattick (in Tischler 1950) from Austria, by Skalinska, Czapik & Piotrowicz (1959) from six localities in the W. Tatra, Poland and by Böcher & Larsen (1955) from various localities in Europe including places in the Faeroe Islands, Switzerland, Poland and France. Also in this paper they record plants with $2n = 36$ from Col du Pillon, Switzerland. This is the only instance of a chromosome number other than $2n = 18$ being found, and Böcher (1959) regards this as an accidental

tetraploid strain, to be regarded as an example of differentiation at the racial level only. Towards the East D. octopetala has been counted by Sokolovskaya & Strelkova (1941) from Kolguev Is. and by the same authors (1948b) from the E. Caucasus and (1960) from Khibini Mt., Kola. Counts have also been made by Maude (1939) and Delay (1948) on material of unstated origin and by Böcher (1938) from plants growing in Copenhagen, in which he notes that meiosis is regular with nine pairs of chromosomes being formed at first metaphase of meiosis.

A number of other Dryas species have also been examined cytologically. Sokolovskaya & Strelkova (1940) have recorded $2n = 18$ for D. caucasica Juz. from the main Caucasus range and in a later paper (1948) the same number is recorded for material from the E. Caucasus. Sokolovskaya & Strelkova have also made counts of two other species; D. oxyodontha Juz. has $2n = 18$ in material from the Altai range (1948a), and D. punctata Juz. from Tiksi, U.S.S.R. (1960) also has this number. The only other species which has been counted is D. integrifolia Vahl in which Böcher & Larsen (1950) also record $2n = 18$, the material being from Ivigtut, S.W. Greenland.

These results indicate that Dryas is a homoploid genus in which polyploidy is exceptional and rare.

Gentiana verna L. ($2n = 28$).

Widdybank Fell, Teesdale, Co. Durham	$n = 14$	P.M.C.
Black Head, Co. Clare	$n = 14$	P.M.C.
Wormhole, Co. Galway	$n = 14$	P.M.C.
Gemmi Pass, near Leukerbad, Valais, Switzerland	$2n = 28$	O.S.

The British plants counted from the above localities all had regular meiosis with $n = 14$ and the Swiss material agreed with this in having $2n = 28$. These agree with all but one of the continental counts. Thus Favarger (1949) in Swiss material from Creux du Van and Preissettes sur Fleurier, Mattick (in Tischler 1950) in Austrian material, and Skalinska (1951) in plants from the Tatra Mts., Poland have all recorded $2n = 28$. This is also the number counted by Quezel (1957) in material of ssp. Peneti from Toubkal m'Goun in the Atlas Mts., N. Africa. Skalinska (1950) however in plants from four localities in the Tatra Mts., Poland records $2n = 26$; whether this number is correct or not is doubtful, especially as in her paper published in 1951 she records $2n = 28$ 'as definitely established' for plants from the same area.

Helianthemum canum (L.) Baumg. ($2n = 22$).

Material of this species from Teesdale has been counted by Tutin (1953) as having $2n = 22$ and this has been confirmed by Proctor (1955a). The latter author has also obtained the same number in material from Glamorgan and Caernarvon, Wales; Kendal, Westmorland; Co. Clare, W. Ireland; near Rouen, France; Oland, Sweden and Saxony, Germany.

Juncus alpinus Vill. (J. alpinoarticulatus Chaix.) ($2n = 40$).

Widdybank Farm, Teesdale, Co. Durham $n = 20$ P.M.C.

Ben Lawers, Perth $n = 20$ P.M.C.

Braemar, Aberdeen $2n = 40$ O.S.

This species shows a large morphological variation and there are a number of papers dealing with this. One of the most comprehensive treatments is by Hylander (1953) who splits it into two subspecies ssp. arthrophyllus (Brenn.) Hyl. with the fruits more or less on the same level, and ssp. nodulosus (Wg.) Lindm. with some fruits borne distinctly higher than the others. Teesdale material, according to Hylander (pers. comm.) belongs to ssp. arthrophyllus. A number of other counts of J. alpinus have been made and all show $2n = 40$. Thus material from S.W. Greenland has been examined by Jørgensen, Sørensen & Westergaard (1958), from Iceland by A. & D. Löve (1956), by these authors (1944a) from Uppland,

also in S. Sweden by Snogerup (1958) and from Bayern, Germany (also by this author). These are thus in agreement with the British counts made. The closely allied species, J. nodulosus Wahl., differs by having some of the flowers pedicelled and the capsule equalling the perianth in length, (whereas in J. alpinus all the flowers are sessile with the capsule slightly exceeding the perianth in length), and has $2n = 80$.

Minuartia stricta (Sw.) Hiern ($2n = 22, 26$).

British material (which must be from Teesdale since it is the only locality) of this species has been counted by Blackburn & Morton (1957) who give $2n = 22$. A. & D. Löve (1956) have counted $2n = 26$ however in material from Iceland and this number has also been recorded by Jørgensen, Sørensen & Westergaard (1958) in material from Clavering Is., N.E.Greenland.

In view of the small number of counts available and the possible taxonomic complexities, comment on this difference in chromosome number must be reserved for the present.

Myosotis alpestris Schmidt ($2n = 14, 24, 48$).

Great Dun Fell, Westmorland	$2n = 48$	O.S.
Little Fell, Westmorland	$2n = 48$	O.S.
Ben Lawers, Perth	$2n = 48$	O.S.

Charbonniere, near Assy, Haute Savoie, France	2n = 48	O.S.	alt.1600 m.
Gemmi Pass, near Leukerbad, Valais, Switzerland	2n = 48	O.S.	alt.2300 m.
Chermignon, near Leukerbad, Valais, Switzerland	2n = 48	O.S.	alt.1940 m.
Clavinenalp, near Leukerbad, Valais, Switzerland	2n = 24	O.S.	alt.1950 m.
Tatra Mts., Poland (grown from seed).	2n = 24	O.S.	

When P.M.C. preparations of this species were examined it was found very difficult to determine accurate chromosome numbers because of the small size of both P.M.C.s and chromosomes; this has also been commented on by Geitler (1936). The ovary wall tissue in which mitoses were plentiful was found to be much easier material, and all counts have been made using this tissue.

The results show that plants from both Teesdale and Scotland have $2n = 48$. The same number has also been counted in three Alpine populations, one from France and two from Switzerland. The other Swiss count however is $2n = 24$, the locality, Chermignon, being at nearly the same altitude and 5 km. distant from Clavinenalp where $2n = 48$ has been recorded. Plants grown from seed collected in the Tatra Mts., Poland have also given a count of $2n = 24$. This latter number has been recorded by Geitler (1936) in material from Schneekar,

Tirol, Austria and by Griesinger (1937) from three localities in N. Tirol, Austria. This number has also been reported by Sokolovskaya & Strelkova (1948) in material from the E.Caucasus range. The same authors (1941) give $2n = 14$ however for plants from Kolguev Is. and this number is also given by Mattick (in Tischler 1950) for central European material. Sokolovskaya & Strelkova (1960) however give another count of M. alpestris from Kolguev Is. and here they record that $2n = 24$. The only count of $2n = 48$ which has been recorded in the literature for M. alpestris material is given by Geitler (1936) for plants which were sent to him under the name of M. lithospermifolia from Munich Botanic Garden and which he has called M. alpestris var. lithospermifolia. He states that the specimens corresponded to the alpestris type, but were very small and poorly developed so that determination was uncertain.

It appears therefore that there are at least two chromosome numbers based on $x = 12$ present in M. alpestris. It seems unlikely that the plants with $2n = 14$ belong here, and they may belong to the M. sylvatica group (in which $2n = 14, 18, 32$ have been recorded). The British material of M. alpestris seems to all belong to the tetraploid race. On the continent, as previously pointed out, both tetraploid and diploid races occur. A comparison of plant height and leaf

length of diploid material from Clavinenalp, Switzerland and tetraploid material from Charbonniere, France has been made and the results are given in table III. 2.

	<u>No. of plants</u>	<u>Plant Ht.</u>	<u>Leaf l.</u>
2n Clavinenalp	10	4.3 \pm 0.41	1.5 \pm 0.02
4n Charbonniere	9	12.4 \pm 0.84	2.7 \pm 0.02

Table III. 2. Plant Height and Leaf length means and standard errors of 2n and 4n Myosotis alpestris populations.

Although the diploid plant is much smaller than the tetraploid, as will be shown later (p. 96) ecotypic differentiation of similar magnitude is found in tetraploid populations in Britain so that these characters are of little use in distinguishing diploid from tetraploid material. Samples of 25 pollen grains from plants from four different localities, three tetraploid and one diploid show (table III. 3) that the diploid has pollen slightly smaller in length and breadth than the three tetraploids and both these differences are significant at the 0.1 % level. The tetraploids all have larger pollen than the diploid, although they show a large variation in gross morphological features (for measurements of the Mickle Fell and Cam Creag populations see p. 97). Thus this character provides a means of distinguishing material of differing ploidy.

Locality	Ploidy	Length	Breadth
Cam Creag, Scotland	4n	6.5 \pm .064 units	3.9 \pm .033 units
Mickle Fell, England	4n	5.9 \pm .033	3.8 \pm .051
Charbonniere, France	4n	6.0 \pm .029	3.9 \pm .037
Clavinenalp, Switzerland	2n	5.5 \pm .049	3.1 \pm .044

Scale: 1 unit = 1.4 μ .

Table III. 3. Pollen measurements of tetraploid and diploid Myosotis alpestris.

Little is known of the distributions or habitat preferences of the two races. As already mentioned, in the neighbourhood of Leukerbad in the Valais, Switzerland, both races occur near one another, at similar altitudes, and both in limestone grassland.

Potentilla fruticosa L. ($2n = 14, 28$).

Cronkley Fell, By R. Tees, Teesdale, N. Yorks (plants grown from seed).	n = 14	P.M.C.
Mullaghmore, Co. Clare (plants grown from seed).	n = 14	P.M.C.

The Teesdale count is the same as that already recorded by Bowden (1957) and by Parbrook (1957) for plants from the same area. Parbrook in her work on this species in Teesdale made observations on both male and female plants and could find no observable differences in the chromosome complements. She found, as I did, that 14 bivalents were regularly formed at first metaphase of meiosis. Material from Öland, Sweden, counted first by Turesson (1938) and confirmed by Bowden (1957) and Parbrook (1957), also has $2n = 28$. Thus the W. Irish count is the same as these, which are all the records of wild European material which have been made. A number of cultivated varieties also have this number. In N. America however a large number of counts have been made by Bowden (1957) and these are all $2n = 14$. These include plants from many localities, from Nova Scotia and Quebec in the East to British Columbia in the West, and Alaska in the North to Ontario, Ottawa and New York in the South.

It seems likely therefore that northern N. American material at least is uniformly diploid, while the disjunct European material is tetraploid.

A number of crosses have been made between $2n$ and $4n$ representatives of the species with the formation of well filled seeds, and a small amount of germination has taken place from these. From the hybrids it should be possible to gain information on the relation of the tetraploid to the diploid, i.e. whether it is an allo- or auto-tetraploid. The hybrid plants are, however, only at seedling stage so that it is not possible to determine this at the present time.

Primula farinosa L. ($2n = 18, 36$).

Cetry Bank, Teesdale, Co. Durham $n = 9$ P.M.C.

This count is the same as has been recorded for plants from Widdybank Fell, Teesdale by Davies (1953) and for over 100 collections made in the North of England by Dovaston (1955). Counts made on this species from unspecified localities have been made by Marchal (1920), Hagerup (1941) and Mattick (in Tischler 1950) who have all recorded $2n = 18$. Bruun (1932) also records this number in material from Vickelby, Oland, but Davies (1953) from the nearby island of Gotland has recorded tetraploid plants with $2n = 36$, in addition to diploid

plants. It thus seems that the Teesdale together with all the British material has the same chromosome number as the majority of continental material.

Saxifraga aizoides L. (2n = 26).

Widdybank Farm, Teesdale, Co. Durham	n = 13	P.M.C.
Ben Lawers, Perth. alt. 900'	n = 13	P.M.C.
Ben Lawers, Perth. alt. 2750'	n = 13	P.M.C.
Durness, Sutherland.	n = 13	P.M.C.

These British counts are uniform with all previous ones which have been made. The material examined had regular meiosis with 13 pairs at first metaphase. Material from central Europe has been counted from Austria by Mattick (in Tischler 1950) and by Hamel (1953) from the Pyrenees; the latter author has also given karyotype analyses for this material. To the north Skovsted (1934) has counted plants from Norway and Böcher (1938) has also confirmed 2n = 26 in plants from Finse. Further east Sokolovskaya (1958) has examined plants from Khibini Mt., Kola, U.S.S.R. and 2n = 26 is also given for material from this area by Sokolovskaya and Strelkova (1960). Towards the Arctic A. & D. Löve (1951) give counts from Iceland, and from Greenland Böcher (1941) gives 2n = 26 from Clavering Island plants and Jørgensen, Sørensen & Westergaard (1958) confirm this in N.E. Greenland.

Thalictrum alpinum L. ($2n = 14$).

Ben Lui, Perth.	$2n = 14$	O.S.
Inchnadamph, Sutherland.	$2n = 14$	R.T.S.
Durness, Sutherland.	$2n = 14$	R.T.S.
Bonne Bay, W. Newfoundland.	$2n = 14$	R.T.S.

The British counts made are, as in Saxifraga aizoides, the same as those from all other localities. In Japan, material has been counted by Sakai (1935). In the U.S.S.R. material from Tiksi has been examined by Sokolovskaya (1958), from the Altai range by Sokolovskaya & Strelkova (1948a) and by the same authors (1960) from Kolguev Island. Further west A. & D. Löve (1944b) have recorded $2n = 14$ from Njulla in Scandinavia; the same authors (1956) have also counted plants from Iceland confirming the counts made by Kuhn (1930) on material from Akureyri in the same country. In Greenland Böcher (1938) has counted the same number in plants from Disko on the West coast while Jørgensen, Sørensen & Westergaard (1958) have counted plants from N.W. Greenland. T. alpinum has also been counted by Langlet (1927) using plants from an unstated source.

Thlaspi alpestre L. ($2n = 14$).

Riley (1956) has counted plants from seven populations in Teesdale from Wynch Bridge, Co. Durham to Moorhouse,

Westmorland and these all have $2n = 14$. This is the same number as he has counted from populations elsewhere in Britain, from Derbyshire, the Mendips and from Wales. Counts have also been made on Scandinavian material by A. & D. Löve (1944b) and the same authors (1956) have recorded $2n = 14$ from Icelandic plants also. Manton (1932) has also counted this number in plants grown from seed from Darmstadt Botanic Garden.

Tofieldia pusilla (Michx.) Pers. ($2n = 30$).

Cetry Bank, Teesdale, Co. Durham	$n = 15$	P.M.C.
Durness, Sutherland	$2n = 30$	R.T.S.
Bonne Bay, W. Newfoundland.	$2n = 30$	R.T.S.

The Teesdale material shows a regular meiosis with 15 pairs at first metaphase. The number of $2n = 30$ which has been recorded from British and Newfoundland material is the same as has been recorded previously. Counts have been made from Khibini Mt., Kola, U.S.S.R. by Sokolovskaya & Strelkova (1960), from Iceland by A. & D. Löve (1956) and from N.W.Greenland by Jørgensen, Sørensen & Westergaard (1958). $2n = 30$ has also been reported by Miller (1930) for plants from an unstated source.

Trollius europaeus L. ($2n = 16$).

Cronkley Farm, Teesdale, N. Yorks.	$n = 8$	P.M.C.
Caenlochan Glen, Angus.	$2n = 16$	R.T.S.
Glen Lochay, Perth.	$2n = 16$	R.T.S.
Ben Chaistal, Argyll.	$2n = 16$	R.T.S.
Lac Vert, near Assy, Haute Savoie, France.	$2n = 16$	O.S.
Clavinentalp, near Leukerbad, Valais, Switzerland.	$2n = 16$	O.S.

The plants from Teesdale show 8 pairs in first metaphase of meiosis. All the counts I have made show $2n = 16$ and this is the same as all counts which have been made on the species. In Scotland Hedberg (1958) has examined material from Ben Lui, Perth, while in central Europe Polya (1949) has recorded this number from Hungarian plants as has Mattick (in Tischler 1950) for Austrian material. Skalinska, Czapik & Piotrowicz (1959) give $2n = 16$ for Polish plants of the typical form from the Sudetic Mts. and also for ssp. transsilvanicus from the High Tatra region. In the north T. europaeus has been counted from Scandinavia (Kopparasen) by A. & D. Löve (1944b) and from Iceland by the same authors (1956). Sokolovskaya & Strelkova (1941) in the U.S.S.R. have examined material from Kolguev Island and also (1960) from Khibini Mt., Kola.

To the east Matsuura & Suto (1935) have counted Japanese plants. Counts of $2n = 16$ have also been made by Langlet (1927) and Lewitsky (1931) on plants from unstated sources.

These counts of T. europaeus are the same as for all species of Trollius which have been counted, except for a count of T. americanus by Langlet (1932) who gives $2n = 32$ for plants grown from seed sent from Berlin-Dahlem.

Viola rupestris Schmidt. ($2n = 20$).

The British populations of this species (Widdybank Fell, Teesdale, Co. Durham; Long Fell, Westmorland; and Arnside, Westmorland) have been examined by Valentine and Harvey (1961) and chromosome counts show that $2n = 20$. This number has also been counted in stocks from Czechoslovakia by the same authors (1960), from near Munich, Germany by Schofer (1954) and in material from Caucasia by Clausen (1929). Schmidt (1961) in material from S. Tirol, Austria has recorded $2n = 20$ plus from four to eight B chromosomes.

Discussion.

No species have been found in which Teesdale or other British material has a different chromosome number from that found in continental Europe, except in the case of Minuartia strica where, for the reasons stated, no conclusions can be

drawn at the present time. In the case of Myosotis alpestris, although most of the previous counts have given $2n = 24$, my own results show that some Alpine plants at least have the same number, $2n = 48$, as the British material.

Since there are no polyploids found which do not occur also in Europe there is no evidence for the idea that Teesdale representatives might have, in a long isolation period, developed polyploid races.

Since there has been no chromosome change from the point of view of number in any British material studied it is probable on this evidence that migration would have taken place post-glacially.

CHAPTER IV.STUDIES ON INDIVIDUAL SPECIES.Introduction

Four species have been selected for detailed studies. They are all well known members of the Teesdale flora and, as described earlier, display different types of distribution both in the dale, in Britain and in their world distributions. Thus Gentiana verna has a wide distribution in the dale, is restricted to Teesdale and W. Ireland in Britain and is an Alpine species in its world distribution. Potentilla fruticosa is rather limited in the dale and is very disjunct both in Britain and in Europe. Myosotis alpestris and Dryas octopetala are both very restricted in the dale and are wide ranging arctic-alpine species, but whereas D. octopetala has quite a wide distribution in Britain, from Yorkshire to Sutherland, and is also found in Ireland, M. alpestris is restricted in Scotland to a few localities in Perth and is not present in Ireland.

A description of each species is given together with some account of its general and breeding biology. A study of the variation in Britain of each species has also been made. For this purpose field samples have been collected as the characters used are usually not easily seen from herbarium

specimens. Samples were always, wherever possible of twenty five specimens, collected at random within the population. Support for the adequacy of this sample size has been obtained from data on samples collected in successive years, from the same populations in Gentiana verna and Potentilla fruticosa. These data are contained in tables IV. 12 (Gentiana verna) and table IV. 16 (Potentilla fruticosa). These show that the variation from year to year is always small and within the limits of the regional groups delimited in the species concerned.

Gentiana verna L.

Taxonomy.

On the classification of Kusnezow (in Engler and Prantl (1891)) Gentiana verna L. belongs to the section Cyclostigma Grisebach in the subgenus Eugentiana Kusnezow.

Description.

Small evergreen hemicryptophyte with a fibrous root system, 2.5 - 8.5 cms. high in flower. Plant with a short stock and a varying number of short underground stolons each ending in a rosette of leaves. Rosette leaves exstipulate, sessile, decussate, ovate to oblong, with obtuse to acute apices, 0.8 - 2.0 cms. long; cauline leaves on the flowering

stem smaller, elliptic. Flowers terminal, solitary, pedicel 0 - 5.5 cms. long, elongating to up to 15 cms. in fruit. Calyx tube 1.0 - 2.2 cms. long, cylindrical, persistent, becoming slightly inflated in fruit, five angled and winged; calyx teeth 2 - 7 mm long, triangular lanceolate. Corolla tube cylindrical c. 2 cms. long, pale; corolla 1.7 - 3.1 cms. in diameter, deep blue, lobes spreading, ovate with obtuse or sub-acute apices, 6 - 12 mm. long and 4 - 8 mm. wide, alternating with small, two pointed appendages. Stamens five, borne below the white, expanded, fimbriate, bilobed stigma. Capsule oblong, gradually narrowing into the style, dehiscent by two longitudinal splits. Seeds many, c. 0.7 mm. long, ellipsoid, dark brown, with a reticulate pattern on the surface.

Relationships.

In Britain there are only two other species of the genus, G. nivalis and G. pneumonanthe; G. verna is distinct from both of these. No variation has been recorded before in this species in Britain. On the continent G. verna is rather a variable species which, according to Hegi (1927) is distinguished from neighbouring species by the winged calyx tube and the elliptic rosette leaves, widest in the middle. It is often confused with G. angulosa M. & B. which, as Soltkovic (1901) pointed out, is a plant of Central Asia to the Caucasus. She

also comes to the same conclusion as Kerner (1899), that G. aestiva, of a number of authors, which has been separated as having narrower leaves and larger wings on the calyx, cannot be maintained as a separate species.

General Biology.

In Britain the flowering season for the species is generally from the end of April to the end of May, but in some seasons flowering may start considerably earlier than this; thus in 1961 it was seen in flower in Teesdale in the middle of April, this being in response to very early warm weather. The flowers in the field are mainly open in sunny weather, tending to close when the weather is cloudy. The flowers appear to be mainly pollinated by bees, which collect the nectar which is secreted at the base of the corolla tube. Frequently the nectar is obtained 'illegitimately' by the insect biting through the base of the calyx and corolla tubes, the holes made being evident in quite a high percentage of flowers. This may be because the bees are unable to reach the nectar with their probosces. Muller (1877), commenting on the pollination of G. verna and a number of allied Gentiana species in the Alps, found that no Alpine species of bees which visited the flowers, had long enough probosces to reach the nectar; he concluded that G. verna is pollinated by

Lepidoptera there. He points out however that repeated attempts to reach nectar by bees may bring about some cross-pollination.

Experiments in an insect-proof greenhouse have shown that although G. verna is self compatible it is not spontaneously self-pollinated, because the anthers are borne below the stigma. Ripe capsules with good seed are certainly produced in both West Ireland and Teesdale, but very rarely survive in the latter area because of the depredations of the sheep, which are very severe. Seed production has been examined in the population at Ballyvaghan, Co. Clare where a sample of 25 capsules had a mean number of 379 ± 20 seeds per capsule, and also at Cetry Bank, Co. Durham where 5 capsules had a mean number of 113 ± 20 . Experimental selfings have shown, however, that plants from these populations produce approximately the same number of seeds in the greenhouse.

Germination has been tested experimentally. Seeds were sown in John Innes seedling compost in November, and kept in a cold greenhouse, so that they were subject to frosting throughout the winter. This was done since seed sown at a similar time and kept in a warm greenhouse gave no germination. It thus appears that frosting is necessary for germination. This was also found to be the case by Kinzel (1913). Thus in one experiment he found that seed sown for 18 months without any

germination, gave 22 % germination after a week's spring frost, when it was illuminated at the same time; Kinzel found that some illumination was necessary as well as frost. This may be the reason for some of the poor germination that I found, since the seeds were covered with approximately 0.5 cms. of fine soil.

A striking feature of my experiments was that germination took place over two years with generally better germination the second spring. No germination was observed the third spring after sowing.

The percentage germination for a number of samples from W. Ireland and Rotenboden, near Zermatt, Switzerland are given in table IV. 1.

	<u>Germination Percentage</u>		
	<u>Spring 1959</u>	<u>Spring 1960</u>	<u>Spring 1961</u>
Black Head, Co.Clare (sown Nov. 1958)	3	11	0
	1	14	0
	5	3	0
	1	13	0
	0	2	0
Rotenboden, Switzerland (sown Nov. 1959)	-	0	6
	-	0	1
	-	0	0

Table IV. 1 Percentage germination in samples of G. verna seed.

The results reflect those obtained from seed sent from various Botanic Gardens, that total germination is in all cases low, although it may be carried on for more than one year. Kinzel (1913) records that in his experiments germination was carried on for four years, also that seeds kept moist for two and a half years needed, after their frost treatment, large amounts of light over several months to produce complete germination. As previously stated, this was probably the reason for my low germination percentages and also, probably, for the well known difficulty in germinating seeds of G. verna. Thus Favarger (1953b) also records a germination percentage of 1 - 10 % only, after a period of frosting.

The relevance of these experimental results to the ecology of the species in Britain is clear. Seed from Co. Clare kept in a warm greenhouse did not germinate, and thus, presumably needs frosting before germination can take place. Frosts on the Burren are rare, and this may be an important factor in the regeneration of G. verna from seed in this area. In Teesdale there is certainly enough frost, but it is doubtful whether more than a small amount of seed ever matures, as the capsules are eaten by sheep as soon as the pedicels begin to elongate.

It seems likely that in Teesdale most of the colonies reproduce by vegetative means. This takes place by the short

underground stolons already mentioned, which develop leaf rosettes at their apices. When the underground parts rot away the rosettes are left as new individuals. In this way quite large clonal colonies could build up over a large number of years; and it is quite possible that some of the populations in Teesdale on isolated exposures of limestone could have been produced from a single seed introduction followed by vegetative reproduction over a long period.

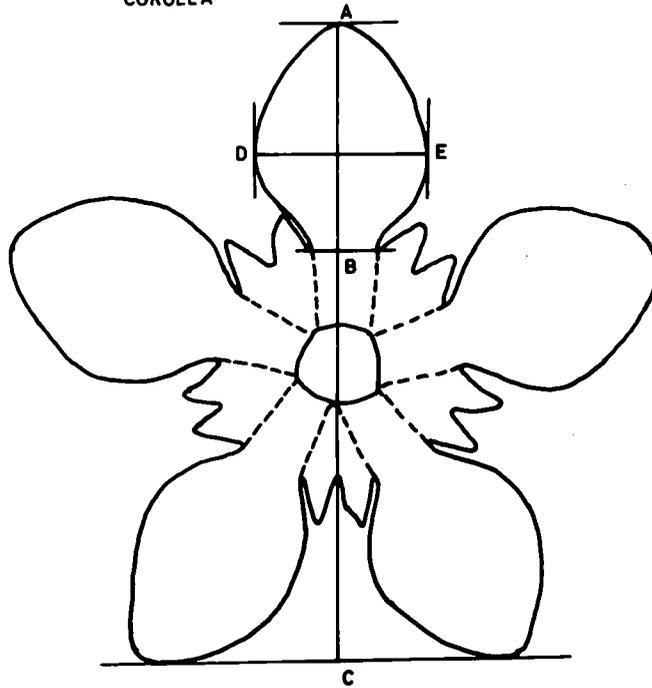
As pointed out earlier chromosome counts have been made on both Irish and Teesdale material, and in both cases $2n = 28$. This is the same as has been recorded on the continent. The variation about to be described is thus not associated with a difference in ploidy.

Variation.

Since the only biometrical work on Gentiana section Cyclostigma has been on the separation of G. verna and G. ^tergestina on leaf length/breadth ratios (Rogenhofer 1905) it was not clear at the start of the study of possible variation which characters might be significant; accordingly as many parts of the plant were preserved as possible so that they would be available for measurement.

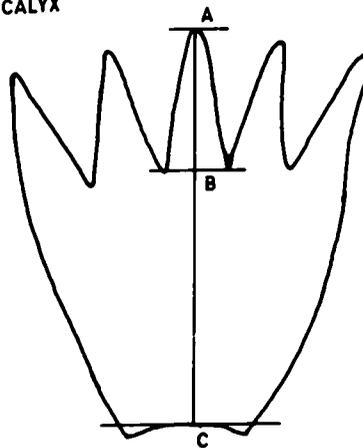
Corolla lobes and calyces were preserved by sticking them on sellotape, a method used by Heslop-Harrison (1949) for

COROLLA



AB Corolla lobe length
DE Corolla lobe breadth
AC Corolla diameter

CALYX



AB Calyx tooth length
AC Calyx length

Diagram

IV. 1. G. verna corolla and calyx characters.

Sample No.	Locality	Date of collection	Corresponding Quadrat No.
1	Tinker's Sike, Widdybank Fell, Co. Durham	7.5.59	6
2	Cow Green, " " , Co. Durham	7.5.59	10
3	Cetry Bank, nr. Widdybank Farm, Co. Durham	12.5.59	2
4	Haugh Hill, Co. Durham	20.5.59	5
6	Poulsallagh, Co. Clare	27.5.59	11
7	Black Head, Co. Clare	28.5.59	12
8	Near Mullaghmore, Co. Clare	30.5.59	13
9	Gentian Hill, Co. Galway	2.6.59	16
10	Ballyvaghan, Co. Clare	3.6.59	18
11	Haugh Hill, Co. Durham	2.5.60	5
12	Cetry Bank, nr. Widdybank Farm, Co. Durham	2.5.60	2
13	Cow Green, Widdybank Fell, Co. Durham	10.5.60	10
14	Tinker's Sike, " " , Co. Durham	10.5.60	6
15	High Hurth Edge, Co. Durham	12.5.60	7
16	W. end of Mickle Fell, Westmorland	16.5.60	1
17	Grains o' th' Beck, N. Yorks	16.5.60	8
18	Bellbeaver Rigg, Cumberland	18.5.60	9
19	Ayere du Mileau, nr. Sallanches, Haute Savoie, France	29.5.60	26
20	Charbonniere, Roc du Fiz, nr. Sallanches, Haute Savoie, France	30.5.60	25
21	Le Leutellet, nr. Megève, nr. Sallanches, Haute Savoie, France	31.5.60	27
22	La Frie, nr. Les Houches, Haute Savoie, France	1.6.60	28
23	Lanche du Pra, nr. Sallanches, Haute Savoie, France	2.6.60	19

Sample No.	Locality	Date of collection	Corresponding Quadrat No.
24	N. end Gemmi Pass, nr. Leukerbad, Valais, Switzerland	4.6.60	22
25	Clavinenalp, nr. Leukerbad, Valais, Switzerland	5.6.60	20
26	Chermignon, nr. Leukerbad, Valais, Switzerland	6.6.60	21
27	Brand, nr. Sass-Balen, Valais, Switzerland	7.6.60	24
28	Riederalp, nr. Mörel, Valais, Switzerland	8.6.60	23
29	Bella Lui, nr. Crans, Valais, Switzerland	9.6.60	-
31	Tinker's Sike, Widdybank Fell, Co. Durham	2.5.61	6
32	Cow Green, " " , Co. Durham	2.5.61	10
33	Cetry Bank, nr. Widdybank Farm, Co. Durham	2.5.61	2
34	Haugh Hill, Co. Durham	2.5.61	5

Table IV. 2. Localities and dates of collection of G. verna samples.

the study of Dactylorhiza and by Moore (1959) for Viola. The leaf rosettes were pressed. A preliminary examination showed that variation was present in a number of characters and the following measurements were made:-

Corolla: corolla diameter, lobe length, lobe breadth.

Calyx: calyx length, tooth length.

These characters are shown in diagram IV. 1.

Leaves: The two largest leaves of the rosette were chosen for measurement and their length and breadth measured. Each pair of measurements from a plant for both characters was then averaged and the averages were used in calculating the mean and standard error for each sample. In this way the intra-plant variation was reduced while not affecting the inter-plant variation within the sample.

Table IV. 2. gives the localities for the sample numbers used.

The characters measured will be considered in turn.

Corolla diameter. The mean corolla diameters are given in table IV. 3. for samples from Teesdale, W. Ireland and the Alps. In Teesdale four localities have been sampled for three years in succession and it will be seen that in the Cetry Bank population the mean corolla diameter varied from 21.00 mm. in 1960 to 26.36 mm. in 1961. Since this range, with the

Locality	1959	1960	1961
Tinker's Sike, Widdybank Fell, Co. Durham	24.28	22.54	25.94
Cow Green, Widdybank Fell, Co. Durham	23.20	21.52	25.60
Cetry Bank, nr.Widdybank Farm, Co. Durham	25.70	21.00	26.36
Haugh Hill, Co. Durham	24.00	22.44	23.54
High Hurth Edge, Co. Durham	-	21.82	-
Mickle Fell, Westmorland	-	24.20	-
Grains o' th' Beck, N. Yorks	-	22.94	-
Bellbeaver Rigg, Cumberland	-	21.76	-
Poulsallagh, Co.Clare	23.90	-	-
Black Head, Co. Clare	24.40	-	-
Mullaghmore, Co. Clare	23.60	-	-
Gentian Hill, Co. Galway	26.60	-	-
Ballyvaghan, Co. Clare	24.50	-	-
Ayere du Mileau, Haute Savoie, France	-	23.82	-
Charbonniere, " " "	-	24.54	-
Le Leutellet, " " "	-	23.38	-
La Frie, " " "	-	24.20	-
Lanche du Pra " " "	-	22.78	-
Gemmi Pass, Valais, Switzerland	-	24.22	-
Clavinenalp, " "	-	24.50	-
Chermignon, " "	-	25.64	-
Brand, " "	-	23.46	-
Riederalp, " "	-	26.56	-
Bella Lui, " "	-	27.22	-

Table IV. 3. Means of corolla diameters of G. verna samples.

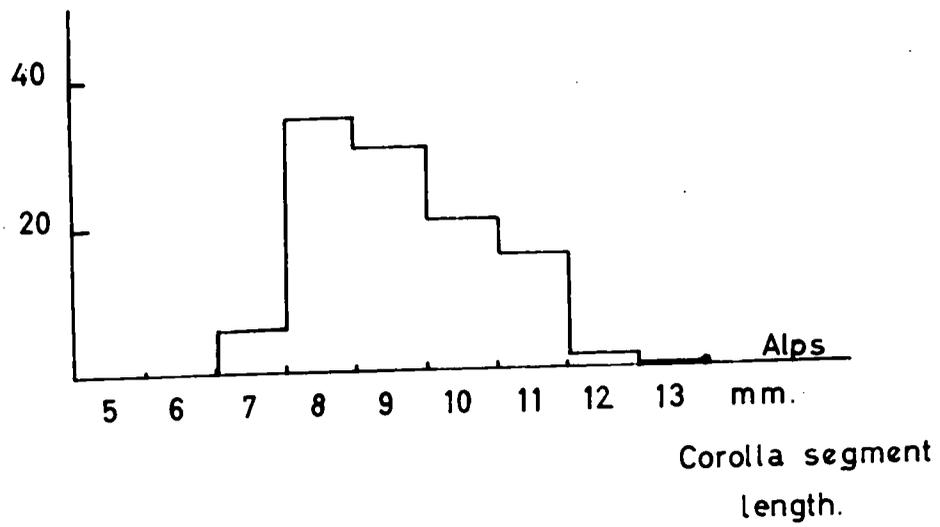
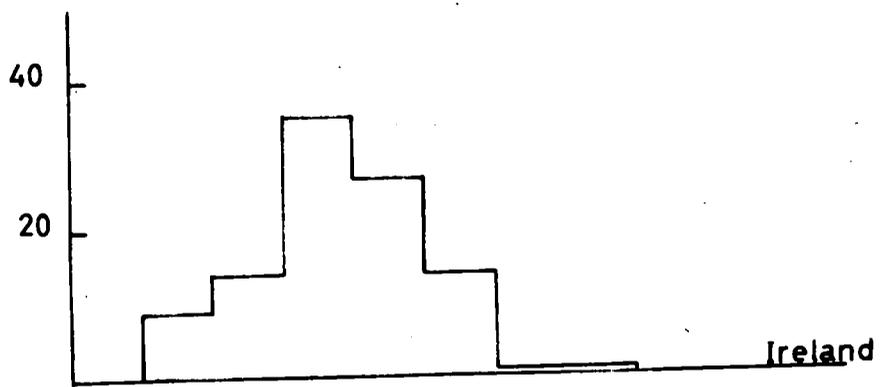
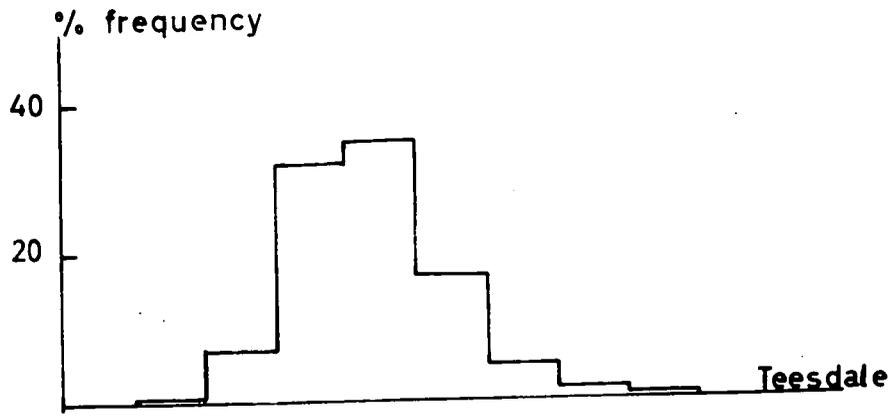
exception of one Irish sample (Gentian Hill, Galway) and two Alpine samples (numbers 28 and 29) includes the total variation of all sites studied it is clear that this character is of little use in studying the population differentiation.

Corolla lobe length. The results from the three regions are given as frequency histograms in diagram IV. 2. There is little difference in the mean corolla lobe length, over 60 % of the measurements falling into 8 and 9 mm. size classes. It is interesting however to note the frequency distribution above and below these two classes in the three groups; this is shown in table IV. 4.

	Ireland	Teesdale	Alps
% frequency in size classes 5, 6 and 7 mm.	22.4	8.2	6.2
% frequency in size classes 10, 11, 12 and 13 mm.	15.2	25.2	40.4

Table IV. 4. Frequency distribution of *G. verna* corolla segment length in size classes of regional groups.

This shows a decreasing frequency of plants in the smaller size classes from Ireland through Teesdale to the Alps and hence an increasing frequency in the larger size classes. It is possible that this shows the beginning of a regional differentiation in this character.



