Biosystematic studies of selected species in the Teesdale flora.

A thesis submitted for the degree of
Doctor of Philosophy in the Department
of Botany, Sheffield University.

by

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Summary.

Studies on the cytological, morphological and ecological variation of a number of species present in Teesdale in the northern Pennines have been made. The species chosen for investigation were selected to represent a range of the different geographical elements in the flora of Teesdale; their distributions which are often highly disjunct are described and discussed.

Intraspecific cytological variation has been found in *Cochlearia alpina* (Bab.) H.C. Watson (2n = 12, 26), *Alopecurus alpinus* Sm. (2n = c100, 117), and *Hippocrepis comosa* L. (2n = 14,28). Attempts have been made to correlate morphological and cytological variation, this being only partially successful in the case of *Hippocrepis comosa*. The distribution of cytotypes of *H. comosa* is discussed and a historical explanation is proposed for the restriction of the diploid (2n = 14) race to open habitats in western Britain, the tetraploid (2n = 28) race being more widespread.

The morphological variation of *Draba incana* L., *Polygala amarella* Crantz and *Hippocrepis comosa* L. has been studied in detail and their breeding systems investigated. Variation is discontinuous in *Draba incana* and *Polygala amarella*, the Teesdale race of each being morphologically and genetically distinct from other populations in Britain. Morphological variation is discussed and related to geographical isolation, small population size and inbreeding. Separate taxonomic status is proposed for the Teesdale race of *Polygala amarella*.

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Introduction.

Introduction

Upper Teesdale is well known for the assemblage of rare species in its flora. Many of these species were discovered in the mid-nineteenth century by John Binks a local lead miner and during the botanical rambles of James Backhouse and his son. More intensive studies since then have thrown light on the phytogeographic and evolutionary importance of the dale.

The species comprising the Teesdale flora belong to a mixture of geographical elements, for instance the Arctic - Alpine species *Dryas octopetala* grows on the summit of Cronkley Fell in the same community as *Helianthemum canum* and *Carex ericetorum* which have continental distribution patterns and with *Hippocrepis comosa* of the southern element. In addition, many species in the assemblage are at or approaching their limits of distribution in Teesdale. Species such as *Alopecurus alpinus* which belongs to the Arctic - Subarctic element are at their southernmost limits in Teesdale, while others such as *Hippocrepis comosa* are at their northernmost limits here. The distribution of many of the Teesdale rarities is highly disjunct, especially in Britain, and as will be shown later, this is an important factor in the evolution of these species.

Many of the plant communities in Teesdale are as interesting as the species which they contain. Often the rare species are confined to a particular community in Teesdale though they may not necessarily be found in the same type of community in other parts of their geographical distribution. It is therefore of interest to compare the Teesdale communities with those in which these species occur in other subarctic and montane areas. It is known for example that several species which have a wide ecological range in continental Europe and southern England become progressively restricted to more calcicolous communities in northern and western Britain towards the edges of their range and in response to the more oceanic climate.

There has been considerable controversy regarding the origin and history of the Teesdale flora. Wilmott (1930) was of the opinion that members of the flora had survived the glacial periods on ice-free nunataks in the Teesdale area, while being destroyed elsewhere. Evidence of glacial plucking on the summits of Cross Fell and Little Dun Fell (Johnson & Dunham, 1963) however shows that even the highest ground in the region was overridden by ice during the period of maximum glaciation. Salisbury (1935) on the other hand maintained that the restricted occurrence of species in the Teesdale flora was due entirely to the presence of specialised ecological conditions. Evidence from pollen analysis and subfossil remains has shown that the majority of species which now belong to the Arctic - Alpine element of the British flora, including many Teesdale species were widespread in Britain during the Late-glacial period and remains of several species have been found to the south of their present areas of distribution (Godwin, 1956). Godwin (1949) and Pigott & Walters (1954) have proposed that floras such as that of Teesdale are remnants of this Late-glacial vegetation which have survived the Post-glacial in open, treeless, base-rich habitats. Except in such isolated "refugia", shade intolerant Arctic - Alpine species have been eliminated firstly by the development of dense forest and later during the wet Atlantic and Sub-Atlantic periods by the extensive development of blanket bog and soil leaching.

Teesdale is perhaps unique in having so many different types of open habitats within a relatively small area. These include river banks, springs and flushes, cliff ledges and outcrops of sugar limestone. It is in the last of these that the largest proportion of rarities are found. The sugar limestone was produced by the intrusion of the Whin Sill which has metamorphosed the surrounding relatively pure Melmerby Scar limestone into a coarsly crystalline rock which weathers into calcite granules with the appearance of sugar, hence its name.

Squires (1971) has found evidence of human interference in Teesdale in the form of deforestation by burning dating back to the Atlantic period and attributes much of the soil degradation and erosion to this factor. The production of various types of unstable habitats such as mine spoil heaps and the verges of roads and tracks by man has also increased the number of open habitats in more recent years, as has overgrazing by sheep and rabbits on Cronkley and Widdybank Fells.

Climatic factors are probably as important as the ecological conditions described above in explaining the present existence of rare species in Teesdale. Dahl (1951) has suggested that Alpine species suffer from high temperatures and are thus restricted to areas with low maximum summer temperatures. Connolly & Dahl (1970) have calculated that during the climatic optimum of the Post-glacial, mean summer temperatures in Britain were 2 - 3°C warmer than at present. Arctic - Alpine species would therefore have been eliminated at this time from all but large or high mountain areas such as the Scottish Highlands, Snowdonia and the northern Pennines.

Recent work by pollen analysts (eg. Squires, 1971) supports the hypothesis that Teesdale has been a refugium for members of its present flora throughout the Post-glacial period. High proportions of herbaceous pollen in Teesdale deposits of the Atlantic period suggest that patches of open ground were present even during the maximum development of forest. It is thought that the bottoms of the dales may have been densely forested while less dense patches of woodland and scrub existed at higher altitudes on the fells. Pollen of several rarities in the present flora has been identified from peat deposits of Atlantic age near Widdybank Fell. These include *Betula nana*, *Dryas octopetala*, *Helianthemum canum*, *Plantago maritima*, *Polemonium coeruleum*, *Rubus chamaemorus* and *Saxifraga stellaris*.

The geographical isolation of populations of several Teesdale species has disrupted gene flow so that variation is now discontinuous and in several cases local races have arisen. Many populations of these species are also very small and it is in such populations that random drift of genes is likely to occur , thus accentuating their differentiation. There is already evidence that the Teesdale populations of several species including *Gentiana verna* (Elkington, 1963), *Viola rupestris* (Valentine &

& Harvey, 1961), *Helianthemum canum* (Proctor, 1957) and *Dryas octopetala* (Pigott, 1956) are morphologically and genetically distinct from other populations in Britain and in continental Europe. The Teesdale populations of *Myosotis alpestris*, for example, are genetically dwarf when compared with populations in Scotland (Elkington, 1964) and leaflets of populations of *Potentilla fruti~~s~~cosa* from northern England differ in shape from the leaflets of Irish populations (Elkington & Woodell, 1963). This variation may result from selection in response to particular environmental conditions, or it may be non-adaptive. Studies of the biology, ecology and variation of these species can therefore give information about the evolution of isolated populations compared with other populations within the main area of distribution.

The species selected for this work have been chosen to represent a number of different geographical elements in the Teesdale flora and to include several species which are at the edge of their range in Teesdale. These distributions are described in Chapter 1. Morphological and cytological variation has been studied in order to compare the variation of British populations with those in continental Europe. Taxonomic implications of the results of these studies are discussed. The ecological range of these selected species has been surveyed both in Britain and in the Alps and results from these areas are compared and contrasted. Studies of general biology have also been made with particular emphasis on reproductive biology and breeding systems as these factors are most important in the evolution of species and populations.

Results of these studies give information about the variation patterns and evolutionary history and probable future of rare species. With this knowledge it is then possible to take steps in conservation to prevent such species from becoming extinct and even to increase their numbers.

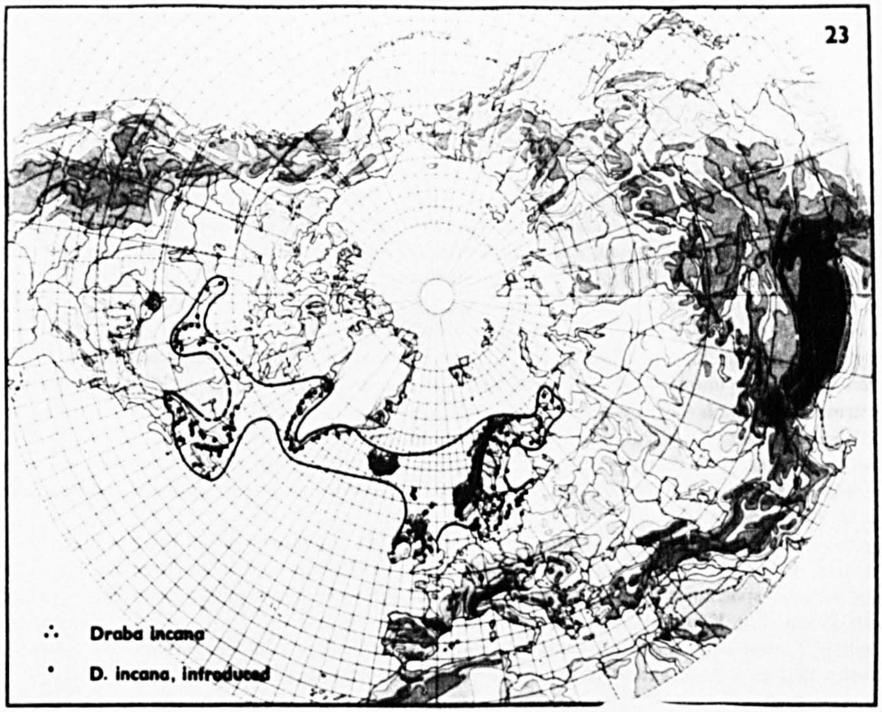
Chapter 1.

Geographical distribution.

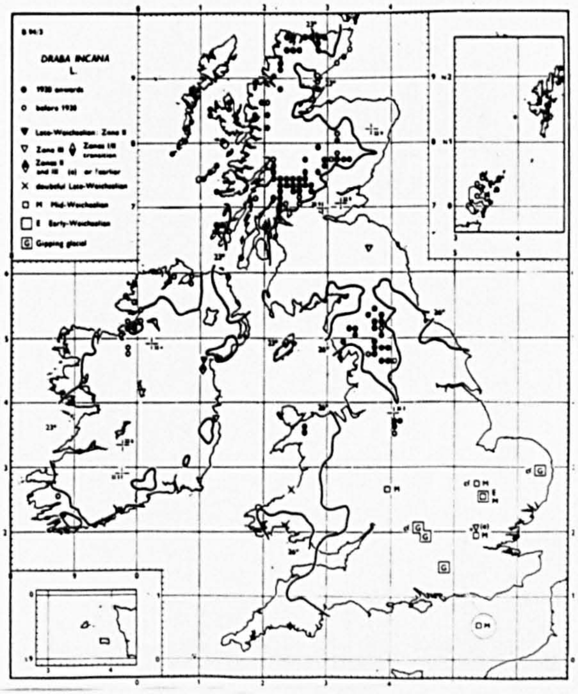
Geographical distribution.

The British flora has been divided into a number of geographical elements which relate the distribution of British species to their distribution in Europe as a whole. In this work the elements proposed by Matthews (1937, 1955) are used. Several elements are represented in the flora of Upper Teesdale and species belonging to a number of different elements have been selected for investigation. The world, British and Teesdale distributions of these species are described.

Draba incana L. was selected as a species representing the Arctic-Alpine element in the Teesdale assemblage. In the terminology of Matthews (loc. cit.) this element includes species which are often circumpolar with their main areas of distribution in arctic or sub-arctic regions, but with outlying occurrences at high altitudes in the mountains of Europe, Asia and sometimes America. The world distribution of D. incana is shown in Map 1:1. Its main area of distribution is in sub-arctic regions of Europe, Greenland and eastern Canada but there are outliers of distribution in the Alps and Pyrenees. Hultén (1958) has called distributions



Map 1:1 World distribution of <u>Draba incana</u> L. (from Hulten, 1958).



Map 1:2 British distribution of <u>Draba incana</u> L., showing subfossil sites. (from Conolly & Dahl, 1970).

of species such as this which occur on both sides of the Atlantic Ocean Amphi-Atlantic. He regards such distribution patterns as remnants of a formerly more widespread circumpolar distribution where the species has, for some reason, died out in the Pacific region. The occurrence of closely related taxa such as D. lanceolata Royle which occurs in Canada and the mountains of Central Asia and D. magellanica Lam. which grows in southernmost South America support the hypothesis that D. incana was formerly much more widespread and that morphological differentation has followed fragmentation of its distribution.

In Britain the distribution of D. incana is disjunct (Map 1:2) with populations in north Wales, Derbyshire, the northern Pennines, the Central Highlands of Scotland, the north-west coast of Scotland and the west coast of Ireland. In the Pennines and north Wales the species is restricted to altitudes above 1,000 feet (305 m.) but in northern and western Britain it occurs at sea level. Conolly & Dahl (1970) have also related its distribution to maximum summer temperature summit isotherms. In the Pennines and north Wales areas of distribution are bounded by the 26°C isotherm, whilst in Scotland and Ireland the limiting isotherm is at 23°C.

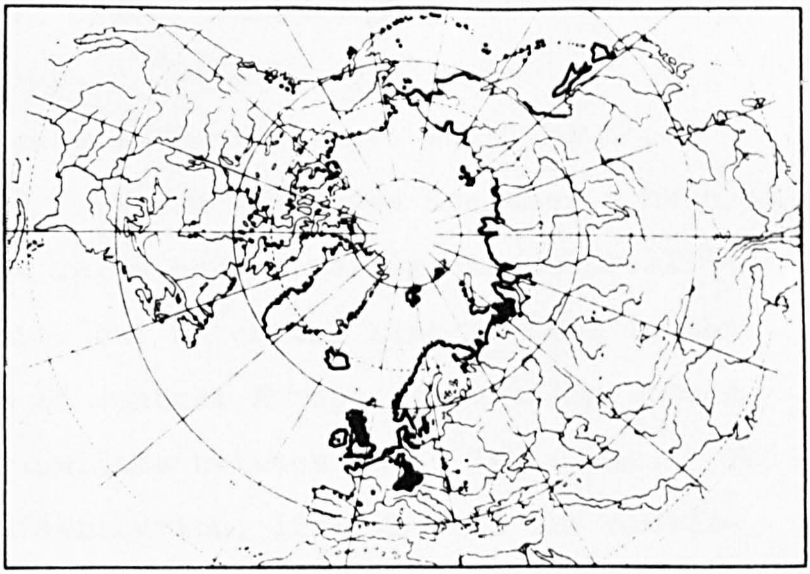
In Teesdale D. incana occurs on ledges of unaltered Carboniferous limestone around the sides of the dale, but it is most abundant where there are outcrops of sugar limestone on Widdybank and Cronkley Fells. It is also found on old lead mine spoil heaps on Widdybank Fell.

Investigations of subfossil plant remains have shown that the species formerly extended to the south of its present limits of distribution in Britain (see Map 1:2). The very characteristic capsule valves and seeds have been identified in full- and late-glacial deposits of Weichselian age and it seems clear that its present British distribution is of a relict nature.

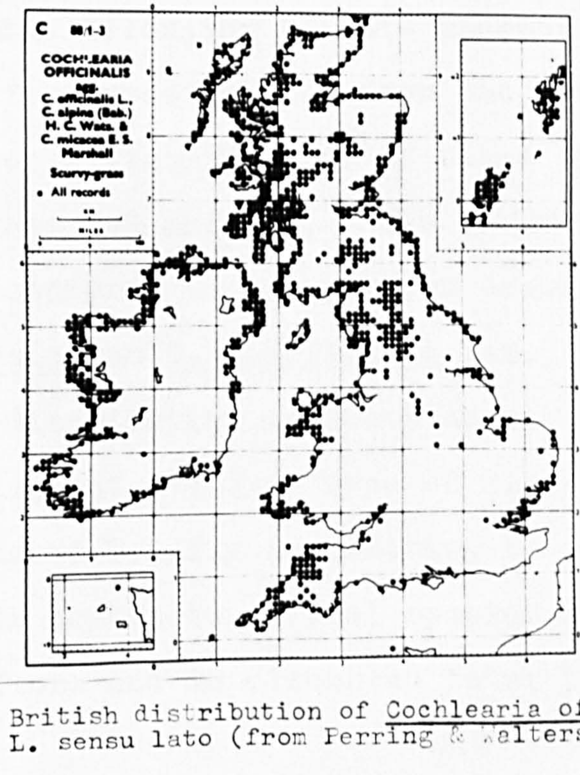
Cochlearia alpina (Bab.) H.C. Wats. is a species belonging to the Alpine element in the Teesdale flora. This element includes species of mountains in central and western Europe but absent from northern Europe and the Arctic. The total distribution of C. alpina is difficult to assess as it is often mapped together with *C. officinalis* L., specific delimitation being difficult in this genus. In Map 1:3 it is probable that most of the inland records refer to *C. alpina* and the coastal records to *C. officinalis*. *C. alpina* is therefore restricted to Britain and montane regions of central Europe.

Map 1:4 shows the British distribution of *C. officinalis* sensu lato and again most of the inland records are probably of *C. alpina*. It is most common in the northern Pennines, where like *Draba incana* it is a colonist of old lead mine spoil heaps, but it is also well distributed in Scotland. It occurs at several localities in Upper Teesdale, from relatively low altitudes in the hay meadows to high altitudes in Moorhouse National Nature Reserve.

Evidence from **subfossil** remains suggests that this species also extended to the south of its present British distribution during the late Pleistocene period. Seeds have been found in the Lea Valley Arctic bed of full-glacial Weichselian age and remains which have been identified as *C. officinalis* found in glacial deposits at Barnwell, Cambridgeshire and



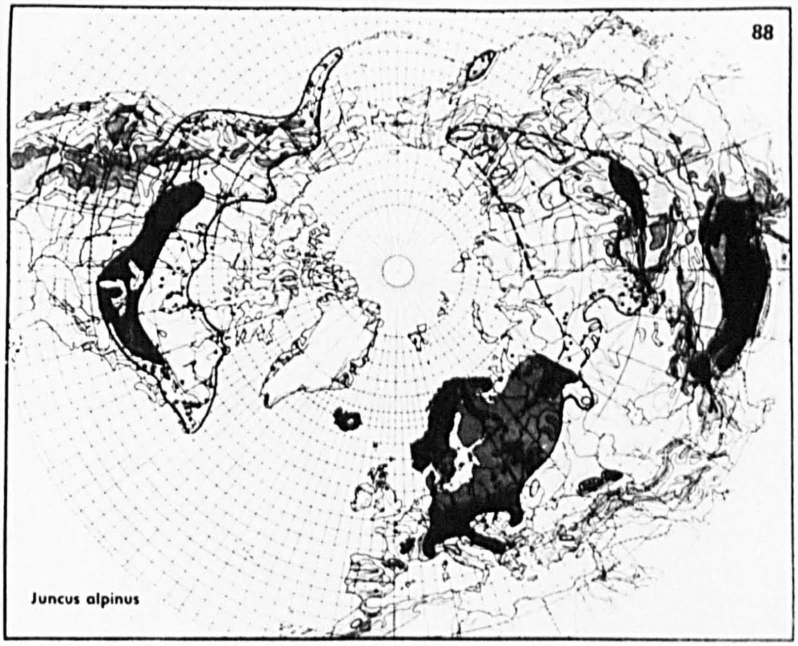
Map 1:3 World distribution of Cochlearia officinalis L. sensu lato (from Meusel, Jäger & Weinert, 1965)



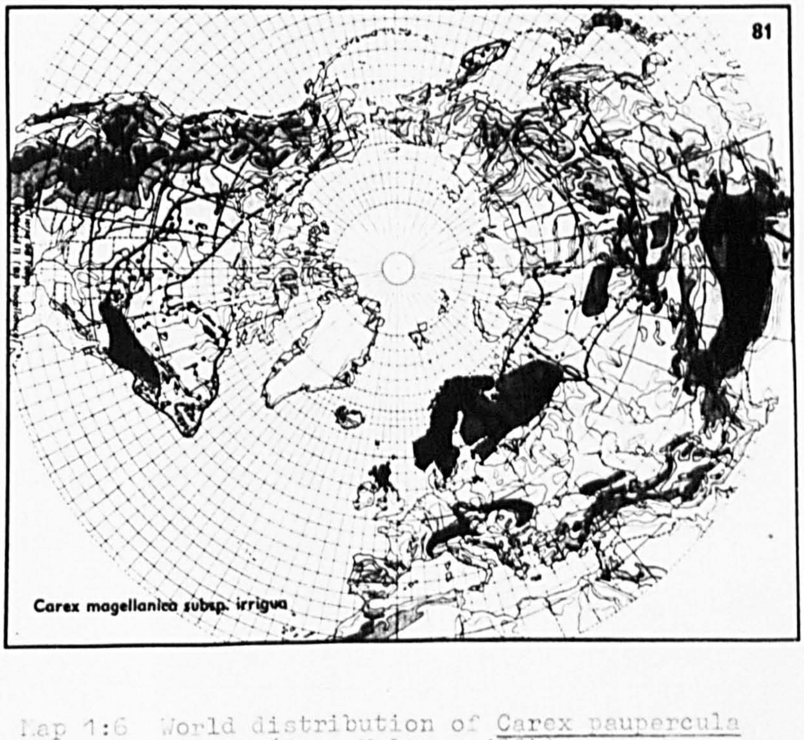
Map 1:4 British distribution of Cochlearia officinalis L. sensu lato (from Perring & Walters, 1962).

Drumurcher, County Monaghan may instead belong to *C. alpina*. (Godwin, 1956)

The geographical element which Matthews has termed Northern - Montane includes a number of species which have a mainly circumboreal distribution but which are also present in the mountains of central Europe, thus being absent from the lowlands between these two areas. This type of distribution, like that of the Arctic-Alpine element, is therefore discontinuous. Two species, *Juncus alpinus* Vill. and *Carex paupercula* Michx. belonging to this element were selected for investigation from the Teesdale flora. The world distributions of these species are shown in Maps 1:5 and 1:6. The distribution of *J. alpinus* conforms to the pattern described, but *C. paupercula* (as *C. magellanica* Lam.) has an outlier of distribution in South America. This highly disjunct bipolar type of distribution has been mentioned briefly in relation to *Draba incana*. It is common to several species in the Teesdale flora and is discussed later in this chapter.



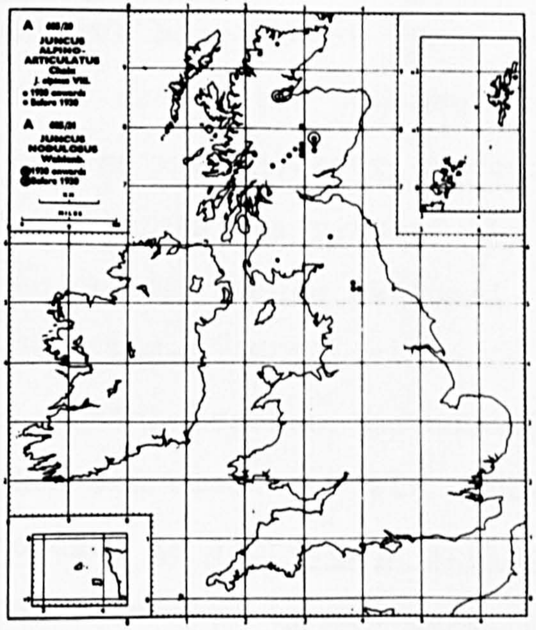
Map 1:5 World distribution of *Juncus alpinus* Vill. (from Hulten, 1964).



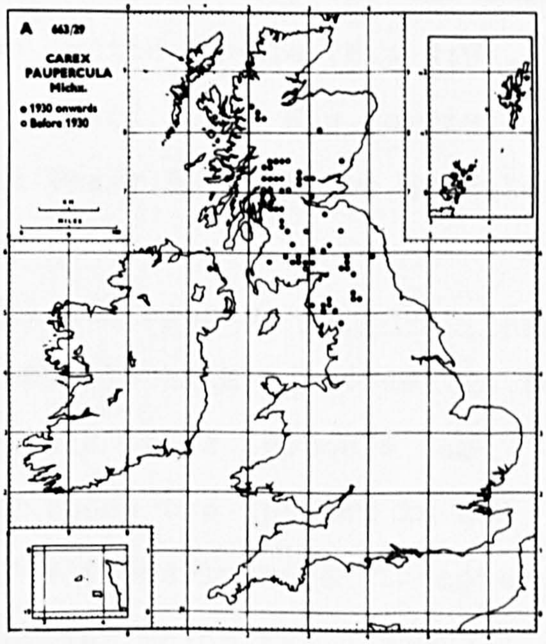
Map 1:6 World distribution of *Carex paupercula* Michx. (from Hulten, 1964).

J. alpinus reaches the most southerly point of its British distribution in Teesdale (Map 1:7). Its pattern of distribution in Britain is highly discontinuous, the main centre of distribution being in the Central Highlands of Scotland. It is completely absent from Ireland. In Teesdale it occurs mainly on and around Widdybank Fell, some of the sites being below the high water line of the reservoir. This species fortunately grows elsewhere in Teesdale, for example near the summit of Cronkley Fell, on a bank of the Tees near Widdybank Farm and also on Whin Sill crags on the edge of the Tees lower down the dale at Winch Bridge. There is no evidence as to its former distribution in Britain.

C. paupercula is much more widely distributed in Britain than J. alpinus, particularly in Scotland, (Map 1:8) though it is not very abundant at any of its localities. Until recently its southernmost limit in Britain was in north Lancashire, but in 1963 a new station for the species was discovered in Merioneth (Benoit, 1963). C. paupercula is a



Map 1:7 British distribution of <u>Juncus alpinus</u> Vill. (from Perring & Walters, 1962).

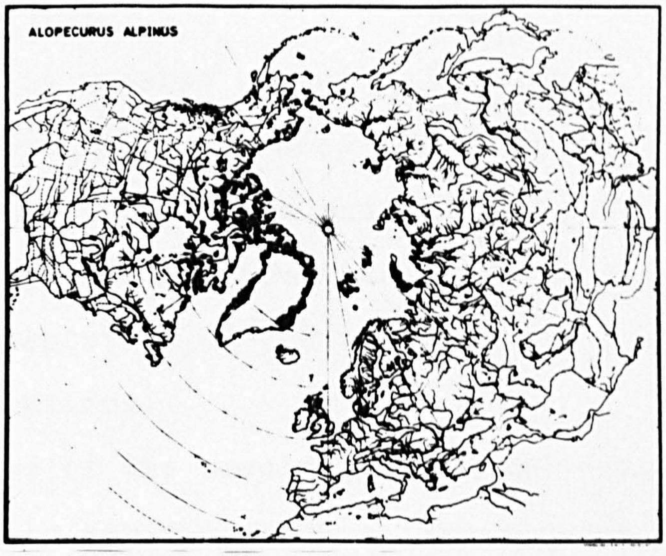


Map 1:8 British distribution of <u>Carex paupercula</u> Michx. (from Perring & Walters, 1962).

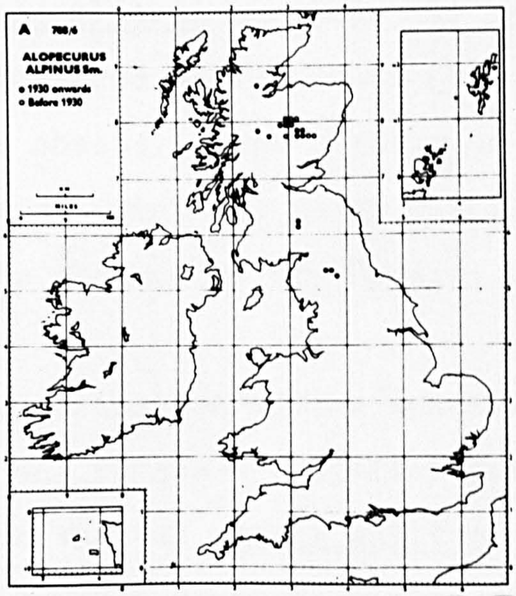
species of deep Sphagnum bogs and in Upper Teesdale several sites are in the Cow Green reservoir basin. There are, however, records for the species higher up in the part of the dale included within the Moorhouse National Nature Reserve (Eddy & Welch 1967).

Another species which reaches the southernmost limits of its British and almost of its world distribution in Teesdale is <u>Alopecurus alpinus</u> Sm. This grass is classified by Matthews within the Arctic - Subarctic element, though its world distribution is circumpolar and almost entirely within the Arctic Circle (Map 1:9). Its most northerly record is at Kap Morris Jesup (83° 39'N) in Peary Land, North Greenland (Frankl, 1955).

The closely related species <u>A. antarcticus</u> Vahl. occurs at similarly high latitudes in the southern hemisphere and it is probable that the distribution of these two species is all that now remains of a formerly more widespread, probably montane species which has become disjunct and morphologically differentiated. Du Rietz (1940) has discussed the problem of bipolar distributions and by using geographical



Map 1:9 World distribution of *Alopecurus alpinus* Sm.
(Hulten, unpublished).



Map 1:10 British distribution of *Alopecurus alpinus* Sm.
(from Perring & Walters, 1962).

evidence based on species of mainly bipolar distributions with isolated occurrences in the Western Cordillera of America has shown that the present disjunct distributions may have arisen by fragmentation of trans-tropical montane distributions.

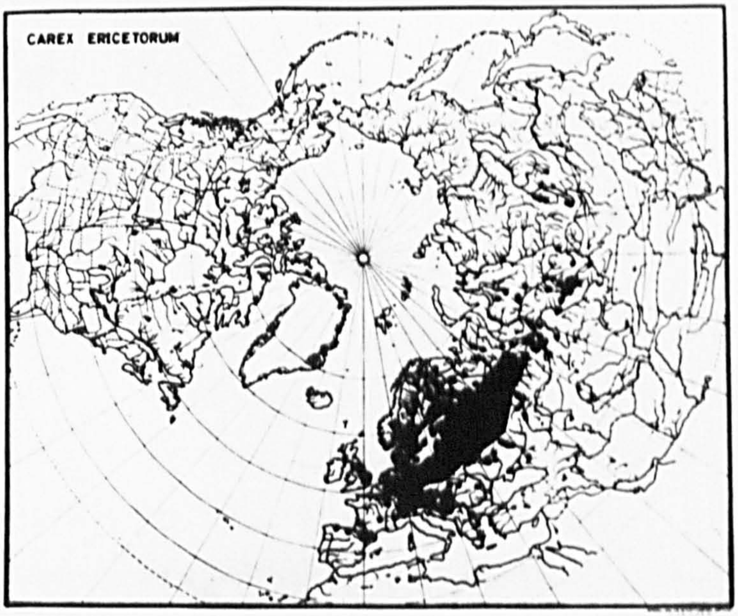
The absence of the species from Scandinavia has been noted by several authors, the nearest extra-British locality being in Greenland. It seems likely that A. alpinus survived the periods of glaciation on ice-free areas around the margins of the ice sheets. The absence of such areas in Scandinavia, which was fully glaciated may account for the absence of the species there today.

The British distribution of the species is shown in Map 1:10 and it shows a similar pattern of discontinuity to that of Juncus alpinus, though it is considerably rarer than that species. Its main centres of distribution are in Teesdale, the Moffat region and the Central Highlands of Scotland. It is restricted to montane flushes at 3,000 to 4,000 feet (915 - 1,220m) and in

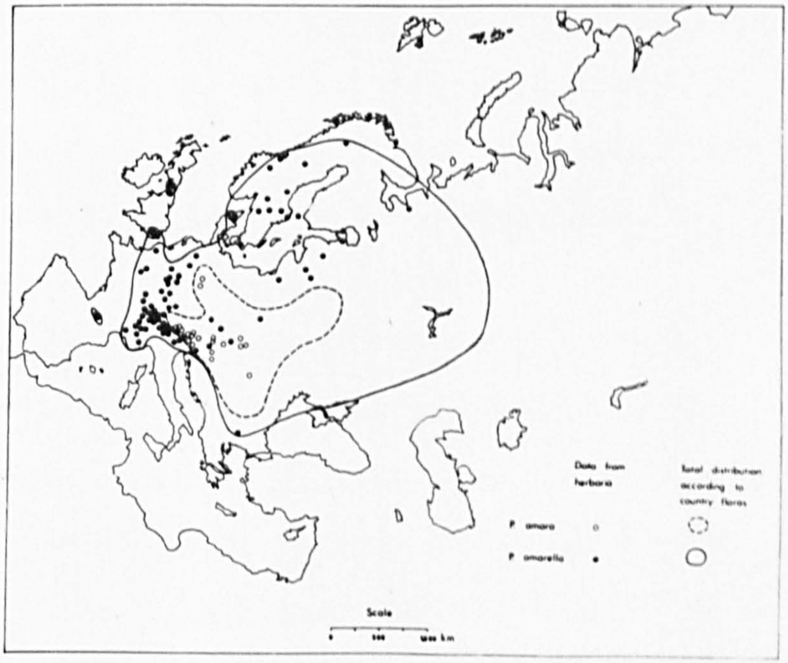
Teesdale it grows near the summits of Little Dun Fell and Cross Fell. It is a very inaptly named plant as it is completely absent from the Alps, but when it was described (Smith, 1804) from a Scottish specimen the knowledge of its geographical distribution was very incomplete.