Diagram

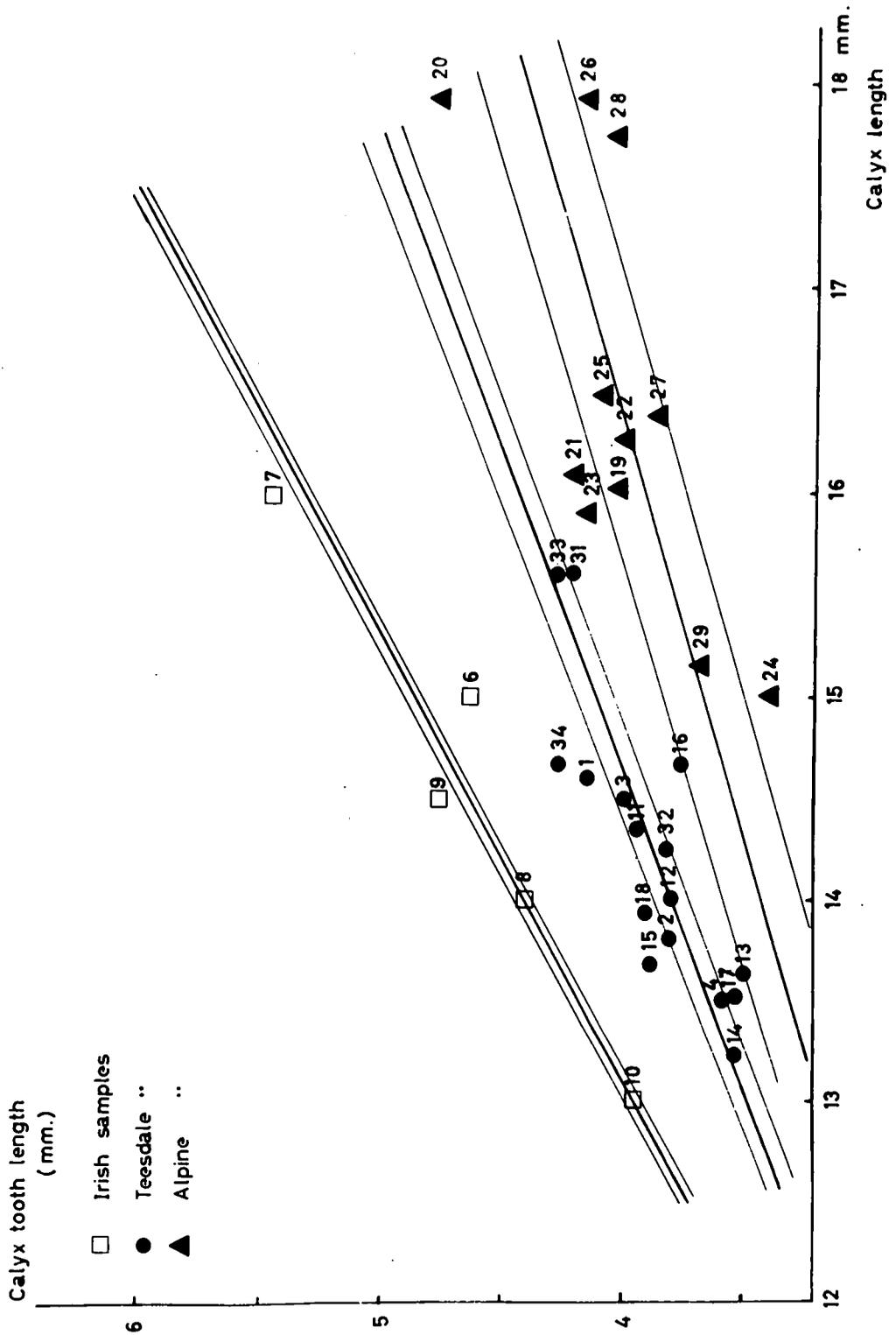
IV. 2. Frequency histograms of *G. verna* corolla segment lengths from Teesdale, Ireland and the Alps.

	<u>Sample No.</u>	<u>Ratio mean</u>
Teesdale	1	1.50
	2	1.50
	3	1.44
	4	1.63
	15	1.55
	16	1.48
	17	1.57
	18	1.27
Ireland	6	1.59
	7	1.44
	8	1.50
	9	1.69
	10	1.43
Alps	19	1.60
	20	1.65
	21	1.50
	22	1.65
	23	1.55
	24	1.45
	25	1.59
	26	1.50
	27	1.70
	28	1.52
	29	1.48

Table IV. 5. Means of Corolla lobe, length/ breadth ratio in population samples of Gentiana verna.

Corolla lobe, length/breadth ratio. The means of the samples for this character are given in table IV. 5. There appears to be a random variation in the means in each region and no differentiation between regions.

Calyx characters. It is convenient to discuss calyx length and calyx tooth length together. The means of these characters together with their standard errors are given in table IV. 6. It became evident in the investigation that there is a regional differentiation in these characters. However when the means of the samples are plotted in a scatter diagram for the two characters as in diagram IV. 3, it is evident that some of the means lie close together. It is therefore necessary to determine whether the regional groups show significant differences from one another. This has been done by carrying out a regression analysis. Since the number of samples is rather large, it would have been impossible in the time available to undertake a full analysis using each member of all the samples. For this reason a modified analysis as recommended by Bailey (1959) was carried out, using the sample means as the original data. The regression lines with 95 % confidence limits are shown in diagram IV. 3. It will be seen that the regional groups are significantly different from one another at the 5 % level. The question



		Calyx length mean	S.E.	Calyx tooth length mean	S.E.
<u>Ireland</u>	6	14.86 mm	± .285	4.64 mm	± .149
	7	15.98	.389	5.46	.189
	8	14.04	.377	4.40	.150
	9	14.60	.362	4.76	.185
	10	12.84	.288	3.96	.141
<u>Teesdale</u>	1	14.60	.292	4.16	.155
	2	13.82	.281	3.80	.115
	3	14.50	.434	4.00	.054
	4	13.54	.497	3.58	.179
	11	14.36	.361	3.94	.162
	12	14.02	.376	3.80	.168
	13	13.62	.395	3.50	.126
	14	13.26	.322	3.52	.110
	15	13.66	.352	3.88	.120
	16	14.66	.278	3.76	.116
	17	13.50	.278	3.54	.135
	18	13.92	.279	3.90	.132
	31	15.60	.320	4.22	.156
	32	14.26	.306	3.82	.104
	33	15.60	.344	4.28	.136
	34	14.64	.429	4.28	.126
<u>Alps</u>	19	16.02	.396	4.02	.114
	20	17.94	.653	4.76	.224
	21	16.10	.474	4.20	.155
	22	16.26	.448	4.00	.173
	23	15.90	.496	4.16	.146
	24	15.00	.450	3.38	.120
	25	16.48	.376	4.10	.144
	26	17.92	.397	4.16	.128
	27	16.36	.409	3.86	.128
	28	17.74	.360	4.04	.132
	29	15.16	.474	3.68	.132

Table IV. 6. Means and standard errors of calyx length and calyx tooth length in G. verna samples.

arises as to how far the sampling procedure is reliable and also how far this variation is genotypic in origin. Two approaches have been made to these problems; in one samples have been taken from the same locality over a number of years and also in one case at several different times in the flowering season, in the other a small number of measurements have been made on calyces from mature capsules to see if the relative dimensions change with the state of maturity.

The results from samples taken at the same localities in successive years are given in table IV. 7. for calyx length and table IV. 8. for calyx tooth length. The sampling dates are included in table IV. 7.

Locality	<u>1 9 5 9</u>		<u>1 9 6 0</u>		<u>1 9 6 1</u>	
	Date of coll.	Mean & S.E.	Date of coll.	Mean & S.E.	Date of coll.	Mean & S.E.
Haugh Hill, Co. Durham	20/5	13.54 [±] .497	2/5	14.36 [±] .361	2/5	14.64 [±] .429
Cetry Bank, Co. Durham	12/5	14.50 [±] .434	2/5	14.02 [±] .376	2/5	15.60 [±] .343
Cow Green, Widdybank Fell, Co. Durham	7/5	13.82 [±] .281	10/5	13.62 [±] .395	2/5	14.26 [±] .306
Tinker's Sike Widdybank Fell, Co. Durham	7/5	14.60 [±] .292	10/5	13.26 [±] .322	2/5	15.60 [±] .320

Table IV. 7. Mean measurements of calyx length in samples of G. verna taken in successive years.

Locality	1959	1960	1961
Haugh Hill, Co. Durham	3.58 \pm .179	3.94 \pm .162	4.28 \pm .126
Cetry Bank, Co. Durham	4.00 \pm .054	3.80 \pm .168	4.28 \pm .136
Cow Green, Widdybank Fell, Co. Durham	3.80 \pm .115	3.50 \pm .126	3.82 \pm .104
Tinker's Sike Widdybank Fell, Co. Durham	4.16 \pm .155	3.52 \pm .110	4.22 \pm .156

Table IV. 8. Means and standard errors of calyx tooth length in samples of G. verna taken in successive years.

There is a small amount of fluctuation in the measurements for both characters, but in all cases the group characteristics are retained. In 1961 there was an exceptionally early and warm spring, with the result that in Teesdale G. verna came into flower in the middle of April, almost three weeks before the normal time, which might have caused environmental size modification. These measurements show that (a) sampling is probably reliable, (b) that there are no significant differences even though climatic conditions were different each year. Thus these characters seem to be reasonably stable so that any significant differences between these and other populations, such as have been found, probably indicate that the differences

are genotypic and not phenotypic.

All the samples were taken approximately in the middle of the flowering season and therefore a second point arises as to whether the characters or ratios change as the season progresses. Two methods have been used to gain information on this. In one samples were taken several times during one flowering season from one population, and in the other a number of fruiting calyces have been measured.

At Haugh Hill three samples were taken in 1961; the results are given in table IV. 9.

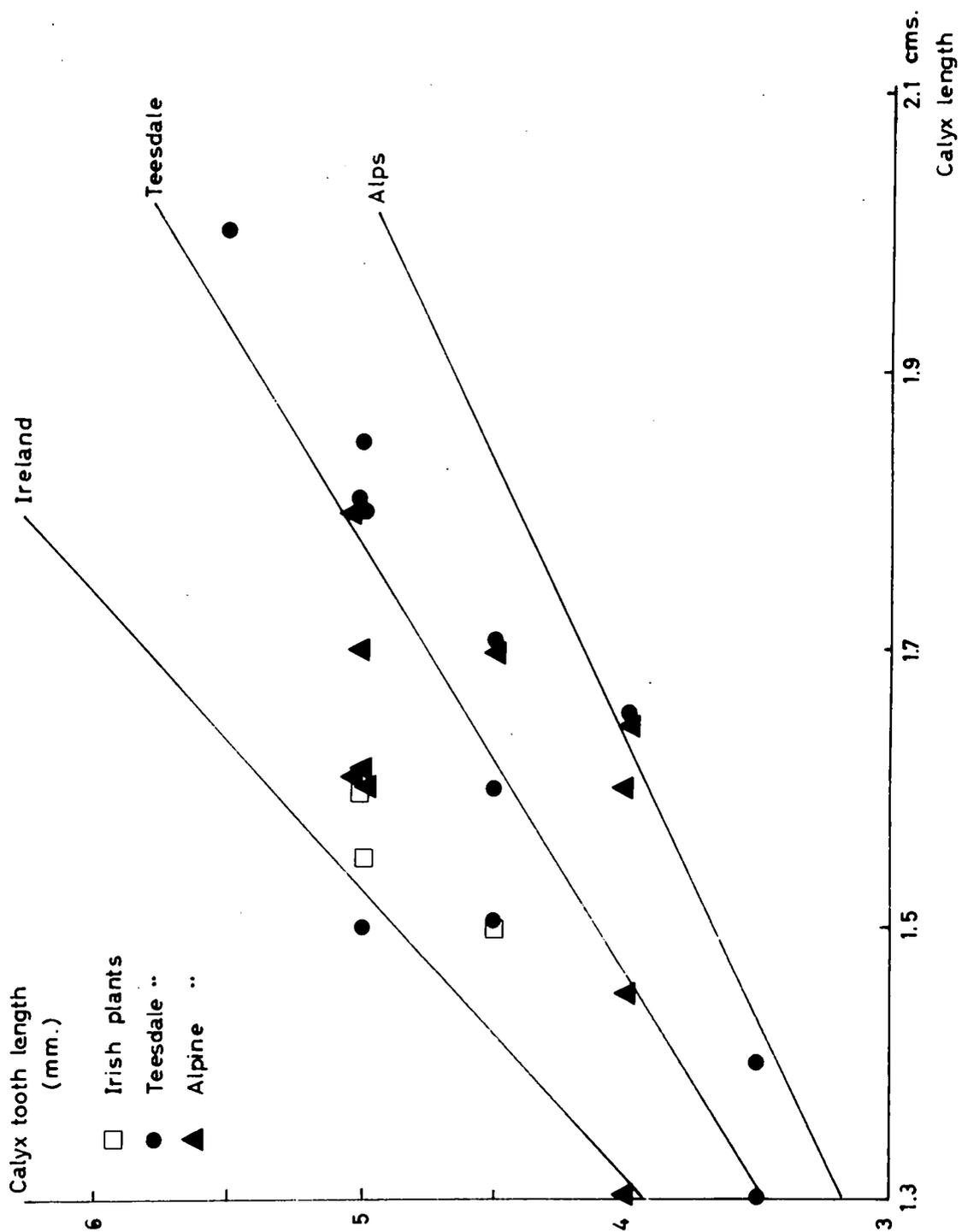
Date of collection	No. in sample	Calyx length	Calyx tooth l.
16. 4. 61.	20	15.20 \pm .390	4.30 \pm .122
2. 5. 61	25	14.64 \pm .429	4.28 \pm .126
19. 5. 61	10	15.35 \pm .435	4.65 \pm .198

Table IV. 9. Means and standard errors of calyx length and calyx tooth length of samples from Haugh Hill, Co. Durham at three times in one year.

Again there is a fluctuation, which in the case of the last sample does differ slightly from the Teesdale group calyx length/ calyx tooth length relationship in that the calyx tooth length is abnormally high; it will be noted that this

sample was small. An example of a character where size has a large phenotypic variation has been given in the corolla diameter, where two samples from the same locality in successive years showed a variation nearly encompassing the total variation recorded.

As already mentioned a number of calyces were removed from ripe capsules which were the results of crosses made in an insect proof greenhouse. Ten from Teesdale plants, three from Irish and four from Alpine plants were available for measurement. The regression lines shown in diagram IV. 4. have been constructed from measurements made on calyces from flowers. Thus if there has been no change in the size of these dimensions during the ageing of the calyces the measurements should still fit these lines. The results, with the regression lines are given in diagram IV. 4. Not enough results are available to come to any firm conclusions, but it will be seen that the Irish calyces fall fairly near the regression line calculated for Irish material and the calyces from Teesdale plants are distributed so that the calculated regression line is true for them also. The calyces from Alpine plants however also seem to be distributed about the Teesdale line rather than the Alpine line. On the limited data available it is impossible to decide whether this is a real difference or not. Nevertheless, both from the field



Diagram

IV. 4. Scatter diagram of calyx length and calyx tooth length of mature calyces from cultivated plants of G. verna.

experiment and the information on the fruiting calyces, there is no evidence of any very marked change in proportions as the flowers mature; and as already pointed out, late flowering or fruiting plants were not used in obtaining the data.

Definite proof that these characters are genotypic can only be gained by studies of families grown from seed. This has not been possible in this species mainly because of the low germination rate already discussed and the slow growth of any resultant seedlings, thus of 500 seeds sown in November 1958 three plants flowered for the first time in 1961.

Having shown that the variation in calyx characters has probably a genotypic basis, and that there is a regional difference between Irish, Teesdale and Alpine material the possible causes for this must now be discussed. It will be seen that the Irish group has diverged further from the Alpine group than has the Teesdale group; there are a number of possible explanations for this situation and for the fact of regional differentiation. It is possible that the regional types were already differentiated on arrival in the two areas. This would seem to be most likely if immigration took place in different directions to the two areas; thus the Irish G.verna might have migrated along the same path as members of the

so-called Lusitanian element of the flora from Spain and W. France, while the Teesdale G. verna may have migrated directly from the Central Alps across E. France. If this took place, it is possible also that migration took place at different times; thus G. verna in Ireland may have migrated there before the last glacial period. In this connection it seems to have been shown that members of the Lusitanian element have survived at least the last glacial period from the preceding interglacial period since fossil material of Daboecia cantabrica and Eriocaulon cf. septangulare have been discovered in an inter-glacial deposit near Gort, Co. Galway (about 14 miles from the middle of the Burren area) by Jessen, Andersen and Farrington (1959). As Jessen (1949) has pointed out survival in glacial refuges off the West coast of Ireland cannot be excluded as a possibility and these finds can be taken as supporting evidence for this theory.

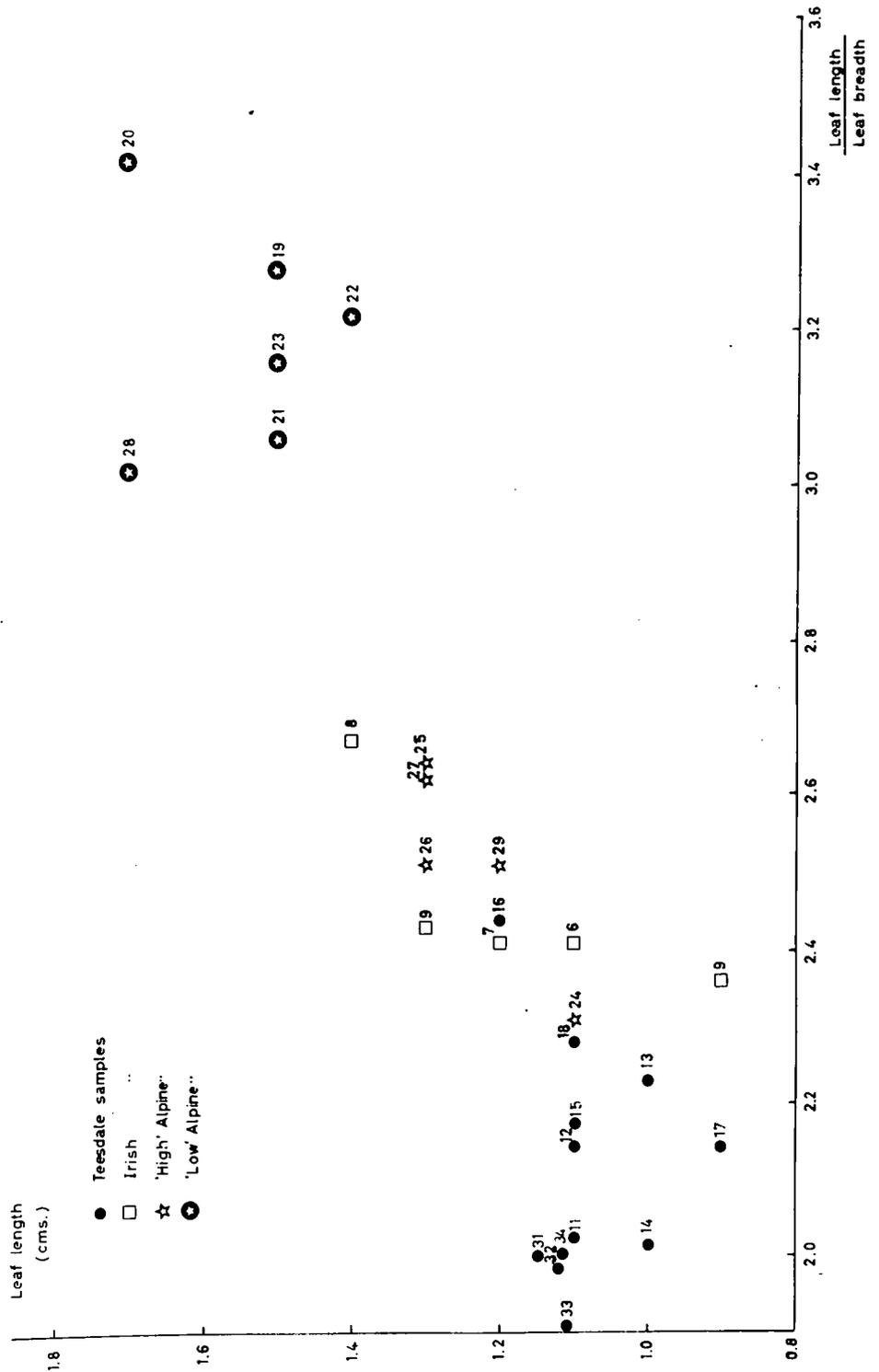
If this is so there seems no reason why G. verna could not also have survived. In this case, even if the original stocks were morphologically identical, then the Irish material would have been isolated for a longer period from the parental populations and might therefore, even assuming equal rates of evolution for this and the Teesdale groups, give a larger differentiation from the Alpine parent stocks. There is no evidence as to rates of evolution, but it is possible that

evolution might occur more rapidly in a more equable climate such as that of W. Ireland, since rates of growth, flowering and fruiting might be higher over a long period than in the generally less clement climate of the N. Pennines, although G. verna is an Alpine plant and it is not known what conditions might be the most favourable.

Another explanation which can be advanced to explain this apparently non-adaptive variation is that of random genetic drift, or the operation of the Sewall Wright effect. This can produce quite large changes, due to chance fluctuations in gene frequency, in a relatively short time, provided that the populations are small. Wright (1948), commenting on changes observed by Fisher and Ford in a population of the moth Panaxia dominula, points out that if the effective number of parents in one particular year was very small (some 100 or less) it is possible to account for all fluctuations as those of small populations, even though the effective number over a period of years may be as much as 1000. It is very difficult to estimate the size of the breeding populations in G. verna in Britain, especially as some of the populations may have been derived from a single seed introduction followed by vegetative reproduction over a long period. Such a population would then act as one effective parent since all individuals would have the same genotype. If this process

has been extensive then the number of effective parents may be small enough for genetic drift to take place. Even if this is not so at the present day, it may have been the case when G. verna, in Teesdale at least, was probably confined to small clearings in the general forest cover.

Leaf Characters. The characters which have been used are leaf length and length/ breadth ratio, and these are considered together. The means and standard errors of the samples collected are given in table IV. 10. and means are plotted in diagram IV. 5. It will be obvious that differentiation has taken place in the characters considered. In Britain, Teesdale plants have, in general, shorter wider leaves than Irish plants. In the Alps variation bears a relation to the altitude of the sample as will be seen from diagram IV. 6. From diagram IV. 5. the Alpine samples are seen to fall into two distinct groups, one of which has long narrow leaves and is found at low altitudes, while the other is similar to a number of Teesdale and Irish samples in having shorter wider leaves; this is typically found at higher altitudes. The differences and similarities between these groups are brought out by the group means given in table IV. 11.



Diagram

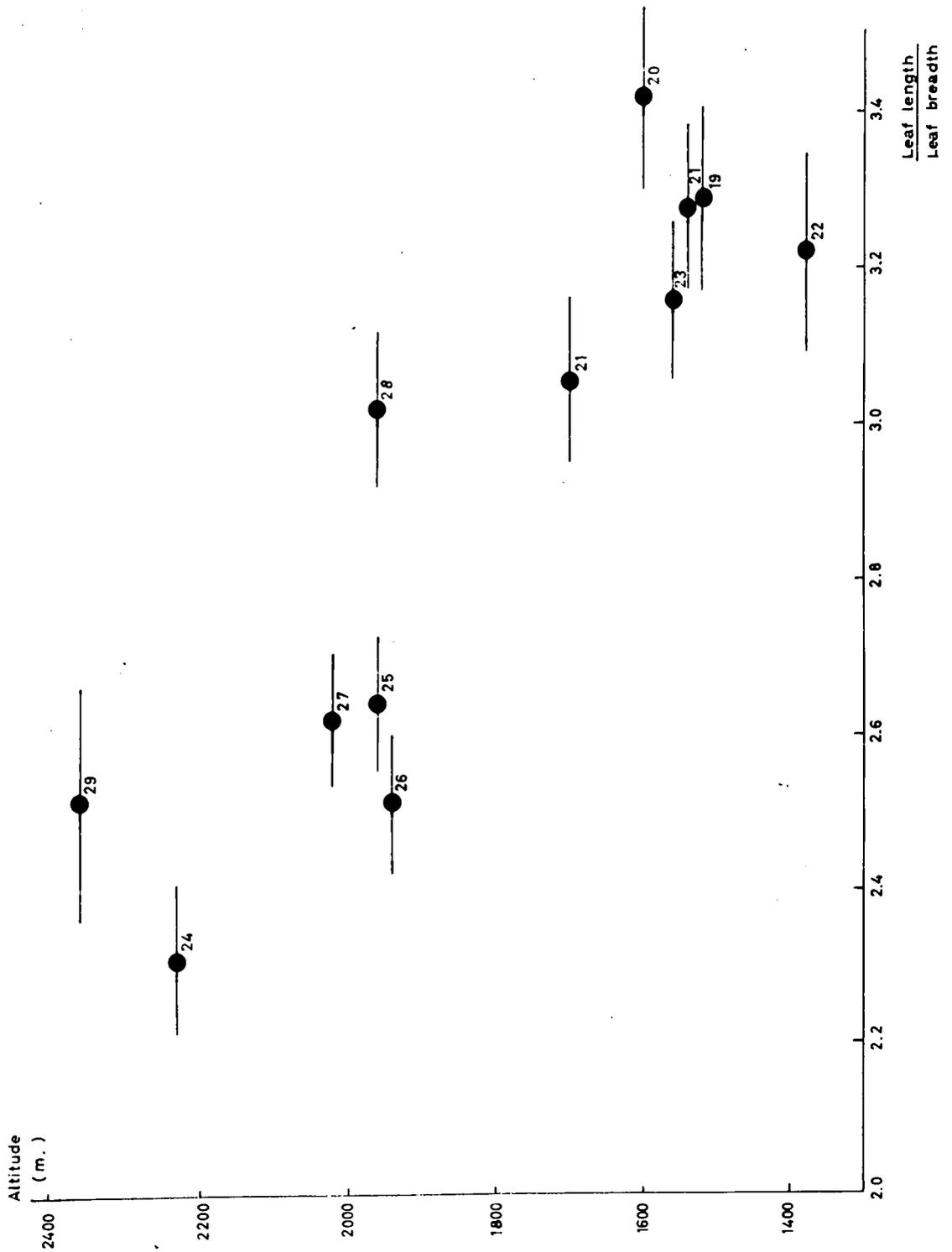
IV. 5. Scatter diagram of means of leaf length and length/ breadth ratio in samples of G. verna.

Sample	length mean	S.E.	length/breadth ratio mean	S.E.
<u>Teesdale</u>				
11	1.13	± .048	2.02	± .050
12	1.15	.040	2.14	.059
13	1.02	.026	2.23	.055
14	1.05	.025	2.01	.049
15	1.09	.030	2.17	.075
16	1.19	.051	2.44	.067
17	.92	.021	2.14	.042
18	1.11	.031	2.28	.048
31	1.15	.036	1.97	.063
32	1.12	.030	1.95	.059
33	1.13	.035	1.90	.148
34	1.18	.048	1.99	.052
<u>Ireland</u>				
6	1.12	.061	2.41	.083
7	1.25	.072	2.41	.080
8	1.37	.066	2.67	.067
9	1.33	.048	2.43	.065
10	.94	.039	2.36	.050

Table IV. 10.

Sample	length mean	S.E.	length/breadth ratio mean	S.E.	Altitude
<u>'High' Alps</u>					
24	1.07	±.058	2.31	±.098	2230 m.
25	1.28	.056	2.64	.087	1960
26	1.28	.051	2.51	.090	1940
27	1.34	.057	2.62	.085	2020
29	1.16	.066	2.51	.149	2360
 <u>'Low' Alps</u>					
19	1.53	.065	3.28	.117	1540 m.
20	1.72	.074	3.42	.118	1600
21	1.54	.058	3.06	.106	1700
22	1.36	.079	3.22	.123	1380
23	1.46	.054	3.16	.101	1560
28	1.72	.073	3.02	.098	1960

Table IV. 10. Means and standard errors of leaf length and length/breadth ratio in samples of G. verna.



Diagram

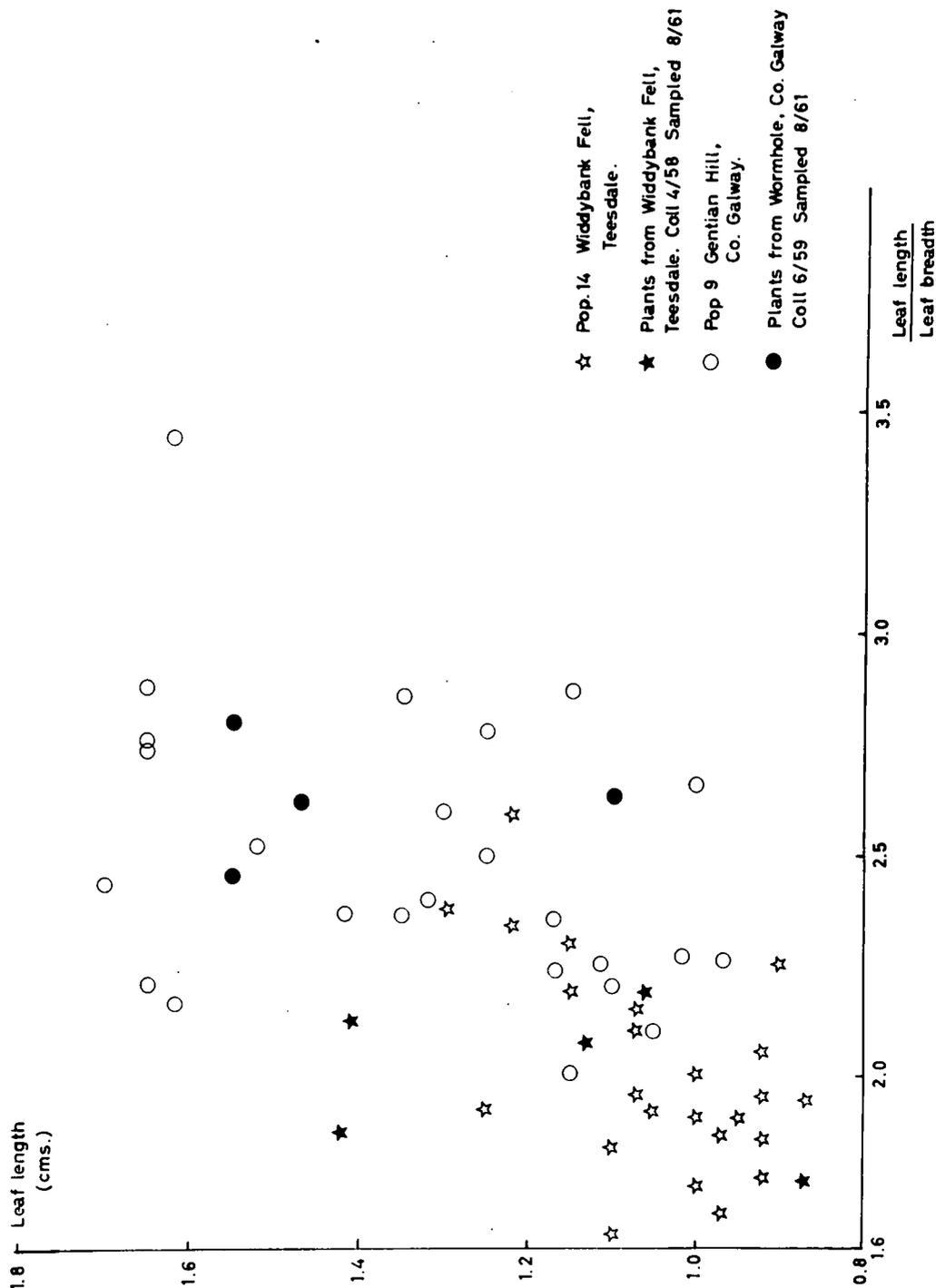
IV. 6. Scatter diagram of means and standard errors of leaf length/ breadth ratio of Alpine samples plotted against altitude of locality.

Area	Mean leaf length	Mean length/breadth ratio
Teesdale	1.10	2.10
Ireland	1.21	2.47
High Alps	1.22	2.51
Low Alps	1.56	3.19

Table IV. 11. Regional leaf length and length/ breadth means in G. verna.

To gain information on whether these differences in leaf size and shape are genotypic or not, a number of plants have been grown together at Durham. They have all been potted in John Innes potting compost and grown in a cold frame to give protection from dampness in the winter. Only a small amount of information is available, as G. verna is rather a rare plant and hence only a small number of plants were collected; in addition quite substantial losses have occurred[†] over the time that the plants have been in cultivation.

Results for Teesdale and Irish plants are presented in diagram IV. 7. Here two population samples are plotted, one from Teesdale (number 14 from Widdybank Fell collected in 1960), and one from Ireland (number 9 from Gentian Hill, Galway collected in 1959); measurements of pot plants have been added to these, five from Widdybank Fell, Teesdale



Diagram

IV. 7. Scatter diagram of leaf length and length/breadth ratio measurements from two samples of G. verna, together with measurements of cultivated plants from the same areas.

collected in 1958, and four from Wormhole, Co. Galway, another population in the same area as Gention Hill, collected in 1959. All the pots were sampled in August 1961. The values used have been compiled from measurements on two leaves from each of two rosettes on a plant; these have been averaged. It will be seen that the Teesdale and Irish plants retain the difference in length/breadth ratio. Plants brought back from the Alps had a low survival rate so that not enough material is available for measurements to be presented. One plant from a low Alpine site, Charbonniere, Haute Savoie, France (from which sample 20 was collected) is however shown in plate A, together with one each from Teesdale and Ireland. The differences, certainly in Teesdale and Irish plants, probably in Alpine plants, are thus retained over a number of years when plants are cultivated under similar conditions, so that it is probable that these are genotypic. This is supported by measurements on samples from the same Teesdale localities made in successive years.



Plate A. *G. verna* plants from Cetry Bank, Teesdale; Poulsallagh, Co. Clare; and Charbonniere, Haute Savoie, France, showing differences in leaf size and shape.

Measurements from four Teesdale localities made in 1960 and 1961 are given in table IV. 12, together with the dates of collection.

Locality:	Haugh Hill		Cetry Bank		Cow Green, Widdybank Fell		Tinker's Sike, Widdybank Fell	
	Date of coll.	Mean & S.E.	Date of coll.	Mean & S.E.	Date of coll.	Mean & S.E.	Date of coll.	Mean & S.E.

<u>Length:</u>								
1960	2/5	1.13 ± .048	2/5	1.15 ± .040	10/5	1.02 ± .026	10/5	1.05 ± .025
1961	2/5	1.18 ± .048	2/5	1.13 ± .035	2/5	1.12 ± .030	2/5	1.15 ± .036

<u>Length/breadth ratio:</u>								
1960		2.02 ± .050		2.14 ± .059		2.23 ± .055		2.01 ± .049
1961		1.99 ± .052		1.90 ± .148		1.95 ± .059		1.97 ± .063

Table IV. 12. Means and standard errors of length and length/breadth ratio of samples of leaves taken in successive years.

There is a small amount of variation from year to year, but this is small compared with the variation between regional groups. The measurements show that (a) sampling is probably reliable, (b) that there are no significant differences even though, as mentioned in connection with the corolla and calyx measurements, climatic conditions were different each year. Thus the leaf characters also seem to be reasonably stable, so that the differences found indicate that these are probably genotypic.

It is also of interest to see whether the leaf shape and size change during the flowering season. Three samples were collected at Haugh Hill in the 1961 season to gain information on this and the results are given in table IV. 13.

Date of collection	No. in sample	Leaf length	Leaf l/b ratio
16. 4. 61	20	1.23 \pm .061	2.05 \pm .069
2. 5. 61	25	1.18 \pm .048	1.99 \pm .052
19. 5. 61	7	1.09 \pm .056	2.07 \pm .085

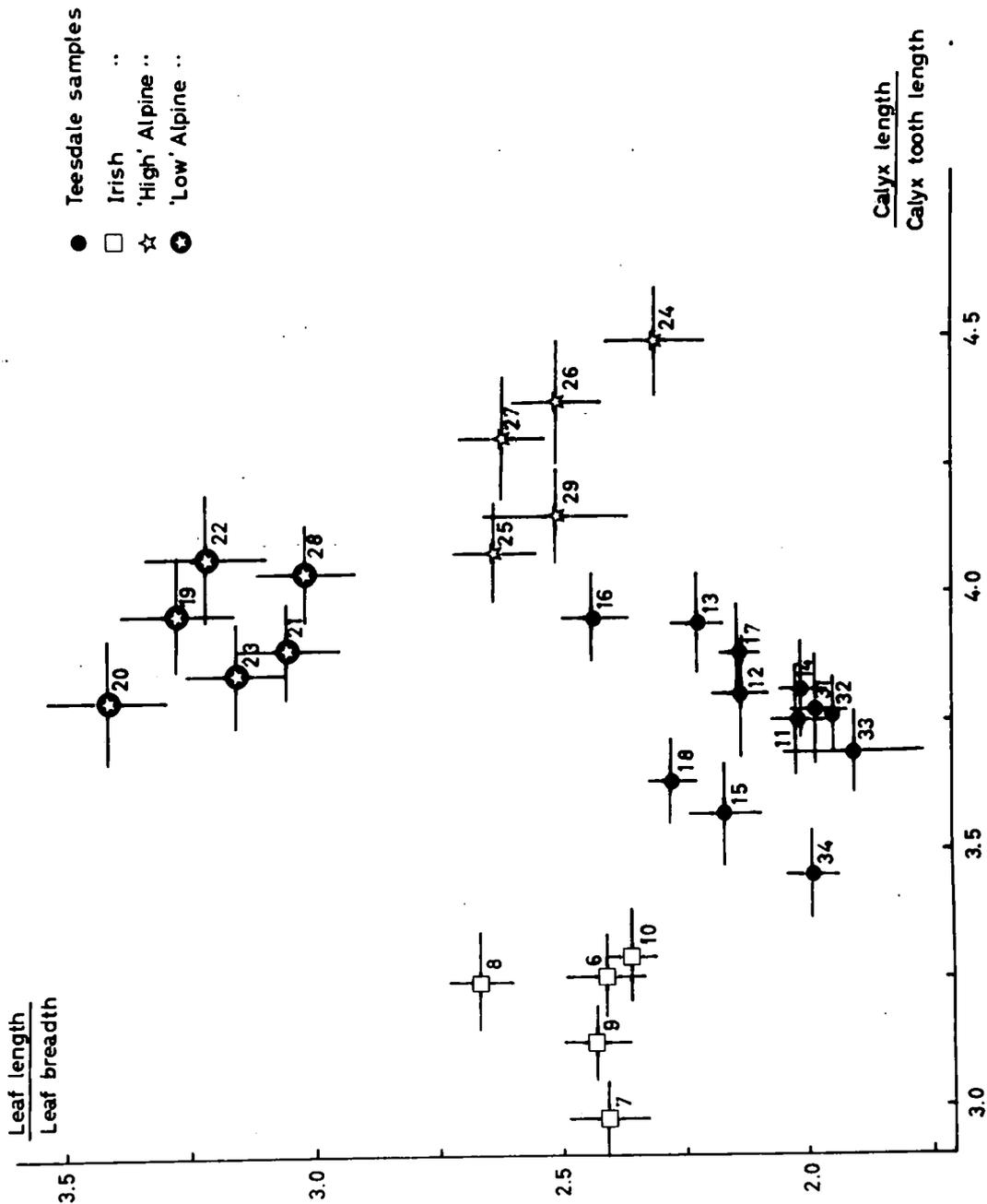
Table IV. 13. Means and standard errors of leaf length and length/ breadth ratio of samples from Haugh Hill, Co. Durham at three times in one year.

There is a small amount of variation, but again this is small compared with the variation between groups. Thus there

is no indication that the leaf size and proportions change during the flowering season.

Again it may be mentioned that seedling populations are needed to settle this point conclusively; the poor germination and slow growth of seedlings have not made this possible.

As in the case of the calyx characters the differentiation must be discussed. It is to be noted that differentiation has here reached a different end point, as it is the Irish and not the Teesdale group that is most similar to the Alpine samples; there is also the added complication that the Alpine samples are themselves differentiated in a manner that bears a relation to altitudinal and presumably the associated climatic conditions. It seems most probable that the short wide leaves of the high Alpine type are an adaptation to the harsher climatic conditions, since these tend to give a tight compressed rosette and a morphologically more dwarf plant than the longer leaved form from lower altitudes. This would tend to explain why sample 28, morphologically a low alpine population (and treated as such here) is from as high ~~an~~ an altitude as some of the High Alps samples, because it was collected from a hay meadow where the vegetation was much higher and more closed than in natural grassland at this altitude. It was thus in a less exposed and presumably more favorable microclimate than the other samples from natural communities at similar altitudes. If this theory



Diagram

IV. 8. Scatter diagram of leaf length/ breadth ratio and calyx length/ calyx tooth length ratio of samples of G. verna.

is right then the difference between the Teesdale and Irish groups may be a reflection of the differing climatic regimes, in that the Teesdale group being in a harsher climate had smaller leaves than the Irish one from a more equable climate.