There is only one historical record of A. alpinus. Remains of this species were found in the stomach of the Mammoth preserved in the Siberian ice of the Berezovka River in north-eastern Siberia. (Tikhomirov & Kupriyanova 1954).

Several species in the flora of Upper Teesdale have a continental distribution in Europe. Carex ericetorum Poll. and Polygala amarella Crantz are two such species and belong to Matthews' Continental Northern Element. This element includes species whose main area of distribution is in central and northern Europe. Both C. ericetorum and P. amarella are close to their western limits of distribution in Britain with Teesdale being one of the most westerly localities. The world distributions of these two species are shown in Maps 1:11 and 1:12. Both species are widely distributed in central and northern Europe as far eastwards as



Map 1:11 World distribution of *Carex ericetorum* Poll. (Hulten, unpublished).

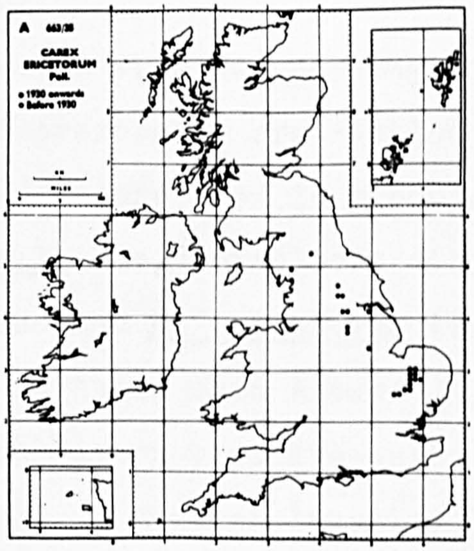


Map 1:12 World distribution of *Polygala amara* L. and *P. amarella* Crantz.

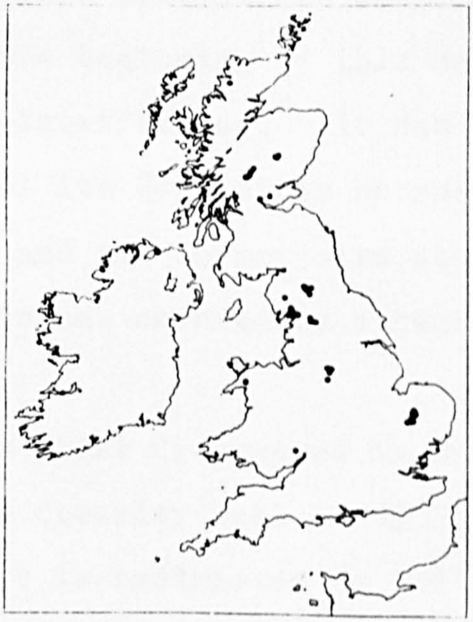
the Ural mountains, though C. ericetorum extends well into Siberia in scattered localities.

In Britain, C. ericetorum has a predominantly eastern distribution (Map 1:13), although it reaches the west coast on Carboniferous limestone in Lancashire. In view of this, it is surprising that the species is absent from the Carboniferous limestone region of Derbyshire, but it may be that it has been overlooked as it flowers early and is very similar to C. caryophyllea in the vegetative condition. Until 1930 C. ericetorum was thought to be restricted to the Breckland of East Anglia, but since then many new localities have been discovered on the Permian magnesian limestone belt of eastern England and on Carboniferous limestone in northern England. Its distribution is strikingly similar to that of the moss Rhytidium rugosum (Map 1:14) which also has a continental distribution in Europe.

In Teesdale C. ericetorum is restricted to the outcrops of sugar limestone and occurs on both Cronkley and Widdybank Fells. It is probably one of the most common species in this habitat, especially on Cronkley Fell and has spread vegetatively over wide areas in the short



Map 1:13 British distribution of Carex ericetorum Poll.
(from Perring & Walters, 1962).

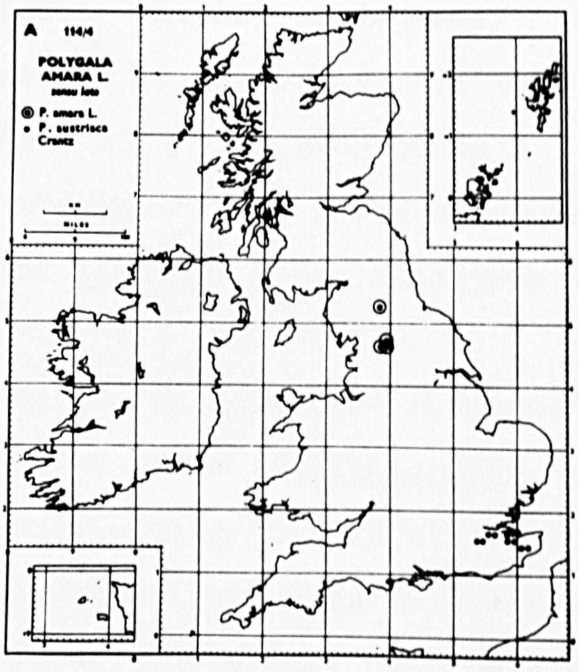


Map 1:14 British distribution of Rhytidium rugosum
(from Pigott, 1956).

turf. It is prevented from reproducing sexually as the inflorescences are nibbled off by sheep long before mature seed is produced.

Polygala amarella has a much more disjunct British distribution than C. ericetorum (see Map 1:15). It occurs in three main areas: Teesdale, the Craven district of mid-west Yorkshire and in Kent. Another locality has recently been discovered near Orton in Westmorland. The distribution of this species has declined considerably since the beginning of this century mainly due to man's interference. It has become extinct in several of its Kent sites because of changes in land use and the former site at Caterham in Surrey is now covered by a housing estate.

The species was first discovered in Britain by the Backhouses on Cronkley Fell in 1852. Like C. ericetorum it is restricted to the outcrops of sugar limestone in Teesdale, though it is much less abundant than that species. It has been known on Widdybank Fell since at least 1883 according to a specimen in the herbarium at Kew, but the site was lost and not rediscovered again until the mid-1960's. The species has

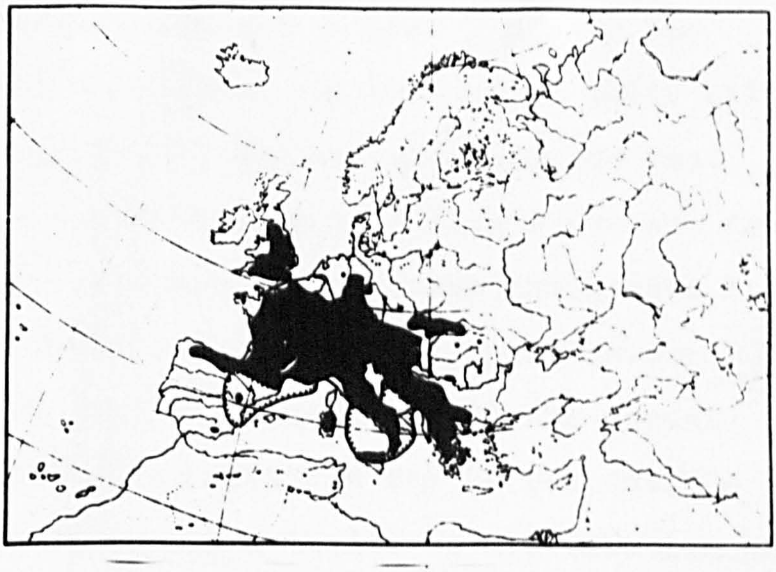


Map 1:15 British distribution of *Polygala amarella* Crantz. (from Perring & Walters, 1962).

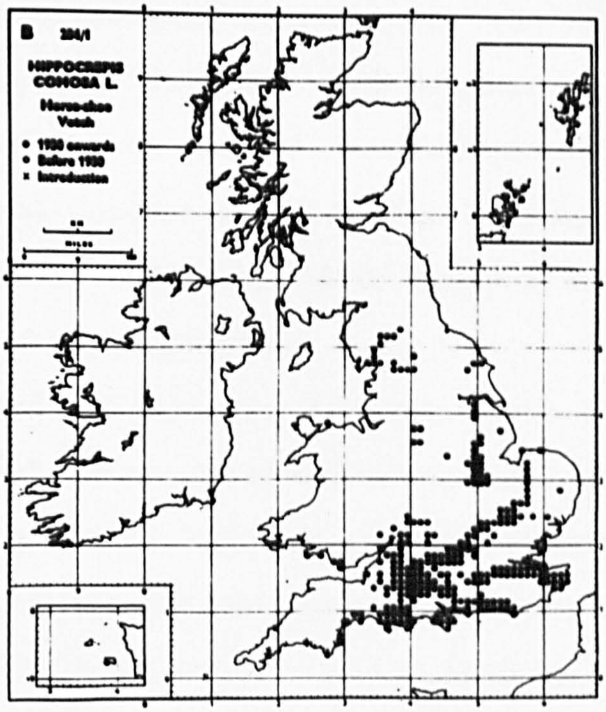
often been reported as extinct on Cronkley Fell, but observations in the summers of 1968 and 1969 showed that it occurs over quite a wide area in the shallow valley known as Black Ark, wherever there is short sugar limestone turf.

The species chosen to represent Matthews' Continental Southern element is Hippocrepis comosa L. Plants belonging to this element have their main distributional area in central and southern Europe and those that have reached Britain are at the northern limits of their range here. The world distribution of H. comosa is shown in Map 1:16 and its British distribution is shown in Map 1:17.

The main concentration of the species in Britain is in the south-east where its pattern of distribution is closely related to the outcrops of chalk and limestone. It becomes progressively rarer and more scattered in the north and west and reaches the most northerly point of its world distribution on Cronkley Fell in Teesdale. There are one or two old records from Scotland but these may be introductions (Matthews, 1937) and there are no records from Ireland. Matthews (1923) has discussed the



Map 1:16 World distribution of Hippocrepis comosa L. (from Meusel, Jäger & Weinert, 1965).



Map 1:17 British distribution of Hippocrepis comosa L. (from Perring & Walters, 1962).

distribution pattern of a number of species restricted to England and Wales with their main area in south-west England and suggests that such species, according to Willis's Age and Area hypothesis are relatively recent immigrants from northern France. In a later paper, however (Matthews, 1937) he suggests that the Oceanic climate of western Britain may be responsible for the north-western limits of distribution of H. comosa by preventing seed production and thus providing an alternative reason for the absence of the species in Ireland. It is however possible that its distribution extended further north and west during the climatic optimum period of the Post-glacial when temperatures were warmer than at present.

The Teesdale site was discovered in about 1840 and plants apparently flowered well until the 1930's, possibly because of lighter grazing pressure or higher summer temperatures at the beginning of this century. Since then no flowers have been seen and the species has been reported as extinct (e.g. Pigott, 1956). In 1965 the site was rediscovered and in 1969 an enclosure erected around it in the hope that the absence of grazing pressure may encourage the plants to flower again. It is probable that the growing season in Teesdale may now be too short to allow the formation of mature seeds which normally takes about four months (See Chapter 4, part 3).

Chapter 2.

Cytology.

Cytology.

I. Introduction.

Chromosome counts have been made on Teesdale representatives of a number of species, but so far there are few records of intraspecific cytological variation within them. The chromosome numbers and cytological behaviour of several of these species are described below and in species where variation in chromosome number is present, an attempt is made to distinguish cytotypes morphologically.

II. Materials and methods.

Plants and seed were collected from a number of native localities and grown in the experimental garden at Sheffield. Somatic chromosome counts were obtained from root-tips which were pretreated with .002 M 8-hydroxyquinoline, fixed in 1:3 acetic-alcohol, stained by the Feulgen method and made into permanent squash preparations using a specially designed hand press and the carbon-dioxide freeze technique.

This method was varied slightly according to the species, e.g. the length of pretreatment in hydroxyquinoline was 2 hours for most species, but for *Alopecurus alpinus* roots, the best results were obtained after 5 hours pretreatment. Chromosome measurements always refer to pretreated material unless otherwise stated. *Juncus alpinus*, *Draba incana* and *Cochlearia alpina* roots stained inadequately with Feulgen stain alone and so were double stained by squashing out in a 1% solution of propionic orcein. The tough fibrous roots of *Alopecurus alpinus* were softened by maceration in a 10% aqueous solution of pectinase at 60° C. for one hour before staining. It was found to be impossible to make adequate squash preparations of somatic *Carex* chromosomes by any of these methods as root-tips are difficult to squash, both cells and chromosomes are very small and the chromosomes do not stain well with any of the dyes available.

Haploid counts were obtained from anther pollen mother cells which were mainly collected and fixed in the field though some were from wild plants now in cultivation. They were stained with either propionic orcein or alcoholic - HCL - carmine (Snow 1963) and made into permanent squash preparations. Alcoholic - HCL - carmine gave the best results with flower buds of Cochlearia alpina, Draba incana, Polygala amarella and Hippocrepis comosa, while propionic orcein worked well with monocotyledonous species.

Photographs were taken with a Zeiss Ultraphot microscope and automatic camera. For karyotype analysis photographic plates and G5/52 sheet film were used, but for all other photographs an Adox KB 14 35 m.m. film was used and enlargements printed on Kodak Bromide Grade 4 paper.

The detailed cytology of individual species is presented below in systematic order.

III . *Cytology of individual species*.

Cochlearia alpina (Bab.) H.C. Watson.

Green Castle, Moorhouse N.N.R. Westmorland.	n = 6	P.M.C.	2 plants.
Woodall, Wensleydale Yorkshire.	n = 6	P.M.C.	several plants
Grassington, Yorkshire	n = 6	P.M.C.	1 plant.
Dirtlow Rake, Derbyshire (seedling)	2n = 12	R.T.	2 plants.
Glas Maol, Angus.	2n = 26	R.T.	3 plants.
Glas Maol, Angus.	n = C.13	P.M.C.	1 plant.

In the root-tips studied, chromosomes are approximately 1/um long and metacentric. **Meiosis in** those cells examined is regular (Plate 2. 1). Gill (1965) and Saunte (1955)record the presence of 1 - 4 B chromosomes in a small proportion of plants, but none were seen in my examination, though population samples may have been too small to adequately sample the variation.

Several chromosome numbers are recorded for *Cochlearia alpina* (Bab.) H.C. Watson and inland populations of *C. officinalis L*. which have been referred to as *C. alpina* (Bab.) H.C. Watson or *C. officinalis* ssp. *alpina* (Bab.) Hook. Gill (1965) records a number of counts of 2n = 12 for *C. alpina* and doubts the only previous record for this species, that of 2n = 28 for plants from an unspecified locality (Crane & Gairdner 1923). Böcher (1938) records

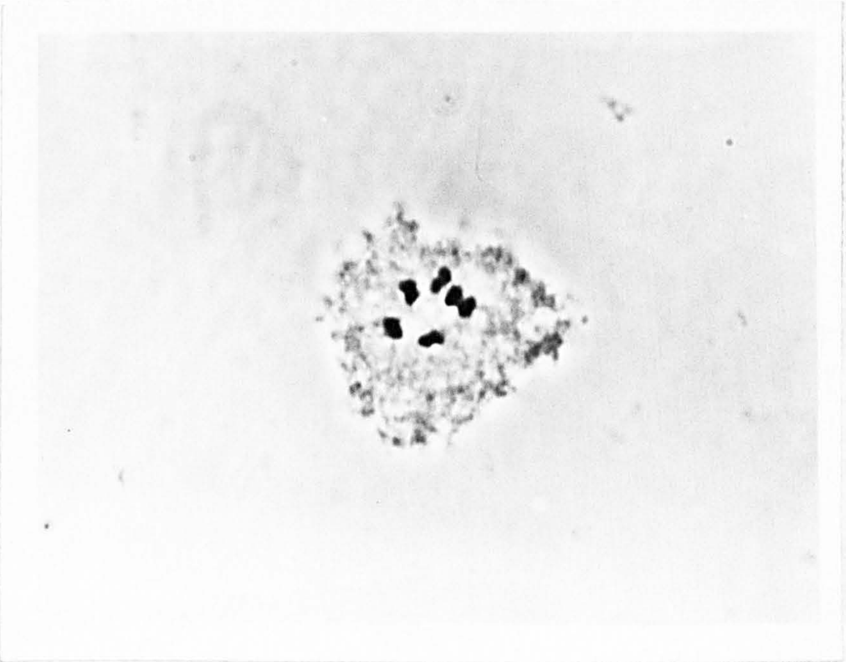


Plate 2:1

Metaphase I of Cochlearia alpina (Bab.) H.C. Watson with 6 bivalents.

C. officinalis L. (var. alpina) from an altitude of 800 m. in the Faeroes as having $2n = 24$ and Saunte (1955) records all the British inland populations of *C. officinalis* which she examined as having $2n = 24$, including one population from Teesdale. Closely related taxa for which chromosome counts are available include *C. pyrenaica* D.C. from the mountains of central Europe for which Rohner (1954) gives counts of $2n = 12$ and the Scottish species *C. micacea* E.S. Marshall for which Crane and Gairdner (1923) give $2n = 34 - 36$.

In general *C. officinalis* is a coastal plant with fleshy leaves and globose fruits, while *C. alpina* is an inland montane species which is not fleshy and has ovoid fruits. These distinctions, however, often break down in practice, fruit shape being particularly variable. All the chromosome counts I have made refer to plants lacking fleshy leaves and with approximately ovoid fruits. Both *C. alpina* and *C. micacea* have recently been united under *C. pyrenaica* by Chater & Heywood (1964), but in view of the different chromosome numbers involved, it is clear that this complex needs a thorough cytotaxonomic revision.

Two base numbers have been postulated for the polyploid series in the genus, $x = 6$ and $x = 7$.

All counts recorded for plants referable to <u>C. alpina</u> belong to the $x = 6$ series. Counts of $2n = 12$ are regarded as diploid, those of $2n = 24 - 28$ as aneuploid at the tetraploid level and of $2n = 34 - 36$ as aneuploid at the hexaploid level. My count of $2 n = 26$ in plants from Glas Maol could be interpreted as being tetraploid with 2 B chromosomes, but as the extra chromosomes are similar in size to other members of the karyotype, occur in all three plants counted and pair regularly at meiosis, it is probable that the plants are aneuploid. Diploid and tetraploid counts have both been recorded from Teesdale, the diploid count from plants in Moorhouse National Nature Reserve and the tetraploid count from an unspecified locality.

<u>Draba incana L.</u>

Widdybank Fell, Co. Durham (seedling)	$2n = 32$	R.T.	1 plant.
Widdybank Fell, Co. Durham.	$n = 16$	P.M.C.	several plants.
Cronkley Fell, Yorkshire.	$n = 16$	P.M.C.	several plants.
Askrigg, Yorkshire.	$n = c16$	P.M.C.	1 plant.
Miller's Dale, Derbyshire.	$n = 16$	P.M.C.	several plants.

This chromosome number has been previously recorded for material from Great Dun Fell in Britain

(Elkington 1962), from Switzerland (Buttler 1967), Norway and Sweden (Heilborn 1927), Denmark (Jörgensen, Sörensen & Westergaard 1958), Iceland (Löve & Löve 1956) and south-west Greenland (Böcher & Larsen 1950).

Related species in the D. incana complex also have 2n = 32. Thus counts of this number have been recorded for the alpine species D. stylaris Gay ex Koch (Merxmüller & Buttler 1965, Buttler 1967) which has been included in D. incana L. by Walters (1964). The North American species D. lanceolata Royle also has 2n = 32 in Greenland (Böcher 1966) and Canada (Mulligan 1966), but Mulligan (loc. cit.) has also made a count of n = 24 for this species in the North West Territories of Canada, though this may refer to a misidentified specimen of another species in this taxonomically complex group.

Root-tip chromosomes are all approximately 1 µm in length and are metacentric. They tend to clump together on the metaphase plate, making counting difficult (Plate 2:2). Meiosis is completely regular (Plate 2:3).

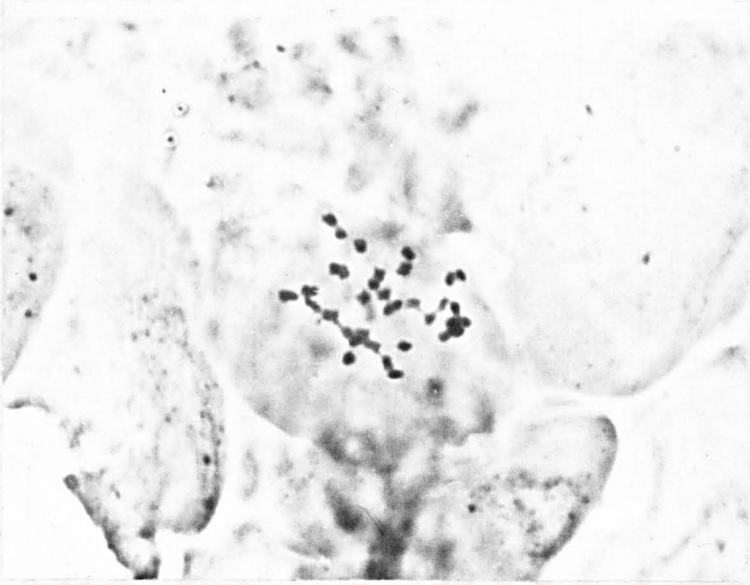


Plate 2:2 R.T. metaphase of Draba incana L.

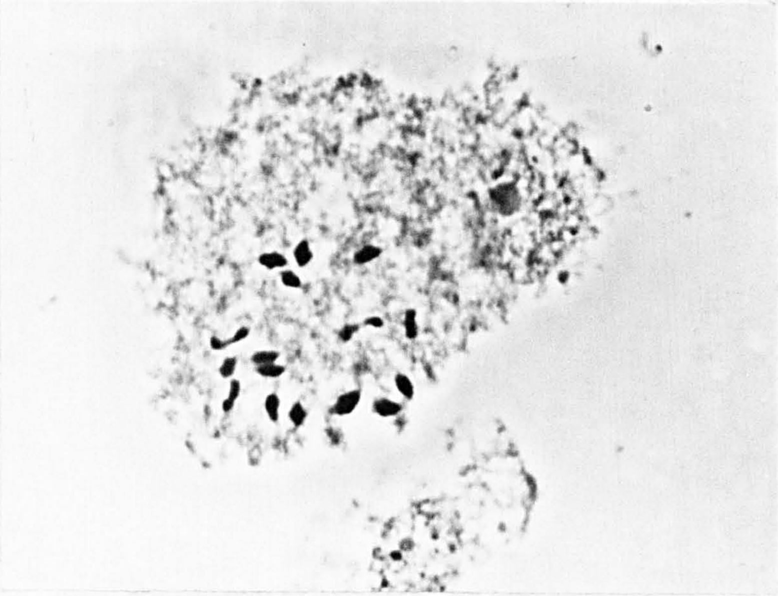


Plate 2:3 Metaphase I of Draba incana L. with 16 bivalents.

Polygala amarella Crantz

Widdybank Fell, Co. Durham.	n = 17	P.M.C.	several plants.
Cronkley Fell, Yorkshire (seedling)	2n = 34	R.T.	1 plant.
Dib Scar, Grassington, Yorkshire.	n = 17	P.M.C.	several plants.
Mastiles Lane, near Grassington, Yorkshire.	n = 17	P.M.C.	several plants.
Gordale Beck, Malham, Yorkshire.	n = 17	P.M.C.	several plants.
Crundale Downs, Kent.	n = 17	P.M.C.	several plants.
Magpie Bottom, Kent.	n = 17	P.M.C.	1 plant.
Couvet, Jura, Switzerland.	n = 17	P.M.C.	3 plants.
Near Couvet, Jura, Switzerland.	n = 17	P.M.C.	4 plants.
Fugière, near La Mure, Isère, France.	n = 17	P.M.C.	2 plants.
Near Seyne, Basses Alpes, France.	n = 17	P.M.C.	5 plants.

Glendinning (1960) has previously recorded 2n = 34 in plants of this species originating from Yorkshire, Kent and Switzerland. Other authors have recorded this number for Scandinavian material (Bjorsa 1961, Sorsa 1963).

The closely related species *P. amara L.* with which *P. amarella* Crantz was long regarded as synonymous has a more eastern distribution in Europe

(See Map 1:12 p. 25) and a different chromosome number. Baksay (1956) has recorded 2n = 28 for this species in Hungary and this number has also been reported for Polish material (Skalinska et al. 1959). *P. amara* is in general a more robust plant with larger flowers than *P. amarella*, but its main distinguishing feature is the presence of an articulated corolla, lacking in *P. amarella*. Other distinguishing characters given by McNeill (1968) fall within the overall range of variation of both species and are not very satisfactory especially when applied to British material of *P. amarella*, local populations of which show a high degree of morphological differentation (See Chapter 4 pt. II).

Unshortened somatic chromosomes vary in size from 0.4 to 1 µm and are approximately metacentric (Plate 2:4). Meiosis is regular and exhibits several characteristic features. At diakinesis there is always one chromosome attached to the nucleolus (Plates 2:5 and 2:6). At first metaphase the nuclear spindle is very clear and tends to be pressed out of the pollen mother cell when squashed, so that the metaphase plate is invariably seen in lateral view. One bivalent, possibly the one previously attached to the nucleolus, is much larger than the others and has a number of constrictions

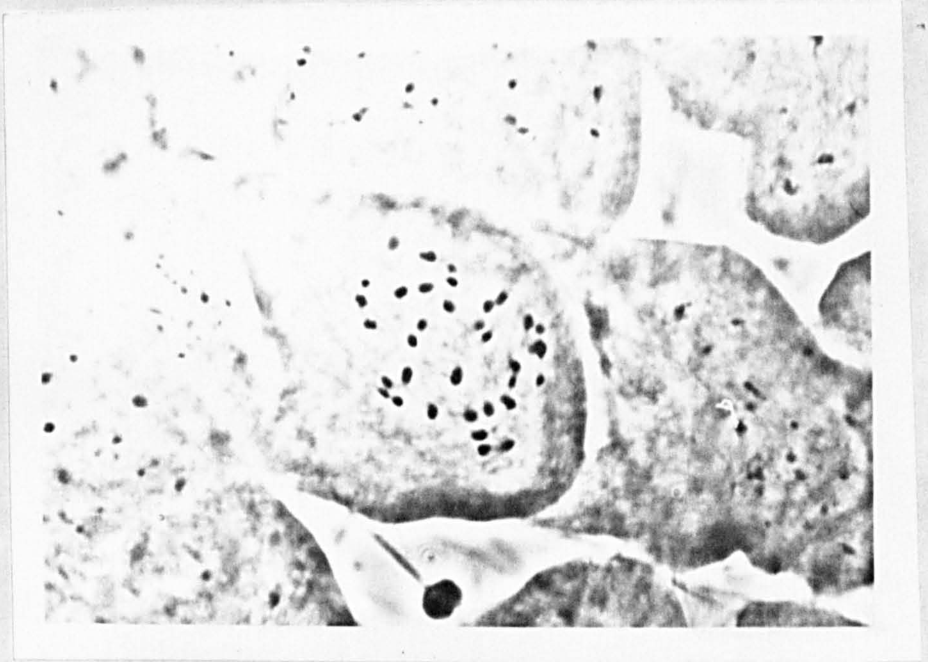
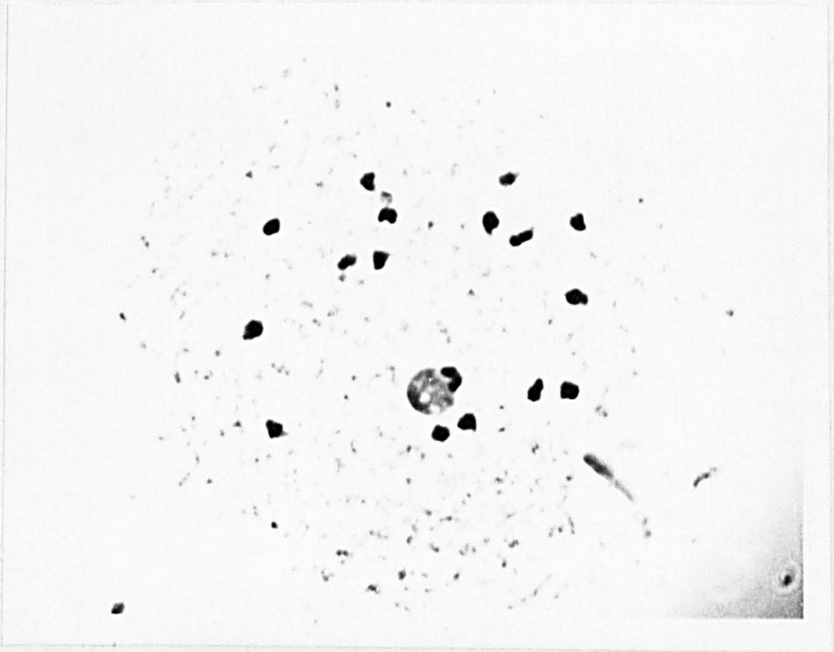
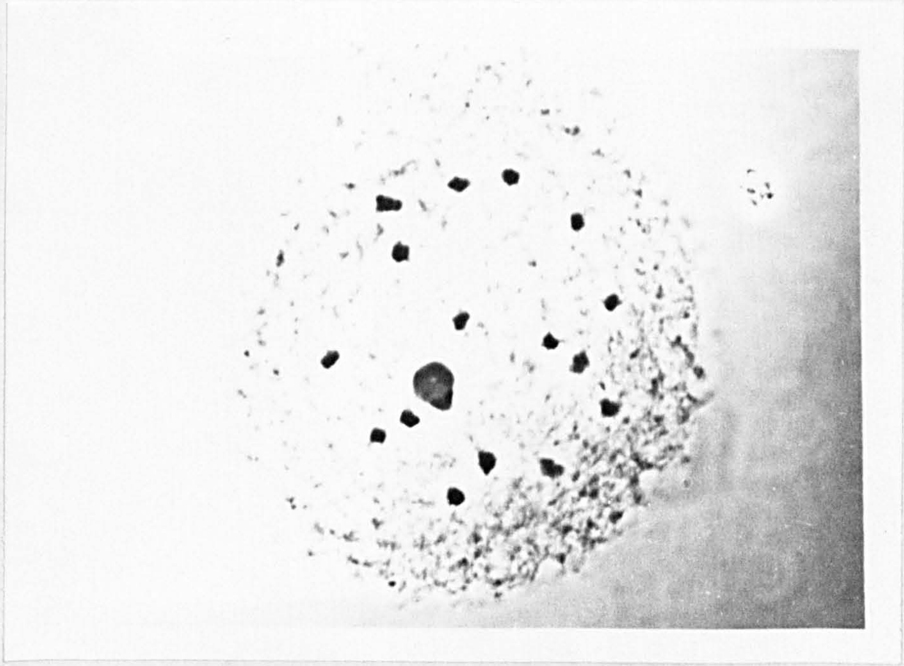
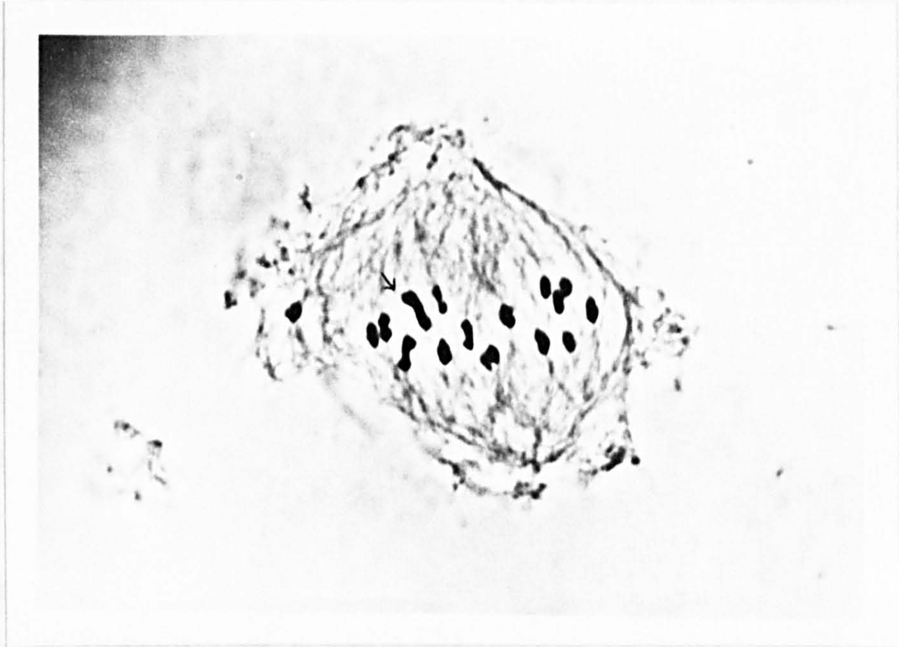


Plate 2:4 R.T. metaphase of Polygala amarella Crantz.