Finally, the four groups which have been distinguished may be completely separated from one another by considering combinations of characters. In diagram IV. 8. a scatter diagram has been constructed of leaf length/ breadth ratio against calyx length/ calyx tooth length ratio. It will be seen that complete separation is given between the four groups previously distinguished. It will be noted that the two Alpine groups are as well separated as any other pair of groups. Whether this is a true estimate of the situation, that there are in fact two climatic ecotypes, or whether there is a clinal variation between the two extremes is impossible to say on the number of samples collected. More collecting at selected altitudes is necessary for a decision on this point.

Potentilla fruticosa L.

Taxonomy.

The name Potentilla fruticosa was published by Linnaeus (1753) and has remained without change to the present day, apart from a number of suggestions that this species, together

with the other shrubby Potentilla species, should be placed in a separate genus. Thus Rydberg (1898) and Juzepczuk (1941) have removed them to a new genus Dasiphora, while Löve A. (1954) has argued that the generic name should be Pentaphylloides, first published validly by Duhamel (1755). From an experimental taxonomic viewpoint there is little to recommend this change in view of the wide crossability of P. fruticosa. In particular the crosses with Fragaria made by Ellis (1958) may be cited.

Description.

Deciduous, branched, ~~woody~~ shrub, the branches white, pubescent in their first year, becoming brown and glabrous in their second, with the bark beginning to flake off in the second and third years. Both erect and prostrate branches are present in the mature plant; the latter are able to root adventitiously and thus increase the diameter of the plant up to 5 - 6 m. or even more. Average height of bushes about 0.5 m., but plants in exposed and grazed localities down to 10 cms., and in sheltered localities up to 2 m. Leaves numerous, with (3-) 5-7 (-9) leaflets; leaflets oblong lanceolate to elliptic, acute, with revolute margins, dark green on the upper surface with impressed veins, paler on the lower surface, more or less pubescent with long white hairs on both surfaces, leaflet length (0.5-) 1 - 3 cms., petioles 0.2 - 1.2 cms.; stipules scarious, sheathing, entire, persisting until the second or

third year. Flowers terminal, occasionally solitary, usually in many flowered cymes (up to 35). Flowers 5-merous; sepals triangular ovate, epicalyx segments oblanceolate, linear, whole calyx pubescent, persistent in fruit and surrounding the achenes. Petals yellow, orbicular ovate, 0.6 - 1.6 cms. long and 0.6 - 1.7 cms. wide. British material, in common with that from Oland, Sweden, is dioecious. In the male flowers the numerous stamens are well developed and the receptacle bears a bunch of hairs. In the female flower the receptacle bears numerous one seeded carpels, while the stamens, although often as large as in the male, produce no good pollen. Achenes c. 1 mm. long, dark brown at maturity, surrounded with a ring of hairs produced from the base of the achene.

The only shrubby Potentilla species found in Europe.

General Biology.

In Teesdale P. fruticosa has two main periods of flowering, one in June and the other in August with occasional flowers until September. In Ireland the first maximum period seems to be somewhat earlier, towards the end of May. This is a much longer flowering period than given in most floras; thus both Smith (1824) and Clapham, Tutin and Warburg (1952) give the flowering season as June and July, whereas the maximum flowering time is August.

As already stated the species is, in Britain, dioecious so that cross pollination is obligatory. In Teesdale pollination seems to be carried out mainly by various Diptera. Knuth (1908) records a large number of Dipteran species, also Coleoptera and Hymenoptera. In Britain cross-pollination is quite successful, plenty of good seed being produced on the female bushes. Seed counts of 13 flower heads from Lake District plants gave an average of 50 seeds per flower while a mean figure of 70 ± 4 seeds per flower was obtained from 25 flower heads collected from High Force, Teesdale. The reason for this difference in seed number is not known; it may be a result of the more severe climatic conditions in the Lake District, especially of higher rainfall and lower summer temperatures than in the bottom of the Tees valley.

Germination experiments have been carried out on Teesdale material collected from the bottom of Cronkley Fell, N. Yorks. Seed was sown in John Innes seed compost in November and kept in a cold greenhouse so that frosting took place throughout the winter. Germination took place in the spring, with an average germination percentage of 22%. Although germination also took place in a warm greenhouse, it did not take place until the same time as the seed in the cold greenhouse and germination was lower (average 6 %). Small amounts of

germination also took place from seed sown in March, the seeds germinating in the late spring. A few seeds were germinated in the second spring after sowing, from seed sown both in autumn and spring.

The seedlings are quick growing under garden conditions and when planted out in a bed a few became mature enough to flower at the end of their first season. Flowers are usually freely produced the second season when the plants are 40-50 cms. in height. A number of populations were grown, each from seed collected from one wild plant. These were sampled for leaves and petals and also scored for sex, as described in the section on variation.

As seed is freely produced in Teesdale and it has a reasonable germination with quick growing seedlings, in the garden at least, it is interesting that P. fruticosa should be so restricted in the dale, especially as it grows typically along the river bank where there is always open ground available for colonisation. Plants have been recorded as far down as Greta Bridge and Egglestone Abbey, both below Barnard Castle, by Ray (1689). They do not seem to have been seen at these places however for many years, and the lowest point now seems to be just below Middleton, 13 miles up the river from Greta Bridge. It is difficult to account for this restriction in

range in view of the facts of the reproductive capacity.

As well as sexual reproduction there is also a form of vegetative reproduction. This is by the rooting of prostrate branches, as already mentioned in the description. The branches quickly become covered by shingle brought down by the river when in flood, and when the old branch decays a new plant is formed. This appears to be an effective method of increasing the size of the population in some of the Teesdale sites.

Variation.

The main part of the study of variation in this species has been carried out on leaf characters, since it was observed that there were marked differences between Teesdale and Irish material. Samples consisted of twenty five mature shoots (those with mature wood only were collected as young branches sometimes bear very large abnormal leaves) collected at random from different bushes in the population. From these shoots the largest leaf was chosen for measurement, and the apical leaflet measured since this was easily recognizable. The origins of all samples used in the study are given in table IV. 14. The length and breadth of each apical leaflet was measured and the means and standard errors calculated for length and length/ breadth ratio.

Code		Year of collection	Population
A	High Force, Co. Durham	1959	Field
B	Lowcroft Pool, N. Yorks	1961	Field
C	Wynch Bridge, Teesdale	1961	Field
D	Bottom of Cronkley Fell, N. Yorks	1961	Field
E	Ex bottom " " "	1960	Seed
F	" " " " "	1960	Seed
G	" " " " "	1960	Seed
H	" " " " "	1960	Seed
I	(same population as H)	1961	Seed
J	Ballyvaghan, Co. Clare	1959	Field
K	Castle Lough, Co. Clare	1959	Field
L	Ballynatty, E. Mayo	1959	Field
M	Ex Mullaghmore, Co. Clare	1960	Seed
N	(same population as M)	1961	Seed
O	Wastwater Screes, Cumberland	1959	Field
P	Pillar Mt., Ennerdale, Cumberland	1959	Field
Q	Ex Pillar Mt., Cumberland	1961	Seed
R	Coal Brook, W. Newfoundland	1958	Field
S	Table Mt., W. Newfoundland	1960	Seed
T	Val d'Eyne, Pyrénées Orientales, France	-	Herbarium
U	Oland, Sweden	-	Herbarium

Table IV. 14. Origins of P. fruticosa samples.

The means and standard errors for the samples of wild material are given in table IV. 15. and plotted on a scatter diagram in diagram IV. 9.

It will be seen that the Lake District and Teesdale populations are not significantly different from one another, so that English material is statistically homogeneous in this respect. There is, however, a regional differentiation between the English and Irish material, the Irish samples having consistently smaller apical leaflets than the English ones; this is also true for the other leaflets of the leaves.

Sample R is a field sample from W. Newfoundland, from a marsh community developed on shale. As pointed out above, Bowden (1957) found no obvious differences between the typical North American diploid plant and the tetraploid European one, and my data are not in disagreement with this. It may be pointed out here that Löve (1954) does not hold this view; he reports, for example that leaves of American plants are subglabrous to silky while European material is soft hairy; but this difference cannot be valid, as a similar difference in hairiness has been observed between Irish and Teesdale plants which are both tetraploid. He has also reported that leaflets of European material are flat, while American material is revolute; again this is not valid as Teesdale material at least is revolute.

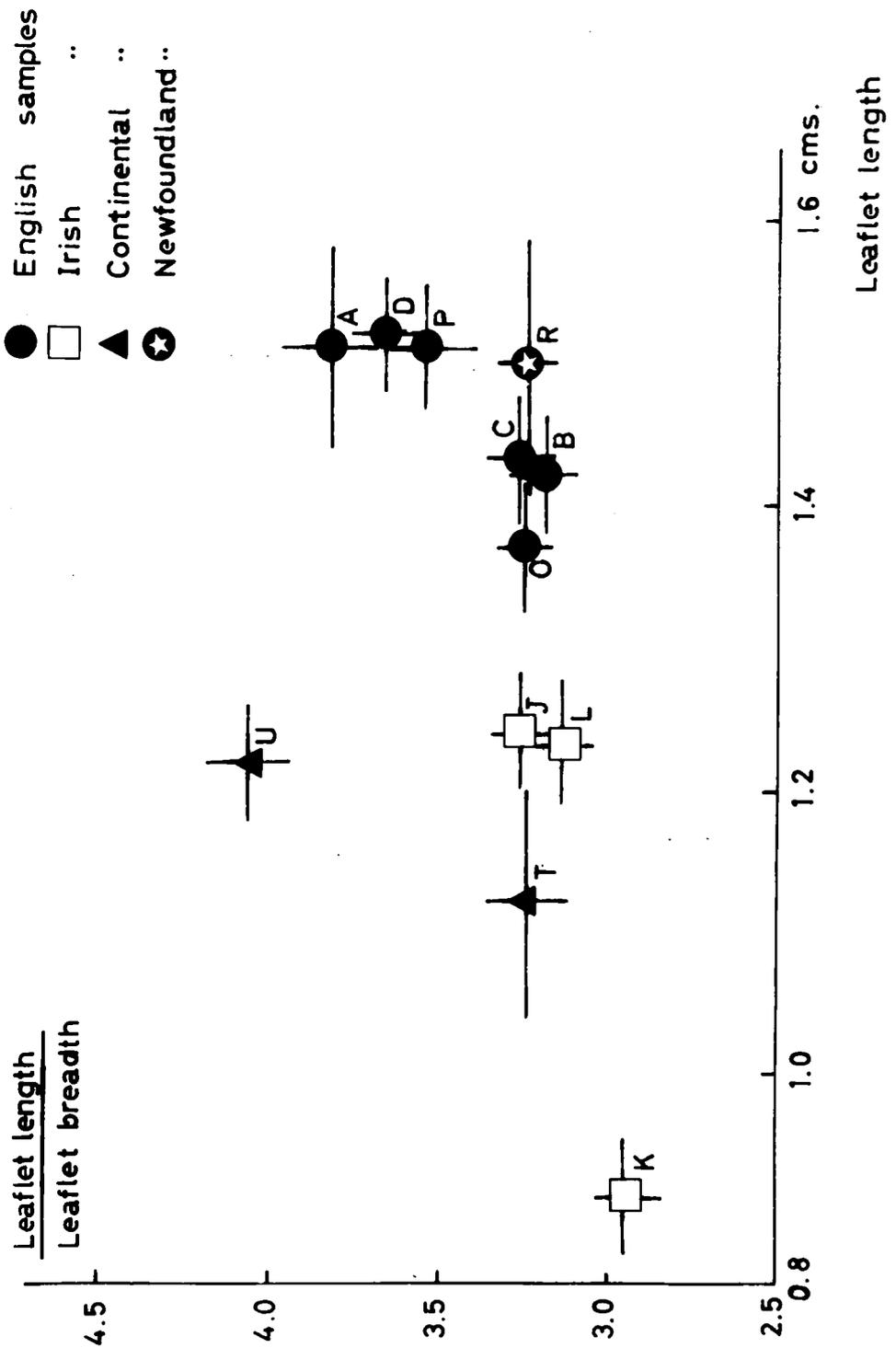


Diagram.

IV. 9. Scatter diagram of means and standard errors of P. fruticosa samples of wild origin.

Sample	length mean	S.E.	length/breadth ratio mean	S.E.
<u>Teesdale (wild)</u>				
A	1.51 cm	± .073	3.83	± .134
B	1.42	.040	3.01	.092
C	1.43	.047	3.07	.101
D	1.52	.043	3.66	.104
<u>Lake District (wild)</u>				
O	1.37	.047	3.26	.079
P	1.51	.047	3.55	.137
<u>Ireland (wild)</u>				
J	1.24	.044	3.27	.084
K	.91	.043	2.95	.084
L	1.23	.047	3.14	.078
<u>Newfoundland (wild)</u>				
R	1.50	.093	3.25	.094
<u>Pyrénées, France (herbarium)</u>				
T	1.12	.080	3.25	.122
<u>Oland, Sweden (herbarium)</u>				
U	1.22	.044	4.06	.118

Table IV. 15. Mean and standard errors of P. fruticosa samples of wild origin.

It may well be that in the material he looked at these differences may have existed, but it was evidently insufficient. However much these two groups may deserve specific rank, the morphological criteria given by Löve would be no use in determining herbarium material.

Also included in table IV.15 and diagram IV.9 are two samples measured from herbarium material (the largest leaf was measured on not less than fifteen specimens). These are from two of the best known continental localities, Öland in the Baltic (sample U) and the Val d'Eyne in the Pyrénées Orientales (sample T). Diagram IV.9 shows that T is similar to the Irish samples whereas U is somewhat intermediate although in a rather isolated position and significantly different from all the other population samples.

As well as samples from wild populations, samples were also taken from the populations grown from seed and planted in beds at Durham as already described. Those originating from Ennerdale, Cumberland and the Burren, Co. Clare are however, from seed originating from a number of plants. From these, information was gained as to the nature of the variation found in the wild populations. Samples consisted of the largest leaf from a shoot mature enough to bear flowers, on each bush. Two of the populations have been sampled in successive years. The results for these

1960

1961

Teesdale	Length mean	S.E.	length/ breath ratio mean	S.E.	sample	Length mean	S.E.	length/ breath ratio mean	S.E.	sample
From Bottom Cronkley Fell, N.Yorks	1.78	± .073	3.58	± .105	E	-	± -	-	± -	-
From " N.Yorks	1.75	± .090	3.22	± .090	F	-	-	-	-	-
From " N.Yorks	1.78	± .071	2.92	± .093	G	-	-	-	-	-
From " N.Yorks	1.65	± .062	3.42	± .118	H	2.02	± .038	3.30	± .054	I
<u>Lake District</u>										
Pillar Mt. Cumberland	-	-	-	-	-	1.70	± .041	2.87	± .080	Q
<u>Ireland</u>										
Burren, Co. Clare	1.44	± .055	2.81	± .074	M	1.61	± .075	2.63	± .089	N
<u>Newfoundland</u>										
Table Mt., W.Newfoundland	1.70	± .073	4.71	± .250	S					

Table IV. 16. Means and standard errors of leaf samples from P.fruticosa plants grown from seed.

measurements are given in table IV.16.

It will be seen that the leaflet length of the Irish sample remains significantly smaller than those of the English samples, and although both the Irish and Teesdale samples have larger leaves in 1961 than 1960 the size difference is maintained. The sample originating from the Lake District, collected in 1961 is really comparable with the other measurements taken in 1960 since the plants are a year younger than those from Teesdale and Ireland. If the comparison is made in this way they fall within the Teesdale group, as did the samples from wild plants. Although no definite differences are apparent in the length/ breadth means of wild samples, in the samples grown from seed, the English ones have longer, narrower leaflets than have the Irish samples as indicated by the higher ratios. This difference is also maintained over two years. These measurements on populations grown from seed indicate that the differences recognised in the wild state are genotypic.

Plants collected from Ireland and Teesdale are shown in plate B. Together with these is shown a plant collected from a serpentine area in W. Newfoundland (described by Fernald 1933). A sample collected from plants grown from seed originating from the area is also included in table IV.16. (sample S). It is very distinct in its very narrow leaves and

leaves from plants collected wild are also much smaller altogether.



Plate B. P. fruticosa plants from High Force, Teesdale; Table Mt., W. Newfoundland; and the Burren, Co. Clare.

As well as the leaves the whole plant is smaller and slower growing (it should be pointed out that this as all N. American material which has been counted is diploid) and it is probably an edaphic serpenticolous ecotype. This type of ecotype is now well known, having been recognised in a number of species, e.g. Streptanthus glandulosus, Gilia capitata, and Achillea borealis described by Kruckeberg (1951). It may be contrasted with sample R, also from W. Newfoundland, which has already

been commented on.

In considering the regional differentiation between English and Irish material it must be remembered that the European continental distribution is very disjunct, thus making the directions of migration almost impossible to trace. As in the differentiation of calyx characters in Gentiana verna a number of explanations are possible. It seems unlikely that the differentiation is due to a Sewall Wright effect since if there were genetic drift it might be expected that the Teesdale and Lake District populations would be different. It is more possible that either the migrating populations were differentiated on arrival (presuming that migration took place in two different directions), or that differentiation took place after isolation. This latter explanation would account for the Teesdale and Lake District populations being similar to one another since they would presumably have been isolated from one another at a later date than the Irish from the English populations.

An interesting feature of the species which seems to be restricted to the tetraploid is the presence of dioecism. This occurs in all the British populations and is also recorded for Oland by Tornblom (1911). On examination of 5,110 bushes he found that 63 % were female and 37 % male. In Teesdale Parbrook (1957) counting 314 bushes between High Force and

Wynch Bridge found that 202 (64 %) were female and 112 (36 %) were male, a remarkably good agreement. The Lake District and West Ireland populations are also dioecious, but no counts have been carried out.

To investigate this difference in proportion, a number of populations, each originating from seed from one parent plant, cultivated as already described, were scored for sex. The results are given in table IV. 17.

Pop.No.	Locality	No. plants	% Female	% Male
PFrS 1	Bottom Cronkley Fell, Teesdale.	18	55.5	44.5
PFrS 3	"	15	60	40
PFrS 4	"	36	50	50
PFrS 15, 16	Mullaghmore, Co.Clare. (mixed heads).	17	47	53

Table IV. 17. Sex ratios of P. fruticosa populations grown from seed.

A chi square test using Brandt and Snedecor's formula shows that these results are not significantly different from a 1:1 ratio. The differences in the field populations may possibly be due to a difference in vigour between plants of the two sexes, although none has been observed in the plants grown from seed. Alternatively there may be a difference in the

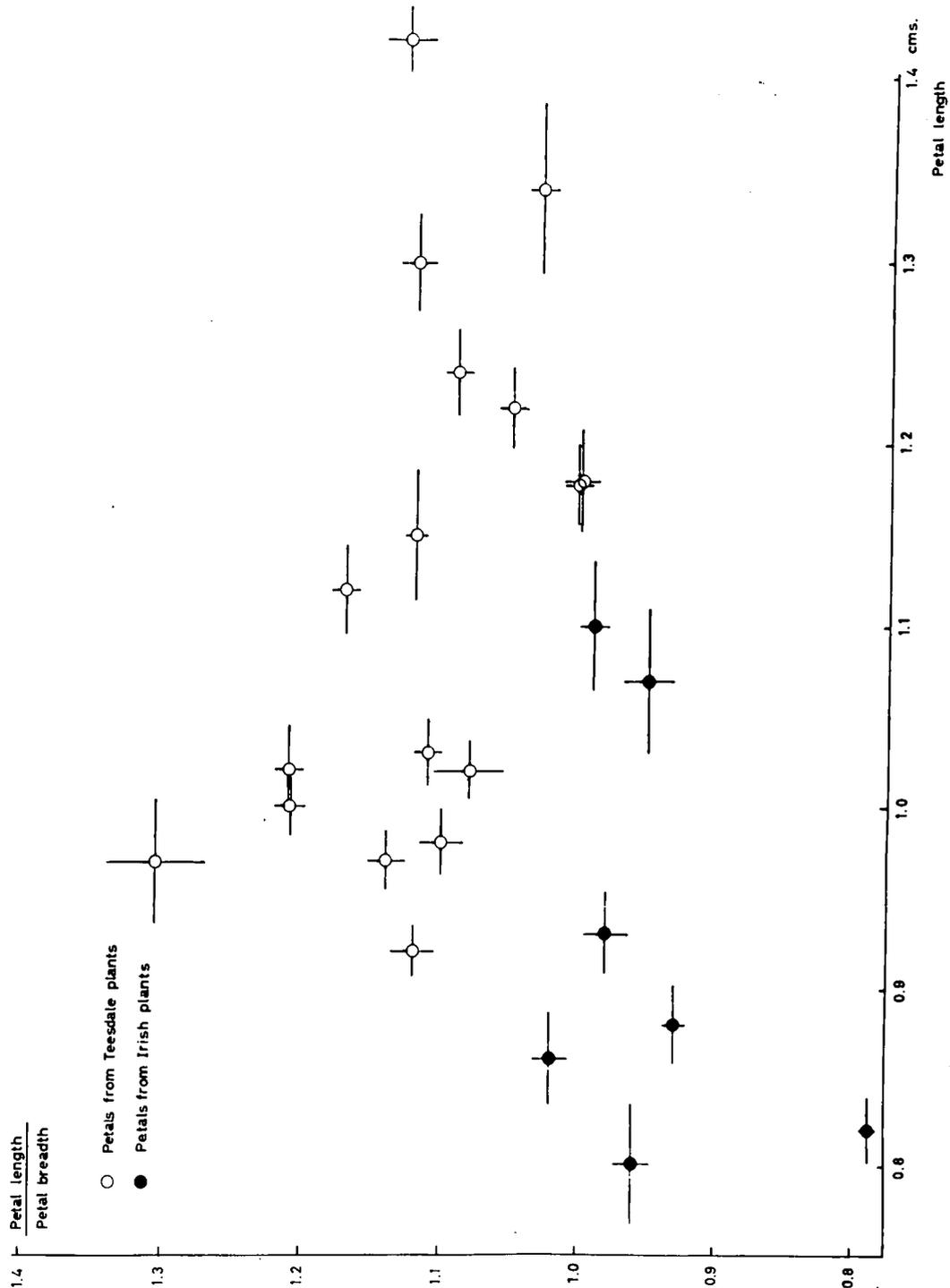
length of life of the two sexes. No information is available on this point.

An attempt has been made to see if there is any morphological differentiation in petal size and shape. For this purpose, the young plants listed in table IV. 17. were used. One petal was removed from each of twenty flowers on a plant and stuck onto sellotape and the length and breadth measured; length and length/ breadth ratio means were calculated. The group means for Teesdale and Irish material are given in table IV. 18.

	<u>length</u>	<u>length/ breadth ratio</u>
Ireland male	0.93	0.95
Ireland female	0.97	1.03
Teesdale female	1.07	1.05
Teesdale male	1.13	1.10

Table IV. 18. Length and length/ breadth ratio group means for P. fruticosa petals.

It will be seen that the groups form a series from the petals of Irish males, which are shortest and relatively widest, to the petals from Teesdale males which are the longest and narrowest. When the groups are considered in pairs the Irish and Teesdale females are not significantly different from one another, nor are the Irish males and females



Diagram

IV. 10. Scatter diagram of means and standard errors of petals from cultivated plants of P. fruticosa.

or the Teesdale males and females. There is however a significant difference when the Irish and Teesdale males are compared together. A scatter diagram of petal length against length/ breadth ratio with the means and standard errors plotted for petals of these groups of plants is given in diagram IV. 10. Even the nearest means (M 2 and L 13) are significantly different at the 5 % level with respect to length. Thus there is a differentiation between English and Irish material and also a sexlinked difference between males and females, although this appears to have taken place in different directions in each area. The amounts of each type of differentiation are small so that statistical separation is only observed between the two extreme groups, the Teesdale and Irish males.

Myosotis alpestris Schmidt.

Description.

Small, perennial hemicryptophyte with a shallow fibrous rooting system, from 2 - 23 cms. high in flower. Plant with a short root-stock bearing oblong lanceolate to spatulate, subacute leaves which are long petioled. Cauline leaves smaller becoming sessile, all hairy. Flowers borne in rather short, dense, ebracteate cymes. Pedicels short, ascending,

as long as the calyx or slightly shorter when fruiting. Calyx tube campanulate, silvery with more or less spreading hairs and with a few short stiff hooked ones on the tube, teeth narrow, lanceolate, half to three quarters the length of the tube, erect or rather spreading in fruit. Corolla tube short, white, corolla lobes spreading, bright blue, more or less rounded; tube partially closed by five short notched scales, yellow in recently opened flowers, fading to white. Stamens five, enclosed in the corolla tube and borne above the capitate stigma. Style short, longer than the calyx tube. Nutlets roundish ovoid, keeled on one surface, black and shiny.

Relationships.

M. alpestris is closely allied to M. sylvatica Hoffm. and is included in this as a subspecies by Hegi (1927). It has fruiting pedicels as long as the calyx and black nutlets, while M. sylvatica has fruiting pedicels 1½ - 2 times the length of the calyx and brown nutlets. M. alpestris is also usually smaller with denser inflorescences. In Britain, the species are also separated altitudinally. The highest records found by Wilson (1949) for M. sylvatica are from Baker (1906) who gives 1050' at Stonesdale Moor in Swaledale, N. Yorks, and from Lees (1888) who records it up to 1250' in the Craven

district of N.W. Yorks. These are much lower than the lowest record of M. alpestris, which is at 2350' in Teesdale.

While these characters serve to separate the two species in Britain, on the continent the situation is much more complex with intermediates occurring between the two, and with a number of other forms differing in characters such as leaf shape, length of corolla tube and hairiness; intermediates also appear to be common between these forms.

General Biology.

M. alpestris, in Britain, has its main flowering season in July and August. Insects have not been seen visiting plants in Teesdale or Scotland although Muller (1881) and Knuth (1909) record a large number of Lepidopteran, Hymenopteran and Dipteran visitors in the Alps. In Britain it seems much more likely that the flowers are mainly self fertilised since the flowers are spontaneously self pollinated and this results, under greenhouse conditions at least, in the production of good seed.

Germination has been tested experimentally. Seed was sown in John Innes seed compost. The species is distinct amongst those tested in not needing a frosting period; seed sown both in the autumn and spring germinates about three

weeks after sowing with up to 50 % germination. The main germination experiments however, were carried out using seed collected from spontaneous selfings and these were sown in November and kept in a cold greenhouse, when germination took place the following spring. The results are given in table IV. 19.

Parent Plant	Origin	Seeds sown	Seeds germ.	Germ. %
A1	Great Dun Fell, Westmorland.	35	32	91
B2	Little Fell, Westmorland.	45	40	89
C1	Mickle Fell, N. Yorks.	28	19	68
D1	Ben Lawers, Perth.	9	4	44
D5	Cam Creag, Perth.	48	12	25
G1	Tatra Mountains, Poland	100	54	54

Table IV. 19. Germination of M. alpestris seed.

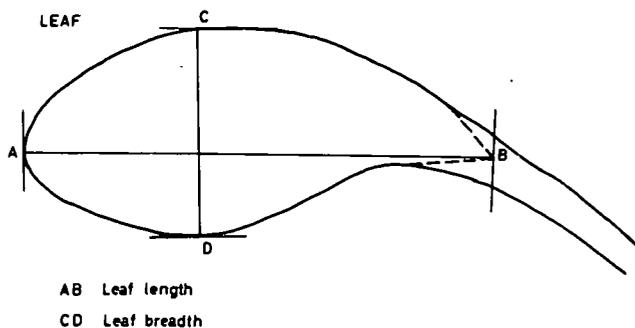
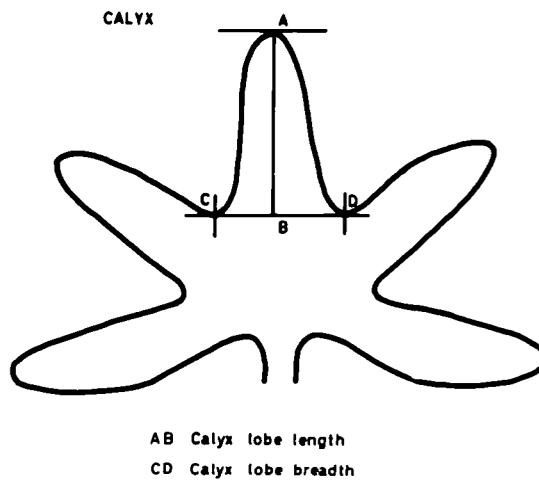
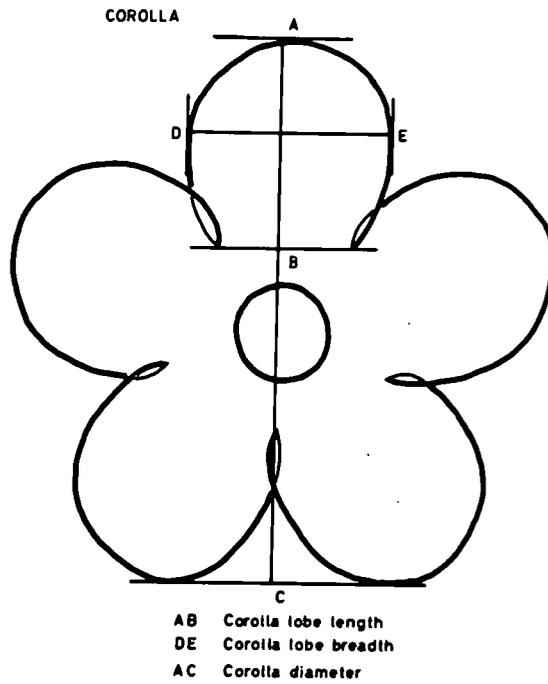
The results show that compared with the other species tested M. alpestris has a good percentage germination. No germination has been observed in the second spring after sowing. Seed production and germination under natural conditions are very difficult to determine, especially as

the main localities are difficult to visit. No fruiting stems have been observed in the wild, but it is not known whether this is due to the depredations of the sheep or to visiting too late in the summer. Likewise no seedlings have been observed. There appears to be no method of vegetative reproduction.

When grown at Durham the plants show a tendency for the centre of the overwintering leaf rosettes to rot off in the late autumn and it is necessary to keep the plants under a cold frame during the winter for adequate survival. That this does not happen under natural conditions may be due to the fact that the ground is largely frozen and often covered with snow for the major part of the winter. It may be noted in this connection that the lowest Teesdale locality is at 2350' and the Scottish ones are at over 3000'. Manley (1942) commenting on the observations he made on Dun Fell (where there is a colony of M. alpestris) points out that in winter the temperature remains persistently below freezing point with a very small range.

Variation.

Biometrical studies in this species have been restricted to a comparison of the English (Teesdale) material and Scottish material. No attempt has been made to compare



Diagram

IV. 11. Corolla, calyx and leaf characters measured in Myosotis alpestris samples.

British and continental material because of the complicated situation mentioned earlier. As described in an earlier chapter M. alpestris is confined to three localities in Teesdale and a number of localities in Perth. From these, two populations in Teesdale have been sampled and two in Scotland. There appears to be little variation between populations in each area and there is no doubt that the conclusions drawn from these samples are applicable to the species as a whole in Britain. As well as field samples, families have been grown from seed produced from spontaneous self-pollination of plants from each area. These will be considered separately.

Field samples consisted of twenty five plants; the largest flower was picked and the corolla and calyx stuck on sellotape and the largest rosette leaf picked and pressed for measurement. The height of the plant was also measured. Corolla and calyx characters were measured using a microscope with low power objective and eyepiece and with a micrometer scale. Parts measured are as in diagram IV. 11. This also indicates the leaf characters measured.

Diagram IV. 12. shows a scatter diagram for corolla lobe length and corolla diameter. The Teesdale samples are significantly smaller in both characters. The results for

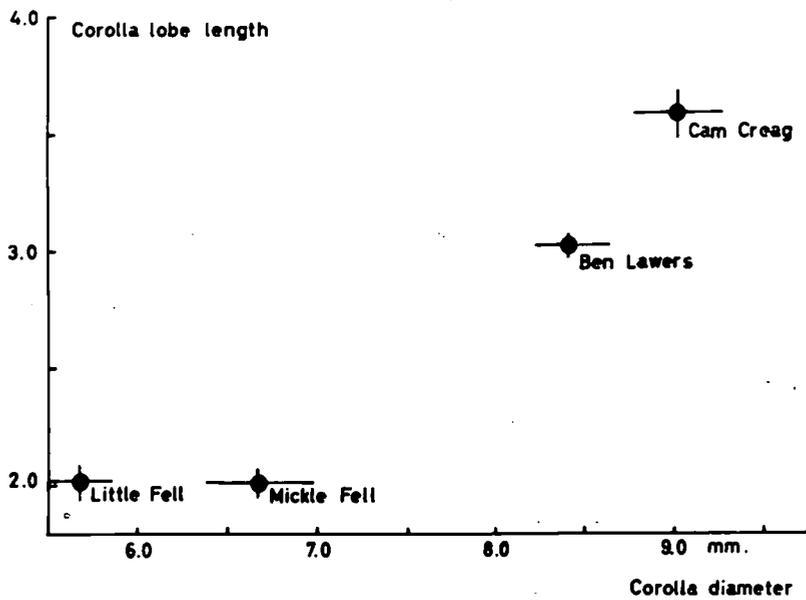


Diagram IV. 12. Scatter diagram of *Myosotis alpestris* corolla diameter and corolla lobe length means and standard errors of field samples.

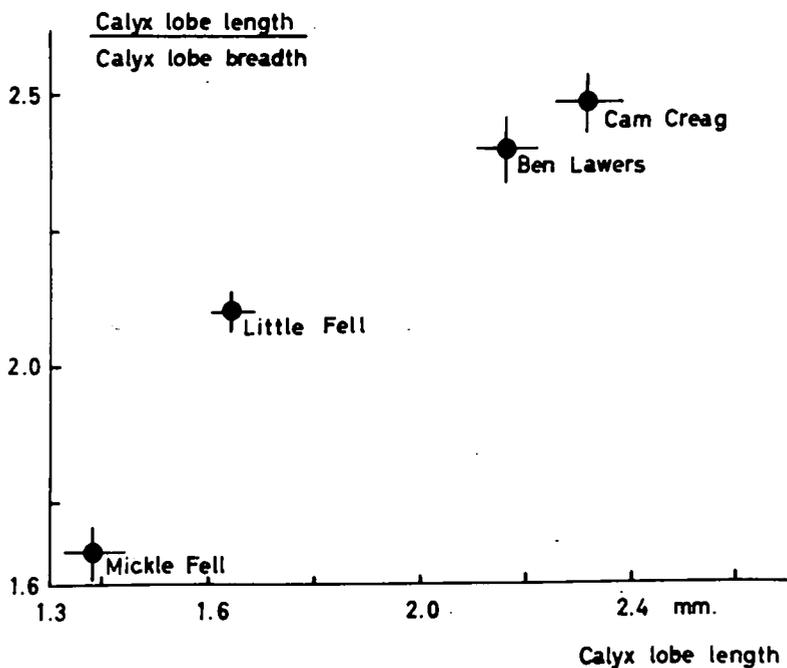


Diagram IV. 13. Scatter diagram of *Myosotis alpestris* calyx lobe length and calyx lobe length/ breadth ratio means and standard errors of field samples,

calyx lobe length and calyx lobe length/ breadth ratio are shown in diagram IV. 13, again the Teesdale samples are much smaller in both characters.

Leaf length and length/ breadth ratio means and standard errors are shown in diagram IV. 14. The Teesdale samples are composed of plants with smaller leaves than the plants in the Scottish samples. Means of the heights of the flowering plants have been added to diagram IV. 14; thus the Little Fell plants are much shorter than the Scottish plants.

Similar leaf measurements for the families grown from seed are shown in diagram IV. 15. It will be seen that the samples of Teesdale origin have smaller relatively wider leaves than the Scottish samples. The means of heights of the non-flowering plants show that the Teesdale ones are much shorter. Plate C shows two of the Teesdale families and the Scottish family, the Teesdale plants are relatively prostrate while the leaves of the Scottish plants are upright.

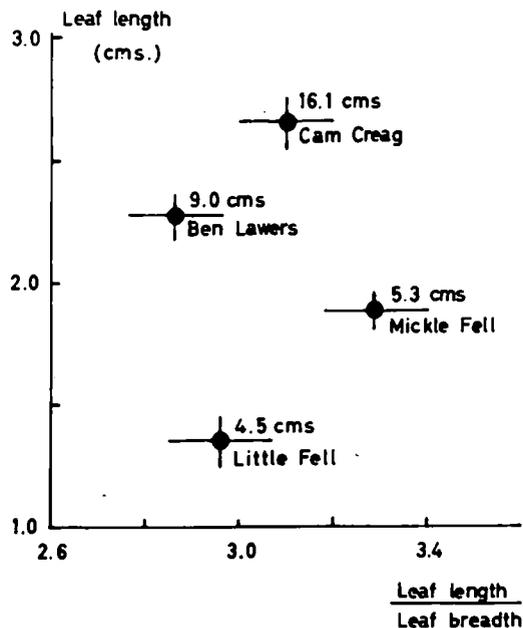


Diagram IV. 14. Scatter diagram of Myosotis alpestris leaf length and leaf length/ breadth means and standard errors of field samples. Means of flowering plant heights added.

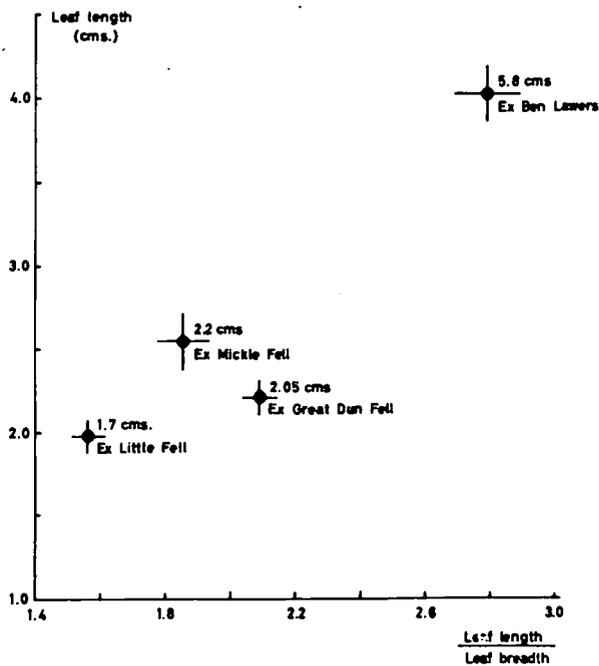


Diagram IV. 15. Scatter diagram of Myosotis alpestris leaf length and leaf length/ breadth means and standard errors of families grown from seed. Means of non-flowering plant heights added.



Plate C. Families of M. alpestris plants grown from seed from Little Fell and Great Dun Fell, Westmorland, and Ben Lawers, Perth.

Thus the Teesdale plants are short, prostrate leaved plants smaller in all parts than the Scottish ones which are larger, taller and more upright leaved.

As pointed out on p.40 chromosome counts have been carried out on plants from both areas and in both cases the number is $2n = 48$. Thus these differences are not due to a difference in ploidy.