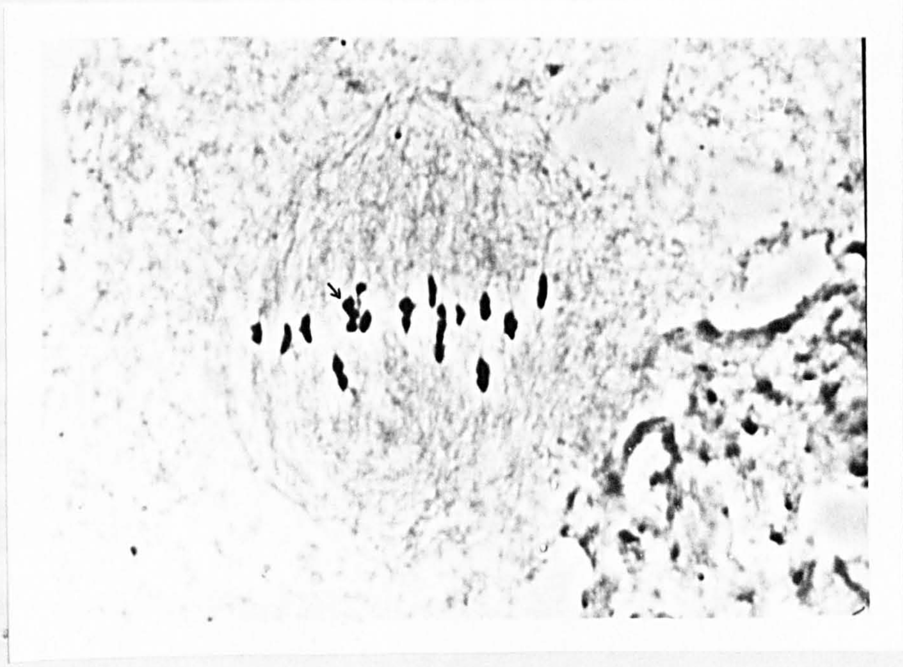


Plates 2:5 (above) and 2:6 (below) showing diakinesis in Polygala amarella Crantz with one bivalent attached to the nucleolus.





Plates 2:7 (above) and 2:8 (below) showing late metaphase I in *Polygala amarella* Crantz with one of the 17 bivalents (arrowed) larger than the rest.



which none of the others possess. (Plates 2:7 and 2:8)

Chromosome numbers recorded for *Polygala* show that there is an aneuploid series in the genus, counts of $2n = 28, 32, 34, 38, C40, 48 - 56, C56, 68$ and C70 having been recorded (Glendinning 1960, Larsen 1959). It is possible that the series is monobasic with $x = 7$ or it may be dibasic with $x = 7$ and $x = 8$. If there are two base numbers, then the two chromosome numbers within the *P. amara* group can be interpreted as a euploid in the $x = 7$ series ($2n = 4x = 28$) and an aneuploid tetraploid in the $x = 8$ series ($2n = 4x = 32 + 2$).

Hippocrepis comosa L.

Cronkley Fell, Yorkshire (leaf cutting)	$2n = 28$ R.T.	1 plant.
Great Close Scar, Malham, Yorkshire.	$2n = 28$ R.T.	1 plant.
Grassington, Yorkshire.	$2n = 28$ R.T.	1 plant.
Ayesgarth Falls, Yorkshire.	$2n = 28$ R.T.	1 plant.
Cave Hole Wood Scar, Yorkshire.	$2n = 28$ R.T.	1 plant.
Silverdale, Lancashire.	$2n = 28$ R.T.	1 plant.
Ermine Street, Lincolnshire.	$2n = 28$ R.T.	2 plants.
Aston Rowant, Oxfordshire.	$2n = 28$ R.T.	2 plants.
Pegsdon, Bedfordshire.	$2n = 28$ R.T.	2 plants.

Streatly, Berkshire.	2n = 28 R.T.	2 plants.
Shaftesbury, Dorset.	2n = 28 R.T.	1 plant.
Maiden Castle, Dorset.	2n = 28 R.T.	1 plant.
Durlston Head, Dorset.	2n = 28 R.T.	1 plant.
Branscombe, Devon.	2n = 28 R.T.	1 plant.
Ventnor, Isle of Wight.	2n = 28 R.T.	1 plant.
Carisbrooke Castle, Isle of Wight.	2n = 28 R.T.	2 plants.
Birling Gap, Sussex.	2n = 28 R.T.	3 plants.
Wye Downs, Kent.	2n = 28 R.T.	3 plants.
Wye Downs, Kent.	n = 14 P.M.C.	several plants.
Burham Downs, Kent.	2n = 28 R.T.	2 plants.
Burham Downs, Kent.	n = 14 P.M.C.	several plants.
Biggin Hill, Kent.	n = 14 P.M.C.	1 plant.
Bredhurst, Kent.	2n = 28 R.T.	1 plant.
Bredhurst, Kent.	n = 14 P.M.C.	several plants.
Durl Head, Devon.	2n = 14 R.T.	1 plant.
Wye Dale, Derbyshire.	2n = 14 R.T.	1 plant.
Wye Dale, Derbyshire.	n = 7 P.M.C.	8 plants.
Topley Pike, Derbyshire.	2n = 14 R.T.	1 plant.
Dovedale, Derbyshire.	2n = 14 R.T.	2 plants.
Great Orme's Head, Caernarvonshire.	2n = 14 R.T.	3 plants.
Overton, Gower Peninsula, Glamorgan.	2n = 14 R.T.	1 plant.
Couvet, Jura, Switzerland.	2n = 28 R.T.	2 plants.

Couvet, Jura, Switzerland.	n = 14	P.M.C.	1 plant.
Oberalp Pass, near Andermatt, Switzerland.	2n = 28	R.T.	3 plants.
Vue des Alpes, Jura, Switzerland.	n = 14	P.M.C.	3 plants.
Val dal Fain, Engadin, Switzerland.	2n = 28	R.T.	4 plants.
Pontresina, Engadin, Switzerland.	2n = 28	R.T.	1 plant.
Pontresina, Engadin, Switzerland.	n = 14	P.M.C.	3 plants.
St. Moritz, Engadin, Switzerland.	2n = 28	R.T.	2 plants.
Bex, Vaud, Switzerland.	2n = 28	R.T.	1 plant.
Lescheres, Haute Marne, France.	2n = 28	R.T.	2 plants.
Lescheres, Haute Marne, France.	n = 14	P.M.C.	1 plant.
Mt. Nivolet, near Chambéry, Savoie France.	2n = 28	R.T.	1 plant.
Quet - en - Beaumont, Isère, France.	2n = 28	R.T.	2 plants.
Seyne, Basses Alpes, France.	2n = 28	R.T.	4 plants.
Col du Lautaret, Hautes Alpes, France.	2n = 28	R.T.	1 plant.

As will be seen from the table of chromosome numbers given above, two cytological races have been found within this species in Britain. Maud (1939, 1940) recorded only 2n = 28 in British material from an unspecified locality, but more recent work has shown the existence of an intraspecific polyploid series. Diploid (2n = 14) and tetraploid (2n = 28) races have been discovered in France (Guern & Gorenflot 1966, Guern 1969) and in England (Guern 1969) and a hexaploid (2n = 42) race has been found in the Pyrenees (Guern 1969). A detailed account of the distribution of cytotypes is given in Chapter 4, part III.

Chromosome counts made on other species in the genus confirm that the base number is 7. The centre of variation and thus the possible centre of origin of *Hippocrepis* is in Spain and the majority of species have a Mediterranean distribution. Guern & Gorenflot (1966) report that all the annual species they examined are diploid. They also report that both diploid and tetraploid populations of the Mediterranean plant *H. comosa ssp. glauca* (Ten.) Rouy (syn. *H. glauca* Ten.) exist.

The morphology of somatic chromosomes of diploid and tetraploid plants was examined in root-tip squash preparations (Plates 2:9 and 2:10). Idiograms were constructed by photographing a metaphase plate and cutting out the chromosomes from an enlarged print after numbering them randomly. Distinguishing features such as centromere positions

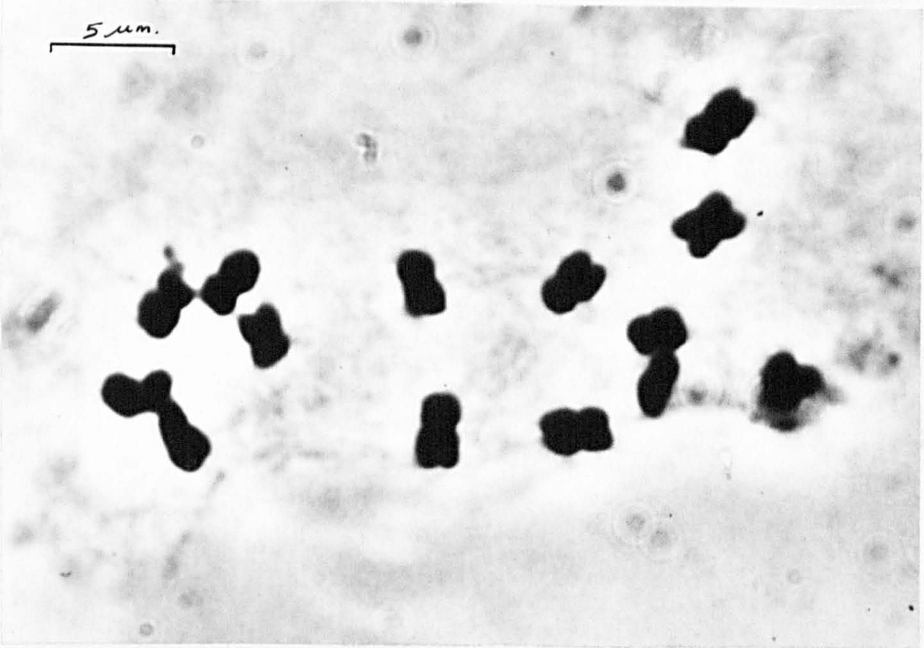


Plate 2:9 R.T. metaphase of diploid *Hippocrepis comosa* L.

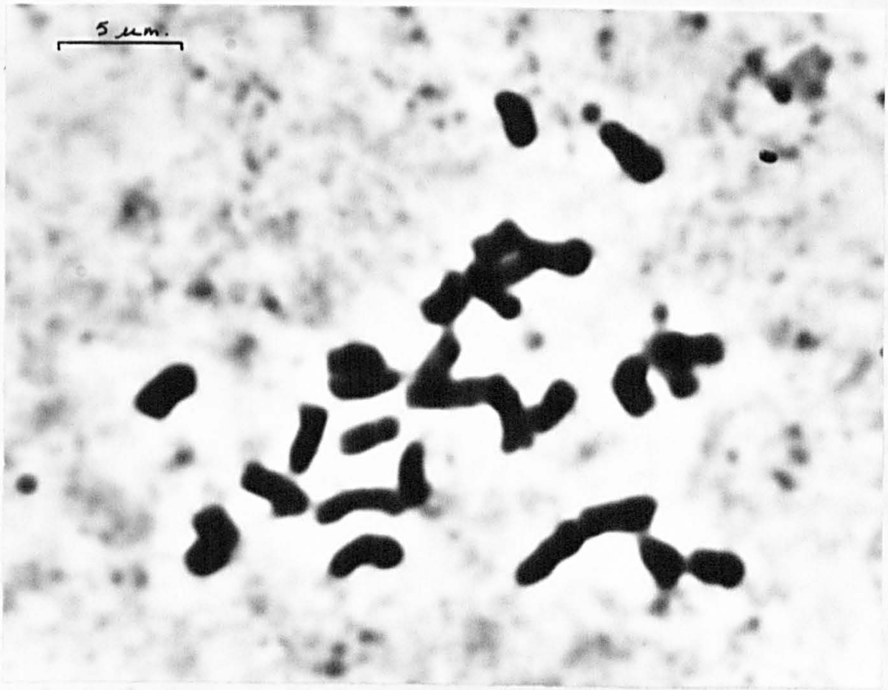


Plate 2:10 R.T. metaphase of tetraploid *Hippocrepis comosa* L.

and satellites were noted and the length of each chromosome arm was measured using dividers. Chromosomes with similar features were paired and placed in a line. Diploid and tetraploid karyotypes are shown in Fig. 2:1 and it can be seen that the diploid karyotype is duplicated exactly in the tetraploid. The haploid complement consists of one long submetacentric chromosome with a satellite, four metacentric chromosomes gradually decreasing in size, one short submetacentric chromosome and one very short chromosome with an almost terminal centromere. Guern & Gorenflot (1966) report that one of the chromosomes in the genome has a secondary constriction, but none were seen during this examination. A diagrammatic representation of the haploid karyotype is shown in Fig. 2:2. Diploid chromosomes are slightly longer than those of tetraploid plants and are affected more by hydroxyquinoline, so that after 2 hours pretreatment comparable diploid and tetraploid chromosomes are almost the same length. Table 2:1 illustrates the effect of hydroxyquinoline on the mean lengths of the longest and shortest chromosomes in the karyotype. Mean values were calculated from measurements of ten chromosomes of each type, a sample which is possibly rather small

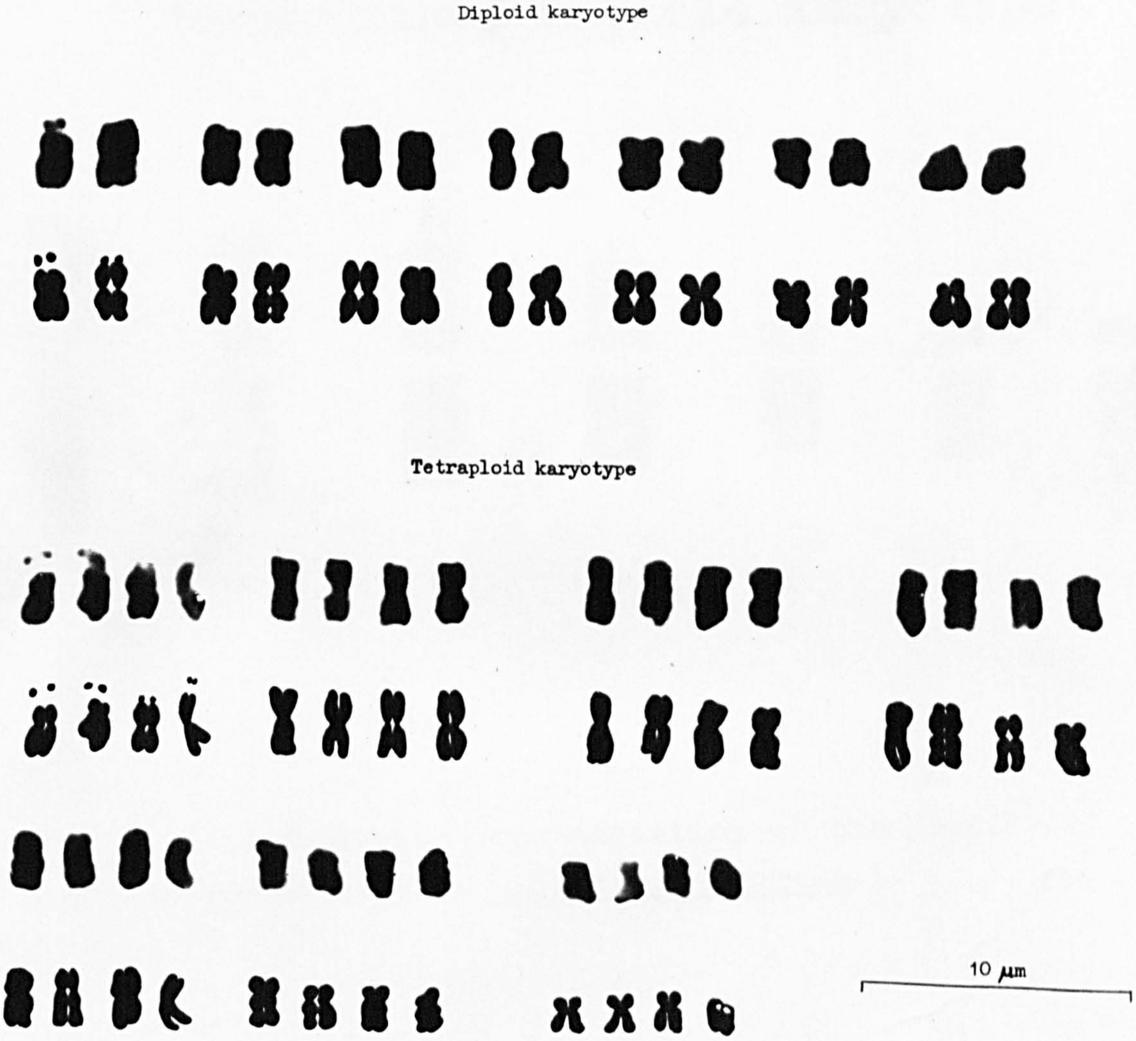


Fig. 2:1 Karyotypes of diploid and tetraploid Hippocrepis comosa L. (photographic prints above and interpreations below).