The explanation for these genetically controlled size differences seems to lie in the ecology of the two races, described in detail on p. 140. The Teesdale populations grow in short, very heavily sheep grazed limestone grassland, while the Scottish plants are confined to mica schist rock ledges

inaccessible, or nearly so, to sheep. Hence in Teesdale small short prostrate leaved plants may be at a selective advantage, as both leaves and inflorescences will be less liable to damage. Since damage will be concentrated in the upper parts i.e. the inflorescences, it might be expected that selection pressure on these parts would be high. In Scotland however selection may tend to work in the opposite way, as in the rich ungrazed herb vegetation of the cliff ledges, small prostrate plants will tend to be shaded out. The Teesdale plant can thus be regarded as a biotic ecotype, which has developed in response to heavy sheep grazing.

Some work on ecotypic variation in M. sylvatica sensu lato has been carried out by Turesson (1925). He states that the mountain type in Scandinavia (in which the plants have an average height of 26 cms.) is similar, although not identical, to M. alpestris as found in the Alps. He concludes that the differences between the montane and the lowland types, which are mainly size differences, are genetically controlled, but does not come to a decision as to whether they are due to different directions of selection pressures within the populations, due to climatic differences, or to chance isolations.

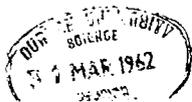
It is clear that the British populations of M. alpestris are again distinct from these forms. Thus, for example, the maximum height recorded in the Scottish plants is 23 cms. and the means of the two populations sampled were 16.1 and 9.0 cms.

It is unlikely that the differences in Britain are due to chance isolations and the explanation put forward, of differing selection pressures, seems much more probable.

Dryas octopetala L.

Description.

A much branched espalier- or under-shrub with stems generally up to 0.5 m. long, which are strongly dorsiventral and bear adventitious roots. Stems creeping with more or less two lines of leaves, except at the apices which are orthotropic and bear leaves all round. Stems green in their first year, developing reddish brown to blackish bark in the second year; with the leaf bases persistent. Leaves numerous with the petioles about as long as the blades. Blades oblong to oblong-ovate, cordate or truncate at base, widest in the middle, 1.5 to 2.5 times as long as broad, crenate dentate, sometimes revolute at the edges especially in plants from exposed situations. Leaves leathery, evergreen, dark green on the upper side, somewhat rugose with impressed veins,



usually glabrous but sometimes covered with white simple hairs (f. argentea (Blytt) Hultén). Undersides of leaves densely white tomentose with simple white hairs, sometimes with much larger yellow to brown multicellular hairs with white branches (in the following account known as branched hairs), and short golden stalked capitate glands, which may be borne both on the side veins and the main vein and petiole or may be confined to the main vein and petiole only. Stipules linear lanceolate, partially fused with the petiole, green at first, becoming brown and scarious, covered with white simple hairs. Pedicels solitary, 2 - 8 cms. long, erect, white tomentose hairy with also blackish glandular hairs above. Flowers usually 8 merous, but often 7 - 10 merous, or even more. Sepals oblong 4 - 8 mm. long acute to obtuse, tomentose, with blackish glandular hairs and the margins ciliate hairy. Hypanthium covered with purplish to black capitate glands. Petals oblong, white, 0.7 - 1.7 cms. long. Flowers typically hermaphrodite, but sometimes male staminate only with hairs on the receptacle. Stamens numerous. Carpels numerous, each with one ovule, styles terminal, increasing to 2 - 3 cms. at maturity, covered with white hairs and acting as a parachute for the achenes which are formed.

Taxonomy and Relationships.

Since the variation which has been studied bears on the classification and taxonomy of the genus a rather detailed account will be given.

The fullest classificatory system for the genus has been given by Juzepczuk (1929). In this paper the genus is divided into two sections, Nothodryas and Eudryas. The section Nothodryas is characterised as follows; leaves acute at the base, petals and sepals erect - spreading or quite erect, receptacle flattened. There are three species included here, D. Drummondii, D. tomentosa (usually reduced to a variety of the last now), and D. grandis. The first two are N. American and the third Siberian. D. Drummondii (including D. tomentosa) is a well defined species with yellow flowers, while D. grandis is thought by Hultén (1959) to be a very doubtful species, but very little material is available for study. None of the members of this group is relevant to the present study and will not be considered further.

The section Eudryas is characterised as follows:- leaves mostly rounded, truncate or subcordate at the base, petals and sepals spreading, receptacle convex. Juzepczuk has divided this section into three subsections. One of these, subsection Punctatae, is chiefly distinguished by the leaves

being punctate-glandular. Hultén (1959) has pointed out however that this is a variable character and in his opinion of little taxonomic value. The other two subsections are the Chamaedrifoliae, with the leaves crenate or dentate along their whole length and the lateral veins more or less deeply impressed, and the Tenellae with the leaves entire, dentate along the basal part only, or minutely crenulate along their whole length, the lateral veins not or little impressed. The main species included in the subsection Chamaedrifoliae is D. octopetala; together with a number of Russian and Asiatic taxa. The subsection Tenellae includes three species, according to Juzepczuk, D. integrifolia, D. chamissonis and D. crenulata. Porsild (1947) added another character to those used by Juzepczuk, i.e. the occurrence of branched hairs both on the main vein on the underside of the leaf, and also sometimes on the lateral veins. Such hairs are present in the Chamaedrifoliae, and absent in the Tenellae.

These hairs have also been described as 'minute, linear, pellucid, fringed scales' by Babington (1842, 1862) and as 'octopetala scales' by Hultén (1959). In this account they will be called branched hairs following Juzepczuk (1929, 1941) and Porsild (1947, 1958). It may be pointed out that although Juzepczuk was aware of the presence of branched hairs and used them in his species diagnoses, it was Porsild who made

them a subsectional character. It follows that a specimen without branched hairs should be placed, according to Porsild, in the subsection Tenellae. Moreover this treatment has been given to specimens which are crenate along the whole length of the leaves, since Juzepczuk, although using the degree of crenation as an important character in the differentiation of these two subsections, has placed one species, D. Chamissonis in the Tenellae, although according to him it may sometimes have completely crenated leaves. Following this lead Porsild (1958) has described a new Dryas species, D. Babingtoniana which is based on British material; this is entirely crenately leaved as is all British Dryas material and differs only in not bearing branched hairs. It should thus, according to Porsild, not only be placed in another species from D. octopetala, but should be placed in the subsection Tenellae and not in the Chamaedrifoliae. The wisdom of these decisions will be questioned in later discussion.

General Biology.

In Teesdale D. octopetala flowers very irregularly, some years apparently producing no flowers at all, whereas in others abundant flowering is said to take place. In the last three years (1959-1961) very few flowers have been observed. In these three years no seed has been seen at all and this is undoubtedly due to sheep grazing, the mat of D. octopetala

being very closely grazed so that anything projecting above the surface has a very small chance of survival. Because of this, there is little chance that D. octopetala in Teesdale can extend its range; and it appears at present to be completely stationary in the area where it was first recorded at the end of the eighteenth century. In this connection, Kihlman (1890) records finding a plant over 108 years old in Lapland and Schroeter (1904), one of over 50 years old in the Alps.

In Scotland and Ireland good flowering and seed production takes place in at least some localities; the main flowering season in Scotland is in June, with some flowers in May and July. In Ireland the maximum is somewhat earlier, in the latter part of May.

The flowers appear to be more or less homogamous in Britain; they are visited by insects for the nectar which is secreted by a ring inside the stamens, and thus may be cross-pollinated. Self-pollination can easily take place, however, since anthers and styles are close together and at the same level. Experiments in an insect-proof greenhouse have shown that well-filled seeds are produced by self-pollination and these are capable of germinating, so that the species is self compatible.

Seed production has been counted in flowers from a number of localities, and the results are given in table IV. 20.

Locality	No. flowers	Mean Seed No.
Tungaa R., Iceland	5	58
Gemmi Pass, Valais, Switzerland	2	52
Ben Lui, Perth, Scotland	3	62
Knockan, Sutherland, Scotland	3	64
Rannagh, Co. Clare, Ireland	3	66

Table IV. 20. Mean seed numbers in D. octopetala.

These counts seem to be representative of the general situation, and show little variation in the seed production per flower.

Germination has been studied under greenhouse conditions. Seed was sown in November in John Innes seedling compost and kept in a cold greenhouse for the winter so that frosting took place. This appears to be necessary since no seed was found to germinate when kept in a warm greenhouse. Germination took place mainly in April and May. Typical results for seed collected in the wild are shown in table IV. 21.

Locality	No. of seeds		% germination
	Sown	germinated	
Black Head, Co. Clare	100	30	30
	100	22	22
	100	35	35
	100	29	29
Inchnadamph, Sutherland	46	3	7
	59	38	64
Durness, Sutherland	26	4	15
Bettyhill, Sutherland	118	60	51
	49	10	20
	38	23	61
	50	28	56

Table IV. 21. Germination rates of D. octopetala seed.

The results show a substantial but rather variable germination rate. Some of the lower germination rates may be due to the seed not being completely mature when collected.

The seedlings are slow growing, they reach a maximum of c. 6 cms. in diameter at the end of their first year and are frequently much smaller. Flowering does not seem to take place until at least the third year. This has meant that the study of variation has had to be made largely on field material.

As Jessen (1921) points out there is little vegetative reproduction, although it may occasionally take place through decay of old stems, the younger parts having rooted adventitiously.

Variation.

Introduction.

Most of the results on variation in vegetative characters have been obtained from field samples. Each sample has consisted, wherever possible, of 25 branches collected at random in a population, at a sufficient distance apart to minimize the risk of collecting two pieces from the same plant. Some samples which have been sent to me have consisted of rather less than 25 pieces.

The main characters which have been investigated, are all leaf characters. Leaf length and breadth have been measured and means and standard errors calculated; a measure of the amount of crenation has also been made. The branched hair and gland characters have been scored into classes of presence since some populations are polymorphic in these respects.

It has not been possible to carry out any detailed work on floral characters because many of the populations were not in flower when they were visited, and flowering in cultivated plants was poor.

Locality	Sample No.	Quadrat No.
Cronkley Fell, N. Yorks	1	48
Glyder Fawr, Caernarvon	2	83
Cowside Beck, Arncliffe, N. Yorks	3	82
Yew Cogar Scar, Arncliffe, N. Yorks	3a	81
Caenlochan Glen, Angus	4	54
Creag an Lochan, Perth	5	53
Ben Lui, Perth	6	51
Knockan, Sutherland	7	-
Loch Mhaoloch-coire, Inchnadamph, Sutherland	8	65
R. Tralagill, " "	9	67
Durness, Sutherland	10	66
Bettyhill (dune), Sutherland	11	79
Bettyhill (grassland), Sutherland	12	75
Creag na Bruaich, Raasay	13	71
S. Screapadal, Raasay	14	72
Druim an Aonaich, Raasay	15	73
Rubha na Leac, Raasay	16	74
Black Head, Co. Clare	17	78
Croagh, Co. Clare	18	77
Rannagh, Co. Clare	19	76
<u>France</u>		
Ayere des Perrieres, nr. Sallanches, Haute Savoie	20	
Le Leutellet nr. Megève, Haute Savoie	21	86
Lanche dur Pra, nr. Sallanches, Haute Savoie	22	88
Col du Lauteret, Hautes Alpes	23	
Tinee Valley, nr. Nice, Alpes Maritimes	24	
<u>Austria</u>		
Radstadter Tavern Pass, Salzburg	25	
<u>Italy</u>		
Sassolunga, Val Gardena, Dolomites	34	

Locality	Sample No.	Quadrat No.
<u>Switzerland</u>		
Gemmi Pass, nr. Leukerbad, Valais	26	84
Clavinenalp, " " "	27	89
Chermignon, " " "	28	85
Bella Lui, nr. Crans, Valais	29	
Bourg St, Pierre, Valais	30	
Combe de là, E. Aspect, Valais	31	
Combe de là, Valais	32	
Zermatt, Valais	33	
<u>Norway</u>		
Tana Head, Finnmark	35	
Varanger Peninsula, Finnmark	36	
Kistrand Head, Finnmark	37	
Sørdal, Troms, Finnmark	38	
Kongsvoll, Dovrefjell, Sor-Trondelag	39	
Memurelo	40	
Alta	41	
<u>Sweden</u>		
Abisko, railway bank.	42	
Foot of Njulja, nr. Abisko	43	
N. side " " "	44	
Vassijaure, nr. Abisko	45	
Laktatjakko, " "	46	
<u>Finland</u>		
Kiutakongas, Kuusamo prov.	47	
<u>Iceland</u>		
Hveravellir	48	
Tungaa River	49	
<u>Spitzbergen</u>		
King's Bay	50	

Table IV. 22. Localities and numbers of D.octopetala samples.

Localities of the samples which have been used are given in ^Ttable IV. 22.

Leaf size and shape. For the measurements of the length and length/ breadth ratio of the leaves the two largest leaves from each branch have been measured; these have then been averaged and the resultant figures used to calculate the means and standard errors. These are given in ^Ttable IV. 23, which has been split into the three parts comprising the results from Britain, Scandinavia and the Alps respectively. An examination of the leaf measurements shows that there is a great deal of variability. The Cronkley Fell, Teesdale population has the smallest leaves of any sample measured and it is nearest in shape and length to the samples from Kistrand Head, Arctic Norway and from Spitzbergen and thus closely resembles these arctic types, as was pointed out by Pigott (1956). The locality on Cronkley Fell is a small plateau of metamorphosed (sugar) limestone which is likely to be very exposed in the winter, since the ground drops away towards the West, and the plateau will probably tend to be blown clear of snow. It is interesting to note that the only other place in Britain where leaves approaching the same size have been found is on the Cairnwell, Perth, where the species grows on a windswept saddle, also on metamorphosed limestone.

Sample No.	Length mean	S.E.	Length/breadth mean	S.E.	Crenations per cm.
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British Isles.

1	0.86	± .028	2.02	± .047	7.5
2	1.25	.041	1.63	.024	5.0
3	1.47	.056	2.14	.043	5.2
4	1.67	.057	1.98	.041	4.3
5	1.38	.047	1.62	.027	4.6
6	1.41	.054	1.58	.037	4.5
7	1.14	.033	1.87	.047	5.8
8	1.29	.033	1.76	.025	5.1
9	1.33	.044	1.87	.031	5.4
10	1.12	.034	1.76	.033	6.2
11	1.21	.033	1.81	.035	6.1
12	1.02	.030	1.94	.044	6.8
13	1.68	.057	1.82	.035	4.2
14	1.20	.045	1.68	.040	5.2
15	1.56	.045	1.86	.039	4.6
16	1.43	.055	1.91	.053	5.0
17	1.52	.038	1.88	.038	4.9
18	1.39	.044	2.10	.053	5.5
19	1.49	.047	1.86	.032	5.0

Table IV. 23.

Sample No.	Length mean	S.E.	Length/breadth mean	S.E.	Crenations per cm.
<u>Alps.</u>					
<u>France.</u>					
20	1.75	± .049	1.96	± .040	4.9
21	1.55	.059	1.88	.046	5.1
22	1.78	.065	1.98	.054	4.6
23	1.86	.054	1.93	.040	4.2
24	1.52	.061	2.05	.056	5.6
<u>Austria.</u>					
25	1.17	.055	1.80	.035	5.2
<u>Switzerland.</u>					
26	1.25	.027	1.93	.033	5.6
27	1.74	.047	1.91	.029	4.4
28	1.60	.044	2.06	.032	4.9
29	1.40	.024	1.98	.026	5.3
30	1.90	.087	1.98	.031	4.1
31	1.70	.059	1.88	.036	4.6
32	1.95	.059	1.97	.034	4.3
33	2.68	.088	2.01	.046	3.3
<u>Italy.</u>					
34	1.47	.053	2.27	.047	5.0

Table IV. 23..

Sample No.	Length mean	S.E.	Length/breadth mean	S.E.	Crenations per cm.
<u>N. Europe.</u>					
<u>Norway.</u>					
35	1.24	± .045	2.23	± .046	6.3
36	1.32	.039	2.19	.025	5.8
37	0.92	.030	2.04	.043	7.1
38	1.52	.057	1.86	.045	4.7
39	1.53	.050	2.40	.104	5.1
40	1.39	.039	1.99	.051	5.6
41	2.02	.047	2.44	.048	4.4
<u>Sweden.</u>					
42	1.15	.040	2.07	.059	6.5
43	1.50	.044	2.15	.053	5.5
44	1.38	.047	2.06	.048	5.7
45	1.26	.047	1.87	.047	5.7
46	0.88	.029	1.79	.041	7.1
<u>Finland.</u>					
47	1.83	.125	2.65	.053	5.5
<u>Iceland.</u>					
48	1.27	.035	2.00	.032	5.7
49	1.44	.053	1.88	.041	5.0
<u>Spitzbergen.</u>					
50	1.00	.030	2.05	.051	6.7

Table IV. 23. Means and standard errors of leaf length and length/breadth ratio and mean number of crenations per cm. in samples of D. octopetala.

These dwarfed plants, in which the leaves are also very revolute, have been known and named for a considerable time. Thus Hooker (1824) examining material from Spitzbergen described it as var. minor with leaves 'parvis angustis profunde crenatis'. Nøto (1902) has also recognised small dwarfed plants from N. Norway and has separated them as var. minima, with leaves c. 5 mm. long.

In Britain the most similar populations to the Teesdale one, in respect of leaf size, which have been sampled, are from Sutherland, at Bettyhill, Knockan and Durness. The large leaved populations in Scotland are mainly found along the central Scottish mica schist belt from Glen Clova, Angus in the East to near Ballachulish, Argyll in the West. The samples from Caenlochan Glen, Angus; Creag an Lochan, Perth; and Ben Lui, Perth are characteristic of these. Large leaved populations are also found in the Hebrides as some of the samples from Raasay show. The samples from W. Ireland are also fairly large leaved, as is the sample from Cowside Beck, Arncliffe, N. Yorks, which is from a grassland community also on Carboniferous limestone, and which shows a 50 % floristic similarity with one of the W. Irish sites (no. 76, Rannagh, Co. Clare.).

It is impossible to comment in detail on most of the continental sites since I have not seen them personally. Of those visited the smallest leaved populations, from the Gemmi Pass and Bella Lui, both in the Valais, Switzerland were from the highest altitudes and the most severe climatic conditions. At the other extreme is the population from near Zermatt, Valais, Switzerland from a sheltered clearing in coniferous forest, where the leaves are more than three times as long as those from Teesdale plants.

It seems probable that, in general, leaf size is correlated with climatic and exposure factors, but the microclimate is apparently often as important as the macroclimate in this respect, and careful meteorological and microclimatic data would be necessary to establish a true correlation. There is also the possibility that edaphic factors may have an influence on leaf size.

Apart from these detailed correlations there also appears to be a more general regional differentiation, in both length and length/ breadth ratio, between British, Central European and North European samples. This is shown by the group means given in table IV. 24.

	Length	Length/ Breadth ratio
Britain	1.34	1.85
Central Europe	1.69	1.97
North Europe	1.35	2.10

Table IV. 24. Regional group means for leaf length and length/ breadth ratio in Dryas octopetala.

The combination of these characters clearly separates these three groups.

Plants which have been brought back from a number of the populations have been grown in pots at Durham in John Innes compost to gain information on whether the size differences are genetic in origin or not. Samples, consisting of the two largest leaves, have been removed once a year and three years records are available for most of the plants.

The results for leaf length are given in table IV. 25. together with the means and standard errors for the samples collected from the same populations as the plants grown at Durham.

In most cases leaf length has increased over the three years. A number of plants however have shown a decrease in leaf length or have not changed.

The plants from Cronkley Fell, Teesdale have all increased in leaf length except one which was collected in

Sample No.	Locality	Field population sample mean & S.E.	Plant	1959	1960	1961
			Code No.			
1	Cronkley Fell, N. Yorks	0.86 [±] .028	E1	0.70	0.75	0.95
			E2	0.80	0.80	1.02
			E3	0.60	1.10	1.10
			E4	-	0.90	1.27
			E5	-	0.87	1.15
			E6	-	1.12	1.10
6	Ben Lui, Perth	1.41 [±] .054	H2	1.17	1.02	1.65
			H3	1.52	1.40	1.65
7	Knockan, Sutherland	1.14 [±] .033	I1	1.05	1.05	1.40
			I2	0.90	0.92	1.20
			I3	0.75	0.75	0.75
8	Loch Mhaolach- coire, Inchnadamph	1.29 [±] .033	K1	0.77	0.67	0.90
			K2	0.85	-	0.77
9	R. Tralagill, Inchnadamph	1.33 [±] .044	J1	1.32	1.07	1.65
			J3	1.00	1.15	1.75
			J4	0.70	0.90	1.45
10	Durness, Sutherland	1.12 [±] .034	L1	0.77	0.65	1.45
			L2	0.87	-	0.92
			L3	0.85	1.05	1.30
			L4	1.02	1.27	1.42

Table IV. 25.

Sample No.	Locality	Field population sample mean & S.E.	Plant			
			Code No.	1959	1960	1961
11	Bettyhill (dune), Sutherland	1.21 [±] .033	M1	1.25	1.17	1.25
			M2	0.95	1.05	1.25
			M3	1.17	1.07	1.30
12	Bettyhill (grassland), Sutherland	1.02 [±] .030	N1	-	1.32	1.40
			N2	0.95	0.95	1.42
			N3	0.87	0.90	1.55
			N4	0.85	1.10	1.30
17	Black Head, Co. Clare	1.52 [±] .038	C1	1.45	1.75	1.90
			C2	1.42	1.62	2.45
			C3	1.87	1.45	1.55
19	Rannagh, Co. Clare	1.49 [±] .047	D1	0.92	1.05	1.70
			D2	1.02	1.30	1.32

Table IV. 25. Leaf length measurements in cultivated plants of D. octopetala.

1960 and shows a 2 % decrease from then to 1961. The increases are rather variable, the final figures being from 27 to 83 % larger than the originals. They have, however, never increased to a size comparable with the plants collected from Ben Lui, Perth (H2 and H3). These, although becoming smaller in 1960 became larger leaved again in 1961 so that in H2 there was an overall length increase of 41 % and in H3 one of 9 %. In both cases the lengths in 1961 are larger than the population sample mean.

The sample mean of the Knockan, Sutherland population indicates an intermediate leaf size to these two populations. Two of the plants were intermediate in 1959 and although they have both increased in leaf length over the three years in cultivation the recorded measurements in 1961 are still intermediate to those from Cronkley Fell and Ben Lui plants made in the same year. One plant (I3) has remained identical in leaf length throughout the three years.

Although the sample mean from the population at Loch Mhaolach-coire, Inchnadamph, Sutherland is somewhat larger than that from Knockan, the two plants collected were much shorter leaved in the year of their collection (1959) and they have remained so throughout the next two years, one plant having shown a length increase of 17 % and the other a further

decrease of 9 %. The population from R. Tralagill, Inchnadamph although having a similar sample mean includes plants showing a rather different behaviour; of the three grown one had a similar leaf length in 1959 while the other two were smaller and J4 in fact had as small a leaf length as some of the Teesdale plants. They have all increased to approximately the same size in 1961 however, so that J1 shows an average increase of 25 % while J4 shows one of 107 %. Dwarfing here is obviously a phenotypic effect.

The figures for plants from Durness and Bettyhill (dune community), Sutherland, show that increase in length is somewhat irregular; in the plants from Bettyhill this has meant that the final lengths are very close to one another; the differences recorded in 1959 for the plants from Durness have however, been accentuated in the three years of cultivation. As in the plants from the dune community at Bettyhill, those from the grassland community have increased in leaf size until they are all fairly close to one another and here, while the values recorded in 1959 are lower than the wild sample means, the increase in length has resulted in leaves considerably larger than these.

The results from Black Head, Co. Clare show that the plants were large leaved when collected as was the natural population and this feature has been maintained in successive

years. The plants collected from Rannagh, Co. Clare were rather small leaved in 1959, compared with the sample mean, but have increased in leaf length so that the leaf size in 1961 is comparable with this.

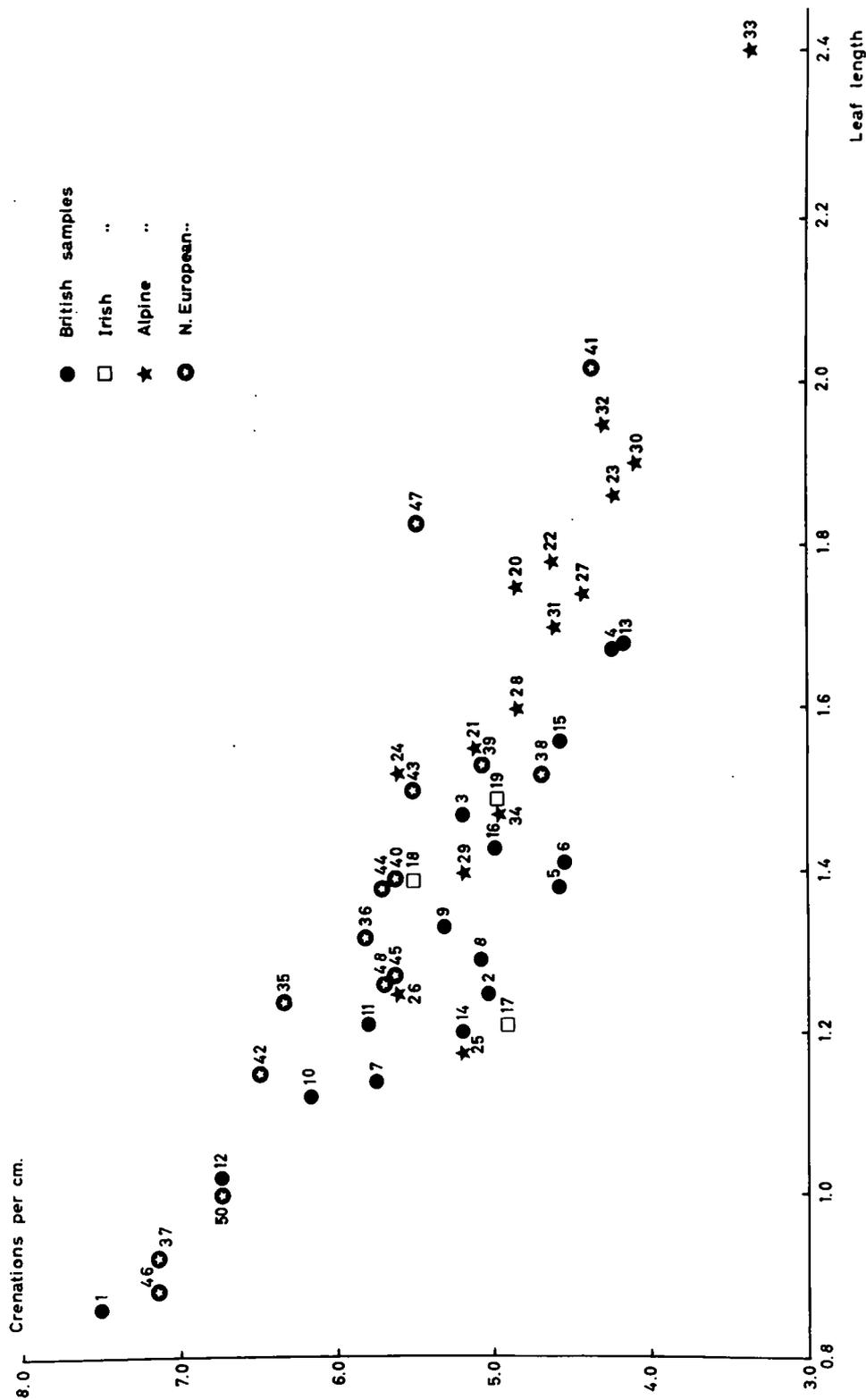
These results are rather variable, but show that in some populations at least size differences in the leaves are maintained although the absolute size may increase. This is particularly true of plants from Cronkley Fell, Teesdale; Ben Lui, Perth; Knockan, Sutherland and Black Head and Rannagh, Co. Clare. The other plants from Sutherland are more variable in their behaviour and small leaf size in some of these seems to be a phenotypic effect. In the above mentioned localities at least though, leaf size variation appears to have a genotypic origin. Plate D shows plants from a number of areas, which have been grown at Durham, and which have retained differences in leaf size.



Plate D. D. octopetala plants from Black Head, Co. Clare; Durness, Sutherland; Caenlochan Glen, Angus; Ben Lui, Perthshire; and Cronkley Fell, Teesdale, after cultivation at Durham for two years, showing differences in leaf size.

Conclusive proof as to whether the leaf variation in D. octopetala is genotypic or not can only be gained from plants grown from seed. This has not been possible due to the slow growth of the seedlings.

The cultivation experiments give evidence however that at least some of the size variation described is ecotypic and



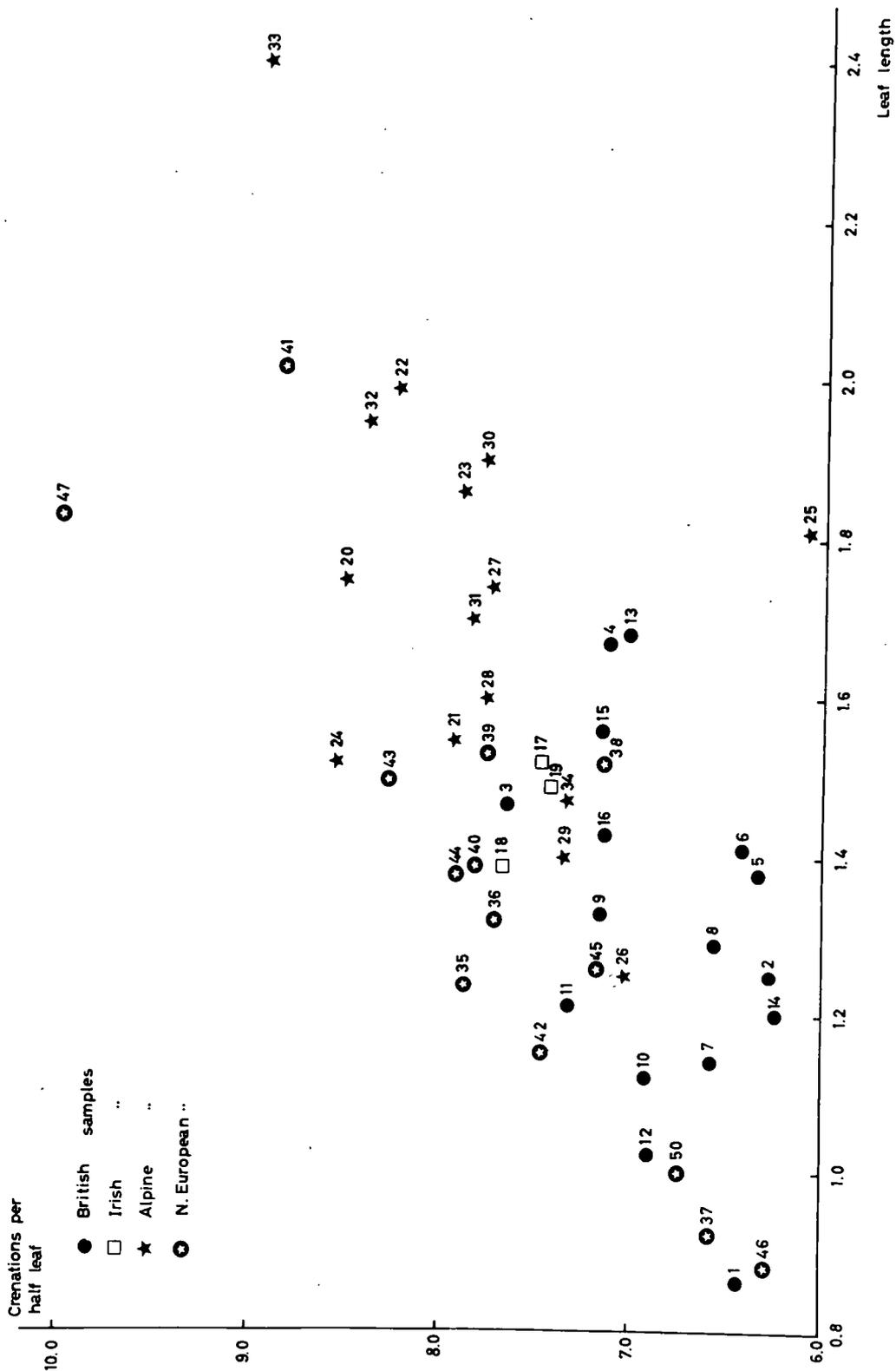
Diagram

IV. 16. Scatter diagram of mean number of crenations per cm. of leaf and mean leaf length in samples of D. octopetala.

this is especially so of the Teesdale population. Here a small leaved type seems to have been selected out in response to the exposed conditions. A similar response has taken place on the Cairnwell, Perth, although it is not known if small size here is genotypic.

Similar measurements have been made for leaf length/breadth ratio, but no conclusive results have been obtained. This is probably due to the much smaller variability in the British populations in this respect and also the fact that the samples from the plants were, of necessity, rather small.

The amount of crenation has been studied in all the population samples and the mean number of crenations per cm. is given in table IV. 23. The samples have also been plotted on a scatter diagram of mean number of crenations per cm. against mean leaf length; this is given in diagram IV. 16. It will be seen that there is a relation between the two and that the smaller leaves have more crenations per cm. than the larger ones. The effect is that the smaller leaves appear to have many small crenations whereas the larger ones have fewer much larger crenations. The number of crenations per half leaf is plotted against leaf length in diagram IV. 17. There is general correlation for most samples between leaf length and number of crenations, but two samples in particular diverge



Diagram

IV. 17. Scatter diagram of mean number of crenations per half leaf and mean leaf length in samples of D. octopetala.

very considerably from this. These are the samples from Radstadter ^uTavern Pass, Austria (no. 25) with a mean of 6.1 crenations per half leaf and from Kiutakongas, Finland (no. 47) with a mean of 10.1. Both samples have a very similar leaf length. However all the other Central and North European samples seem to follow the general correlation of number of crenations to leaf length so that there are no simple geographical correlations. It can be noted however that the sample means of crenations per cm. from Kistrand Head, Norway (no. 37) and Spitzbergen (no. 50) are close to the Teesdale (no. 1) value, and the figures for absolute numbers of crenations are also very similar.

Leaf hair and gland characters. Since the presence or absence of branched hairs has been used as an important diagnostic character all the samples have been scored for these. At the same time they have been scored for the presence of small capitate glands which also occur on the main and lateral veins on the undersides of the leaves. It should be noted that these are smaller than those used by Hultén (1959) in his species diagnoses and are not thought by him to be similar (pers. comm.). Each character has been scored into four classes of presence; since both of them are somewhat variable in their distribution from leaf to leaf the

classes have had to be defined in rather general terms.

Classes for branched hairs.

1. Branched hairs present on all leaves, some leaves at least with branched hairs on the lateral veins also.
2. Branched hairs present on all leaves, but confined to the main veins.
3. Branched hairs present on some leaves, but not on all.
4. No leaves with branched hairs.

Classes for capitate glands.

1. Glands present on all leaves and numerous on at least some leaves.
2. Glands present on all leaves, but never numerous.
3. Glands present on some leaves, but not on all.
4. No leaves with capitate glands.

Before the results are described and discussed the evidence for believing that the presence or absence of branched hairs and capitate glands is genetically controlled will be discussed. Two sets of data are available; those collected from plants in cultivation, and those from two samples from one population in Scotland collected in different years. Records have been kept of 38 plants collected from 14 localities (12 British and 2 Norwegian) and grown in the garden at Durham from 1959,

when they were collected, to 1961. In this time no plants have lost their branched hairs, if they had them in the wild condition, or grown them if they lacked them when collected. Also all plants with branched hairs had capitate glands when first examined in 1959, and all those with branched hairs in 1961 also had capitate glands. No plants without branched hairs had developed capitate glands. These data indicate that presence and absence of these characters remains stable over several years, so that their expression is probably genetically controlled.

In the other approach data have been collected from the population at Creag an Lochan, Perth in 1959 and 1961; the results are compared in table IV. 26.

	Branched hair classes.				Capitate gland classes.			
	1	2	3	4	1	2	3	4
1959	17	60	23	-	-	-	70	30
1961	92	8	-	-	-	16	84	-

Table IV. 26. Percentage composition of D. octopetala population from Creag an Lochan, Perth with respect to branched hairs and capitate gland.

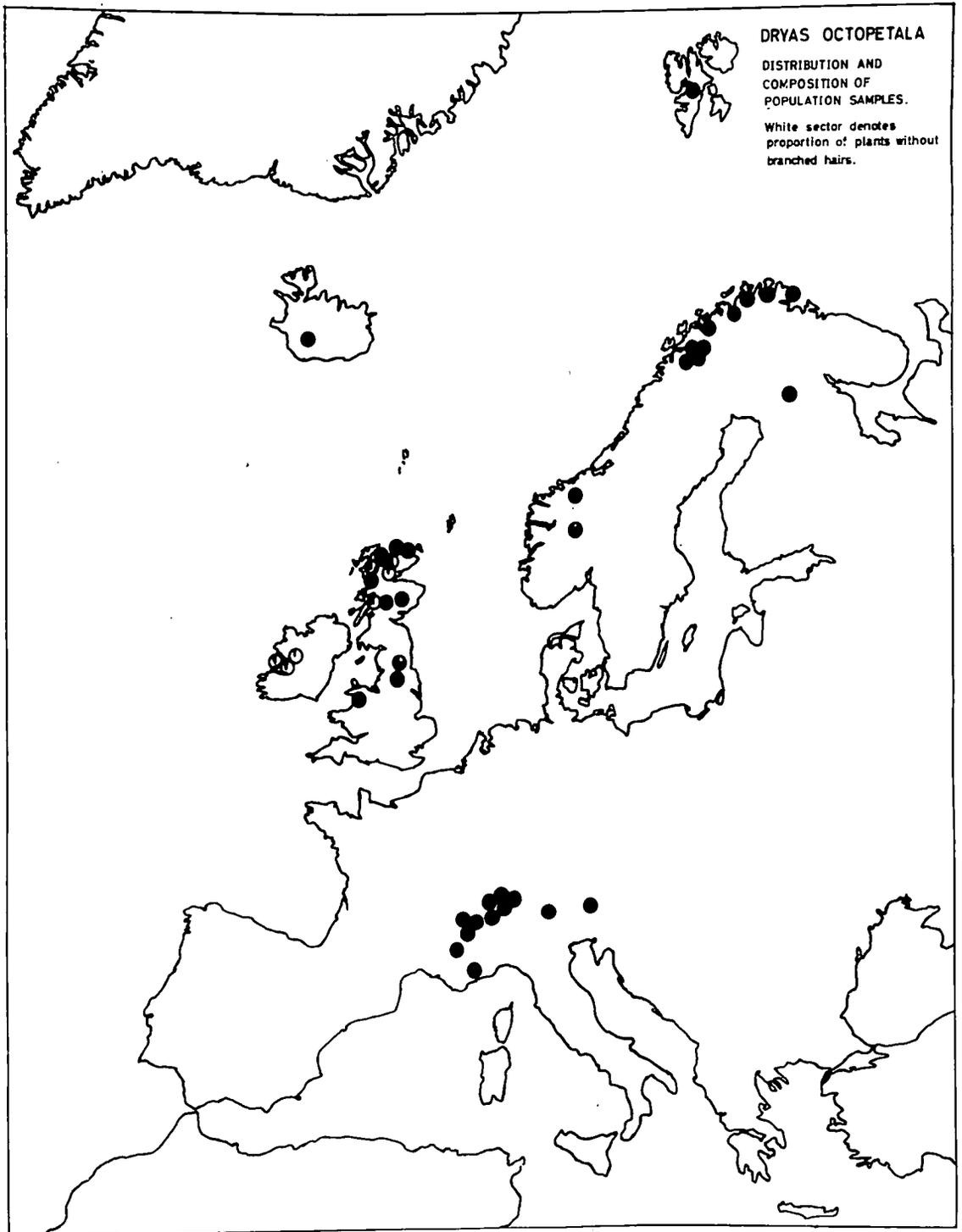
The detailed distribution has changed, but the general situation is similar. Many more of the plants in 1961 have branched hairs on the lateral veins, but there are still no plants without branched hairs; the major proportion still have glands on some leaves, but none were found to be completely lacking glands in 1961 and some specimens appeared to bear them on all leaves. Thus so far as the presence of branched hairs is concerned the two samples give very similar results, also indicating a stable situation which is probably due to genetic control of the character. Much more variation is shown in the presence of capitate glands. The reasons for this are not clear. The cultivation experiments indicate that their presence is genetically controlled, but it is possible that their expression may be modified by other factors. When wild plants are examined the numbers of capitate glands often varies greatly from leaf to leaf possibly indicating that the time of year that the leaves are produced has an influence on the number of glands produced; the state of maturity of the leaf may also be important in this respect. Their production is, however, linked to that of the branched hairs; plants which are without branched hairs never bear capitate glands.

Attempts have been made to gain information on the genetic control of these characters by studying families, each

of which has been grown from seed from one flower head. However it has not been possible yet to do this as it appears that, due to the slow growth of the seedlings, they only become mature enough for reliable scoring when they are several years old. Thus a family of 51 seedlings (seed from Bettyhill, Sutherland) scored on 23. 11. 60 had three plants (6 %) with branched hairs, none of which had capitate glands. When scored again on 15. 8. 61, of the 41 surviving plants, 23 (55 %) now had branched hairs, although there were still none with capitate glands.

The results which have been gained from the field samples are presented in table IV. 27. This has been divided into three parts comprising the British, Central European (Alpine), and North European samples respectively. The number of specimens in the samples is variable, as mentioned before, so that the class representations are also presented as percentages for comparative purposes. A map giving the positions and compositions of the populations with respect to presence and absence of branched hairs is given in diagram IV. 18. From the table and map it will be clear that by far the greatest variation recorded is in Britain.

The general pattern of variation in Britain is complicated. In Wales, where one of the only two known populations



Diagram

IV. 18. Map showing distribution of D. octopetala samples and indicating composition of samples with respect to presence or absence of branched hairs.

Sample	No. of plants	Branched hairs								Capitate Glands							
		Numbers				Percentages				Numbers				Percentages			
		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
<u>British Isles.</u>																	
1	25	12	8	-	5	48	32	-	20	-	8	11	6	-	32	44	24
2	25	25	-	-	-	100	-	-	-	20	5	-	-	80	20	-	-
3	25	24	1	-	-	96	4	-	-	7	7	10	1	28	28	40	4
3a	6	6	-	-	-	100	-	-	-	-	2	2	2	-	33	33	33
4	27	21	4	2	-	78	15	7	-	2	14	10	1	7	52	37	4
5	30	5	18	7	-	17	60	23	-	-	-	21	9	-	-	70	30
6	27	2	4	2	19	7	15	7	71	-	2	6	19	-	8	22	70
7	26	-	-	1	25	-	-	4	96	-	-	1	25	-	-	4	96
8	29	11	2	2	14	38	7	7	48	1	1	9	18	3	3	31	63
9	26	24	1	-	1	92	4	-	4	3	5	17	1	12	19	65	4
10	30	19	11	-	-	63	37	-	-	3	8	19	-	10	27	63	-
11	27	16	10	1	-	59	37	4	-	9	7	11	-	33	26	41	-
12	25	9	10	5	1	36	40	20	4	3	3	18	1	12	12	72	4
13	25	3	-	-	22	12	-	-	88	-	2	1	22	-	8	4	88
14	25	4	-	2	19	16	-	8	76	-	3	3	19	-	12	12	76
15	25	2	-	-	23	8	-	-	92	-	1	1	23	-	4	4	92
16	23	18	2	2	1	78	9	9	4	3	12	7	1	13	52	30	5
<u>Ireland.</u>																	
17	24	1	-	1	22	4	-	4	92	-	1	1	22	-	4	4	92
18	27	-	-	1	26	-	-	4	96	-	-	1	26	-	-	4	96
19	25	2	-	-	23	8	-	-	92	-	1	1	23	-	4	4	92

Table IV. 27.

Sample of plants	No.	<u>Branched hairs</u>								<u>Capitate Glands</u>							
		Numbers				Percentages				Numbers				Percentages			
		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
<u>Alps.</u>																	
<u>France.</u>																	
20	25	25	-	-	-	100	-	-	-	18	7	-	-	72	28	-	-
21	25	25	-	-	-	100	-	-	-	12	13	-	-	48	52	-	-
22	24	24	-	-	-	100	-	-	-	12	12	-	-	50	50	-	-
23	27	25	2	-	-	93	7	-	-	1	11	14	1	4	40	52	4
24	18	17	1	-	-	94	6	-	-	3	12	3	-	17	66	17	-
<u>Austria.</u>																	
25	18	8	10	-	-	44	56	-	-	-	4	8	6	-	22	44	34
<u>Switzerland.</u>																	
26	24	23	1	-	-	96	4	-	-	10	12	2	-	42	50	8	-
27	23	23	-	-	-	100	-	-	-	16	7	-	-	70	30	-	-
28	25	25	-	-	-	100	-	-	-	11	14	-	-	44	56	-	-
29	25	25	-	-	-	100	-	-	-	13	12	-	-	52	48	-	-
30	25	24	1	-	-	96	4	-	-	-	13	12	-	-	52	48	-
31	25	23	-	-	2	92	-	-	8	11	8	2	2	44	32	8	8
32	25	25	-	-	-	100	-	-	-	13	11	1	-	52	44	4	-
33	25	25	-	-	-	100	-	-	-	1	15	9	-	4	60	36	-
<u>Italy.</u>																	
34	34	25	-	-	-	100	-	-	-	-	18	7	-	-	72	28	-

Table IV. 27.

Sample of plants	No.	Branched hairs								Capitate Glands							
		Numbers				Percentages				Numbers				Percentages			
		2	3	4		1	2	3	4	1	2	3	4	1	2	3	4
<u>N. Europe.</u>																	
<u>Norway.</u>																	
35	25	18	7	-	-	72	28	-	-	-	-	8	17	-	-	32	68
36	24	16	7	1	-	67	29	4	-	-	1	7	16	-	4	29	67
37	25	8	15	2	-	32	60	8	-	-	-	3	22	-	-	12	88
38	20	18	2	-	-	90	10	-	-	-	9	9	2	-	45	45	10
39	10	4	6	-	-	40	60	-	-	-	2	6	2	-	20	60	20
40	25	13	7	2	3	52	28	8	12	-	5	13	7	-	20	52	28
41	25	25	-	-	-	100	-	-	-	-	6	13	6	-	24	52	24
<u>Sweden.</u>																	
42	23	15	7	1	-	65	30	5	-	-	5	13	5	-	22	56	22
43	25	25	-	-	-	100	-	-	-	2	15	8	-	8	60	32	-
44	25	22	3	-	-	88	12	-	-	3	12	9	1	12	48	36	4
45	24	24	-	-	-	100	-	-	-	11	12	1	-	46	50	4	-
46	29	26	2	1	-	90	7	3	-	-	9	17	3	-	31	59	10
<u>Finland.</u>																	
47	19	18	1	-	-	95	5	-	-	4	8	7	-	21	42	37	-
<u>Iceland.</u>																	
48	25	24	1	-	-	96	4	-	-	9	11	5	-	36	44	20	-
49	19	19	-	-	-	100	-	-	-	-	15	4	-	-	79	21	-
<u>Spitzbergen.</u>																	
50	19	19	-	-	-	100	-	-	-	-	15	4	-	-	79	21	-

Table IV. 27. Class representation of branched hair and capitate gland characters in D. octopetala samples, in terms of numbers of plants and percentage composition.

was sampled, all the plants had branched hairs and glands, and appeared similar in this respect to the majority of the continental populations. In England three populations from two localities were scored. Those in Littondale, near Arncliffe, N. Yorks all have branched hairs although some specimens without glands were recorded. In Teesdale the only population, on Cronkley Fell, is mixed with respect to both branched hairs and glands. In Scotland there is a large amount of variation as will be seen from table IV. 26. Thus the populations at Knockan, and by the R. Tralagill, Inchnadamph both in Sutherland, are at approximately the same altitude, both on Durness limestone, are seven miles apart, and have entirely opposite proportions of plants without and with branched hairs and glands; the population at Inchnadamph has 96 % plants with branched hairs and glands while that at Knockan has 96 % plants without either. This type of situation is repeated both in the central Scottish localities on mica schist and on the Hebrides, as evidenced by the samples from Raasay. The samples from the Burren, Co. Clare do however show continuity with one another, nearly all the plants in each sample having neither branched hairs nor glands. It is important to note however that in each of the samples there is at least one plant with branched hairs and glands, i.e. the populations are not homogeneous in these characters.

The samples from the Alps are homogeneous in all having branched hairs, except for two plants in a sample from the Combe de la, Valais, Switzerland. This appears to be the first record of such plants from the Alps. The same two plants are also lacking glands, as are plants from two other samples, one from France and the other from Austria. In general however the Alpine plants show little variation in these characters, the typical plant having branched hairs on all leaves with some leaves bearing them on lateral veins as well, and capitate glands on all leaves.

The typical Scandinavian plant has a similar distribution of branched hairs. One sample, from Memurelo, Opland, Norway contains three specimens without branched hairs and a few other specimens from Norway examined by Porsild (1958) also lacked them. The leaves have in general, in Scandinavia, fewer glands; most of the plants do bear them, but they are seldom numerous.

The reasons for the distribution of branched hairs in the populations must now be discussed. It is possible that in the Alps the presence of a small number of plants without branched hairs can be explained by mutation from the normal condition. Little information is available on the occurrence and frequency of gene mutation in natural populations of plants, but mutations, identical to those produced under laboratory conditions, are well known in wild populations of Drosophila

species (see Dobzhansky 1951), although they are infrequent due to selection against them in many cases.

The situation in Britain however differs greatly from this, since nearly all populations are heterogeneous for this character. This situation can possibly be regarded as an example of stable polymorphism. However it is not possible to see how each population structure is kept in balance by selection. For example, on Raasay in the Inner Hebrides, populations are present which are completely different in composition with respect to branched hairs, but which grow in the same type of community on cliffs facing the sea, about four miles apart. It is difficult to visualise differing selective pressures which will maintain a different balance of polymorphism in each population. Indeed there appear to be no correlations between population composition and geographical habitat, or climatic factors, as far as can be seen. Although it is possible that the W. Ireland population composition is correlated with the extreme oceanic climate this does not seem very likely as some populations on the N.W. coast of Scotland, also in very oceanic conditions, are known to have a very different composition. It is perhaps conceivable that the variation in Britain is due to past hybridisation with a species without branched hairs, so that the British populations would then be regarded as a series of more or less stabilised

hybrid swarms. The most widespread species without branched hairs is D. integrifolia, a species of N. America and Greenland in which the leaves are entire, or toothed at the base only. D. integrifolia is not present in Europe at the present day and little evidence is available to show if it was in the past. One quaternary record has been made of this species by Kulczynski (1932) at Przemyśl in Poland. The material was a single entire leaf 2.5 mm. long. Although similar leaves to that described and figured can be found in D. integrifolia plants, in view of the paucity of the material it is very desirable that confirmatory records should be made elsewhere. Hultén (1959) has identified specimens from Alaska and Greenland which have leaves crenulated to the tips and which lack branched hairs as D. octopetala x D. integrifolia. Whether this is a reliable diagnosis is quite uncertain. If it were, then it might be morphologically possible to interpret the British plants as of hybrid origin. What is clear is that Dryas octopetala in Britain is composed of different biotypes ~~from~~ those found on the Continent.

The population in Teesdale is of special interest. As pointed out earlier it is heterogeneous with respect to branched hairs. Thus the Teesdale population must be regarded as a true population and not as a clone derived from a single

seed introduction. Since no seed is now produced, due to sheep grazing, evolution has now presumably stopped so that the population can be regarded as the surviving remnant of a normal breeding population. The small leaved ecotype now present must have evolved before breeding was stopped. There is evidence that grazing took place in the upper dale in the 17th century (see p. 190), but no other information is available. It seems most likely that the small leaf size is a response to the severe exposure of the site. At the time when the surroundings were wooded the microclimate would probably have been much less severe due to the sheltering effect of the trees, so that possibly at this time a population with larger leaves existed and the ecotype now present has been evolved since the woodland disappeared. M.E. Johnson (pers. comm.) has shown that at Moorhouse blanket bog rapidly extended in the Atlantic period (zone VII a) so that nearly all the forest was invaded and covered by bog at this time. This change must have given large alterations in the microclimate on Cronkley Fell. However T.W. Böcher (pers. comm.) has pointed out that in the Faeroe Islands D. octopetala, growing under conditions of extreme exposure, is present in a large leaved form. Thus it is possible that the leaf size in the Teesdale population is not a result of climatic influence, but the result of the survival unchanged of the original form which first migrated there.

The heterogeneity of the British populations is also important in discussing the taxonomic status of the forms. Plants without branched hairs were first separated from the species by Babington (1842) who designated them as var. pilosa. The plants he used were cultivated ones from Co. Clare. Porsild (1958) in a revision of British material has considered this variety to be distinct from D. octopetala and has removed it to a new species, D. Babingtoniana, the type material being from Co. Clare. Porsild has also placed specimens from Scotland, including ones from Inchnadamph and Bettyhill, Sutherland; Ben Lui, Perth; Knockan, W. Ross; and Caenlochan Glen, Angus into this new species. Both the Irish and these Scottish populations have been shown to be heterogeneous, including both plants possessing and lacking branched hairs. It would therefore seem unjustifiable to separate one part of such a population as a different species.

While examining material in the British Museum it has been noticed that plants from Teesdale without branched hairs closely resemble specimens from Alaska and the Aleutians identified by Porsild as D. Chamissonis. Thus the means of leaf length and length/ breadth ratio of the Teesdale population are 0.86 and 2.02 while those of D. Chamissonis specimens measured was 0.87 and 1.90 (mean of 19 specimens from Alaska). According to Porsild (1958) this taxon is

endemic to the Bering Sea region and N. Pacific coast of Alaska. Böcher, Holmen and Jakobsen (1957) state that it also occurs in the east of Greenland. Hultén (1959) comes to the conclusion that in Alaska, at least, this morphological type is a stabilised hybrid between D. octopetala and D. integrifolia.

CHAPTER V.ECOLOGY.Introduction.

It has been pointed out that the distributions of the species considered are disjunct. The question arises as to whether these disjunct localities bear any similarity to one another in their floristic composition, their soils and their climate. It is also necessary to determine whether the variation already described for some of the species is linked to their ecology. The floristic lists and soil analyses which are detailed in the following chapter have been collected for these purposes. They also have a bearing on the question of whether species are more restricted ecologically towards the edge of their geographical and climatic range.

The general method, which has been used for each species, is to arrange the floristic lists in groups of floristic similarity and to compare these groups, picking out the correlations with the species' distribution and variation. The soil analyses have been arranged in the same order as the floristic lists so that any differences in soils between the floristic groups are brought out.

Little climatic information is available for some of the areas concerned and a more general account has been presented.

Vegetation and Floristics.Collection of data.

The methods used for vegetational description are based on those of Poore (1955a); the detailed procedure is as follows. The basic quadrat area for description usually chosen was 1 sq.m. Sometimes in communities which occupied smaller areas in extent a smaller basic area had to be chosen, and in some cases e.g. the Bartsia alpina hummock samples and a number of cliff ledge samples the whole sample was described. In each case a floristic list was made scoring cover-abundance on the Domin scale.

Cover about 100 %	10
Cover greater than 75 %	9
Cover 50-75 %	8
Cover 33-50 %	7
Cover 25-33 %	6
Abundant, cover about 20 %	5
Abundant, cover about 5 %	4
Scattered, cover small	3
Very scattered, cover small	2
Scarce, cover small	1

The basic quadrat areas were normally doubled twice and additional species added to the list. Notes of the aspect, slope and altitude were made, and the soil profile described as far as possible; soil samples were also taken for analysis.

Analysis of data.

The data have been analysed statistically using the method developed by Kulczynski (1928); this method has also been discussed and compared with other similar methods by Sørensen (1948). Indices of similarity (V) are calculated for each pair of samples,

$$\text{where } V = \frac{\left(\frac{c}{a} + \frac{c}{b}\right) \times 100}{2}$$

and where a = number of species in sample A, b = number of species in sample B, and c = number of species common to both. The results are transferred to a triangular diagram using the following code system for 10 % levels of similarity.

90 - 100%	
80 - 89%	
70 - 79%	
60 - 69%	
50 - 59%	
40 - 49%	
30 - 39%	

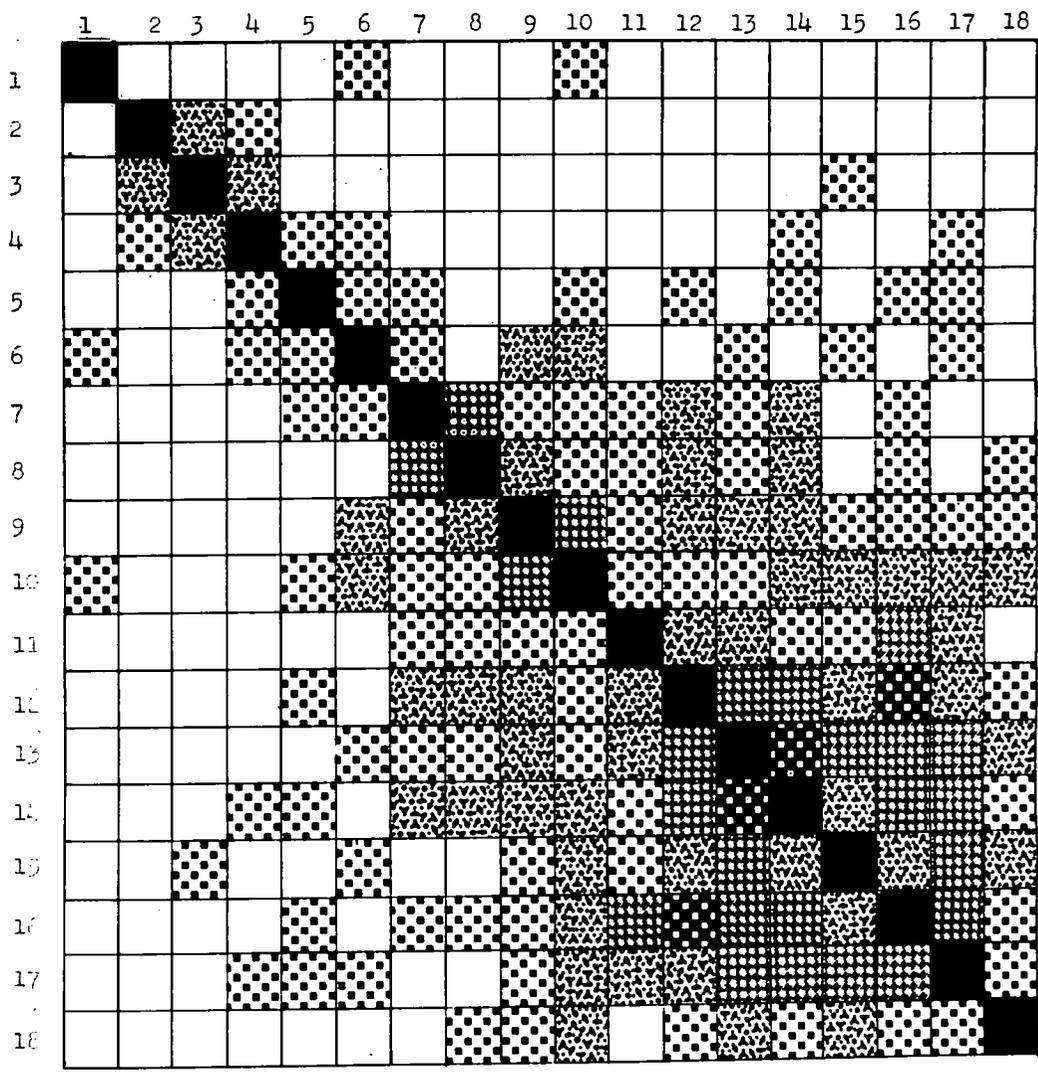
No similarities of less than 30 % are included in the diagram. The samples are then rearranged until the groups of high similarity are brought together; the results of this procedure are best appreciated by examination of the following examples. In these the original sample lists have been rearranged according to this order, and species of presence class V, also known as constant species (those with over 80 % presence) underlined. Tables comparing the groups delimited, with respect to species of presence classes V and IV (species with 60-80 % presence) are also given.

Gentiana verna.

A full range of sites in Teesdale and a number in West Ireland have been described and used in a Kulczynski analysis. Floristic lists have also been made for the sites sampled in the Alps and these results have been given separately in table V. 4.

Reference to diagram V. 1. shows that two main blocks of similarity are present in the British quadrat samples and these fit the two main types of habitat, flushes and limestone grassland. The floristic lists arranged as in the diagram are given in table V. 1. The community developed in flushes is represented by samples 2, 3, 4, 5 and 6. Of these all, except sample 6, are characterised by being developed on calcareous

GENTIANA VERNA



Diagram

V. 1. Kulczynski diagram of quadrat samples from British sites of Gentiana verna.

glacial drift, the vegetation being kept wet and flushed by springs and seepages. Sample 6 is interesting as being a site on sugar limestone, physiognomically more allied to the limestone grassland group, but floristically showing much greater affinities with the flush group. Overall constants for all the lists are Festuca ovina, Euphrasia officinalis agg. and Gentiana verna. The flushes are rather varied floristically and there are only three constant species, these being Molinia caerulea, Primula farinosa and Ctenidium molluscum. Of these the first two are confined, in the Gentiana verna sites examined, to the flush community.

All the other sites examined except 1 fall into the limestone grassland set. This is characterised by the following constant species; Carex caryophylla, Bellis perennis, Hieracium pilosella, Lotus corniculatus, Plantago lanceolata and Thymus drucei. The first of these species is not found in any of the flush sites. It is interesting to note the very close floristic relationship between the Teesdale and Irish grassland sites, which do not show any indication of separating into two groups in the Kulczynski analysis. This is borne out by examination of the floristic makeup. Thus although some species are commoner in one of the areas e.g. Achillea millefolium, Trifolium repens and Viola riviniana are commoner in Teesdale while Sesleria caerulea, Carex panicea,

<u>Flushes</u>		<u>Grasslands</u>	
<i>Selaginella selaginoides</i>	IV		
<i>Briza media</i>	V	<i>Briza media</i>	V
<i>Festuca ovina</i>	V	<i>Festuca ovina</i>	V
<i>Molinia caerulea</i>	V		
<i>Sesleria caerulea</i>	IV	<i>Sesleria caerulea</i>	IV
<i>Sieglingia decumbens</i>	IV		
		<i>Carex caryophyllea</i>	V
		<i>Carex panicea</i>	IV
		<i>Carex pulicaris</i>	IV
<i>Kobresia simpiciuscula</i>	IV		
		<i>Bellis perennis</i>	V
		<i>Campanula rotundifolia</i>	IV
		<i>Cirsium arvense</i>	IV
<i>Euphrasia officinalis</i>	V	<i>Euphrasia officinalis</i>	IV
<i>Gentiana verna</i>	V	<i>Gentiana verna</i>	V
		<i>Hieracium pilosella</i>	V
<i>Linum catharticum</i>	V	<i>Linum catharticum</i>	V
		<i>Lotus corniculatus</i>	V
<i>Pinguicula vulgaris</i>	IV		
		<i>Plantago lanceolata</i>	V
<i>Plantago maritima</i>	IV	<i>Plantago maritima</i>	IV
<i>Potentilla erecta</i>	IV	<i>Potentilla erecta</i>	IV
<i>Primula farinosa</i>	V		
<i>Prunella vulgaris</i>	IV	<i>Prunella vulgaris</i>	IV
		<i>Thymus drucei</i>	V
		<i>Trifolium repens</i>	IV
		<i>Viola riviniana</i>	IV
<i>Ctenidium molluscum</i>	V	<i>Ctenidium molluscum</i>	IV
		<i>Dicranum scoparium</i>	IV
		<i>Hypnum cupressiforme</i>	IV

Table V. 2. Comparison of flushes and grasslands containing *Gentiana verna*, with respect to species in presence classes IV and V.

GENTIANA VERNA									
Sample No.	1	2	3	4	5	6	7	8	9
Locality	Wickle Fell, Westmorland.	Cetry Bank, Teesdale, Co. Durham.	Widdybank Farm, Teesdale, Co. Durham.	Birkdale, Teesdale, Westmorland.	Haugh Hill, Teesdale, Co. Durham.	Widdybank Fell, Teesdale, Co. Durham.	High Eurther Edge, Teesdale, Co. Durham.	Grains o' th' Beck, Lunedale, N. Yorks.	Bellbeaver Rigg, near Gerrigill, Cumberland.
Grid Ref.	55/797242	55/845298	55/837299	55/810283	55/860296	55/823288	55/864313	55/856204	55/758353
Altitude	2300'	1250'	1300'	1450'	1200'	1600'	1600'	1400'	1950'
Aspect	WSW	S	- (Hummock 15 cms. high)	SE	SW	W	SW	E	WSW
Slope	36°	20°	-	25°	36°	2-3°	27°	31°	10°
Cover (%)	20	80	100	100	90	100	100	100	100
Sample Area (sq. m.)	4	1	0.5	4	4	1	4	4	4

GENTIANA VERNA									
Sample No.	10	11	12	13	14	15	16	17	18
Locality	Widdybank Fell, Teesdale, Co. Durham.	Pouleslough, Co. Clare.	Black Head, Co. Clare.	Near Mullaghmore, Co. Clare.	Ballinacorney, Co. Kerry.	Torbale, Co. Kerry.	Gentian Hill, near Torbale, Co. Kerry.	Menlough, Co. Kerry.	Ballyvaghan, Co. Clare.
Grid Ref.	55/815304	N08/02	N17/13	R31/96	H39/14	M23/39	M26/23	M30/29	M25/10
Altitude	1650'	100'	50'	150'	50'	50'	50'	150'	25'
Aspect	W	ENE	ENE	ENE	S	S	ENE	W	W
Slope	5°	10°	10°	2°	2°	2-3°	8°	6°	2°
Cover (%)	100	100	100	100	100	100	100	100	100
Sample Area (sq. m.)	1	4	4	4	4	4	4	4	4

Table V. 3. Localities and habitat details of British G. verna sites.

Campanula rotundifolia, Plantago maritima and Potentilla erecta are commoner in Ireland, the only species showing a clear separation is Antennaria dioica, which is present in the Irish and absent in the Teesdale lists. Thus there is no clear ecological separation corresponding to the morphological differentiation in the species as already described. One of the Irish samples, number 18, from Ballyvaghan is from a stabilised sand dune community on top of calcareous drift and from the diagram it is seen that this groups itself with the rest of the grassland samples. The only sample which does not group with either of the two blocks is number 1 from Mickle Fell, Westmorland. This is from a steep limestone slope and appears to be a pioneer stage of the grassland community, but with a rich moss flora at this stage. This would explain why of the two floristic correlations shown with other samples, one is with a sample of the flush community and the other with one of the grassland samples. The flush and grassland groupings are compared with respect to species of presence classes IV and V in table V. 2.

Habitat details for these sites are given in table V.3. The soils data will be considered in a separate section.

Floristic lists from the alpine sites sampled are given in table V. 4. and the habitat details in table V. 5. Since

GENTIANA VERNA (ALPS).

	19	20	21	22	23	24	25	26	27	28
Calluna vulgaris	-	-	-	-	-	1	-	1	-	-
Dryas octopetala	-	-	-	3	-	-	-	-	-	2
Picea abies (seedlings)	-	-	-	-	-	-	-	-	-	-
Salix sp.	-	-	-	5	-	-	-	-	-	-
Vaccinium myrtillus	-	-	-	-	-	1	-	2	-	-
Botrychium lunaria	1	-	-	2	2	3	-	-	3	-
Selaginella selaginoides	-	-	-	-	-	-	-	-	-	-
Anthoxanthum odoratum	-	-	4	-	7	6	4	-	6	4
Briza media	-	7	-	-	-	-	-	-	-	-
Deschampsia caespitosa	-	-	-	-	-	-	2	-	-	-
Pestuca ovina agg.	6	-	7	5	-	5	-	7	6	5
Koeleria gracilis	-	5	-	-	-	-	-	-	-	-
Nardus stricta	6	-	-	-	5	5	-	-	-	-
Poa alpina	-	-	-	-	-	-	-	-	-	-
Sesleria caerulea	-	5	-	2	-	-	5	-	-	-
Carex caryophyllica	-	-	-	-	-	-	2	-	2	3
C. flacca	1	-	-	-	-	-	-	-	-	3
C. ornithopoda	-	-	-	-	8	3	-	-	-	-
C. rupestris	-	-	-	-	-	-	-	-	-	-
C. sempervirens	6	4	3	5	2	3	-	-	-	-
Coeloglossum viride	-	-	-	-	-	-	-	1	-	-
Listera ovata	-	-	-	-	-	-	-	-	1	1
Luzula campestris	3	-	-	-	-	3	-	-	1	-
Orchis fuchsii	-	-	-	-	-	-	-	1	-	-
Orchis latifolia	-	-	-	-	-	-	-	-	2	-
Achillea millefolium	-	2	3	-	3	-	-	-	-	-
Ajuga reptans	1	-	-	-	-	-	-	3	2	-
Alchemilla alpina	4	-	-	-	-	-	-	-	-	3
A. colorata	-	3	-	-	-	-	-	-	-	-
A. monticola	1	-	4	-	4	4	-	3	1	-
Anthyllis vulneraria	-	2	-	1	-	2	-	-	-	-
Astragalus glycyphyllos	-	5	-	-	-	-	3	-	-	-
Bellis perennis	-	-	-	2	-	-	-	-	4	4
Cherleria sedoides	-	-	-	-	-	-	-	-	5	3
Chrysanthemum leucanthemum	1	2	3	-	2	3	-	-	1	1
Cirsium sp.	-	-	2	-	-	-	-	-	-	-
Corydalis solida	-	-	4	-	4	-	-	3	-	-
Crocus albiflorus	-	-	2	-	-	-	3	2	-	-
Euphorbia cyparissias	3	-	-	-	-	-	2	-	-	-
Galium pumilum	-	1	1	-	-	-	-	-	-	-
Gentiana Kochiana	-	1	1	-	3	3	-	2	-	-
G. verna	4	4	3	3	3	3	4	2	3	4
Geranium sylvaticum	-	-	-	-	3	-	-	2	-	-
Geum rivale	-	-	-	-	3	-	-	-	-	-
Globularia cordifolia	-	3	-	-	-	-	3	-	-	-
Helianthemum alpestre	-	5	6	-	-	-	7	-	-	-
Hieracium pilosella	-	3	3	-	-	-	2	4	-	-
Hutchinsia alpina	-	-	-	2	-	-	-	-	-	-
Hypochaeris radicata	1	-	-	-	5	2	-	-	1	-
Leontodon hispidus	-	-	3	-	-	-	-	-	-	2
Linum catharticum	3	3	-	-	-	-	2	-	-	-
Lotus corniculatus	4	4	-	1	-	6	2	5	5	4
Maianthemum bifolium	-	-	-	-	-	-	-	-	-	2
Myosotis alpestris	-	-	-	1	-	2	-	-	-	-
Pedicularis sp.	-	-	-	-	-	-	-	-	1	-
Petasites sp.	-	-	-	-	-	2	-	-	-	-
Plantago lanceolata	5	2	3	-	3	-	-	3	3	2
P. maritima	1	2	5	-	-	-	-	6	-	-
P. media	3	2	-	-	-	1	-	3	-	5
Polygala alpina	3	4	3	-	-	3	-	-	3	3
P. chamaebuxus	-	3	-	-	-	-	-	3	-	-
Polygonum viviparum	-	-	-	4	-	-	-	-	-	-
Potentilla aurea	-	-	-	4	-	-	-	-	-	-
P. rupestris	-	-	-	-	4	-	-	-	-	-
P. tabernaemontani	4	3	3	-	-	-	1	4	3	3
Primula farinosa	-	4	-	4	-	-	-	-	2	-
Prunella vulgaris	-	-	-	-	-	4	-	-	-	-
Pulsatilla alpina ssp. sulphurea	-	-	-	-	-	3	-	-	-	-
Ranunculus acris	3	2	3	-	3	-	-	2	2	-
R. bulbosus	-	-	-	-	-	-	-	-	-	2
R. montanus	-	-	-	3	-	-	-	-	-	-
Rhinanthus minor	-	2	-	-	-	-	3	-	-	-
Sieversia montana	-	-	-	2	2	-	-	-	4	-
Soldanella alpina	-	-	3	-	3	-	-	2	-	3
Taraxacum officinale agg.	2	-	-	-	-	3	-	-	-	-
Thlaspi alpestre	-	-	-	-	-	4	6	-	4	-
Thymus drucei	4	4	4	-	-	4	-	-	-	4
T. serpyllum	-	-	-	-	4	-	-	-	-	-
Trifolium pratense	-	3	-	-	4	-	-	-	-	-
T. repens	4	4	4	-	3	-	3	3	4	2
Trollius europaeus	-	-	-	-	3	4	-	2	-	2
Tussilago farfara	-	-	-	-	-	-	-	-	2	-
Valeriana sp.	-	-	-	-	-	-	-	-	-	1
Veronica chamaedrya	-	-	-	-	-	3	-	-	-	-
Viola biflora	-	-	-	-	-	-	-	-	-	1
Brachythecium glareosum	1	-	-	1	-	-	-	-	-	-
Bryum sp.	-	-	-	1	-	-	-	-	-	-
Campylium chrysophyllum	-	1	-	-	-	-	-	-	-	1
Cirriphyllum piliferum	-	-	-	-	-	-	-	-	1	-
Hylocomium cf. pyrenaicum	-	-	-	-	-	-	-	-	1	-
Mnium pseudopunctatum	-	-	-	-	-	-	-	-	1	-
Polytrichum juniperinum	-	-	-	-	-	5	-	-	-	-
Rhytidadelphus squarrosus	3	-	-	-	-	-	-	-	-	2
R. triquetrus	3	-	-	-	-	-	-	-	-	-
Thuidium cf. abietinum	-	1	-	-	-	-	-	-	-	1
T. philberti	-	-	-	-	-	-	-	-	-	-
Tortella tortuosa	-	1	-	-	-	-	-	-	-	-
Plagiogchila asplenoides	-	-	-	-	-	-	-	-	1	-
Alectoria ochroleuca	-	-	-	3	-	-	-	-	-	-
Cetraria islandica	-	-	-	3	-	-	-	-	-	-
C. nivalis	-	-	-	3	-	-	-	-	-	-
Cladonia cf. cervicornis	-	-	-	-	-	-	-	-	-	-

Table V. 4. Floristic lists from Alpine sites of G. verna.

GENTIANA VERNA (ALPS).

Sample No.	Locality	Rock Type	Altitude	Aspect	Slope	Cover (%)	Sample area (sq. m.)
19	Lanche du Pra, near Sillanches, Haute Savoie, France.	Limestone	1580m.	NE	22°	100	4
20	Clavinsalp, near Leukerbad, Valais, Switzerland.	Limestone	1940m.	SSW	30°	100	4
21	Cherdignon, near Leukerbad, Valais, Switzerland.	Limestone	1940m.	WSW	26°	100	4
22	Gemmi Pass, near Leukerbad, Valais, Switzerland.	Limestone	2230m.	SE	19°	100	4
23	Riedersalp, near Mirel, Valais, Switzerland.	Schist	1980m.	SE	5°	100	4
24	Brond, near Saas-Salen, Valais, Switzerland.	Schist	2020m.	SW	42°	100	4
25	Charbonniere, near Assy, Haute Savoie, France.	Limestone	1600m.	S	38°	100	4
26	Ayere du Milrou, near Assy, Haute Savoie, France.	Limestone	1520m.	SE	15°	100	2
27	Le Leutellet, near Megeve, Haute Savoie, France.	Schist	1700m.	NE	25°	100	4
28	La Prie, near Les Houchea, Haute Savoie, France.	Shale	1360m.	N	21°	100	4

Table V. 5. Localities and habitat details of Alpine G. verna sites.

the sites were chosen to give as wide a variation as possible in the areas visited (amply confirmed by the soil analyses) it is not surprising that the samples given do not show a great deal of homogeneity. However reference to Braun-Blanquet and Jenny (1926) shows that Gentiana verna in the Central Alps is a characteristic species of the alliance *Seslerion caeruleae* in the order *Seslerietalia caeruleae*; this also seems to be true for the French Alps (Braun-Blanquet 1954). The same conclusion has been reached by Ludi (1948) working on the Schinigeplatte near Interlaken in Switzerland. On examination of some of my lists it seems probable that at least some of them can be put into this alliance and within this into the association *Seslerieto-Semperviretum* with Carex sempervirens as one of its most characteristic species.

It is difficult to fit the British samples into the Braun-Blanquet scheme of classification; from an examination of the data as they stand it would appear that many of the grassland samples would be placed in the alliance *Seslerion caeruleae*. However Braun-Blanquet and Tuxen (1952), in their survey of Irish vegetation, certainly put sample 18 and probably many of the calcareous grassland samples into the alliance *Mesobromion erecti*, although it may be mentioned that the species Bromus erectus appears nowhere in their lists. Their

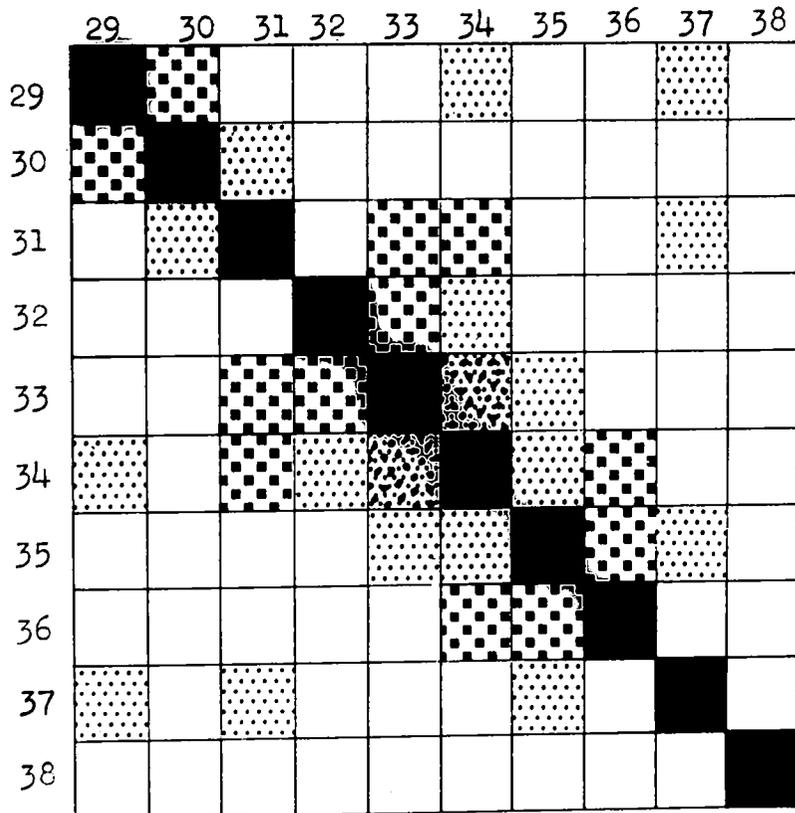
reasons for doing this are that there are a large number of characteristic species of this alliance present in the area. It is interesting that in Teesdale G. verna is present in two distinct types of habitat. In Ireland however it is restricted to the limestone grassland community, never occurring in flush communities. In the Alps it is also most characteristic of grassland communities, although it is possible that it may be present in some flush communities.