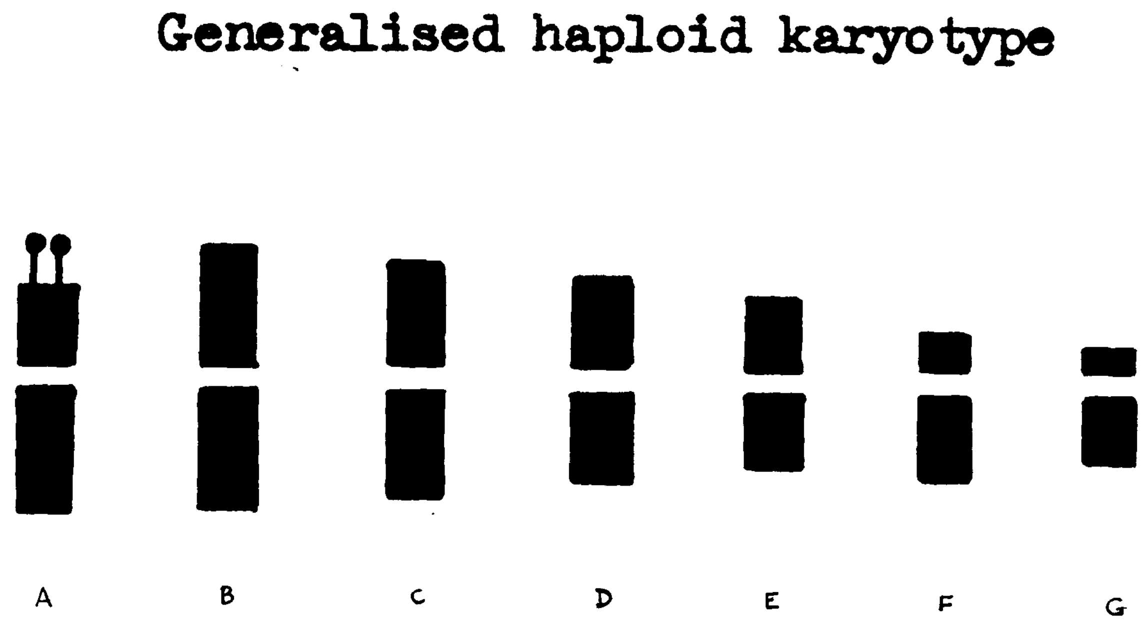

Generalised haploid karyotype

Fig. 2:2 Diagrammatic representation of the haploid chromosome complement of Hippocrepis comosa L.

but which nevertheless gives some indication of the effect of this chemical.

TABLE 2:1.

A comparison of chromosome lengths of diploid and tetraploid *Hippocrepis comosa*, showing the effect of .002 M 8-hydroxyquinoline.

	DIPLOID		TETRAPLOID	
Chromosome	B	G	B	G
Untreated	3.72	2.09	3.07	1.62
After 2 hrs pretreatment with hydroxyquinoline.	2.32	1.31	2.15	1.02

At first metaphase of meiosis pairing of homologous chromosomes is quite regular in diploid plants and seven bivalents are formed, see Plate 2:11. One bivalent has several constrictions when seen in lateral view (Plate 2:12) and is thought to be the pair of satellited chromosomes. In approximately 5% of the cells examined lagging chromosomes are seen at both first and second anaphase. As a result some of the pollen grain nuclei are genetically unbalanced and give rise to a low percentage of inviable pollen.

In tetraploid plants the majority of chromosomes

Plate 2:11 Diplotene of diploid Hippocrepis comosa L. showing 7 bivalents with few chiasmata.

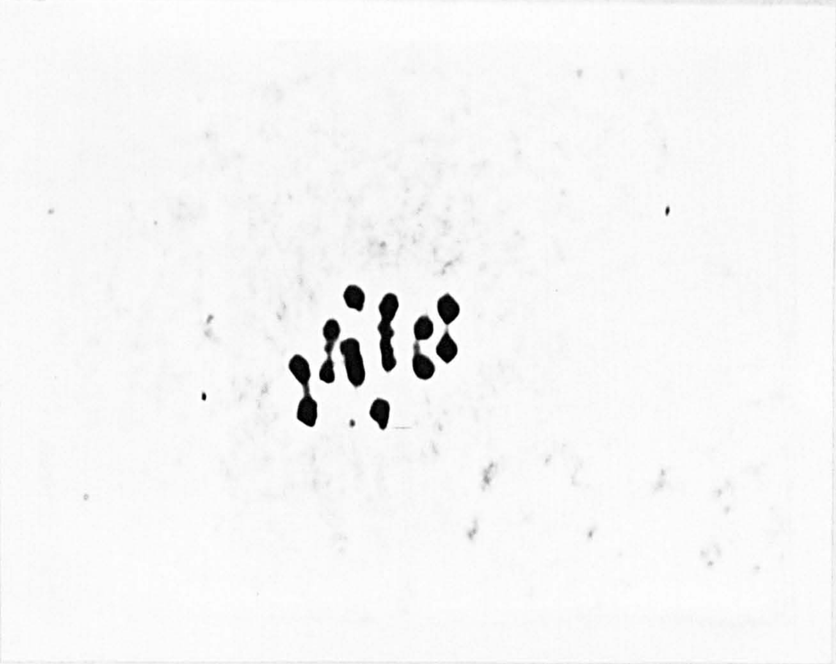


Plate 2:12 Anaphase I of diploid Hippocrepis comosa L. showing one large bivalent with several constrictions.

form bivalents, but quadrivalents in the form of chains and rings with adjacent or alternate arrangements have been seen in a variable proportion of cells. The majority of cells contain only one, but some may have up to three quadrivalents (Table 2:2 and Plates 2:13 - 2:15). No trivalents have been seen and bivalents are by far the most common association (Table 2:3).

TABLE 2:2

Frequency distribution of cells with from 0 - 3 quadrivalents in tetraploid *Hippocrepis comosa*.

		Percent frequency of cells with stated number of quadrivalents.				
Plant No.	Origin	0	1	2	3	Cells exam.
Bredhurst 4	Kent, England.	75.0	25.0	0	0	20
Burham 4	Kent, England.	45.0	40.0	15.0	0	20
C12/3	Pontresina Switzerland	55.0	35.0	5.0	5.0	20
C12/2	Pontresina Switzerland	41.7	58.3	0	0	12
C5/2	Jura, Switzerland.	70.0	30.0	0	0	20

Diakinesis in tetraploid *Hippocrepis comosa* L. showing a cell with no quadrivalents (Plate 2:13), a cell with 1 quadrivalent (Plate 2:14), and a cell with 2 quadrivalents (Plate 2:15).

Plate 2:13.

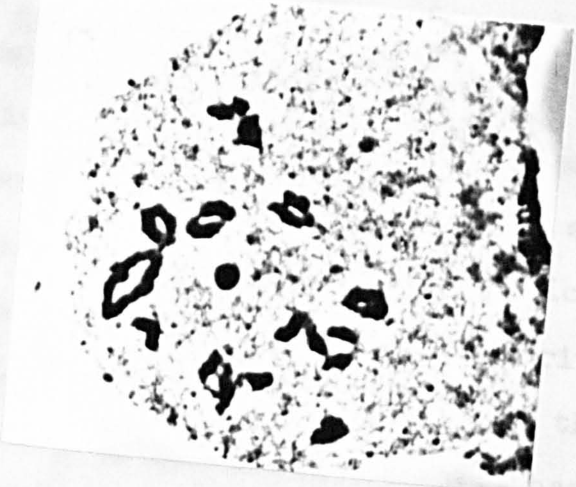


Plate 2:14.

Plate 2:15.

TABLE 2:3

Chromosome pairing in tetraploid *Hippocrepis comosa*

		Mean associations per cell.				
Plant No.	Origin	IV	III+I	II	I	Cells exam.
Bredhurst 4	Kent, England.	0.25	0	13.50	0	20
Burham 4	Kent, England.	0.60	0	12.60	0	20
C12/3	Pontresina, Switzerland	0.50	0	13.00	0	20
C12/2	Pontresina, Switzerland	0.58	0	12.83	0	12
C5/2	Jura, Switzerland	0.30	0	13.40	0	20

As in the diploids, lagging chromosomes are seen at anaphase in about 5% of the cells examined but on the whole meiosis results in genetically balanced gametes and the presence of quadrivalents has little if any effect on pollen fertility, there being regular separation of chromosomes at anaphase even when quadrivalents occur. (Plate 2:16)

Chiasma frequency was examined at diakinesis to see if this varied amongst plants from different areas and different ploidy levels. As will be seen from table 2:4 chiasma frequency is low and also remarkably constant at c0.7 per chromosome, whatever the origin or ploidy of the plant.

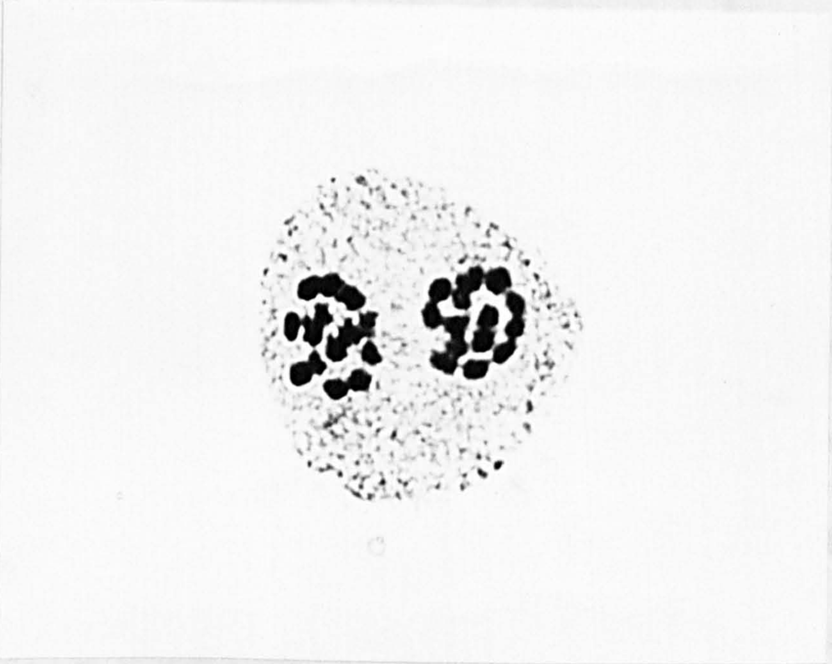


Plate 2:16 Metaphase II of tetraploid <u>Hippocrepis comosa</u> L.

TABLE 2:4

Chiasma frequency in Hippocrepis comosa.

Plant No.	Origin	Ploidy	Mean Xta/cell	Mean Xta/ Chromosome	No.cells examined
Bredhurst 4	Kent, England	4x	18.25	0.652	20
Burham 4	Kent, England	4x	17.95	0.641	20
C12/3	Pontresina Switzerland	4x	19.75	0.705	20
C12/2	Pontresina Switzerland	4x	20.16	0.720	12
C5/2	Jura Switzerland	4x	20.45	0.730	20
Wye Dale 1	Derbyshire, England	2x	9.50	0.678	20
Wye Dale 3	Derbyshire, England	2x	9.85	0.704	20
Wye Dale 4	Derbyshire, England	2x	9.80	0.700	20
Wye Dale 5	Derbyshire, England	2x	9.85	0.704	20

The three cytotypes of H. comosa are almost completely morphologically indistinguishable. Attempts have been made to relate chromosome number to external morphological features in diploids and tetraploids using a number of floral and vegetative characters but the only ones where any separation is possible are those relating to pollen grain and stomatal guard cell sizes.

Pollen grains of this species are ovoid and maximum and minimum diameters were therefore measured and the mean diameter calculated. 20 pollen grains were examined in each sample and the results are shown in Table 2:5. Mean pollen grain diameter of tetraploid plants is slightly greater than that of diploid plants. The difference between mean values of maximum and minimum pollen grain diameter of diploid and tetraploid plants is statistically significant at the 1% and 2% levels respectively, and the difference between mean pollen grain diameter of diploids and tetraploids is significant at the 1% level. These differences, however, are too slight to be used as a reliable character for distinguishing diploid and tetraploid herbarium material.

TABLE 2:5

Pollen grain diameter (μm), showing mean values and standard error.

Origin	Maximum	Minimum	Mean
Diploid			
Gt. Orme's Head, Caernarvonshire.	22.12 ± 0.27	19.40 ± 0.25	20.76
Wye Dale, Derbyshire.	20.79 ± 0.31	18.21 ± 0.18	19.50
Overton, Glamorgan.	22.36 ± 0.23	19.70 ± 0.21	21.03
Mean	21.76	19.10	20.43
Tetraploid			
Marne Valley, France.	23.68 ± 0.21	20.80 ± 0.22	22.24
Marne Valley, France.	23.81 ± 0.27	20.87 ± 0.20	22.34
Andermatt, Switzerland.	23.59 ± 0.29	20.39 ± 0.18	21.99
Bredhurst, Kent.	24.99 ± 0.37	20.65 ± 0.36	22.82
Mean	24.02	20.68	22.35

Ockenden (1968) and others have shown that polyploidy often increases the number of apertures per pollen grain and may be accompanied by variation in surface ornamentation when examined under the scanning electron microscope. However, both diploid and tetraploid pollen grains of H. comosa show three longitudinal furrows and have similar surface features when examined in this way (Plates 2:17 and 2:18).

Stomatal guard cell length is the only reasonably reliable morphological character which can be used to separate diploid and tetraploid plants. Tetraploids tend to have longer guard cells than those of diploids and though there is quite a large overlap in the range of variation, there is far less overlap when mean values are compared (Fig. 2:3). The ploidy of plants in the population on Cronkley Fell was correctly predicted by this method before any cytological preparations were made. Even so, some plants cannot be identified as to cytotype using this character.