Potentilla fruticosa.

The samples in table V. 6 include lists from all the British areas known. The species has been able to survive in a number of different types of habitat and since the number of examples of each is so limited it has been difficult to arrange the samples in groups. Reference to diagram V. 2. however shows that the main relationships have been brought out. This variation is further shown by the fact that there are only two species common throughout the samples, these being Festuca ovina and Thymus drucei.

The most ecologically distinct community is found in the two Lake District localities (samples 29 and 30) where the species grows on rock ledges and in crevices. The species common to both localities are Calluna vulgaris, Lycopodium selago*, Festuca vivipara*, Carex pulicaris, Achemilla alpina*

POTENTILLA FRUTICOSA



Diagram

V. 2. Kulczynski diagram of quadrat samples from British sites of Potentilla fruticosa.

Sedum rosea*, Succisa pratensis, Thalictrum minus*, Breutelia chrysocoma* and Rhacomitrium lanuginosum, of which, the species starred are not found in association with Potentilla fruticosa elsewhere in Britain. The most similar habitat for P. fruticosa in Teesdale is at Wynch Bridge (sample 31), where it grows in crevices of the dolerite rock. Floristically however it is not allied, only four of the above mentioned species of the Lakeland localities being present, those above which are not starred.

The next and largest group is composed of samples from both Teesdale and Ireland and is physiognomically rather varied. Samples 32 and 33 are from pioneer communities on recent sandy alluvial deposits by the River Tees with the plants of P. fruticosa being scattered, while 36 is from a dense patch developed higher up the bank from 33 on a maturer soil. Although this sample obviously belongs to this group on its total floristic composition it has not any of the constant species of the group. Samples 34 and 35 are from Ireland, 34 from Ballynatty where the locality is a small promontory, probably of calcareous drift, projecting into Lough Corrib, and 35 from the characteristic Potentilla fruticosa zone round one of the turloughs or temporary lakes developed on Carboniferous limestone in Co. Clare. This group of localities

POTERYLLA FRUTICOSA										
Sample No.	29	30	31 *	32	33	34	35	36	37	38
Locality	Westwater Screes, Pillar, Cumberland.	Knnerdale, Cumberland.	Wynch Bridge, Teesdale, Co. Durham.	Dent Bank, Teesdale, Co. Durham.	High Force, Teesdale, Co. Durham.	Ballymitty, L. Corrib, Co. Mayo.	Castle Lough, Teesdale, Co. Durham.	Crosbley Scar, Teesdale, Co. Durham.	Mallyveghan, Co. Clare.	
Grid Ref.	55/195041	55/178122	55/904280	55/913261	55/875281	8200/91	816/99	55/875281	55/837295	823/06
Altitude	1450'	2000'	900'	800'	1100'	50'	50'	1100'	1300'	90'
Aspect	NE	NW	WSW	SW	SSW	-	WV	SSW	ENE	-
Slope	50°	65°	45°	2-5°	2-5°	-	5°	1-2°	15°	-
Cover (%)	100	80	60	80	80	100	80	100	100	100
Sample Area (sq. m.)	1	2	4	4	4	4	4	4	4	4

Table V. 7. Localities and habitat details of P. fruticosa sites.

has four species as constants, these being Briza media, Sesleria caerulea, Campanula rotundifolia and Leontodon hispidus. Other common species in this group are Koeleria gracilis, Bellis perennis, Cerastium vulgatum, Euphrasia officinalis agg., Lotus corniculatus, Plantago lanceolata, Plantago maritima, Polygala vulgaris, Succisa pratensis, and Ctenidium molluscum. Sample 37 is from a mature patch of the shrub by the River Tees by Cronkley Fell and is floristically distinct, showing only low similarities to a number of different types of community. The last sample, from the community at Ballyvaghan, Co. Clare (sample 38), is from a very tall shrub layer of Potentilla fruticosa (upto nearly 2 m. high) and shows no similarity above 20 % with any other sample.

Habitat details of the samples are given in table V.7.

Scattered information only is available to compare these habitats with other European sites. Tornblom (1911) reports that at Oland in the Baltic the species grows in crevices in limestone pavement and also in hollows with a deeper soil which are damp. The species seems to favour the same conditions in Latvia (Vilbaste 1953). This type of habitat appears to bear some resemblance to the turlough zones in Ireland. In the Pyrenees Despaty and Conill (1920) report

it in the Eyne valley growing in damp ground by the river, a situation which would appear to be similar to that by the Tees. Gorchakovsky (1960) in his world wide survey of the habitat conditions of the species states that in the Urals it appears mainly in the scrub covered gravel on river beds, again a situation similar to the Tees-side occurrences. In general from his account it seems that P. fruticosa is a colonist species requiring open nonshaded conditions for its growth and the British data do, on the whole, fit in with this hypothesis.

It is interesting to note that in Britain P. fruticosa displays a wide ecological tolerance in that it is present in a range of habitats, from pioneer rock ledge to closed shrub communities. It can thus, apparently, survive through a number of seral stages, being limited in the sere by not being able to withstand shaded conditions. As pointed out again later it is surprising in view of this tolerance and the species' performance in Teesdale that it is not more widespread.

Myosotis alpestris.

This species is, in Britain, confined to two areas, Teesdale, and the Breadalbanes in Scotland. In each area it occupies one type of habitat and the samples in table V. 8.

MYOSOTIS ALPESTRIS

	39	40	41	42	43	44	45	46
Asplenium viride	-	-	-	-	-	-	-	1
Botrychium lunaria	-	-	-	-	1	-	-	-
Polystichum lonchitis	-	-	-	-	-	-	-	1
Selaginella selaginoides	-	-	-	2	-	-	-	-
<u>Prasaca ovina</u>	7	7	6	9	8	-	-	4
P. rubra	-	-	-	-	-	-	-	4
P. vivipara	-	-	-	-	-	5	4	5
Helictotrichum pratense	-	-	-	2	-	-	-	-
Koeleria gracilis	-	-	-	-	3	-	-	-
Poa alpina	-	-	-	-	-	-	1	-
Sealeria caerulea	-	1	1	-	1	-	-	-
<u>Carex caryophylla</u>	2	3	2	3	3	-	-	-
<u>Luzula carpestris</u>	-	-	1	2	1	-	-	-
L. pilosa	-	-	-	-	-	-	-	1
<u>Achillea millefolium</u>	2	-	-	2	1	-	-	-
Adoxa moschatellina	-	-	-	-	-	-	-	2
Alchemilla acutidens	-	-	-	-	-	-	-	4
A. alpina	-	-	-	-	-	5	3	3
A. glabra	-	-	-	-	-	-	5	4
A. vestita	-	-	-	1	-	-	-	-
Campanula rotundifolia	-	-	-	1	-	-	-	3
Cerastium alpinum	-	-	-	-	-	3	-	-
C. vulgatum	1	2	2	1	2	-	-	-
Cherleria sedoides	-	-	-	-	-	4	-	-
Cochleria alpina	-	-	-	1	-	3	-	2
Draba incana	-	1	2	-	1	-	-	1
Euphrasia officinale agg.	-	-	-	-	2	-	-	-
<u>Galium pumilum</u>	1	1	1	2	3	-	-	1
Gentiana verna	-	-	-	-	1	-	-	-
Geum rivale	-	-	-	-	1	-	-	5
Hieracium sp.	-	-	-	-	-	-	3	-
<u>Minuartia verna</u>	2	3	3	1	2	-	-	-
<u>Myosotis alpestris</u>	3	3	2	3	2	5	2	4
Oxyria digyna	-	-	-	-	-	-	-	3
<u>Polygonum viviparum</u>	-	-	-	-	-	2	2	3
Potentilla crantzii	-	-	-	-	-	-	3	-
P. erecta	-	-	-	3	-	-	-	-
Saxifraga aizoides	-	-	-	-	-	-	3	-
S. hypnoides	-	-	1	1	-	3	-	4
S. nivalis	-	-	-	-	-	1	-	-
<u>S. oppositifolia</u>	-	-	-	-	-	4	4	1
Sedum rosea	-	-	-	-	-	5	-	5
Silene acaulis	-	-	-	-	-	-	4	-
Taraxacum officinale agg.	-	-	-	-	-	-	-	2
Thalictrum alpinum	-	-	-	-	-	3	-	2
Thymus drucei	5	4	4	4	4	-	3	4
Trifolium repens	-	-	-	-	-	-	-	2
Viola lutea	-	-	-	1	-	-	2	-
<u>V. riviniana</u>	-	1	-	2	1	-	-	-
<u>Acrocladium cuspidatum</u>	7	-	-	-	-	-	1	-
Barbula cylindrica	-	-	-	-	-	-	1	-
Bartramia ithyphylla	-	-	-	-	-	-	-	1
Ctenidium molluscum	1	1	1	1	-	-	1	1
Dicranella heteromalla	-	-	-	-	-	-	1	-
D. varia	-	-	-	-	-	-	-	1
<u>Dicranum sponarium</u>	2	1	2	1	-	3	1	3
Drepanocladus uncinatus	-	-	-	-	-	-	-	1
Encalypta streptocarpa	-	-	-	-	-	2	-	-
Entodon orthocarpus	-	-	1	-	-	-	-	1
Fissidens cristatus	-	-	1	-	1	-	-	-
Hylocomium splendens	1	-	1	1	-	1	-	1
<u>Hypnum cupressiforme</u>	1	1	1	1	1	-	-	1
Mnium punctatum	-	-	-	-	-	-	-	1
M. undulatum	-	-	-	-	-	-	-	3
Plagiothecium denticulatum	-	-	-	-	-	-	-	1
Pleurozium schreberi	-	-	-	1	-	-	1	-
Polytrichum alpinum	-	-	-	1	-	-	-	-
P. juniperinum	-	-	-	-	-	-	-	1
P. urnigerum	-	-	-	-	-	1	-	-
Pseudoleskea catenulata	-	1	-	-	-	-	-	-
Pseudoscleropodium purum	-	-	-	-	-	-	-	1
Rhacomitrium sciculare	-	-	-	-	-	-	1	-
R. canescens	1	-	-	-	-	1	-	-
R. heterotichum	-	-	-	-	-	-	1	-
<u>R. lanuginosum</u>	4	4	3	1	1	3	4	2
Rhodobryum roseum	-	-	-	-	-	-	-	2
Rhytidadelphus loreus	-	-	1	-	-	-	-	-
R. squarrosus	1	-	-	-	-	-	-	1
R. triquetrus	1	-	-	-	-	1	-	1
<u>Thuidium tamariscinum</u>	1	1	1	1	1	-	-	-
<u>Tortella tortuosa</u>	2	1	2	2	1	3	2	1
Barbilophozia barbata	-	-	-	-	-	-	1	-
B. hatcheri	-	-	-	-	-	-	-	-
B. lycopodicoides	-	-	-	-	1	-	-	-
Cephalozia sp.	-	-	-	-	-	-	-	-
Frullania tamarisci	-	-	-	-	-	-	1	-
Lophozia ventricosa	-	-	1	-	-	-	-	-
Mylia anomala	-	-	-	-	-	-	-	-
Plagiochila asplenioides	-	-	1	-	-	-	1	-
Scapania curta	-	-	-	-	-	-	-	1
<u>Tetraria aculeata</u>	1	-	1	1	1	-	-	-
<u>T. islandica</u>	1	-	-	1	1	-	-	-
Cladonia cervicornis	-	-	-	1	-	-	-	-
C. crispata	-	-	-	1	-	-	-	-
C. furcata	-	-	-	1	-	-	-	-
C. gracilis	-	-	-	-	-	1	-	-
C. pocillum	1	-	-	-	-	-	-	-
C. cf. pyxidata	-	-	-	1	-	-	-	-
C. rangiformis	-	-	-	-	1	-	-	-
Peltidea apthosa	1	-	-	-	-	-	-	-
Peltigera canina	-	-	-	-	1	-	-	-
P. polydactyla	-	-	1	-	1	-	-	-

Table V. 8. Floristic lists from M. alpestris sites.

show a simple floristic division into these two. In Teesdale the species grows in short grazed limestone grassland and here the constant species are Festuca ovina, Carex caryophyllea, Luzula campestris, Achillea millefolium, Cerastium vulgatum, Galium pumilum, Minuartia verna, Viola riviniana, Hypnum cupressiforme, Thuidium tamariscinum, Cetraria aculeata and Cetraria islandica. In addition there are a number of overall constants to both Teesdale and the Breadalbanes, these being Thymus drucei, Dicranum scoparium, Rhacomitrium lanuginosum and Tortella tortuosa.

In the Breadalbanes the species is confined to mica schist rock ledges which are largely inaccessible to sheep. The constants here are Festuca vivipara, Alchemilla alpina, Polygonum viviparum and Saxifraga oppositifolia. Comparative lists of species of presence classes IV and V in the two communities are given in table V. 9.

It is interesting to note that in Teesdale the species is confined to steep slopes with a southerly aspect. (see table V. 10). It is impossible to determine whether the aspect is significant or not at the present. In this position the whole community is subject to very heavy sheep grazing since the patches of grassland developed on the successive altitudinal bands of the Yoredale limestones of the district are preferentially grazed in comparison with surrounding

Teesdale Limestone
grasslands

Scottish mica schist
rock ledges

<i>Festuca ovina</i>	V	<i>Festuca vivipara</i>	V
<i>Sesleria caerulea</i>	IV		
<i>Carex caryophyllea</i>	V		
<i>Luzula campestris</i>	V		
<i>Achillea millefolium</i>	V	<i>Alchemilla alpina</i>	V
		<i>Alchemilla glabra</i>	IV
<i>Cerastium vulgatum</i>	V	<i>Cochleria alpina</i>	IV
<i>Draba incana</i>	IV		
<i>Galium pumilum</i>	V		
<i>Minuartia verna</i>	V		
<i>Myosotis alpestris</i>	V	<i>Myosotis alpestris</i>	V
		<i>Polygonum viviparum</i>	V
<i>Saxifraga hypnoides</i>	IV	<i>Saxifraga hypnoides</i>	IV
		<i>Saxifraga oppositifolia</i>	V
		<i>Sedum rosea</i>	IV
		<i>Thalictrum alpinum</i>	IV
<i>Thymus drucei</i>	V	<i>Thymus drucei</i>	IV
<i>Viola riviniana</i>	V		
<i>Ctenidium molluscum</i>	IV	<i>Ctenidium molluscum</i>	IV
<i>Dicranum scoparium</i>	V	<i>Dicranum scoparium</i>	V
<i>Fissidens cristatus</i>	IV		
<i>Hylocomium splendens</i>	IV	<i>Hylocomium splendens</i>	IV
<i>Hypnum cupressiforme</i>	V		
<i>Rhacomitrium lanuginosum</i>	V	<i>Rhacomitrium lanuginosum</i>	V
		<i>Rhytidiadelphus triquetrus</i>	IV
<i>Thuidium tamariscinum</i>	V		
<i>Tortella tortuosa</i>	V	<i>Tortella tortuosa</i>	V
<i>Cetraria aculeata</i>	V		
<i>Cetraria islandica</i>	V		
<i>Peltigera polydactyla</i>	IV		

Table V. 9. Comparison of Teesdale and Scottish communities containing *Myosotis alpestris*, with respect to species in presence classes IV and V.

MYOSOTIS ALPESTRIS

Sample No.	39	40	41	42	43	44	45	46
Locality	Great Dun Fell, Westmorland.	Great Dun Fell, Westmorland.	Great Dun Fell, Westmorland.	Little Fell, Westmorland.	Wickle Fell, N. Yorks.	Ben Lovers, Perth.	Ben Lovers, Perth.	Cam Craig, Perth.
Grid Ref.	35/713312	35/713312	35/713312	35/786214	35/816248	27/636411	27/632410	27/580384
Altitude	2400'	2400'	2400'	2350'	2400'	3250'	3200'	3250'
Aspect	SE	SE	SE	WSW	S	SW	SE	SE
Slope	25°	25°	25°	20°	28°	Ledge	Ledge	Ledge
Cover (%)	80	90	80	100	100	100	100	100
Sample Area (sq. m.)	1	1	1	1	1	-	-	2

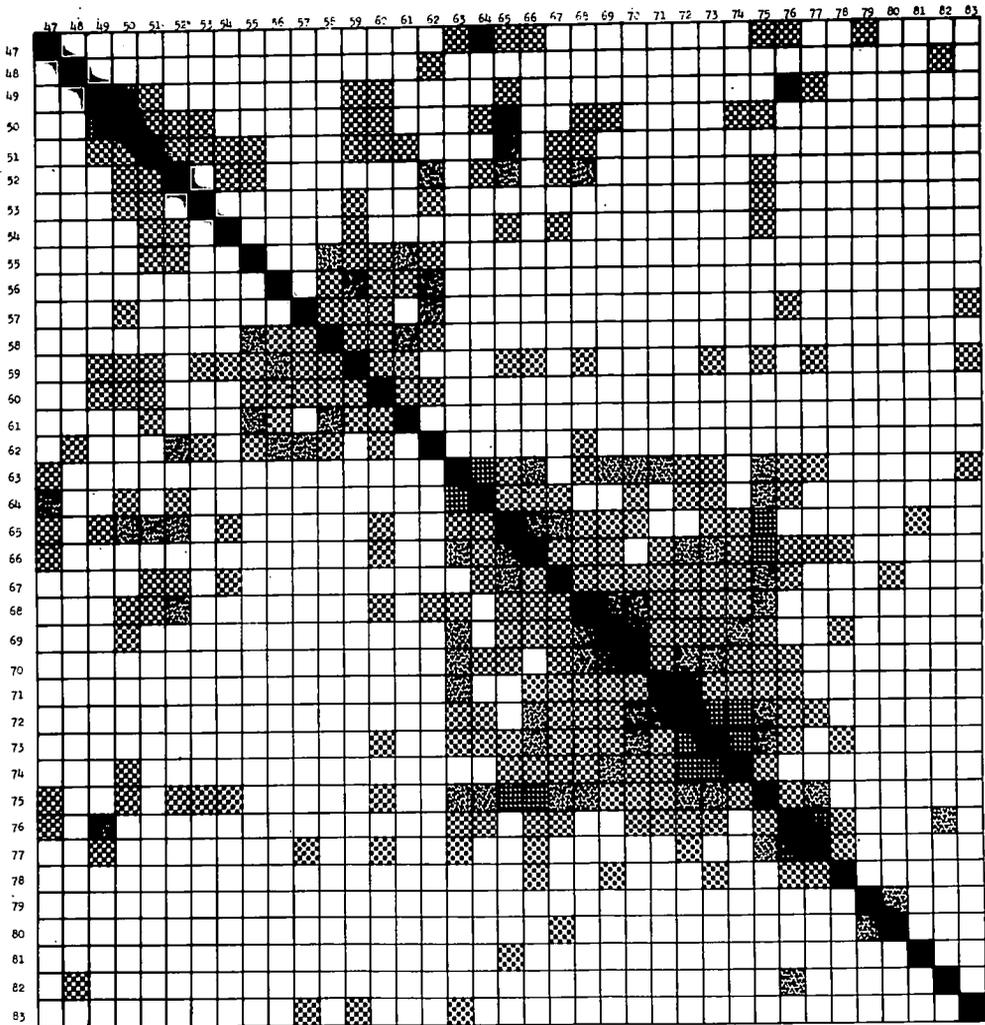
Table V. 10. Localities and habitat details of M. alpestris sites.

mineral poor communities. As has already been pointed out (p. 98) this biotic influence has probably led to the development of a distinctive ecotype. In the Breadalbanes however the species seems to be restricted to the rock ledges which the sheep find impossible or certainly very difficult to reach. It is striking that the species is almost entirely absent from the steep grassland below the cliffs.

A feature which is common to both habitats is that they are both kept somewhat open and the vegetation never becomes completely stabilised. In Teesdale this is due to the phenomenon of soil creep. This is most marked on Dun Fell, but is also present in the other sites; it is correlated with the steep slopes already mentioned. It seems likely that this situation has been maintained for a considerable part at least of the post glacial period, since it is postulated (M.E. Johnson pers. comm.) that the maximum tree line in the area was at approximately 2350'. In the Breadalbanes the rock ledges undergo a cyclical development, a rich herb community building up until the whole system becomes unstable and drops away, so that a series of open habitats at the right stage is always maintained.

Thus Myosotis alpestris is more ecologically restricted than Gentiana verna in Teesdale since this can maintain itself in stabilised and closed grassland.

DRYAS OCTOPETALA



Diagram

V. 3. Kulczynski diagram of quadrat samples from British sites of Dryas octopetala.

DRYAS OCTOPETALA								
Sample No.	47	48	49	50	51	52	53	54
Locality	Borrailie, Sutherland.	Cronkley Fell, N. Yorks.	Glas Cnoc, Kishorn, Ross.	Glas Cnoc, Kishorn, Ross.	Ben Lui, Perth.	Conival, Ben More Assynt, Sutherland.	Creag an Lochan, Perth.	Gaenloch an Glen, Angus.
Grid Ref.	29/388652	35/840283	18/865451	18/865451	27/270272	29/303191	27/590411	37/175764
Altitude	200'	1750'	1050'	1050'	1750'	1700'	2100'	2750'
Aspect	SE	-	NW	NW	NE	SW	NE	SE
Slope	5°	-	50°	50°	65°	25°	80°	30°
Cover (%)	100	90	75	75	100	95	100	100
Sample Area (sq. m.)	4	1	2	1	4	4	1	4
DRYAS OCTOPETALA								
Sample No.	55	56	57	58	59	60	61	62
Locality	Creag Mhor, Loch Lyon, Perth.	Gaenloch an Glen, Angus.	Glen Doll, Glova, Angus.	Sanna Shrasigh, Ross.	Glen Doll, Glova, Angus.	Glen Doll, Glova, Angus.	Coire na Coichille, Ardwickie, Inverness.	The Cairnwell, Perth.
Grid Ref.	27/389357	37/185772	37/240767	28/385867	37/240767	37/242763	27/463744	37/128782
Altitude	3000'	2800'	2300'	2550'	2100'	2250'	3000'	2750'
Aspect	S	S	NE	SW	NE	N	N	-
Slope	50°	45°	40°	15°	55°	50°	45°	-
Cover (%)	90	100	80	100	85	100	100	100
Sample Area (sq. m.)	2	4	4	4	4	4	4	4

Table V. 11. Localities and habitat details of British D. octopetala sites.

DRYAS OCTOPETALA

Sample No.	63	64	65	66	67	68	69	70	71	72
Locality	Heilan, Sutherland.	Smoo Cave, Durness, Sutherland.	Loch Mhaoloch-coire, Inchnadaph, Sutherland.	Durness, Sutherland.	R. Tralegill, Inchnadaph, Sutherland.	Weall Mor, Glencor, Sutherland.	Monadh Dubh, Rhun.	Monadh Dubh, Rhun.	Craig na-Bruich, Rassy.	Near S. Screaspadal, Rassy.
Grid Ref.	29/453604	29/421767	29/278193	29/399676	29/263215	27/108567	18/330027	18/330028	18/583657	18/578439
Altitude	150'	100'	900'	200'	450'	1500'	200'	150'	750'	500'
Aspect	SW	W	NW	SE	N	N	W	W	ENE	W
Slope	30°	40°	20°	20°	5°	40°	10°	30°	55°	50°
Cover (%)	90	80	70	100	100	100	95	100	100	100
Sample Area (sq. ft.)	4	4	4	1	4	4	4	4	4	4

DRYAS OCTOPETALA

Sample No.	73	74	75	76	77	78	79	80	81	82	83
Locality	Drain on Aonach, Rassy.	Rubhs na Leac, Rassy.	Bettyhill, Sutherland.	Rannagh, Co. Clare.	Crough, Co. Clare.	Black Head, Co. Clare.	Bettyhill, Sutherland.	Bettyhill, Sutherland.	Yew Cogar Scar, N. Yorks.	Cowside Beck, Arncliffe, N. Yorks.	Llyn Idwal, Glynor Fawr, Caernarvon.
Grid Ref.	16/563024	16/598379	29/705605	N27/61	N19/07	N16/12	29/706605	29/706605	34/923908	34/918706	23/648594
Altitude	850'	250'	30'	400'	800'	100'	15'	15'	1200'	900'	1750'
Aspect	SE	EW	NE	NW	SE	NW	-	NE	NW	SE	SW
Slope	50°	65°	13°	27°	7°	17°	-	32°	74°	40°	75°
Cover (%)	100	100	100	100	100	100	100	100	50	100	40
Sample Area (sq. ft.)	4	4	1	4	4	4	1	1	1	4	4

Table V. 11. Cont.

Dryas octopetala.

The communities within which Dryas octopetala grows have been the most complex to deal with of the species considered. This is partly because of the range of localities studied (from Caernavonshire to N. Sutherland), and partly because of the fragmentary nature of some of the communities, especially in central Scotland. However, using Kulczynski's technique, it has been possible to recognise four main groups and to show the relationships of the remaining samples to these groups. The degree to which these groups are distinguished from one another will be seen by reference to diagram V. 3. In constructing this diagram, as well as using my own results I have also used a number of lists made by Dr. D. A. Ratcliffe; these are numbers 47, 49, 50, 52, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 68, 69, and 70. This has been done so that the results should have as wide a validity as possible. The full floristic lists for the British sites are given in table V. 12.

It is difficult to define the differences between the first and second groups of samples although from diagram V. 3. it is clear that when compared on total species content they do form two distinct units. Both are mainly based on lists from central Scotland although each includes one sample from

Sutherland; also the second group tends to be composed of more species-rich samples than the first although there is no clear differentiation. From the habitat factors in table V. 11. it will be observed that the only factor here which tends to delimit the two is altitude, the second group being on the whole at higher altitudes, but even here there is some overlap between the groups. Floristically the groups can be separated by means of their constant species, some of these acting as indicator species. The first group has the following constants (besides Dryas octopetala, Festuca ovina and Thymus drucei which are constant throughout the whole range of *Dryas* communities); Selaginella selaginoides, Alchemilla alpina, Linum catharticum, Polygonum viviparum, Saxifraga aizoides, Viola riviniana, and Ctenidium molluscum. Reference to table V. 13. shows that the best indicators for separating this group from the second are Linum catharticum and Viola riviniana, although it must be stressed that the total number of constant species must be used to decide to which groups any particular sample belongs since the third group has both these species as constants, although it has other distinctive constant species. The second group has as its constants Selaginella selaginoides, Polygonum viviparum, Saxifraga oppositifolia, Silene acaulis, Ctenidium molluscum, Hylocomium splendens and Tortella tortuosa. The best of these species for separating samples from the first

group is the presence of Saxifraga oppositifolia, Silene acaulis and Hylocomium splendens. These two groups are mostly (although not without exception) developed on rock of the mica schist type. Visits to some of Ratcliffe's localities indicate that one of the differences between the habitats, in which these two groups exist, is the degree of damp flushing. Sites in the first group are frequently very wet, the soil almost saturated with moisture and with water dripping down from the crags above, while those in the second group usually appear to be considerably drier with the soil, although damp, not saturated and with the rock faces dry.

The third group is sharply differentiated from the first two in a number of features. It appears to be confined to the North and West coast of Scotland and the Hebrides (samples from Rhum and Raasay) and is developed on a number of different rock types, but apparently not on mica schist. Thus the first five from Sutherland are developed on the mainly Ordovician Durness limestone, while number 75 from Bettyhill is on a banded gneiss (containing biotite amphibole, garnet and plagioclase feldspar. (R.W. Nesbitt pers. comm.)) which however gives a soil with a fairly high base status (see soil analysis p.166). The well known fact that the mountain flora grows at progressively lower altitudes towards the North of Scotland is well shown here. The most southerly sample, at Glencoe, is

at 1500', while none of the other samples is higher than 900'; thus this group appears at lower altitudes than the first two. The constant species are Hypericum pulchrum, Linum catharticum, Plantago lanceolata, and Viola riviniana, of which Hypericum pulchrum and Plantago lanceolata are good indicator species. Other common species in the group are Calluna vulgaris, Euphrasia officinalis agg., Prunella vulgaris and Succisa pratensis. It is interesting to note that although there are no constant bryophytes to the group Ctenidium molluscum is constant and Tortella tortuosa also common in the mainland samples, although they do not occur in the Hebridean ones.

The fourth group is, from diagram V. 3, obviously closely related to the third although distinct. It is composed of samples from Co. Clare, W. Ireland all on Carboniferous limestone. The constant species are for the most part very characteristic; they are Sesleria caerulea, Polygala vulgaris, Viola riviniana, Breutelia chrysocoma, Ctenidium molluscum and Pseudoscleropodium purum. A comparison of the species in presence classes IV and V in the four groups is given in table V. 13.

Apart from these four groups there are a number of samples which appear to be distinct. Three of these, numbers 28 and 29 from Bettyhill and 12 from Borralie are communities developed on shell sand; they have correlations with one another and

Group 1.	Group 2.	Group 3.	Group 4.
Dryas octopetala.	V Dryas octopetala Empetrum nigrum agg. Salix reticulata Vaccinium vitis-idaea Selaginella selaginoides Deschampsia caespitosa Festuca ovina.	V Calluna vulgaris Dryas octopetala	IV Calluna vulgaris V Dryas octopetala
Selaginella selaginoides	V		
Festuca ovina	V	Festuca ovina	V Festuca ovina V Sesleria caerulea
Carex capillaris	IV Carex capillaris	Sieglingia decumbens	IV
Alchemilla alpina	V Coeloglossum viride		IV Carex flacca IV Carex panicea
Hieracium sp.	IV Campanula rotundifolia Euphrasia sp.	Bellis perennis Euphrasia sp.	IV Campanula rotundifolia IV Cirsium arvense
Linum catharticum	V Hypericum pulchrum	Hypericum pulchrum	IV Hypochoeris radicata
Pinguicula vulgaris	IV Linum catharticum	Linum catharticum	IV Lotus corniculatus

Table V. 13.

Group 1.

Group 2.

Group 3.

Group 4.

Polygonum viviparum	V	Polygonum viviparum	V	Plantago lanceolata	V	Polygala vulgaris	V
Saxifraga aizoides	V	Saxifraga aizoides	IV	Plantago maritima	IV	Potentilla erecta	IV
Thymus drucei	V	Saxifraga oppositifolia	V	Potentilla erecta	IV	Succisa pratensis	IV
Viola riviniana	V	Silene acaulis	V	Prunella vulgaris	IV	Thymus drucei	V
Ctenidium molluscum	V	Succisa pratensis	IV	Succisa pratensis	IV	Viola riviniana	V
		Thymus drucei	IV	Thymus drucei	V	Breutelia chrysocoma	V
		Ctenidium molluscum	V	Viola riviniana	V	Ctenidium molluscum	V
		Ditrichum flexicaule	IV			Neckera crispa	IV
		Hylacomium splendens	V			Pseudoscleropodium purum	V
		Rhytidiadelphus triquetrus	IV			Rhytidiadelphus triquetrus	IV
Tortella tortuosa	IV	Rhacomitrium lanuginosum	IV				
		Tortella tortuosa	V				

Table V. 13. Comparison of British D. octopetala groups with respect to species in presence classes IV and V.

slight ones with the N. Scotland group, but are certainly distinct from it. The remaining samples are disjunct ones from the North of England and Wales and diagram V. 3. shows that as well as being geographically disjunct they are also floristically disjunct. The only correlations greater than 30 % that the Teesdale sample (number 20) has, are with one of the samples from Arncliffe, N. Yorks and the sample from the Cairnwell, Perth which is notable in that it is the only other site on metamorphosed limestone - "sugar limestone". The Arncliffe samples, 18 and 19, are on Carboniferous limestone and the only other samples that are similar to these are one from W. Ireland on Carboniferous limestone at 400' and one from Inchnadamph, Sutherland on Ordovician limestone at 450'. The sample from above Llyn Idwal, N. Wales is also disjunct floristically, having scattered similarities with samples from Glen Clova, Angus and Heilam, Sutherland. The locality is itself very restricted and developed on a craggy outcrop (slope 75°) of a small intrusion or lava flow into the surrounding slate (see footnote).

This system of division of Dryas communities bears no simple relation to the noda put forward by Poore and McVean (1957) and each sample must be examined separately. This is

The rock is fine grained and siliceous with prominent laths of an albitic plagioclase feldspar in fine section, quartz is also common and there is a small amount of calcite (up to 5%), chemically it is probably rich in Na_2O , SiO_2 and Al_2O_3 with lesser amounts of K_2O and Fe_2O_3 . My thanks are due to Dr. H. Emeleus, Geology Dept., Durham for this description.

also the case for the noda suggested by McVean and Ratcliffe (in press).

Correlations with phytosociological units is again rather difficult. The Irish samples are placed by Braun-Blanquet and Tuxen (1952) in a new association, *Asperuleto-Dryadetum* which belongs to the alliance *Mesobromion erecti*; the reasons for this are stated as follows, "together with Sesleria which is the most frequent associate of Dryas in the Alps there also occur isolated plants of Euphrasia salisburgensis, in Central Europe an indicator of the *Seslerion caeruleae* alliance of the Central European mountains, but there is also a whole series of thermophilous *Bromion* species which indicate the floristic relationship of the association with the *Bromion*". This view is interesting as from limited experience of the Central Alps the communities certainly appear to have distinct affinities with the *Seslerion caeruleae* alliance. The N. England communities of Dryas in the Craven and Teesdale districts certainly have affinities with the *Seslerion caeruleae* alliance. The Scottish communities seem to be more closely allied to the Scandinavian Dryas associations than to those of the Alps; Poore and McVean (1957) have classed the Sutherland communities on the Durness limestone and sand dunes as allied to the *Elyno-Dryadion* alliance described by Nordhagen (1943).

It may be emphasized at this point that there appears to be no correlation between the complex pattern of morphological differentiation described earlier and the ecological groups which have been described above. It is possible, as has been mentioned, that there may be a correlation between leaf size and climate, but the detailed microclimatic information which would be necessary to establish this is not available.

Quadrat lists for the Alpine sites sampled are given in table V. 14. and the habitat details in table V. 15. It is well established (Braun-Blanquet and Jenny 1926, Braun-Blanquet 1954, Ludi 1948) that in the Alps Dryas octopetala is the dominant in the pioneer stage of a number of associations in the alliance *Seslerion caeruleae*. The majority of lists appear to belong to the association *Seslerieto-Semperviretum* which is present in both the French Alps (Braun-Blanquet 1954) and the Central Alps (Braun-Blanquet and Jenny 1926). Thus samples 87 and 88 from France and 89 from Switzerland are typical examples of the pioneer stage of this association developed on steep calcareous slopes with Sesleria caerulea and Carex sempervirens as characteristic species. Sample 84 although lacking Carex sempervirens seems to be an early stage in the same association developed on gently sloping limestone pavement, since there are maturer examples of the same association

DRYAS OCTOPETALA (ALPS)

	84	85	86	87	88	89
Arctostaphylos uva-ursi	-	-	-	4	-	-
<u>Dryas octopetala</u>	<u>8</u>	<u>9</u>	<u>8</u>	<u>6</u>	<u>8</u>	<u>6</u>
Salix repens	1	-	5	-	-	-
Festuca ovina	3	3	-	-	-	4
<u>Sesleria caerulea</u>	<u>4</u>	<u>4</u>	<u>3</u>	<u>7</u>	<u>5</u>	<u>5</u>
Carex rupestris	3	-	-	-	-	-
<u>C. sempervirens</u>	-	-	-	<u>6</u>	<u>5</u>	<u>3</u>
Tofieldia calyculata	-	-	2	-	1	-
Alchemilla alpina	-	-	-	-	3	-
Androsace chamaejasme	-	-	-	-	-	2
Anthyllis vulneraria	-	3	2	1	2	-
Astragalus glycyphylus	-	3	-	2	-	-
Bartsia alpina	-	3	-	-	-	-
Bellis perennis	-	-	-	-	3	-
Cherleria sedoides	3	-	-	-	-	-
Chrysanthemum leucanthemum	-	-	3	-	-	-
Cirsium arvense	-	-	2	-	-	-
Cirsium sp.	-	-	-	-	1	1
Draba aizoides	2	1	-	-	-	-
Galium pumilum	-	-	-	-	-	1
Gentiana Kochiana	-	-	-	1	1	1
G. verna	1	-	-	-	-	2
Globularia cordifolia	-	2	-	-	-	5
G. nudicaulis	-	-	-	-	1	-
Helianthemum alpestre	-	3	-	1	4	-
Hieracium sp.	-	4	-	-	-	2
Homogyne alpina	-	2	-	-	1	-
Hutchinsia alpina	1	-	-	-	-	-
Leontodon hispidus	-	-	1	-	-	-
Lotus corniculatus	-	-	-	3	2	2
Myosotis alpestris	-	1	-	-	-	-
Oxytropis sp.	-	-	-	1	-	-
Petasites paradoxus	-	-	2	-	-	-
Polygala alpina	-	-	-	-	-	4
P. chamaebuxus	-	-	-	3	4	2
Plantago maritima	-	-	3	-	-	-
Polygonum viviparum	-	2	-	-	-	2
Potentilla tabernaemontani	-	-	1	-	-	-
Primula farinosa	-	-	3	-	-	-
Pulsatilla vernalis	-	2	-	-	-	-
Ranunculus montanus	3	-	-	-	-	-
Sagina sp.	-	-	3	-	-	-
Saxifraga aizoon	-	3	-	-	-	1
S. oppositifolia	3	-	-	-	-	-
Sedum sp.	1	-	-	-	-	-
Silene acaulis	-	-	-	1	-	-
Soldanella alpina	-	3	-	-	3	3
Taraxacum officinale agg.	-	-	-	-	2	-
Trifolium alpinum	-	-	-	-	3	-
T. repens	-	-	2	-	-	-
Valeriana sp.	-	-	1	-	-	-
Viola riviniana	-	-	-	-	-	2
Brachythecium glareosum	-	-	1	-	-	-
Bryum sp.	1	-	-	-	-	-
Campylium chrysophyllum	-	-	1	1	-	1
Ctenidium molluscum	-	-	1	-	1	-
C. procerrimum	1	-	-	-	-	-
Distichium capillaceum	-	-	-	-	-	1
Ditrichum flexicaule	1	-	-	-	-	-
Encalypta streptocarpa	-	-	-	-	-	1
Fissidens cristatus	-	-	-	1	1	-
Mnium hornum	-	-	-	-	-	1
Rhytidiadelphus triquetrus	-	-	-	-	3	2
Rhytidium rugosum	-	-	-	-	-	1
Thuidium abietinum	1	-	-	-	-	1
Tortella tortuosa	-	-	2	2	1	3
Scapania cf. aequiloba	-	-	-	-	1	-
Alectoria ochroleuca	3	-	-	-	-	-
Cerania vermicularis	3	-	-	-	-	-
Cetraria islandica	6	4	-	-	-	3
C. juniperina	3	-	-	-	-	-
C. nivalis	2	-	-	-	-	-
Cladonia cf. cervicornis	-	-	-	-	-	1

Table V.14. Floristic lists from Alpine sites of D.octopetala.

DRYAS OCTOPETALA (ALPS).

Sample No.	Locality	Rock Type	Altitude	Aspect	Slope	Cover (%)	Sample area (sq. m.)
84	Gemmi Pass, near Leukerbad, Valsis, Switzerland.	Limestone	2300m.	NW	12°	80	4
85	Chermignon, near Leukerbad, Valsis, Switzerland.	Limestone	2060m.	W	42°	95	4
86	Le Leutellet, near Megève, Haute Savoie, France.	Shale	1700m.	E	5°	100	4
87	Charbonniere, near Aesy, Haute Savoie, France.	Limestone	1600m.	E	38°	70	4
88	Lanthe du Pra, near Sallanches, Haute Savoie, France.	Limestone	1600m.	ESE	22°	100	4
89	Clwincnalp, near Leukerbad, Valsis, Switzerland.	Limestone	2000m.	SW	50°	70	2

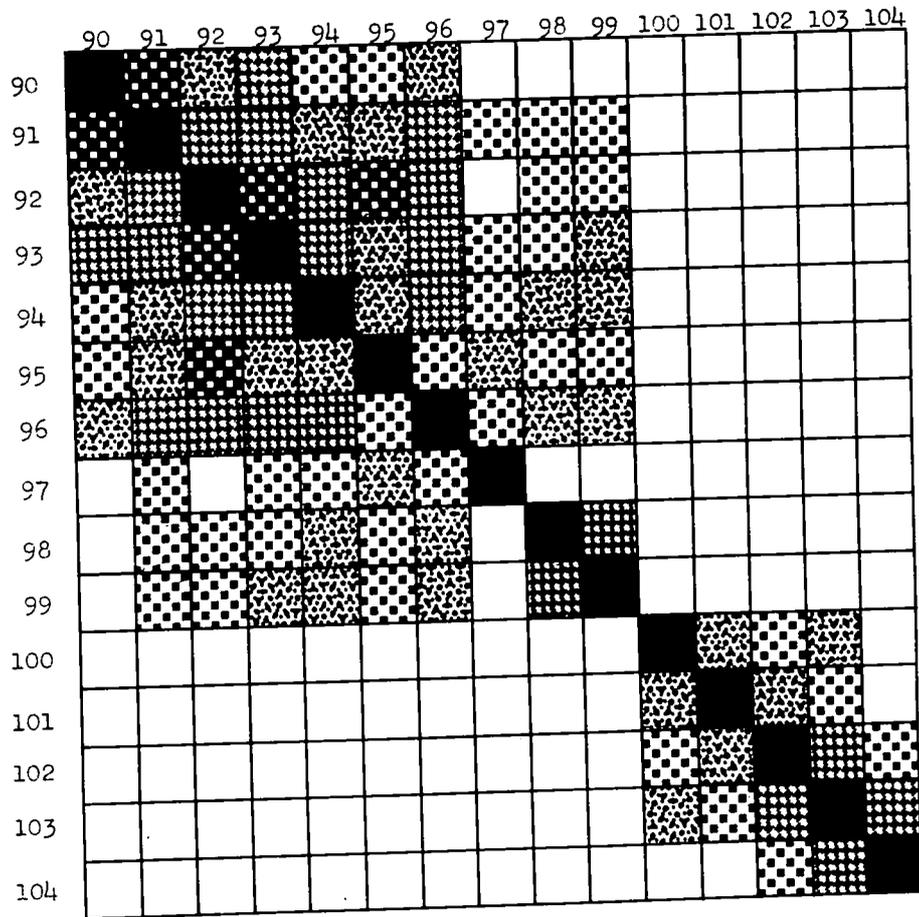
Table V. 15. Localities and habitat details of Alpine D. octopetala sites.

nearby, e.g. sample 22 of table V. 4. of alpine Gentiana verna samples. Sample 85 also falls into a pioneer stage of the same association with scattered Salices and also Globularia cordifolia and Helianthemum alpestre, mentioned by Braun-Blanquet and Jenny (1926) as typical "espalier shrubs" (Spaliersträucher) which are characteristic of the early development of this community. Sample 86 however is somewhat different being developed on an alluvial platform by a stream on a shale lithosol. Floristically it seems to belong to an association recognised by Lúdi (1948) present on flat calcareous areas, which he has called Dryadetum octopetalae. This has a number of Salices and also Tofieldia calyculata and Primula farinosa (both present in 86) included in the differential species separating it from the Seslerieto-Semperviretum. Thus in the Alps Dryas is typically a pioneer species in a number of associations of the order Seslerietalia caeruleae, an order of communities developed under well drained calcareous conditions.

Bartsia alpina.

A number of localities for this species have been studied ecologically. These fall into two distinct groups floristically, this being well shown by diagram V. 4. These two groups are separated geographically and also by habitat.

BARTSIA ALPINA



Diagram

V. 4. Kulczynski diagram of quadrat samples from British sites of Bartsia alpina.

The first group is composed of the English samples which are all from flushed marsh areas and the second from Scotland where the species is characteristically a member of a rich wet mica schist ledge community. Floristically there are a number of overall constants these being Festuca ovina (agg.), Carex panicea, Euphrasia officinalis agg., and Ctenidium molluscum.

In England the species is characteristically found growing on hummocks, which are sometimes composed of a tufa core e.g. at Malham, and sometimes of glacial drift. There is usually a flow of base rich water between the hummocks with an open community developed including such species as Juncus articulatus and Schoenus nigricans. It has been suggested by Pigott (1956) that the formation of the glacial drift hummocks both at Teesdale and Malham is due to cattle trampling. At Orton the process of formation seems to be similar, cattle trampling being quite evident. The process also appears to have taken place at Tarn Moor nearby described by Holdgate (1955), where however Bartsia is not present although nearly all the other constant species of the Bartsia flushes grow here including Primula farinosa, but with the apparent exception of Euphrasia officinalis agg.

The samples studied are listed floristically in table V. 16. with the habitat details in table V. 17. In the majority

BARTSIA ALPINA

Sample No.	90	91	92	93	94	95	96
Locality	Great Close Nire, Malham, N. Yorks.	Great Close Nire, Malham, N. Yorks.	Orton, near Shap, Westmorland.	Orton, near Shap, Westmorland.	Wheysike House, Teesdale, Co. Durham.	Cetry Bank, Teesdale, Co. Durham.	Widdysbank Farm, Teesdale, Co. Durham.
Grid Ref.	34/908665	34/908665	35/627093	35/627093	35/855298	35/843298	35/837299
Altitude	1225'	1225'	850'	850'	1300'	1250'	1300'
Aspect	Hummock (20 cms. high)	Hummock (20 cms. high)	Hummock (15 cms. high)	Hummock (15 cms. high)	NE	S	Hummock (15 cms. high)
Slope					12°	70°	
Cover (%)	100	100	100	100	100	100	100
Sample Area (sq. m.)	0.54	0.66	0.45	0.18	4	1	0.45

BARTSIA ALPINA

Sample No.	97	98	99	100	101	102	103	104
Locality	Widdysbank Farm, Teesdale, Co. Durham.	Sand Sike, Teesdale, Co. Durham.	Sund Sike, Teesdale, Co. Durham.	Stuchd an Lochan, Glen Lyon, Perth.	Ben Lui, Perth.	Ben Lui, Perth.	Ben Chaiatel, Argyll.	Ben Chaiatel, Argyll.
Grid Ref.	35/837299	35/840309	35/840309	27/484451	27/270272	27/270272	27/343368	27/343368
Altitude	1300'	1350'	1350'	2800'	1750'	1750'	1750'	1750'
Aspect	Hummock (15 cms. high)	ENE	ENE	E	NE	NE	EW	EW
Slope		5°	5°	ledge	ledge	ledge	70°	ledge
Cover (%)	100	100	100	100	100	100	100	100
Sample Area (sq. m.)	0.45	1	1	-	1	1	1	0.25

Table V. 17. Localities and habitat details
of B. alpina sites.

of cases the hummock was taken to be the sample and thus the plot area is the hummock area in these. Samples from this type of hummock are numbers 90, 91, 92, 93, 96, and 97. Samples 94, 98 and 99 are from much smaller hummocks, which appear to be natural, in spring head areas. Here the runnels between the hummocks are small and the usual method of quadrating has been followed. Sample 95 is from a moraine^{ic} bank which is being eroded by the River Tees and also by springs and seepages emerging in the bank; here the Bartsia grows on the sides of ridges which undergo a cycle of building up a closed vegetation which then becomes unstable and breaks away. A detailed description is given by Pigott (1956). The constants (apart from the overall constants) are Selaginella selaginoides, Molinia caerulea, Carex lepidocarpa, Primula farinosa, Succisa pratensis, and Cratoneuron commutatum, of which Molinia caerulea, Primula farinosa, Succisa pratensis and Cratoneuron commutatum are exclusive to the English Bartsia sites. As well as a rich angiosperm flora the hummocks also carry an interesting bryophyte flora, listed for Teesdale by Pigott (1956) and for Malham by Proctor (1960).

The Scottish samples are from a very different type of habitat. This is typically a mica schist ledge with water running down the cliff on to and through the rich herb

<u>English marsh community.</u>		<u>Scottish wet ledge community.</u>	
		<i>Vaccinium myrtillus</i>	IV
<i>Selaginella selaginoides</i>	V	<i>Selaginella selaginoides</i>	IV
<i>Festuca ovina</i>	V	<i>Festuca ovina</i>	V
<i>Molinia caerulea</i>	V		
<i>Carex lepidocarpa</i>	IV		
<i>Carex panicea</i>	V	<i>Carex panicea</i>	V
		<i>Carex pulicaris</i>	V
		<i>Alchemilla alpina</i>	V
		<i>Alchemilla glabra</i>	V
<i>Bartsia alpina</i>	V	<i>Bartsia alpina</i>	V
<i>Euphrasia officinalis</i>	V	<i>Euphrasia officinalis</i>	V
		<i>Geum rivale</i>	V
<i>Leontodon hispidus</i>	IV		
<i>Linum catharticum</i>	IV		
<i>Parnassia palustris</i>	IV		
<i>Pinguicula vulgaris</i>	IV	<i>Pinguicula vulgaris</i>	V
		<i>Polygonum viviparum</i>	V
<i>Potentilla erecta</i>	IV		
<i>Primula farinosa</i>	V		
<i>Saxifraga aizoides</i>	IV	<i>Saxifraga aizoides</i>	V
		<i>Saxifraga oppositifolia</i>	V
		<i>Silene acaulis</i>	IV
<i>Succisa pratensis</i>	V		
		<i>Taraxacum officinale</i>	IV
		<i>Thalictrum alpinum</i>	V
		<i>Trollius europaeus</i>	IV
		<i>Viola riviniana</i>	IV
		<i>Breutelia chrysocoma</i>	IV
<i>Campylium stellatum</i>	IV		
<i>Cratoneuron commutatum</i>	V		
<i>Ctenidium molluscum</i>	V	<i>Ctenidium molluscum</i>	V
		<i>Racomitrium lanuginosum</i>	V
		<i>Rhytidiadelphus triquetrus</i>	V

Table V. 18. Comparison of English and Scottish communities, containing Bartsia alpina, with respect to species in presence classes IV and V.

vegetation which is developed on it. The composition of this community is shown by samples 100 to 104 in table V. 16, from three different localities. The constants are Carex pulicaris, Alchemilla alpina, Alchemilla glabra, Geum rivale, Polygonum viviparum, Saxifraga aizoides, Saxifraga oppositifolia, Thalictrum alpinum, Rhacomitrium lanuginosum and Rhytidiadelphus triquetrus all of which except Carex pulicaris, Saxifraga aizoides and Rhacomitrium lanuginosum are exclusive to the Scottish Bartsia sites. This community can be present in the same locality as the Dryas communities on mica schist e.g. at Ben Lui, and then the Bartsia community occupies the wetter ledges and the Dryas the drier ones. Thus Thalictrum alpinum, a species preferring wetter sites, is present in the Bartsia sample from Ben Lui and absent in the Dryas sample (number 24).

The English flush and the Scottish rock ledge communities are compared, with respect to species in presence classes IV and V, in table V. 18.

Soils.

Collection and storage of samples.

The samples were collected from beneath the plants in the rooting layer which was generally at the junction of the A_0 and A_1 horizons. They were air dried, lightly ground in a

pestle and mortar and sieved through a 2 mm. sieve; the resultant samples, on which all the analyses have been carried out, were kept in screw cap aluminium tubes until used.

Analysis methods.

pH. pH was determined electrometrically using an E.I.L. pH meter on a soil:water paste such that the paste was just at the "flow-point" without free standing water on the surface, as recommended by Jackson (1958).

Colour. Colour was assessed on the dry sample using the Munsell soil colour charts.

Texture. The texture was determined by the method of 'feel' which gives a rapid method of approximate textural classification. A small quantity of soil is placed in the palm of the hand and wetted until plastic, it is then kneaded until uniform. If the sample forms a fluid mass on wetting and is very gritty it is a sand. If the sample can be rolled into a ball, which is gritty and readily crumbles it is a loamy sand. If the sample is gritty, forms a cohesive ball which can be rolled into a cylinder, but breaks on gentle bending, it is a sandy loam. If the cylinder can be bent without breaking and there is no grittiness, stickiness (indication of clay) or silkiness (indication of silt) it is a loam.

(Method based on Brade-Birks 1959, modified by D.W.G. Shirlaw pers. comm.) Soils with a loss on ignition of over 25 % are

termed humic (see Hall 1945 p. 278).

Organic matter. This was estimated by loss on ignition.

Approximately 5 gms. of soil were accurately weighed out into a weighed crucible, which had previously been ignited, and then ignited for two hours in a muffle furnace at dull red heat. Carbonates were then reformed with 2N ammonium carbonate solution and after drying in an oven at 110°C . the crucible and sample were reweighed.

Determination of exchangeable cations. Ca, Mg, Na and K were determined on a leachate prepared as follows. 5 gms. of soil were placed in a soil funnel with glass wool in the base of the tube, and covered with a layer of coarse washed sand. This was leached with 250 ml. of N ammonium acetate solution. The leachate was then made up to 250 ml. with ammonium acetate solution.

Na and K were determined directly on the leachate using an EEL flame photometer.

Ca and Mg were determined on the leachate by emission spectrophotometry using a CF 4 Optika grating spectrophotometer with flame attachment. Emission wavelengths used were $383.8\text{ m}\mu$ for Mg and $422.7\text{ m}\mu$ for Ca with an oxy-hydrogen flame.

Exchangeable H was determined by equilibration of 5 gms. of soil and 10 ml. of Woodruff's buffer solution (8 gms. p-nitro-phenol, 40 gms. calcium acetate and 0.625 gms. MgO, dissolved in 1 litre of water and the pH adjusted to 7), allowing to stand for 10 minutes and then measuring the pH. Each change of 0.1 pH is equal to 1 meq. of exchangeable H per 100 gms. soil (Shirlaw and Willimot 1960, Jackson 1958).

Total Exchange capacity. The leached soil is now releached with 250 ml. of N sodium acetate solution giving a sodium saturated soil. The excess sodium acetate is then washed out with methanol, complete washing being indicated by the conductance of the effluent being less than 40 micromhos per cm. measured on a conductivity bridge; at this conductivity the quantity of Na released by hydrolysis just balances the quantity of excess Na (Bower et al 1952). Thus washing is stopped at this point since further washing results in hydrolysis giving a low exchange capacity. The soil is now leached with 250 ml. N ammonium acetate solution and the leachate made up to 250 ml. with ammonium acetate solution. Na is then determined on the flame photometer; corrected into meq. this gives the total exchange capacity.

Available nutrients. These were estimated by extracting the soil with N/2 acetic acid. 2.5 gms. soil were placed in a shaking bottle, 100 mls. of N/2 acetic acid added and the

bottle shaken for one hour on a reciprocating shaker. The suspension was then filtered and cleared by adding a little activated charcoal and refiltering. Available potash and phosphate were determined on this extract. Available potash was determined directly by flame photometry. Available phosphate was determined colorimetrically. 1 ml. of 5 % ammonium molybdate solution was added to 10 ml. extract and shaken. 6 drops of reducing agent (prepared by dissolving .2 gms. 1,2,4 aminonaphtholsulphonic acid, 12 gms. sodium metabisulphite and 2.4 gms. sodium sulphite in 100 ml. distilled water) were then added to reduce this, and let stand for 5 minutes to allow development of the molybdophosphoric blue colour, the colour intensity was then read colourimetrically and the phosphate concentration read off from a graph constructed from standards. These methods give an indication of the 'available' amounts of potash and phosphate present in the soil. Since results vary with the extractant solution the results are given on a status basis. The limits of the groups are as follows.

<u>Phosphate Status.</u>			<u>Potash Status.</u>		
p.p.m. P_2O_5			p.p.m. K_2O		
0 - 1.5	Very low		0 - 6	Very low	
1.5 - 3	Low		6 - 10	Low	
3.1 - 6	Medium		10 - 18	Medium	
6.1 - 10	Medium high		18 - 28	Medium high	
Over 10.1	High		28 - 35	High	
			Over 35	Very high	

Mechanical Analysis. 50 gms. of soil were weighed out and 25 ml. of 'Calgon' (a dispersing agent) and 200 ml. of water added. This was then shaken on a reciprocating shaker for nine hours. The soil suspension was then decanted into a 1 litre measuring cylinder, water added up to the litre mark and a few drops of amyl alcohol added to break up the froth. The cylinder was then shaken end to end for 30 seconds. After standing for 4 minutes 30 seconds a Bouyoucos hydrometer (graduated in terms of gms. of soil per litre of solution) was placed in the suspension and a reading taken at 5 minutes. This gives the weight of silt and clay fractions. At the same time the temperature was read since the hydrometer is graduated at 20°C. and a correction of +.3 units for every 1° above 20° and -.3 units for every 1° below 20° must be made. After 5 hours a second hydrometer and temperature reading was made, this giving the clay fraction per litre. The majority of the suspension was then poured away retaining all the sand fraction. This was then washed into a 400 ml. beaker which was filled to 10 cm. depth with water. The temperature was taken and the suspension allowed to stand the requisite time for fine sand sedimentation on the International system (as given by Piper 1942 p. 70) and the supernatant liquid decanted off; the beaker was then refilled and the process repeated

until the supernatant liquid (containing the clay and silt fractions) was clear. The fine and coarse sand fractions were then separated by sieving through a 0.2 mm. sieve with a jet of water and collecting the fine sand; after oven drying the coarse and fine sand fractions were weighed. It will be noted that the usual procedure has been modified so that limestone fragments are included in the coarse sand fraction; this has been done because of their textural importance.

Results.

Introduction.

The results of the cation exchange analysis are presented both as millequivalents per 100 gms. soil and as a percentage of the total. Where the total capacity as obtained by summing of the individual cations (total calculated - T.C.) is within 25 % of the total capacity as determined experimentally (Total determined - T.D.) the percentages are computed on the basis of the T.C. Where however the T.C. is greater by more than 25 % of the T.D. the percentages are computed on the basis of the latter. This is done by subtracting the sum of the cations Mg, Na, K and H from the T.D. and taking the remainder as the amount of Ca. This procedure is justified by the fact that in all cases where it has been adopted the pH is greater than 7, showing that free carbonate is almost certainly present.

As pointed out by Jackson (1958) under these conditions Ca is dissolved by an ammonium acetate solution "beyond its true activity for plant use".

The analyses and results will be considered under species headings where they have been arranged in the same way as the groups distinguished by the Kulczynski floristic analyses.

Gentiana verna.

As already stated the flush communities are somewhat varied floristically and this feature is reflected in the soil profiles. Thus samples 2, 3 and 5 are from glacial drift deposits azonal in sample 2 and with a zone of medium brown soil developed above the drift in samples 3 and 5. Sample 6 has the following profile:-

2-3 cms. dark medium brown soil
52 cms. light medium brown soil
(earthworms present)
Sugar limestone rock.

This is much deeper than most limestone rendzina profiles and may partly explain the development of what is floristically a flush community.

The limestone grassland samples with the exception of samples 16 and 18 are from short mull rendzina profiles, sample 9 is typical:-

12 cms. medium brown soil
(earthworms present)
Limestone rock.

Sample No.	Locality	Textural Cl.	Colour	pH.
1	Mickle Fell, Teesdale, N. Yorks	Sandy loam	10 YR 3/2 v. dk. grey brown	7.2
2	Cetry Bank, Teesdale, Co. Durham	Loamy sand	10 YR 4/2 dk. grey brown	7.9
5	Haugh Hill, Teesdale, Co. Durham	Sandy loam	10 YR 4/2 dk. grey brown	7.3
6	Tinkers Sike, Widdybank Fell, Co. Durham	Loamy sand	10 YR 3/4 dk. yellowish brown	7.4
7	High Hurth Edge, Teesdale, Co. Durham	Humic	10 YR 3/2 v. dk. grey brown	6.3
8	Grains o' th' Beck, Teesdale, N. Yorks	Loamy sand	10 YR 2/1 black	5.7
9	Bellbeaver Rigg, Teesdale, Cumberland	Humic	10 YR 3/2 v. dk. grey brown	5.6
12	Black Head, Co. Clare	Humic	10 YR 4/2 dk. grey brown	6.8
16	Gentian Hill, Co. Galway	Sandy loam	10 YR 5/2 grey brown	7.7
18	Ballyvaghan, Co. Clare	Sandy	10 YR 5/1 grey	7.9

Table V. 19.

Sample No.	Loss on ignition	meq/ 100 gms soil				Total				% of Total				Available nutrients (status)
		Ca	Mg	Na	K	H	calc.	det.	Ca	Mg	Na	K	H	
1	13.2	61.0	4.17	0.65	0.29	-	66.11	29.57§	82.7	14.1	2.2	1.0	-	M.High Low
2	5.2	29.75	1.79	0.17	t	-	31.71	12.17§	83.9	14.7	1.4	t	-	High V.Low
5	6.5	32.75	1.25	0.41	0.24	-	34.65	17.39§	89.1	7.2	2.4	1.4	-	Med. Low
6	14.7	45.0	2.04	0.39	0.03	-	47.46	23.04§	89.3	8.8	1.7	0.1	-	High V.Low
7	33.4	45.0	5.83	0.59	0.76	1.0	53.18	54.78	84.6	11.0	1.1	1.4	1.9	M.High M. High
8	17.5	41.25	3.96	0.65	0.63	4.0	50.49	50.43	81.7	7.8	1.3	1.2	7.9	High M. High
9	32.0	37.75	2.92	0.61	0.41	4.0	45.69	53.04	82.6	6.4	1.3	0.9	8.8	M.High Low
12	25.4	38.0	6.25	0.43	0.27	4.0	48.95	45.22	77.6	12.8	0.9	0.5	8.2	Low Med.
16	13.1	50.0	2.79	0.70	0.38	-	53.87	24.78§	84.4	11.3	2.8	1.5	-	Med. High
18	2.8	46.0	2.83	0.85	0.01	-	49.69	4.78	82.0	17.8	0.2	0.2	-	Med. Low

§ Percentages computed on the basis of the 'Total Determined'.

Table V. 19. Soil analyses from British G. verna sites.

Samples 16 and 18 are from glacial drift basal material with 20 cms. of medium brown soil developed above in 16, while 18 has 16 - 25 cms. of grey sand on top of the calcareous boulder clay.

The analytical results given in table V. 19. show that the flushes have a uniformly high pH while the grasslands are more varied. This appears to be correlated with the humus content since the lower the loss on ignition the higher the pH. The lower pH of some of the grassland samples is reflected in the presence of exchangeable H. The percentage of exchangeable Ca in the total capacity is uniformly high. It may also be noted that as might be expected the highest amounts of exchangeable Na are found in the sea side samples, numbers 16 and 18. Available nutrients are rather varied in status.

In general there are no distinct soil differences between the English and Irish grassland sites, and this follows the lack of floristic distinction.

The soil analysis of sample 1 supports the view that it is an early stage in development of the limestone grassland type, since it has a higher pH and smaller loss on ignition than the typical mull rendzina sites.

Mechanical analyses have been carried out on four samples from Teesdale sites of Gentiana verna; the results are given

Sample	2	2	6	10
Initial Wt. of sample	50.0 gms.	50.0 gms.	50.0 gms.	50.0gms.
Wt. Clay fraction	7.3	5.3	4.45	6.3
Wt. Silt fraction	10.4	6.25	3.1	9.25
Wt. Fine Sand fraction	20.35	20.8	5.45	8.4
Wt. Coarse Sand fraction	11.45	17.9	36.3	24.05
Total final wt.	49.5	50.25	49.3	48.0
% Clay	14.7	10.6	9.0	13.1
% Silt.	21.0	12.4	6.3	19.3
% Fine sand.	41.2	41.4	11.1	17.5
% Coarse sand.	23.1	35.6	73.6	50.1
% Loss by solution.	1.0	-	1.4	4.0
Texture designation.	Loam.	Loam.	Loamy sand	Loam.

Table V. 20. Mechanical analyses of soil samples from G. verna sites in Teesdale.

Sample No.	Locality	Textural Cl.	Colour	pH.
21	Chermignon nr. Leukerbad, Valais, Switzerland	Loamy sand	10 YR 5/3 brown	6.3
22	Gemmi Pass, nr. Leukerbad, Valais, Switzerland	Humic	10 YR 2/1 black	6.0
23	Riederalp, nr. Mörel, Valais, Switzerland	Loamy sand	10 YR 4/2 dk.grey brown	4.4
24	Briand, nr. Sass-Balen, Valais, Switzerland	Loamy sand	10 YR 5/2 grey brown	4.6
25	Charbonniere, nr. Assy, Haute Savoie, France	Humic	10 YR 4/1 dk.grey	7.2
27	Le Leutellet, nr. Megève, Haute Savoie, France	Loamy sand	10 YR 6/3 pale brown	5.9
28	La Frie, nr. Les Houches, Haute Savoie, France	Loamy sand	10 YR 4/1 dk.grey	7.1
A	Bella Lui, nr. Crans, Valais, Switzerland	Humic	10 YR 2/2 v.dk.brown	6.5

Table V. 21.

Sample No.	Loss on ignition	meq/ 100 gms soil				Total calc.	Total det.	% of Total				Available nutrients (status) PO ₄ K ₂ O			
		Ca	Mg	Na	K			H	Ca	Mg	Na		K	H	
21	12.9	15.5	2.29	0.28	0.40	0.5	18.97	24.78	81.7	12.1	1.5	2.1	2.6	High	Low
22	50.7	77.0	5.63	0.74	0.71	3.0	87.08	80.87	88.4	6.5	0.8	0.8	3.5	High	M. High
23	16.0	4.87	1.29	0.24	0.41	9.0	15.81	28.70	30.8	8.2	1.5	2.6	56.9	M. High	Med.
24	11.3	5.87	1.46	0.24	0.38	6.0	13.95	21.30	42.1	10.5	1.7	2.7	43.0	High	Med.
25	28.5	90.0	7.40	1.30	0.74	-	97.44	66.09§	85.7	11.2	2.0	1.1	-	M. High	M. High
27	12.6	14.0	1.83	0.41	0.24	2.0	18.48	22.17	75.8	9.9	2.2	1.3	10.8	High	Low
28	21.3	63.0	4.58	0.93	0.32	-	68.83	43.04	86.4	10.6	2.2	0.7	-	Med.	V. Low
A	35.5	69.0	5.00	0.52	0.56	1.0	76.08	61.74	90.7	6.6	0.7	0.7	1.3	M. High	M. High

§ Percentages computed on the basis of the 'Total Determined'.

Table V. 21. Soil analyses from Alpine G. verna sites.

in table V. 20. It will be seen that sand accounts for more than 60 % of the sample in each case with the clay content uniformly small, indicating an open soil with good drainage properties.

Results for the analyses of soil samples from a number of Alpine sites are given in table V. 21. The most striking feature is the much greater variation in pH and amounts and percentages of exchangeable Ca and H. Amounts of Mg, Na, and K do not differ and again the nutrient status is variable. The results show that Gentiana verna in Britain is confined to a narrow range of soil conditions, whereas in the Alps it is able to grow on a much wider range of soil conditions.

Potentilla fruticosa.

As noted in the section on vegetation the samples from the Lake District and Wynch Bridge, Teesdale are allied in their habitat conditions, all three being rock ledge or crevice sites with skeletal soils. The rest of the Teesdale sites samples numbers 32, 33, 36 and 37 are all probably allochthonous soils in various stages of development, 32 and 33 at the earliest deposition stage and 36 and 37, higher up the bank and much less often flooded, at rather later stages. The description of 36 is as follows, at least 60 cms. medium brown loam a little darker towards the bottom, very few stones,

Sample No.	Locality	Textural Cl.	Colour	pH.
29	Wasdale, Cumberland	Humic	10 YR 3/2 v.dk.grey brown	6.3
30	Pillar, Ennerdale, Cumberland	Loamy sand	10 YR 2/2 v.dk.brown	6.3
33	High Force, Teesdale, Co. Durham	Sand	10 YR 4/2 dk.grey brown	6.9
34	Ballynatty, Co. Mayo	Humic	10 YR 4/1 dk.grey	7.0
35	Castle Lough, Co. Clare	Humic	10 YR 2/2 v.dk.brown	6.9
36	High Force, Teesdale, Durham	Loamy sand	10 YR 3/3 dk.brown	6.3
37	Cronkley Scar, Teesdale, N. Yorks.	Loamy sand	10 YR 3/4 dk.yellowish brown	5.1
38	Ballyvaghan, Co. Clare	Humic	10 YR 4/1 dk.grey	6.7

Table V. 22.

Sample No.	Loss on ignition	meq/ 100 gms soil.				Total calc. det.	Total	% of Total				Available nutrients PO ₄ -K ₂ O		
		Ca	Mg	Na	K			H	Ca	Mg	Na		K	
29	21.2	30.75	7.71	0.54	0.29	9.0	48.99	44.35	62.8	15.7	1.1	0.6	18.4	Med. Med.
30	28.0	11.75	4.17	0.67	0.54	16.0	33.13	41.30	35.5	12.6	2.0	1.6	48.3	low M. High
33	12.8	5.87	1.25	0.11	0.04	-	7.27	8.26	80.7	17.2	1.5	0.6	-	Med. Low
34	22.6	39.25	7.50	0.26	0.18	1.0	48.19	38.70	81.4	15.6	0.5	0.4	2.1	Med. Med.
35	73.9	212.77	7.15	2.01	0.99	2.0	224.92	-	94.6	3.2	0.9	0.4	0.9	High V. High
36	10.7	11.12	2.88	0.09	0.21	8.0	22.30	21.30	49.9	12.9	4.0	9.4	35.9	Med. Med.
37	19.5	17.97	3.00	0.50	0.26	13.0	34.73	36.09	51.7	8.6	1.4	0.8	37.4	Med. M. High
38	30.4	61.75	2.88	0.65	0.15	4.0	69.43	59.13	88.9	4.2	0.9	0.2	5.8	Med. Low

Table V. 22. Soil analyses from P. fruticosa sites.

earthworms present. According to Kubiens (1953) this would be classed as an allochthonous brown warp soil. The Irish samples seem, with the exception of 34 which is azonal on undifferentiated glacial drift, to be on rendzina profiles which have been modified by the changing water table.

The analytical results are given in table V. 22. The Lake District samples are seen to have comparatively high percentages of exchangeable H although the amounts of exchangeable Ca present are not low. The difference between the frequently flushed site by the Tees 33 and the less flushed and more leached sites higher up the bank 36 and 37 is well shown in the amounts and percentages of exchangeable H and the drop in pH, although the latter two have greater amounts of exchangeable Ca. The Irish sites are all very base rich with high pH and Ca percentages. Again, available nutrients are variable, their levels not apparently being critical to this species.

Three mechanical analyses have been carried out the results being given in table V. 23. They are from the sites by the Tees and show the increase in finer fractions with increase in maturity of the soil profile and the decrease in the coarse sand fraction.

Sample	37	36	33
Initial Wt. of sample	40.0 gms.	50.0 gms.	50.0 gms.
Wt. Clay fraction	3.3	4.3	1.3
Wt. Silt. fraction	5.85	7.25	3.25
Wt. Fine sand fraction	16.75	25.6	9.8
Wt. Coarse sand fraction	12.1	11.45	37.1
Total Final wt.	38.0	48.6	51.45
% Clay.	8.7	8.8	2.5
% Silt.	15.4	14.9	6.3
% Fine sand.	44.1	52.7	19.1
% Coarse sand.	31.8	23.6	72.1
% Loss by solution	5.0	2.8	-
Texture designation	Loamy sand.	Loamy sand.	Sand.

Table V. 23. Mechanical analyses of soil samples from *P. fruticosa* sites in Teesdale.

Sample No.	Locality	Textural Cl.	Colour	pH.
39	Great Dun Fell, Westmorland	Humic	10 YR 3/2 v.dk.grey brown	6.9
42	Little Fell, Westmorland	Humic	10 YR 2/2 v.dk.brown	5.8
43	Mickle Fell, N. Yorks	Humic	10 YR 2/2 v.dk.brown	7.3
44	Ben Lawers, Perth	Loamy sand	10 YR 4/1 dk.grey	6.3
46	Cam Creag, Perth	Loamy sand	10 YR 3/1 v.dk.grey	6.3

Sample No.	Loss on ignition	meq/ 100 gms soil				Total	Total	Total	% of Total				Available nutrients (status)	
		Ca	Mg	Na	K				H	Ca	Mg	Na		K
39	32.1	72.50	4.17	1.48	0.42	1.0	79.57	72.17	91.1	5.2	1.9	0.5	1.3	M.High Med.
42	34.7	47.37	4.17	0.50	0.65	11.0	63.69	60.00	74.4	6.5	0.8	1.0	17.3	M.High M. High
43	45.4	116.25	3.54	1.33	0.59	-	121.71	73.91§	91.3	4.8	1.8	0.8	-	M. High M. High
44	10.9	11.50	3.42	0.02	0.12	7.0	22.06	16.96	52.1	15.5	0.1	0.5	31.7	Low M. High
46	27.5	41.25	4.17	0.52	0.45	10.5	56.87	48.70	72.5	7.3	0.9	0.8	18.5	Med. M. High

§ Percentages computed on the basis of the 'Total Determined'.

Table V. 24. Soil analyses from M.alpestris sites.

Myosotis alpestris.

The simple division into types of habitat is maintained in consideration of the soils data. The Teesdale sites are all on immature mull rendzinas on Carboniferous limestone e.g. sample 42 has 25 cms. of blackish soil with limestone fragments towards the bottom directly on limestone rock. The Breadalbane sites are all on lithosols of developing soil and mica schist fragments on rock ledges. Their more skeletal nature is seen from the smaller loss on ignition percentages in comparison with those from the Teesdale sites, see table V. 24. There are also marked differences in the exchangeable Ca and H percentages between the two groups, reflecting the higher calcium content of limestone over mica schist. It will be noted that the amounts of exchangeable Mg, Na and K are very similar.

Dryas octopetala.

Unfortunately no soils information is available on the second groups of samples distinguished floristically and therefore no comparisons can be made between it and the first group. Also the number of samples which could be analysed from each of the remaining groups was small so that no valid comparisons can be made between groups. However a few points can be made. All the soil profiles from which samples were

taken proved to be immature. The exact type was rather variable; thus samples 51, 53 and 54 are from mica schist ledges, 65 and 66 from immature rendzinas on Durness limestone in N. Sutherland, 76, 77 and 78 from similar soils on Carboniferous limestone in W. Ireland and 81 from Carboniferous limestone at Arncliffe, N. Yorks. The other sample from this region was on a mull rendzina developed on a steep slope where terracing due to soil creep was taking place. The other sites examined, provided a wide range of conditions, but all with the common feature of providing an open habitat. Thus 48 from Teesdale has a maximum of 5 cms. of dark brown soil on sugar limestone and the best growth of Dryas appearing to take place where the substrate is almost entirely limestone fragments. Sample 67 is from an alluvial platform by the R. Tralagill at Inchnadamph with 25 cms. of alluvium resting on limestone rock. Further North 79 and 80 from Bettyhill are on a sand hillock - a complete lithosol. Another sample from Bettyhill, 75, is from a rocky slope on a banded gneiss already described (p.145), while 71, 72, 73 and 74 from Raasay are all on rocky slopes and ledges on what is probably Jurassic Lias. Finally sample 83 from Llyn Idwal, N. Wales is on an entirely skeletal soil derived from the intrusive rock already described (p.147).

Sample No.	Locality	Textural Cl.	Colour	pH.
48	Cronkley Fell, Teesdale, N. Yorks	Humic	10 YR 2/2 v.dk.brown	7.1
51	Ben Lui, Perth	Humic	10 YR 2/2 v.dk.brown	7.0
53	Creag an Lochan, Perth	Loamy sand	10 YR 3/2 v.dk.grey brown	7.1
54	Caenlochan Glen, Angus	Loamy sand	10 YR 3/2 v.dk.grey brown	6.6
66	Durness, Sutherland	Humic	10 YR 3/2 v.dk.grey brown	6.2
67	Inchnadamph, Sutherland	Sandy	10 YR 5/2 grey brown	7.5
75	Bettyhill, Sutherland	Loamy sand	10 YR 4/2 dk.grey brown	6.2
76	Rannagh, Co. Clare	Humic	10 YR 3/2 v.dk.grey brown	7.2
77	Croagh, Co. Clare	Humic	10 YR 2/2 v.dk.brown	6.8
79	Bettyhill, Sutherland	Sandy	10 YR 5/3 brown	7.4
82	Cowside Beck, Littondale, N. Yorks	Loamy sand	10 YR 3/2 v.dk.grey brown	7.3
83	Llyn Idwal, Glyder Fawr, Caernarvon	Humic	10 YR 3/1 v.dk.grey	5.9

Table V. 25.

Sample No.	Loss on ignition	meq/ 100 gms soil							Total					% of Total					Available nutrients (status)		
		Ca	Mg	Na	K	H	calc.	det.	Ca	Mg	Na	K	H	PO ₄	K ₂ O	Med.					
48	27.4	67.5	2.83	0.52	0.14	-	70.99	43.04§	91.9	6.6	1.2	0.3	-	High	Med.						
51	22.2	31.5	3.92	0.37	0.05	4.5	40.34	30.87	78.1	9.7	.9	0.1	11.2	Low	Low						
53	15.0	35.33	4.04	0.66	0.10	-	40.13	-	88.0	10.1	1.6	0.2	-	Med.	Low						
54	17.5	28.75	3.58	0.63	0.08	-	33.04	30.43	87.0	10.8	1.9	0.2	-	Med.	Low						
66	23.0	24.25	1.04	0.80	0.27	13.0	39.36	46.96	61.6	2.6	2.0	0.7	33.0	Low	Med.						
67	4.8	6.25	3.25	0.54	t	-	10.04	8.70	62.2	32.4	5.4	t	-	Med.	V.Low						
75	10.2	10.75	2.21	0.26	0.77	7.0	20.99	19.57	51.2	10.5	1.2	3.7	33.3	V.Low	Low						
76	44.2	118.75	2.64	1.84	0.68	2.0	125.91	-	94.3	2.1	1.5	0.5	1.6	Low	High						
77	77.9	196.43	8.69	2.75	0.94	2.5	211.31	-	92.8	4.1	1.3	0.4	1.2	M.High	High						
79	1.8	6.25	0.92	0.09	t	-	7.26	5.22§	80.6	17.6	1.7	t	-	Low	V.Low						
82	11.0	40.75	2.40	0.41	0.28	-	43.84	19.13	83.8	12.5	2.1	1.5	-	Med.	Low						
83	26.8	20.5	3.13	0.39	0.32	3.0	27.34	35.65	75.0	11.4	1.4	1.2	11.0	M.High	Med.						

§ Percentages computed on the basis of the 'Total Determined'.

Table V. 25. Soil analyses from British D.octopetala sites.

Analyses from a number of these sites are presented in table V. 25. The chief point of note is the maintenance of a comparatively high base status in all the samples despite their varied geological origins; thus the combined exchangeable Ca and Mg percentages do not drop below 60 % in any sample. This is correlated with the pH which is at a minimum of 5.9 in the Welsh sample. Thus although the absolute amount of Ca can be very variable - from 6 meq./100 gms. soil in a humus deficient sand lithosol (79) to nearly 200 meq. in a sample 78 % composed of humus (77) the ratio of bivalent cations to the rest of the exchange capacity and in particular to the exchangeable H is much more important. Amounts of K and Na do not appear to be as important as will be seen from the results.