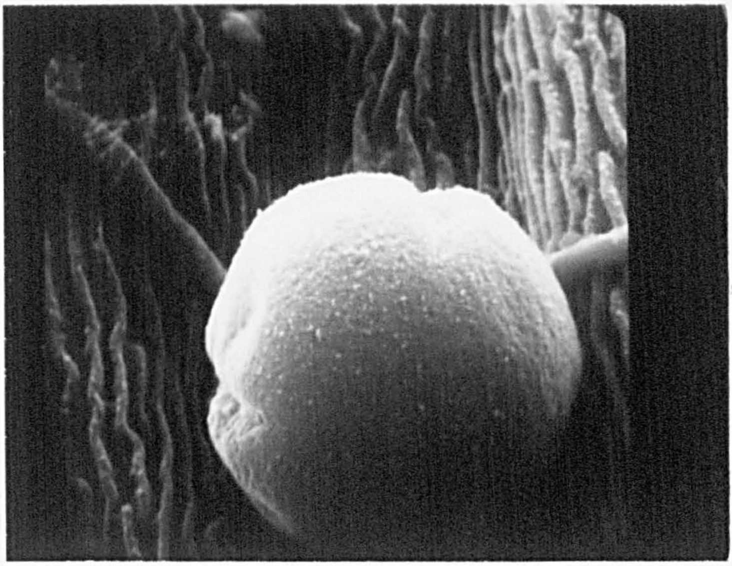


Plate 2:17 Scanning electron micrograph of a pollen grain of diploid <u>Hippocrepis comosa</u> L.

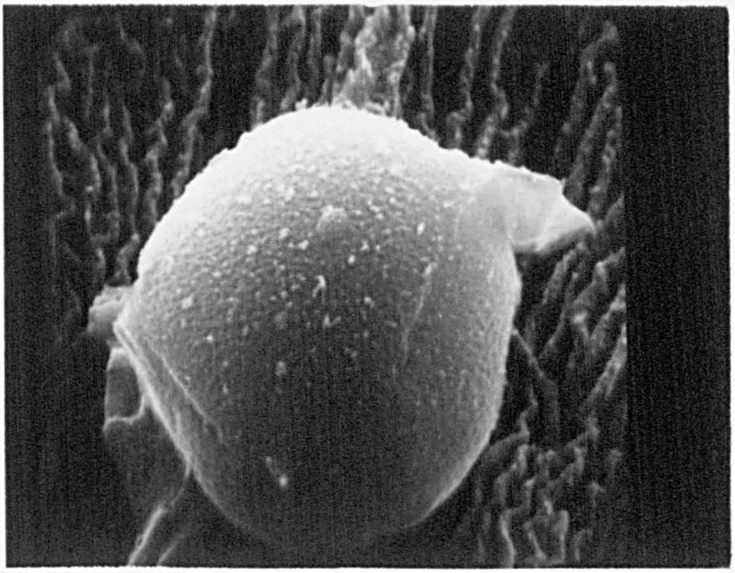
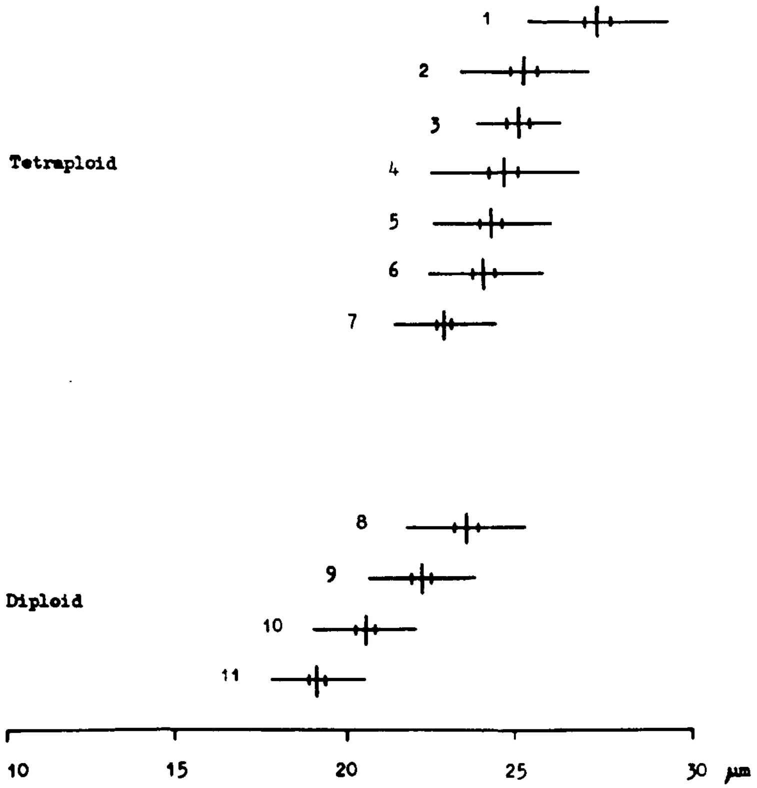


Plate 2:18 Scanning electron micrograph of a pollen grain of tetraploid <u>Hippocrepis comosa</u> L.



1. Burham, Kent.
2. Val dal Fain, Engadin, Switzerland.
3. Cronkley Fell, Teesdale, Yorkshire.
4. Aysgarth, Yorkshire.
5. Bredhurst, Kent.
6. Wye Downs, Kent.
7. Bex, Vaud, Switzerland.
8. Overton, Gower, Glamorgan.
9. Durl Head, Devon.
10. Dove Dale, Derbyshire.
11. Great Orme's Head, Caernarvonshire.

Fig. 2:3 Stomatal guard cell length, showing the mean, twice the standard error and twice the standard deviation.

In the field (in Britain) diploids usually form bushy plants with large leaves and leaflets while tetraploids are relatively small leaved and often prostrate. This is probably a genecological response to grazing, as ungrazed tetraploids are morphologically similar to diploids, which have not so far been found in situations accessible to grazing animals. A detailed account of this variation is given in Chapter 4. pt. III.

The observations described above provide conflicting evidence as to the origin of the tetraploid. The low quadrivalent frequency at meiosis suggests that it may be an allo - or segmental allopolyploid, while the similarities in karyotype and external morphology are more in accordance with an autopolyploid origin, though karyotypes of other diploid species in the genus have not yet been examined and may also prove to be similar. A number of workers (Dawson 1941, Riley & Chapman 1958, Morrison & Rajhathy 1960) have shown, however, that multivalent frequency in polyploids is dependent on a number of factors other than chromosome homology, so that the absence of multivalents does not necessarily indicate allopolyploidy. Dawson (1941) postulated that the tetraploid race of *Lotus corniculatus* is an autopolyploid because inheritance of cyanogenesis is tetrasomic, in spite of the fact that few multivalents are seen at meiosis. However, later work has shown that the natural tetraploid is unable to hybridise with an artificially induced autotetraploid so its origin is still in doubt. In *H. comosa* it seems likely that the low chiasma frequency of only 0.7 per chromosome limits quadrivalent formation, but until there is more evidence available, neither an auto - nor an allopolyploid origin can be postulated with any certainty. Attempts to synthesise an artificial autotetraploid for comparison with the natural tetraploid have been unsuccessful.

Juncus alpinus Vill.

Widdybank Fell, Co. Durham	$2n = 40$	R.T.	3 plants
Widdybank Fell, Co. Durham	$n = 20$	P.M.C.	1 plant
Winch Bridge, Teesdale, Co. Durham	$2n = 40$	R.T.	2 plants
Devil's Elbow, Perthshire	$2n = 40$	R.T.	1 plant
Sand Sike, Teesdale, Co. Durham	$2n = 40$	R.T.	3 plants
Braemar, Aberdeenshire	$2n = 40$	R.T.	1 plant
Shiehallion, Perthshire	$2n = 40$	R.T.	1 plant
Ben Vrackie, Perthshire	$n = 20$	P.M.C.	1 plant
Branxholme, Roxburghshire	$2n = 40$	R.T.	1 plant

* Loch Ussie, E. Ross	2n = 40 R.T.	2 plants
Col du Lautaret, Hautes Alpes, France.	n = 20 P.M.C.	2 plants
Lund, Sweden (seedling)	2n = 40 R.T.	1 plant

* *Juncus alpinus* Vill. ssp. *nodulosus* (Wahlenb.) Lindm. var. marshallii (Pugsley) Lindquist

Juncus alpinus sensu lato is very variable and forms a taxonomically complex group. It has been studied by a number of Scandinavian workers, notably Lindquist and Hylander. It is generally agreed that there are two fairly distinct types and Hylander (1953) separated the more robust artic-alpine race with sessile flowers in the inflorescences as *J. alpinus* Vill. ssp. *arthrophyllus* (Brenn.) Hyl. and the slender circumpolar race with pedicellate flowers in the inflorescences as *J. alpinus* Vill. ssp. *nodulosus* (Wahlenb.) Lindm. A number of varieties have been named within each subspecies and most British plants, with the exception of those from Loch Ussie seem referable to *J. alpinus* Vill. ssp. *arthrophyllus* (Bren.) Hyl. var *fuscoater* (Celak) Buch.

There is considerable variation in capsule shape and degree of capsule exsertion from the perianth within British plants of ssp. *arthrophyllus* even within the Teesdale region, though this variation is mainly due to phenotypic plasticity. Field samples of plants from Widdybank Fell, for example, have capsules which are completely immersed in the perianth. This may be an adaptation to withstand the cold windy climate there which has also caused the tattered appearance of the scarious margins of the perianth segments (Fig. 2:4). The capsules produced after one year in cultivation protrude from the perianth almost as much as those from more sheltered sites in Teesdale.

Alpine material of ssp. *arthrophyllus* from the Col du Lautaret remains distinct in cultivation and has rather sparsely-branched inflorescences with large heads of dark brown sessile flowers with definite "shoulders" on the capsules. The distribution of this arctic-alpine race, referred to as *J. alpinus* Vill. *var. alpestris* (C.J. Hartman) C. Hartman, has been studied by Lindquist (1931, 1940). The name "*alpestris*", however, also includes Scandinavian plants with some shortly pedicellate flowers in the inflorescences and Löve & Löve (1961) include such plants within *J. nodulosus* Wahlenb. Some British populations appear to be intermediate between *var. fuscoater* and the alpine type of *var. alpestris*.

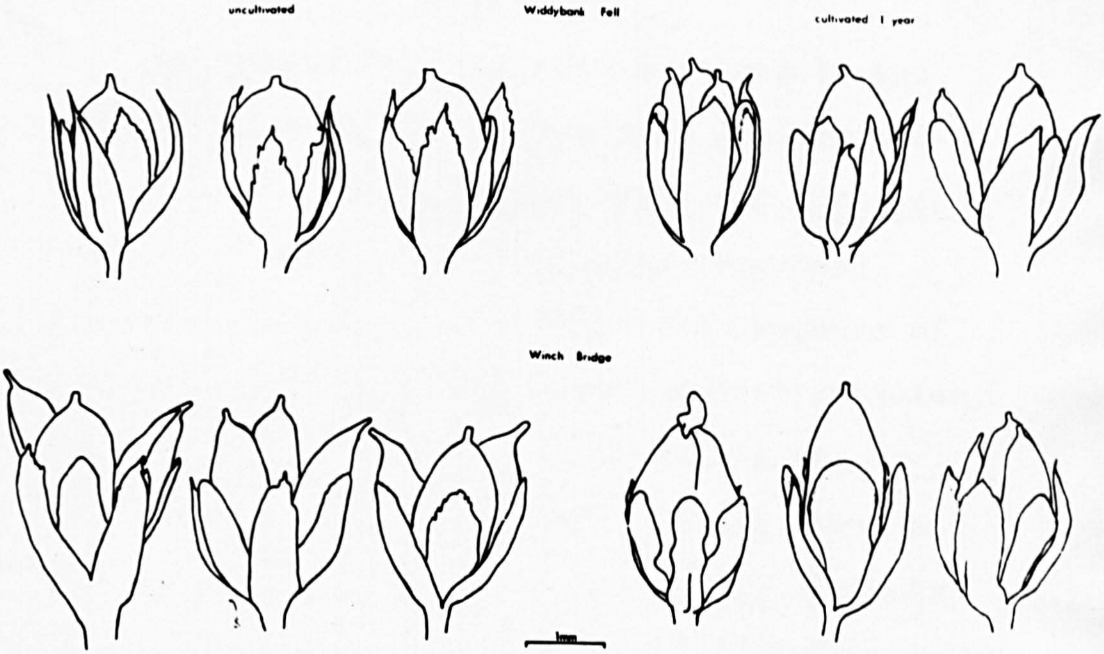


Fig. 2:4 Camera lucida drawings of capsules of Teesdale representatives of Juncus alpinus Vill. showing the effects of cultivation.

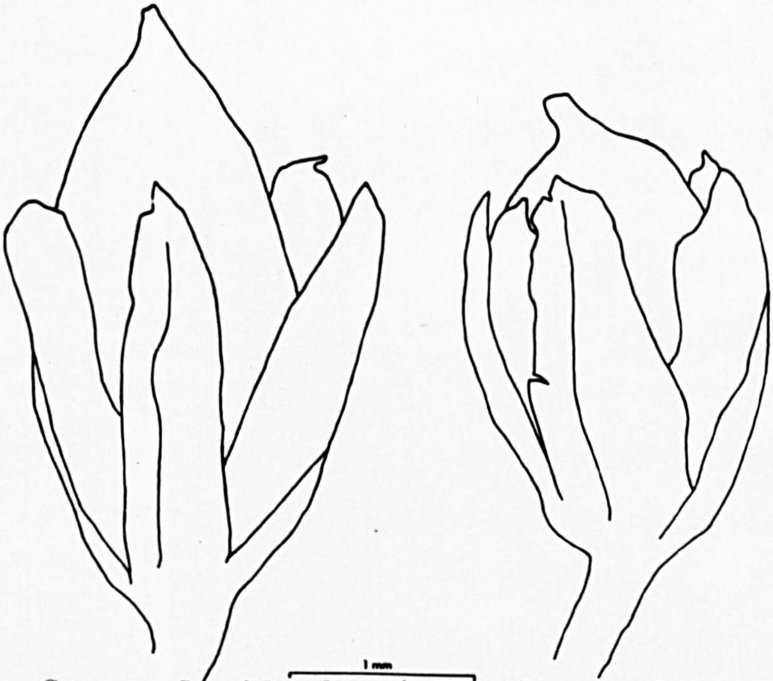


Fig. 2:5 Camera lucida drawings of capsules of Juncus alpinus Vill. ssp. nodulosus (Wahlenb.) Lindm. showing the long pointed capsule of var. rariflorus (E. Fries) C.J. Hartman and the immersed, shouldered capsule of var. marshallii (Pugsley) Lindquist.

The plants from Loch Ussie belong to the circumpolar race with pedicellate flowers and are referable to *J. alpinus* Vill. ssp. *nodulosus* (Wahlenb.) Lindm. var *marshallii* (Pugsley) Lindquist. The slender habit and presence of pedicellate flowers with dark immersed capsules typical of this variety is maintained in cultivation. In Scandinavia another taxon has been described within ssp. *nodulosus.* This is *var. rariflorus* (E. Fries) C.J. Hartman which has long light brown capsules lacking distinct "shoulders" and which protrude from the perianth (Fig. 2:5). There is, however, a complete range of intermediates between these two extreme forms which cannot be designated as belonging to either one variety or the other.

Occasionally, pedicellate flowered plants which are strictly referable to ssp. *nodulosus* arise spontaneously in populations of otherwise normal ssp. *arthrophyllus*. Single specimens of these forms have been noted amongst herbarium specimens from one population near Braemar, Scotland, and also from a population in Teesdale. It therefore seems that too much emphasis has been placed on a single character and for this reason, Hylander's classification of the pedicellate race as a subspecies of *J. alpinus* rather than as a distinct species is followed in this work. Both subspecies are self-fertile and difficult to emasculate, so that, unfortunately, crossing experiments are difficult to carry out.

At first cytological studies suggested that the race with pedicellate flowers has 2n = 80 (counts from Iceland (Löve & Löve 1948, 1956) and Sweden (Vaarama 1948)), while the race with sessile flowers has 2n = 40 (counts from Britain (Elkington 1962), Iceland (Löve & Löve 1956) and Sweden (Löve & Löve 1944)). Snogerup (1958), however, records a count of 2n = 40 for material which he names as <u>J. nodulosus</u>, though he states that the plants did not have pedicellate flowers, the key character. In the same year Jörgensen, Sörensen & Westergaard (1958) recorded 2n = 40 in a Greenland variety of <u>J. alpinus</u> ssp. <u>nodulosus</u>. My count of 2n = 40 for Scottish material of this subspecies therefore adds further evidence that two chromosome races are present within this taxon.