Table V. 26 gives the results for some foreign soil samples. Samples 84, 86, 88, 89 and B are from the Alps, all of them on rendzina soils on Jurassic limestone except 86 which is from a shale alluvial platform by a stream which was azonal, this sample has already been shown to be floristically distinct. Samples C, D, and E are from Iceland from three Dryas sites on recent lava. Finally F, G and H are from Spitzbergen, F and G on limestone lithosols and H from a mica schist lithosol. Here again the importance of a high

Sample No.	Locality	Textural Cl.	Colour	pH.
84	Gemmi Pass, nr. Leukerbad, Switzerland	Loamy sand	10 YR 4/2 dk.grey brown	5.9
86	Le Leutellet, nr. Megève, France	Loamy sand	10 YR 4/1 dk.grey	7.5
88	Lanche du Pra, nr. Sallanches	Sandy loam	10 YR 4/1 dk.grey	7.2
89	Clavinenalp, nr. Leukerbad, Switzerland	Humic	10 YR 3/2 v.dk.grey brown	7.1
B	Bella Lui, nr. Crans, Switzerland	Humic	10 YR 2/2 v.dk.brown	6.5
C	Tuugnaa R., nr. Vatnakokull, Iceland	Loamy sand	10 YR 3/2 v.dk.grey brown	6.1
D	Hrauneyjarvisl, nr. " , Iceland	Loamy sand	10 YR 2/2 v.dk.brown	5.8
E	Hald, nr. Vatnajokull, Iceland	Loamy sand	10 YR 2/2 v.dk.brown	5.7
F	Limestone scree, King's Bay, Spitzbergen	Loamy sand	10 YR 4/2 dk.grey brown	7.0
G	Limestone raised beach, King's Bay, Spitzbergen	Loamy sand	10 YR 4/2 dk.grey brown	6.1
H	Mica schist scree, King's Bay, Spitzbergen	Loamy sand	10 YR 3/3 dk.brown	6.0

Table V. 26.

Sample No.	Loss on ignition	meq/ 100 gms soil							Total				% of Total				Available nutrients (status)
		Ca	Mg	Na	K	H	calc.	det.	Ca	Mg	Na	K	H	PO ₄	K ₂ O		
84	11.3	22.0	3.13	0.28	0.17	1.0	24.58	24.78	81.4	12.6	1.1	0.7	4.1	M.High	Low		
86	8.4	37.75	2.71	0.39	0.35	-	41.20	11.74§	70.6	23.1	3.3	3.0	-	M.High	Med.		
88	21.5	77.0	4.27	0.61	0.71	-	82.59	37.83§	85.2	11.3	1.6	1.9	-	High	M. High		
89	32.6	93.5	5.42	0.80	0.49	-	100.21	59.13	88.6	9.2	1.3	0.8	-	M.High	M. High		
B	35.5	69.0	5.00	0.52	0.56	1.0	76.08	61.74	90.7	6.6	0.7	0.7	1.3	M.High	M. High		
C	7.0	6.25	3.13	0.46	0.36	0.5	10.50	16.96	59.2	29.8	4.4	3.4	4.8	Med.	Med.		
D	6.5	5.0	3.02	0.37	0.42	1.0	9.81	15.22	51.0	30.8	3.8	4.3	10.2	High	Med.		
E	4.8	4.5	2.40	0.35	0.44	1.5	9.19	14.35	49.0	26.1	3.8	4.8	16.3	Med.	Med.		
F	9.7	18.0	5.83	0.37	0.24	-	24.44	19.57	73.6	23.8	1.5	1.0	-	High	Med.		
G	6.9	10.12	2.81	0.24	0.15	0.5	13.82	15.65	73.2	20.3	1.7	1.1	3.6	High	Low		
H	21.2	33.75	8.75	0.46	0.56	4.0	47.52	42.17	71.0	18.4	1.0	1.2	8.4	High	High		

§ Percentages computed on the basis of the 'Total Determined'.

Table V. 26. Soils analyses from European D.octopetala sites.

ratio of bivalent cations to exchangeable H is brought out, the combined exchangeable Ca and Mg percentage not falling below 75 % although again the absolute Ca values are variable ranging from around 5 meq. in the Iceland lava samples up to 93.5 meq. in one of the Alpine rendzina soils. Correlated with this is the relatively small range in pH, from 5.7 to 7.5.

Bartsia alpina.

As has been mentioned earlier (p.151) most of the English samples are from hummocks of glacial drift or tufa and glacial drift banks, all of which are azonal. In the spring head ones, numbers 98 and 99 there is a layer of 11 - 28 cms. of dark brown peaty soil overlaying blue clay. The Scottish samples, already described, are from skeletal soils on mica schist rock ledges.

The analytical results are given in table V. 27. The English samples tend to have rather more exchangeable Ca on the average than the Scottish ones, but the exchangeable Ca and Mg percentage does not drop below 70 % in either group. The only other difference between the two groups is that available phosphate is high in the English samples, but low in the Scottish ones.

Sample No.	Locality	Textural Cl.	Colour	pH.
90	Great Close Mire, Malham, N. Yorks	Loamy sand	10 YR 3/1 v.dk.grey	7.0
92	Orton, nr. Shap, N. Yorks	Loamy sand	10 YR 4/1 dk.grey	7.1
94	Wheysike House, Teesdale, N. Yorks	Humic	10 YR 3/2 v.dk.grey brown	6.3
95	Cetry Bank, Teesdale, Co.Durham	Loamy sand	10 YR 4/2 dk.grey brown	7.9
98	Sand Sike, Teesdale, Co.Durham	Humic	10 YR 3/2 v.dk.grey brown	6.7
100	Stuchd an Lochan, Perth	Loamy sand	10 YR 4/2 dk.grey brown	7.6
101	Ben Lui, Perth	Humic	10 YR 2/2 v.dk.brown	7.0
103	Ben Chaistal, Argyll	Loamy sand	10 YR 3/2 v.dk.grey brown	6.5

Table V. 27.

Sample No.	Loss on ignition	meq/ 100 gms soil				Total		% of Total				Available nutrients (status)		
		Ca	Mg	Na	K	H	calc. det.	Ca.	Mg	Na	K		H	
90	21.8	79.0	4.17	0.89	0.28	-	84.34	36.96§	85.5	11.3	2.4	0.8	-	High Med.
92	13.8	68.0	4.58	0.78	0.32	-	73.68	24.78§	77.1	18.5	3.1	1.3	-	High Low
94	25.7	38.0	4.27	0.67	0.51	0.5	43.95	46.09	86.5	9.7	1.5	1.2	1.1	M.High High
95	5.2	29.75	1.79	0.17	t	-	31.71	12.17	83.9	14.7	1.4	t	-	High V.Low
98	27.4	50.0	1.08	0.55	0.12	3.0	54.75	57.29	91.3	2.0	1.0	0.2	5.5	M.High Low
100	18.1	10.16	2.37	0.35	0.25	-	13.13	13.36	77.4	18.1	2.7	1.9	-	V.Low Med.
101	22.2	31.5	3.92	0.37	0.05	4.5	40.34	30.87	78.1	9.7	0.9	0.1	11.2	Low Low
103	13.2	17.5	3.38	0.46	0.18	7.0	28.52	23.04	61.4	11.8	1.6	0.6	24.5	Low Med.

§ Percentages computed on the basis of the 'Total Determined'.

Table V. 27. Soil analyses from B.alpina sites.

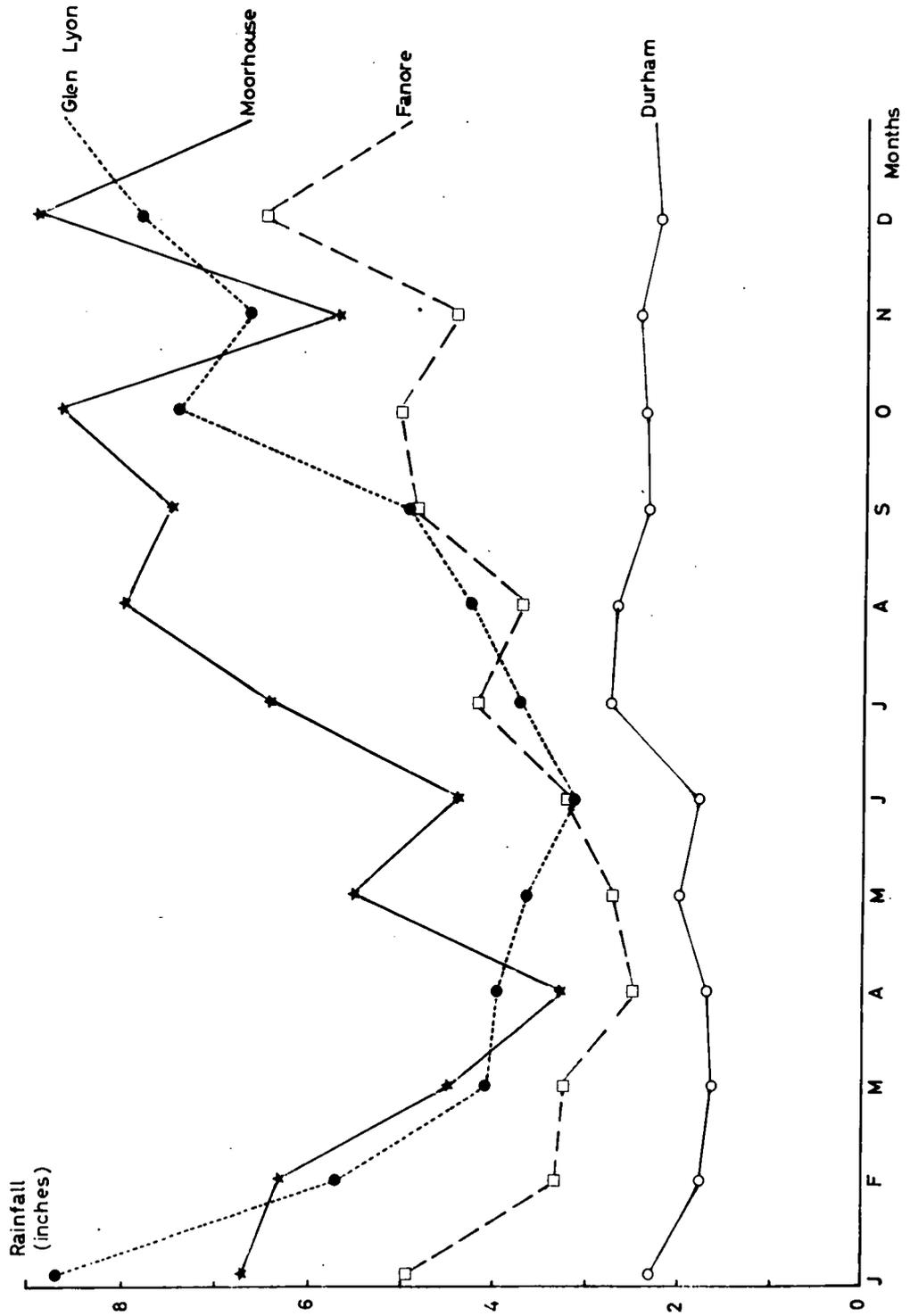
Discussion.

All the soils studied have certain features in common. They have all had a high base status. This is correlated with the high ratio of bivalent cations to exchangeable H which exists in all these samples independent of the actual amounts of exchangeable Ca and Mg present.

The soil profiles also have one feature in common. In nearly all cases they are very shallow and mostly immature, many of them being azonal soils of one type or another. In those cases where the actual soil depth is large (in some samples on glacial drift) there is a constant removal of material from the surface mostly by water erosion. These features all tend to give open unstable habitats, a general point of great importance in trying to understand the reasons for the presence of these species in their disjunct British localities.

Climate.

The climate of Teesdale has a number of interesting features. Data for the rainfall of the region have been given by Glasspoole (1932), and it is clear from his map that annual rainfall increases rapidly towards higher ground to the West of the area. Thus at Middleton (750') it is approximately 35", while at Langdon Beck (1270') it is about 50", rising to



Diagram

V. 5. Average monthly distribution of rainfall at Moorhouse; Teesdale; Durham; Glen Lyon, Perth; and Fanore, Co. Clare.

55" on Widdybank Fell (1700') and Cronkley Fell (1800') and reaching a maximum of over 70" per annum on Mickle Fell (2590') and the high ground of Knock Fell (2600') and Cross Fell (2930'). At Moorhouse (1800') the computed mean rainfall is given as between 60" and 70" per annum; an average over a period of six years there gives a figure of 76.2". It may therefore be necessary to increase Glasspoole's computed figures for the West of the area. The distribution of average rainfall per month at Moorhouse is given in diagram V. 5. Although the amounts are less towards the east of the area the annual distribution will probably be similar. The driest part of the year is the spring, with a wet summer and autumn (although with a decrease in November) and then a high winter precipitation which often falls as snow. This annual distribution may be compared with that at Durham 32 miles to the east at 336' altitude. The contrast is striking; at Durham there is much more even distribution over the year with less rain at all times. Two other monthly distributions are given, one from Glen Lyon, Perth, (station at Meggernie Castle altitude 700' (taken from London Met. Office 1958)) and the other from Fanore, Co. Clare, on the coast at nearly sea level in the Burren area (figures from Irish Dept. of Transport and Power unpublished records). Both, although having less rain than Moorhouse (average 64.17" in Glen Lyon and 49.1" at

Fanore) have a similar type of annual distribution, spring and early summer being dry, and then becoming steadily wetter with December and January being the wettest months.

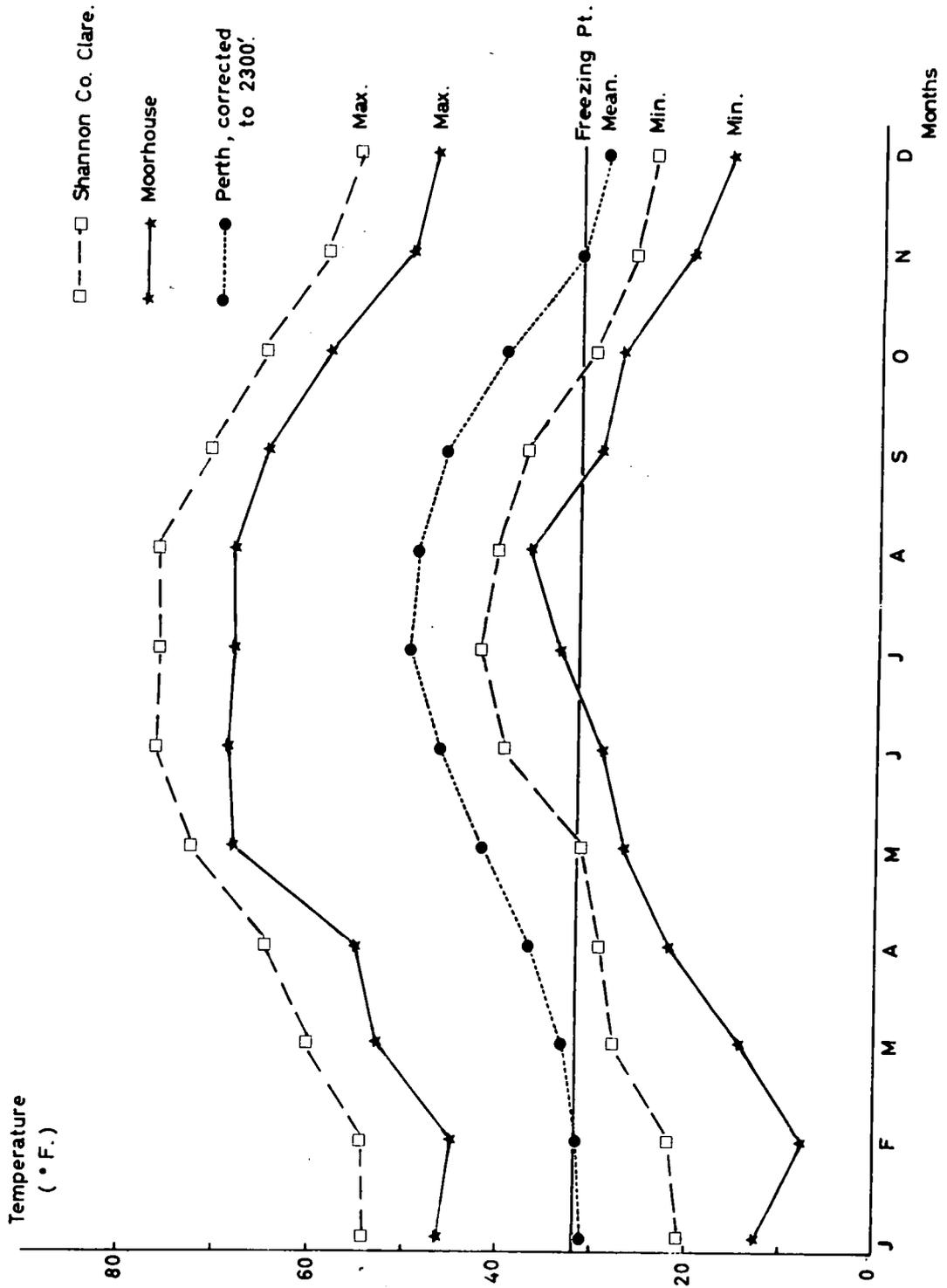
With regard to snow Manley (1936) has suggested that there is a notable increase in the amount of snow-lie above High Force (1000'). The average over six years of the number of snow days at Moorhouse is given in table V. 28.

Month	O	N	D	J	F	M	A	M
Number of snow days.	.2	1.3	7	13	18	13	3	1

Table V. 28. Average number of snow days at Moorhouse.

It may be expected that the situation will be similar at similar altitudes further to the east e.g. at Widdybank and Cronkley Fells. Actual snow lie on a community will, of course, depend on a number of factors such as relief, wind direction and strength etc., but a foot of level snow was observed on the sugar and unaltered limestone grassland communities on Widdybank Fell in February 1960 which was, in general, a rather mild winter.

Information on temperature is more scanty. The monthly average maximum and minimum temperature over a six year period from Moorhouse are plotted on diagram V. 6. They are compared with similar figures from Shannon Airport, Co. Clare (30 miles



Diagram

V. 6. Average monthly maximum and minimum temperatures for Moorhouse, Teesdale and Shannon, Co. Clare, and mean monthly temperatures for Perth corrected to 2300'.

south of the Burren district), and with the mean monthly temperature record from Perth corrected to 2300' assuming a lapse rate of 3°F./1000' (taken from Poore 1955b.). It will be noted that the Moorhouse record has only two months a year in which the average minimum temperature is above freezing point; also the maximum graph shows a very flat peak for the summer months. Manley (1945) remarking on this type of temperature curve, points out that it indicates that a slight increase in elevation will be accompanied by a large decrease in the length of growing season. Manley (1936) has also pointed out that in comparison with other areas, Moorhouse bears a general resemblance, in its climate, to South Iceland; he has also shown (1942) that the temperature conditions on Dun Fell (2750') are similar to those found at about 3500' in Central Norway.

It is clear from this information that Teesdale has a distinctly montane climate. Summer temperatures are not high and are further moderated by the strong and frequent winds and high humidity. Autumn (and the end of the growing season) comes early and the winter is long. Manley (1942) describes Dun Fell, in the West of the area, as having 'an excessively windy and pervasively wet autumn, a very variable and stormy winter with long spells of snow cover, high humidity and

extremely bitter wind, alternating with brief periods of rain and thaw'. A climate of this type compares generally with other mountain areas in Britain and shows similarities with Continental mountain areas.

In contrast to this is the climate to be found on the Burren. The rainfall is still quite high, but the temperature range is markedly different. The figures given for Shannon Airport are, perhaps, somewhat misleading to use as a comparison as temperatures on the Burren must differ considerably from these at times, although no data are available to show this. Frosts, according to local inhabitants, are rare and snow extremely so. Temperatures will be affected by the large masses of bare limestone in the area and the microclimate here, especially in the summer, will probably be several degrees higher at times than the surrounding areas, because of radiation and reflection of heat from the limestone surfaces. Thus the minimum curve is unlikely to be as low as that shown for Shannon and the maximum curve is likely to be higher.

Since Gentiana verna and Potentilla fruticosa especially, seem to be healthy and free flowering in both Teesdale and W. Ireland, it is possible that there are physiological differences between them. It would be interesting to test this by growing plants of the species from the two areas under

different temperature regimes to see if there are any differences in growth rate or flowering vigour etc. which might be revealed by these conditions.

CHAPTER VI.General Discussion.

It has been shown in the previous chapter that the Teesdale populations of the species studied are different from the populations elsewhere in Britain. It has also been shown that part at least of this difference is genotypic. In Gentiana verna, Potentilla fruticosa and Myosotis alpestris variation is not random, but shows regional differences. In G. verna there is, in Britain, a difference between the English (Teesdale) populations and the Irish populations. A similar situation is also found in P. fruticosa, where the Lake District and Teesdale populations have been shown to be similar, so that the difference is also between English and Irish populations. In both these species differences have also been found between the British populations and those on the European mainland. In G. verna it has been found by leaf measurements that this is not a simple regional distinction, but that the Alpine populations show variation which can be correlated with altitudinal and probably with the associated climatic factors. In P. fruticosa a study of continental herbarium material has shown that divergence has occurred between the continental and British populations and also between the material from the two continental localities

studied. A similar situation has been found in Helianthemum canum by Proctor (1958). Here the Teesdale population was found to be very distinct, composed of dwarfed plants with very small glabrous or subglabrous leaves which never show any stellate tomentum on the upper surfaces. This is distinct from the populations on the West coast of England and Wales, which are on Carboniferous limestone and which have pubescent leaves with a fine stellate felt on the upper leaf surface. Both of these types are again distinct from the W. Irish populations which rarely show a stellate pubescence, like the Teesdale plant, but which have much larger and hairier leaves and a coarser growth. Regional differences have also been demonstrated, in Myosotis alpestris, between the Teesdale and Scottish populations, and this has been related to biotic factors. Variation has been demonstrated in Dryas octopetala, and although it has been shown that British populations are different in structure from the majority of Alpine and N. European populations, the reasons for the population structure in Britain are not clear. It has however been shown that the Teesdale plant is distinct in leaf size and crenation from other British populations, being most similar to populations in Arctic Norway and Sweden in these respects. Little detailed work has been carried out on other Teesdale

species. A comparison of plants of Viola rupestris from Teesdale and Arnside, Westmorland by Valentine and Harvey (1961) has shown that when grown under uniform conditions the Teesdale plants remained compact with many very short shoots, while the Arnside plants became less compact with a few long shoots. Although these investigations were only carried out on a few plants, previous investigations by the same authors have shown that differences in these characters are heritable in plants from a number of Czechoslovakian populations, so that it is probable that those in the English populations are also genotypic.

It can thus be seen that the Teesdale populations of these disjunct species which have been studied, show differences from other populations in Britain. It has been shown in Chapter I that the explanation of the presence of refugia must be sought in terms of events which have taken place after the retreat of the ice, since it has been demonstrated by pollen analytical methods that many of the species were widespread in Britain in the early Post-glacial period. The distributional patterns of the disjunct species do not therefore throw any light on whether their arrival was post-glacial or not.

It has also been pointed out that there is geological evidence for ice free areas in Teesdale, but it is conjectural

how suitable the conditions on these would be for plant growth at the maximum period of glaciation. What the climatic conditions were in N. England at the periods of maximum ice extension, is unknown. It has been suggested by Manley (1959) that in the late-glacial period of the post-Allerød recession the climate would be oceanic, as at the present day, with prevailingly damp air and much low cloud at all seasons. If such a picture bears any relation to the weather in the full glacial periods this must have been very unfavorable to plant growth. As already pointed out, in Ireland the probabilities of glacial survival seem somewhat greater, as shown by the discoveries of remains of Eriocaulon cf. septangulare and Daboecia cantabrica in inter-glacial deposits, and also the probability of ice free areas to the west of the present coastline.

Since there are these possibilities it is therefore necessary to discuss whether the variation which has been demonstrated could have arisen during post-glacial times, or whether a longer time would have been necessary. There is no direct evidence on this question. In the case of Dryas it may be possible, at certain sites, to gain direct evidence by the study of sub-fossil material in situ; it is hoped that this will be possible, but no work has been carried out yet.

The most useful indirect method of gaining evidence is by comparing the situation with refugia which are known certainly to have been glaciated. Two of the best known of such refugia in Europe are the Swedish islands of Oland and Gotland in the Baltic. Both these islands have been certainly glaciated. In Oland there are extensive areas of limestone pavement known as 'Alvars', and the disjunct species are closely associated with these. Alvars are also present in Gotland, although to a lesser extent. The rich relict floras of these islands contains a mixture of both southern and northern species. Amongst the northern species a number are of special interest as they are also found in Teesdale. Potentilla fruticosa has its only Scandinavian localities on these islands, and as has been shown, is as different from the Teesdale form as is the Irish form. It is also distinct from plants from one of the Pyrénées localities. Another species found on Oland is Helianthemum oelandicum which Proctor (1958) has shown to be closely related to H. canum, but distinct from the British and Alpine forms. Another northern species, also found in Teesdale is Bartsia alpina, and here Oland is the most southern locality in Scandinavia. Oland, together with Gotland and Sarema (an island near Estonia) also provide the most southern Scandinavian localities of Pinguicula alpina. Amongst

southern species found are Globularia vulgaris, a species which has its main distribution in the E. Alps and Pyrenees, and a number of steppe plants such as Artemisia laciniata, Ranunculus illyricus and Plantago tenuiflora. Iversen (1954) has demonstrated pollen grains of Helianthemum oelandicum and Ephedra cf. distachya (a steppe plant now extinct on Oland) from post-glacial sediments on the island, indicating that these species have had a continuous history there through the post-glacial period. Thus these islands have a rich relict flora composed of species with a large variation in distributional area. In his genealogical studies on a number of common Scandinavian species Turesson (Hereditas 6, 1925) found that some of these, growing on the Alvar in Oland, were genetically and morphologically different, forming distinct ecotypes. Thus he found that the Oland populations of Artemisia campestris, Rumex acetosella and Silene maritima were composed of prostrate plants, while Allium schoenoprasum occurred as a dwarf form and Leontodon autumnalis was different in leaf shape and anatomy from the other transplants which he had in cultivation. Turesson concluded that these ecotypes had been developed in response to the severe exposure to which the unsheltered limestone pavement is subject.

Thus Oland populations of a number of species have morphological differences from other European populations, which are genetically controlled. These differences can be of a similar magnitude to those which have been demonstrated, both between the Teesdale and other British populations in the species which have been studied, and also between these and populations on the European mainland. Since Oland is known to have been glaciated it is therefore possible that the differences in the British populations have arisen during post-glacial times.

Thus both a mixture of distributional types in the floras of the Burren area and Teesdale and the differentiation which has taken place between them, are quite comparable with the situation in Oland and could therefore be explained on the basis of post-glacial introduction.

In Denmark a number of species e.g. Hypochaeris maculata, Dactylis glomerata, Solidago virgaurea and Viola tricolor have distinct coastal races. Böcher (Dansk Natur-Dansk Skole 25 År, 1955) has interpreted these as late-glacial relicts which have survived on the steep coastal slopes, since because of the exposure and instability of the shallow soil on chalk these have probably remained open and free from forest cover throughout post-glacial times. The races do not

appear to be of recent origin and since Denmark was totally glaciated their presence appears to be due to the special ecological conditions which are present in these maritime areas. Again the possibility of the differences in the Teesdale species being explainable on the basis of post-glacial introduction is seen to be reasonable

Although these comparisons show the feasibility of the Teesdale flora being of post-glacial origin, they give no information on whether the differences found are due to divergence in situ or are the result of residual differences from highly variable late-glacial populations. Riley (1955) has discussed this problem in relation to Thlaspi alpestre, an inbreeding species of disjunct distribution in Britain, found in a number of localities in North England from Teesdale south to Derbyshire, and also in the Mendips and N. Wales. The most common habitat is on the spoil heaps of old lead mines, although it is also known on the Whin sill at Wynch Bridge, Teesdale and in limestone pastures in Derbyshire. In Teesdale there is an ecotypic differentiation into a dwarf sub-alpine type found on high ground in the west of the area (on old lead mine spoil heaps) and a much larger low altitude type found at the Wynch Bridge locality. This variability in a restricted area is as great as that found between these

populations and those elsewhere in Britain. Riley has suggested that this situation, which has been arisen largely due to the breeding system, is more likely to be due to divergence in situ than as a result of high variability in the late-glacial populations. None of the species studied have shown population differences within areas and this is perhaps not surprising because the most widespread species in Teesdale which have been studied - Gentiana verna and Potentilla fruticosa, are both normally outbreeding (in the latter species it is obligatory), while Dryas octopetala, which, from its flower structure, appears to be capable of inbreeding has only a single locality in the dale. Myosotis alpestris, a species also capable of inbreeding, appears to be under strong selective pressures in its three localities and again it is not surprising that differences should not be present between them. However it seems more likely that the differences between the Teesdale and Scottish populations of this species are more easily explainable by reference to the differing biotic influences in each area, and thus to a divergence in situ, rather than as a result of survival of part of a variable late-glacial population in each area.

A short account has been given in Chapter I of the vegetational changes that took place in Britain as the climate

ameliorated. It is clear that as the trees encroached upon the open vegetation of the late-glacial period the plants requiring open, unshaded conditions became progressively more restricted. Since Godwin (1956) has suggested that the main reason why Teesdale is a refugium is because of the presence of open areas there throughout the whole of the post-glacial period, including the forest maximum, it is clearly important to consider the habitats in which the relict species grow today and assess whether they would have remained both free of forest and also free from blanket bog after this had invaded and covered the forest in the Sub-Atlantic period. The most obvious habitats which would be certainly free from forest and bog are to be found along the banks of the River Tees. As shown earlier the shingle banks are one of the main habitats for Potentilla fruticosa and such areas would have been free from forest influence at all times. The same will apply to the gorge at Wynch Bridge, which is still fringed by woodland, and supports on the Whin sill crags a rich flora including Potentilla fruticosa, Antennaria dioica, and Potentilla crantzii. In the same area there are small flushes, which although partially shaded by Betula and Alnus, contain such species as Salix phylicifolia, Primula farinosa and Juncus alpinus. A few miles upstream from here the river is

eroding the large calcareous, morainic bank known as Cetry Bank. Today this has an extremely rich flora including Gentiana verna, Bartsia alpina, Carex capillaris, Kobresia simpliciuscula and Tofieldia pusilla. The habitat is very unstable with constant erosion of the surface, partly through the action of small springs in the upper part of the bank, and it seems very unlikely that this would ever have borne any woodland. It has been shown that similar communities, floristically, are to be found in a number of small calcareous marshes in the area. These include some of the examples of the flush communities delimited in the studies on Gentiana verna and Bartsia alpina. One of the main influences that appears to keep these marshes in an open condition, with a series of hummocks surrounded by more or less bare areas, is the influence of sheep grazing and trampling. Pigott (1956) has discussed the possibility of these remaining open during the forest period and points out that large herds of red deer were, at one time, common in the North Pennines and may have used such sites as watering places and thus maintained open conditions, in the same way as at the present day calcareous springs in the forests of central Sweden are kept open, with a similar structure, by the native fauna. As has been mentioned the crags of Whin sill at Wynch Bridge support several of the disjunct species. A number of the rare species

are also found on other Whin sill crags in the district; thus Arctostaphylos uva-ursi is found on Cronkley Scar, while on the opposite side of the river on Falcon Clints, the Holly fern Polystichum lonchitis still survives, while Woodsia ilvensis is known to have grown here in the past. Limestone crags are also common in the district and the larger of these will also probably have been free from closed woodland. Perhaps the most problematical areas in this respect are the outcrops of sugar limestone on Cronkley Fell and Widdybank Fell. Today these are two of the main centres of disjunct species in the dale. The Cronkley Fell outcrop bears the only colonies in the dale of Dryas octopetala, Polygala amara and Helianthemum canum. Those on ^{Widdybank}~~Cronkley~~ Fell include one of the two known colonies of Viola rupestris, while a large number of other rare species especially Gentiana verna and Kobresia simpliciuscula are abundant here; on one of the wetter areas, where there are large areas of bare ground, Minuartia stricta has its only locality in Teesdale and in Britain. Although it would seem that this wetter part with large bare areas of gravel, constantly more or less saturated with water, would be unsuitable for shrub or tree growth at all times, it is possible that on the very shallow rendzina of the drier outcrops an open scrub might have developed.

This is even more likely to be the case on the unaltered limestone outcrops of the district. However Pigott has also pointed out that it is still probable that some of the species would be able to survive under such conditions since Viola rupestris, Carex ericetorum and Dryas octopetala can exist under scrub and on very small outcrops, while he has noted Polygala amara and Gentiana verna in fruit under small openings in the canopy of Sub-Alpine Picea abies forest in the Alps.

Finally some areas in the west of Teesdale would have been above the tree limit at all times, since the limit in the area appears to have been between 2300' and 2400', and some species no doubt were able to survive in such areas. M.E. Johnson (pers. comm.) has carried out pollen analytical studies on a blanket bog profile on Knock Ridge, on the N.E. side of Knock Fell in the west of the area, at 2425'. The profile is only small, but no Betula remains were found, and the diagram shows peaks for Filicales, Selaginella, Cyperaceae and Empetrum. The site is on a gently sloping ridge and such high ground today includes a few Arctic-alpine species, examples being Carex bigelowii and Lycopodium alpinum. There are however a number of limestone crags which would probably have been above the tree limit, the largest of which forms

the southern side of Mickle Fell. Perhaps the most likely species to survive in such habitats was Myosotis alpestris, found today, in all three localities in Teesdale, at not less than 2350' altitude. Gentiana verna is also a species which grows on Mickle Fell, while it is of interest that there is an old record made by a local naturalist, George Bolam, in the last century of Dryas octopetala (pers. comm. D. Ratcliffe); it does not seem to have been seen here this century however. In this connection Lid (1958) has recorded finding Dryas octopetala at two places in the spruce forest zone of S.E. Norway, some 80 km. from the main montane area of Dryas in S. Norway. In these two areas the species grows with a number of other photophilic species including Carex rupestris, Carex capillaris, Potentilla crantzii and Saxifraga aizoides on steep, broken, limestone slopes where the unstable nature of the habitat prevents the encroachment of the forest. Lid has interpreted these occurrences as post-glacial relics from the late-glacial period in Norway. Thus even if the Mickle Fell and other similar exposures were surrounded by forest, there would be a good chance that such areas would remain open. This may also have been the case with some of the lower crags in the area.

In Chapter V it has been shown that the Lake District and Scottish communities of the species studied are primarily

on rock ledges and crags and there can be no doubt that such situations have remained free from tree cover throughout post-glacial times. The Burren area in W. Ireland presents many more problems in this respect however. Today the predominant aspect of the area is of bare limestone, the soil being always thin and often confined to the grikes or crevices in the limestone. Tree cover is limited, trees being generally confined to the valleys although isolated specimens are found scattered on the hills, while Crataegus is also common as more or less isolated bushes. Some of the limestone areas slightly to the north in Co. Galway bear a thick scrub today, mostly of Crataegus and Corylus, and without doubt this will have been much more widespread in the area during the period of maximum forest extension. However Braun-Blanquet and Tuxen (1952) consider that much of the Dryas vegetation on the W. coast of the Burren would probably have existed as grassland throughout the post-glacial period, and Proctor (1955b) has pointed out that in the cool climate with a high degree of exposure and shallow soil this is certainly a plausible suggestion. On Oland with a similar topography, although a much drier climate at present, Iverson (1954) has shown pollen analytically that there was a rather open forest, in which presumably the relict flora was able to survive.

After the invasion of the forest in Teesdale by blanket bog in the Sub-atlantic period, due to the increase in rainfall, the landscape on the fells must have assumed a similar aspect to that at the present day. The sugar and unaltered limestone exposures would probably then, as now, have appeared as small windows in the blanket bog in which the disjunct species would be under very similar conditions to those prevailing at the present time. Since the exposure will have greatly increased due to the diminution in tree cover, even the small limestone exposures which would have been covered by scrub or woodland up to this time would now probably become open, although not covered by blanket bog due to the high base status of the shallow soil. It is therefore possible that at this time there was an extension in range of some of the species, especially perhaps Gentiana verna, which, it has been suggested, could have developed some of its colonies in the dale today from single seed introductions on some of the small limestone exposures, followed by prolonged vegetative reproduction.

It is clear that at the present day sheep have an important influence on many of the sites where the disjunct species exist, especially the calcareous marshes and the sugar and unaltered limestone exposures. It has been noted

that a number of species are directly affected. Thus Gentiana verna is very rarely seen in a fruiting condition due to the capsules being eaten as soon as the peduncles elongate above the general herbage level. Dryas octopetala suffers even more in this respect and it is very doubtful whether any seed reaches maturity at the present day. Although in the calcareous marshes the sheep appear to play an important part in maintaining an open community, they also play a destructive part and one of the species confined to this type of habitat, Bartsia alpina, is rarely seen in flower in the most heavily grazed areas and is rare in fruit in all localities. Finally the case of Myosotis alpestris has already been discussed and it seems likely here that sheep have played a large part in the production of a dwarf ecotype. It is unknown for how long sheep have been grazed in the dale. Singleton (1677) (information from Nature Conservancy 1959) provides the earliest documentary evidence that cattle and sheep were driven to upland pastures for summer grazing in Upper Teesdale and on Alston Moor, while Pigott (1956) has noted that this practice was probably well established during the Norse settlement of the area since the termination -set referring to such upland pastures appears in several of the place names of the district e.g. Scarset, Cornset and Selset in Lunedale.

Thus this type of biotic influence has been in existence a considerable time and is reinforced in some areas, especially those on the sugar limestone, by the activities of rabbits. Because of these influences the species on the upper fells appear to be static at the present day, holding their own in their various localities, but unable to expand their areas further. It is much more problematical why some of the species which grow by the R. Tees are so restricted; in particular, the case of Potentilla fruticosa has already been discussed. It appears that in the last three hundred years this species has suffered a reduction in range in Teesdale to about half that previously known. It has not been possible to find any information on the reasons for this.

So far this discussion has dealt with a number of aspects of the past history and the present situation of some of the Teesdale species; what of their future chances? It has become clear that both the species studied in the course of these investigations and those species which have been studied by others have distinct forms in Teesdale. They have become distinct through their isolation and form a series of unique taxa not found elsewhere. If any of them become extinct in Teesdale, a distinct and irreplaceable biotype will have been lost. Conservation of the flora of Upper Teesdale is thus to

be regarded as of prime importance. This is not to be interpreted as a suggestion that human and biotic influences should be completely withdrawn from a number of areas. It is clear, for example, that the hay meadows in Teesdale which have a rich flora would very quickly revert to a rough Nardus-Agrostis grassland without the traditional management of dung-fertilising and cutting for hay. Again the calcareous marshes have been shown to be, at least partially, dependent on sheep grazing and trampling for the maintenance of open conditions. On the sugar limestone exposures of Cronkley and Widdybank Fells the situation is quite different. Such base-rich areas are very selectively grazed by sheep because of the good quality of the grassland and this pressure is concentrated on these areas to an extent that has become actively destructive. Here, modification of present practices so that grazing pressure is reduced is very desirable.

Finally, although nearly all the species in Teesdale have now been found elsewhere, the combination of species and habitats in the area remains unique, as are the particular biotypes of the species. If they become extinct, as a number already have become, they can never be replaced for study and research.

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