Root-tip chromosomes are approximately 1 µm in length and lack visible centromeres. Strands of nuclear material can be seen linking individual chromosomes into a network (Plate 2:19). Similar nuclear connections, or "chromosome stickiness" have been seen in several genera which are thought to possess diffuse centromeres, including *Carex* and *Luzula* (Davies 1956), two genera quite closely related to *Juncus*, though they have also been seen in *Campanula* (Böcher, 1964), a genus with localised centromeres.

Meiosis in *J. alpinus* appears to be regular (Plate 2:20).

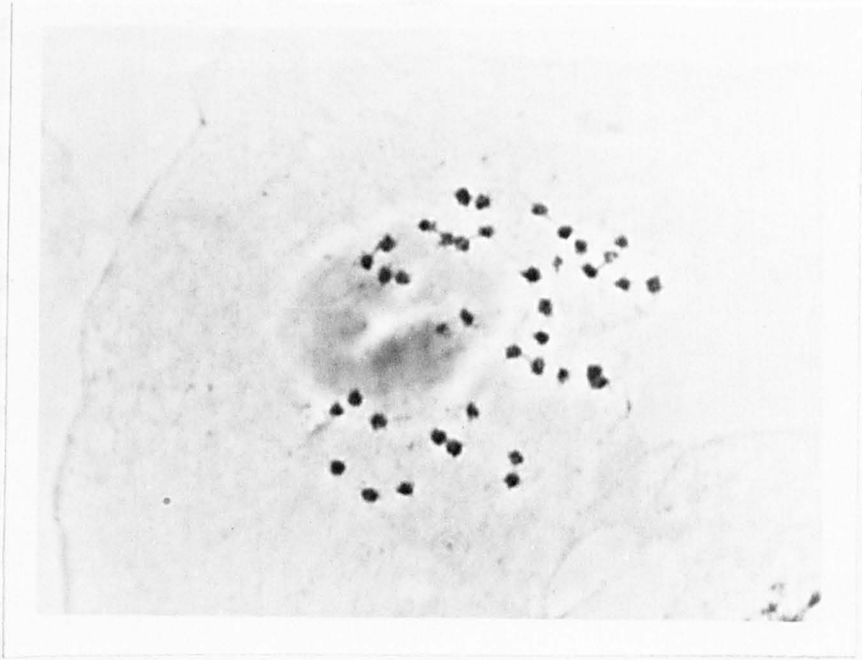


Plate 2:19 R.T. metaphase of <u>Juncus alpinus</u> Vill. showing connecting strands between chromosomes.

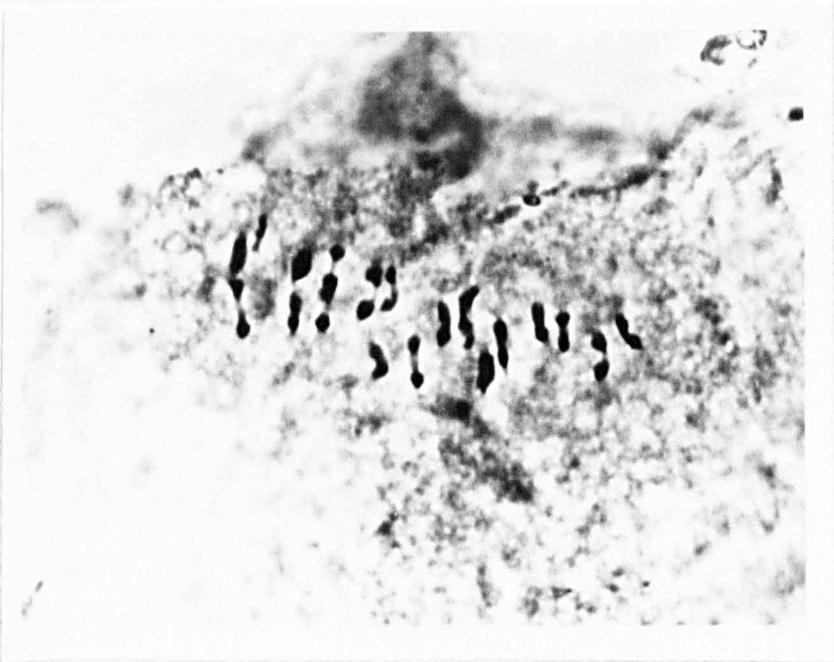


Plate 2:20 Anaphase I of <u>Juncus alpinus</u> Vill.

Carex ericetorum Poll.

Widdybank Fell, Co. Durham	n = 15 P.M.C. 1 plant
Cronkley Fell, Yorkshire.	n = 15 P.M.C. 1 plant
Arnside Knott, Lancashire	n = 15 P.M.C. 1 plant
Jenny Brown's Point, Lancashire	n = 15 P.M.C. 1 plant
Kirk Smeaton, Yorkshire	n = 15 P.M.C. 3 plants
Markland Grips, Derbyshire	n = 15 P.M.C. 1 plant
Grimes Graves, Norfolk	n = 15 P.M.C. 1 plant
Foxhole Heath, Suffolk	n = 15 P.M.C. 1 plant
Col du Lautaret, Hautes Alpes, France.	n = 15 P.M.C. 1 plant

Previous counts agree with those listed above. Thus Davies (1956) has found n = 15 in material from Markland Grips, Derbyshire, and Heilborn (1924), and Dietrich (1964) also record this number from Swedish and Swiss material respectively.

The genus *Carex* is notoriously difficult to examine cytologically. Successful root-tip squashes are impossible to make though a few authors have managed to obtain fairly good results by sectioning methods. Somatic chromosomes are reported to be small and spherical (Jörgensen, Sörensen & Westergaard 1958, Moore & Calder 1964).

Several unusual cytological features are present in the *Cyperaceae*. One of the most striking is the presence of a long aneuploid series, with haploid numbers ranging from n = 6 to n = 56. The sequence of meiosis differs from that found in the majority of higher plants and Wahl (1940) who made an extensive study of the genus came to the conclusion that the first meiotic division is equational and the second is reductional. As evidence for this, he showed that in several hybrid plants, lagging chromosomes and bridge formations were only seen at second anaphase, indicating that during the first division the chromosomes split into their constituent chromatids, the reverse of the usual sequence. Another unusual feature of meiosis is that three of the four nuclei resulting from the second division abort, so that individual pollen mother cells produce single pollen grains instead of tetrads. The first pollen grain mitosis takes place very early while the remains of the aborting nuclei are still visible. Plate 2:21 shows this in C. ericetorum.

Bivalents form regularly in C. ericetorum and at diakinesis and first metaphase are often joined into a network by faint strands (Plate 2:22 and 2:23) similar to those seen in the root-tip cells of Juncus alpinus. Two sizes of bivalent are present and at first anaphase there is regular separation of

Plate 2:21 1st pollen grain mitosis of Carex ericetorum Poll. with remains of three aborting nuclei.

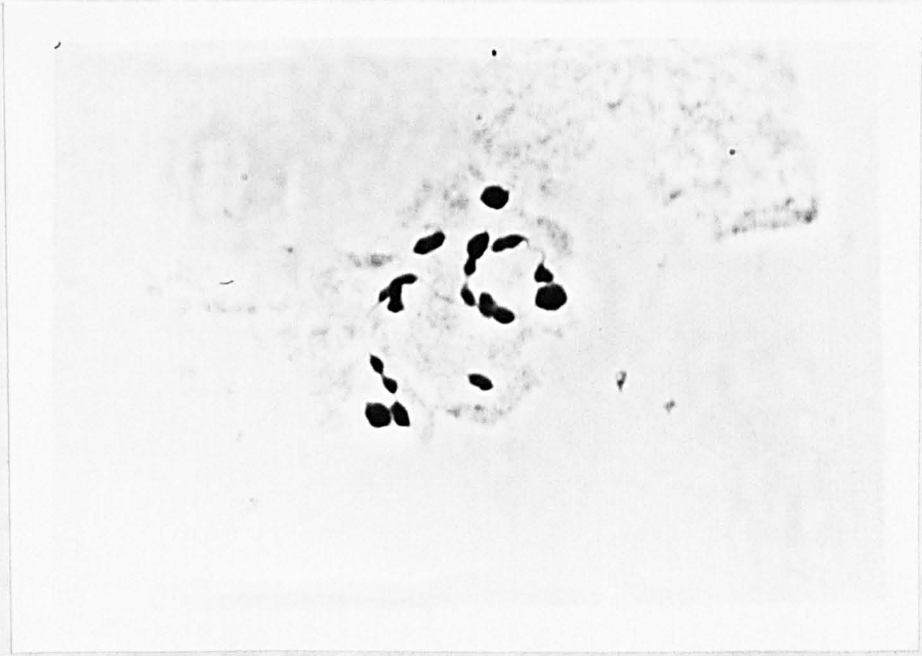


Plate 2:22 Diakinesis of Carex ericetorum Poll. showing connecting strands between bivalents.

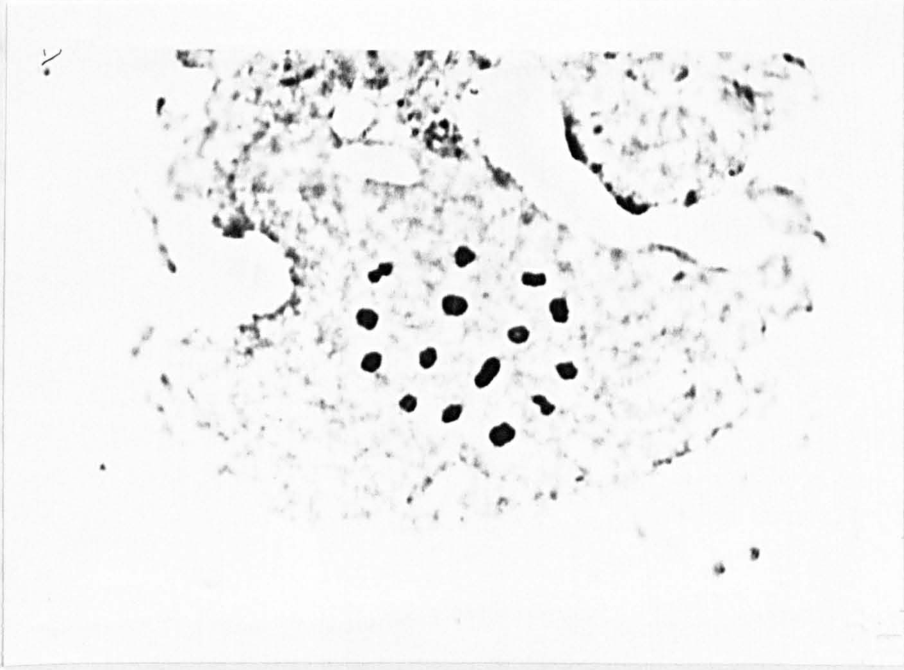


Plate 2:23 Metaphase I of Carex ericetorum Poll. showing 15 bivalents of different sizes.

daughter chromosomes which move apart parallel to one another. Similar observations have been made on several members of the genus by Davies (1956) and she therefore concluded that the chromosomes possess diffuse centromeres. She also deduced that this would aid chromosome fragmentation and postulated this process as a mechanism for the production of the long aneuploid series in the *Cyperaceae*. This theory, however, does not explain why aneuploidy is lacking in the closely related *Juncaceae*, another family in which diffuse centromeres are present, or why aneuploidy can occur in families and genera with localised centromeres.

Several varieties of *C. ericetorum* have been described by continental workers, eg Jalas (1950), based mainly on the shape and marking of the glumes, but all varieties seem to intergrade with one another. British material is also variable in these characters, but intra-population variation is as great as inter-population variation, and no distinct races have been found.

Carex paupercula Michx.

The Weel, Cow Green, Westmorland n = 29 P.M.C. 3 plants
Glengavel, Ayr - Lanark border n = 29 P.M.C. 1 plant

These counts agree with those recorded by other authors, thus 2n = 58 has been recorded for material from Swedish Lappland (Heilborn 1928), the Simplon Pass, Switzerland (Favarger 1959) and Moore & Calder (1964) record a somatic count of 2n = C.60 for material from Mt. Revelstoke National Park in Canada. The vicarious species known as *C. magellanica* Lam. which grows in southern Patagonia and Tierra del Fuego differs only slightly in morphological features from its northern relative, being in general a more robust plant with darker glumes. As it has similar ecological preferences and also the same chromosome number as the northern race (D.M. Moore, private communication) it seems rational to consider the two as subspecies of the same species, as has been suggested by Hultén (1964). He has designated the southern race as *C. magellanica* Lam. ssp. *magellanica* and the northern race as *C. magellanica* Lam. ssp. *irrigua* (Wahl.) Hultén.

Meiosis proceeds as in *C. ericetorum* and again there is some variation in the size of bivalents at first metaphase (Plates 2:24 and 2:25).

Plate 2:24 Metaphase I of Carex paupercula Michx. with 29 bivalents.

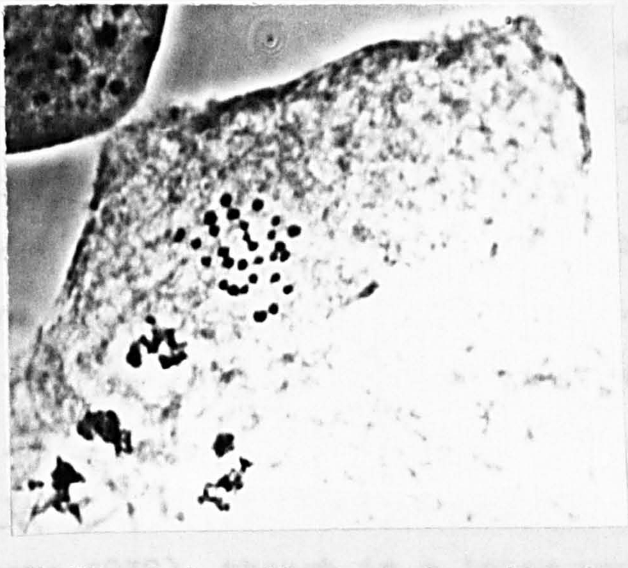


Plate 2:25 1st pollen grain mitosis of Carex paupercula Michx.

Alopecurus alpinus Sm.

Little Dun Fell, Westmorland 2n = C.100 R.T. 1 plant
Little Dun Fell, Westmorland n = 50 P.M.C.2 plants
Glas Maol, Angus 2n = 117,C.116 + 1F. R.T. 2 plants

Authors who have previously examined this species have found that it has a high and rather variable chromosome number. Early workers used a sectioning technique and the chromosome counts they made are probably not very accurate. Flovik 1938, however, counted 2n = >120, 112 + 3 fragments and 114 + 2 fragments in different plants from a population at Isfjorden in Spitzbergen. Plants from north and west Greenland are reported to be 2n = 112 (Holmen 1952, Jörgensen, Sörensen & Westergaard 1958) but Johnsson (1941) counted 2n = 119 - 122 in five different individuals also from west Greenland. Bowden who has examined the species in Canada has obtained counts of 2n = 105, 2n = 112 and 2n = 119 for different clones from the Arctic coast (Bowden 1960) and counts of 2n => 100 and 2n = 110 have been reported for material from northern Siberia (Sokolovskaya & Strelkova, 1960, 1962). In this region there are a number of closely related species in the Alpinae group and counts of 2n = 98 are reported for *A. borealis* Trin. and *A. pseudobrachystachyus* Ovcz. (Strelkova 1938), though in a later paper (Sokolovskaya 1963) A. borealis is given as 2n => 100. There is also a count of 2n = 70 for *A. alpinus* var *elatus* Roshev (Avdulov 1931), but the taxonomic status of

Plate 2:26 R.T. metaphase of Alopecurus alpinus Sm.

this plant is disputed and at present this chromosome number must be considered doubtful. It is of note that A. antarcticus Vahl., the southern hemisphere homologue of A. alpinus is also a high polyploid with 2n = 112 (Johnsson 1941). As the base number of the genus is 7, it seems likely that A. alpinus is approximately 16 - ploid, a ploidy level which has already been suggested for A. antarcticus (Johnsson 1941).

Root-tip chromosomes are 3 - 6 µm in length, or 2 - 4.5 µm after 5 hours pretreatment with hydroxyquinoline. One very clear metaphase plate was obtained (Plate 2:26) and an attempt has been made to analyse the karyotype, using the method described on p. 52. Chromosomes with similar measurements and other features were placed together into seven groups, designated A to G as follows:-

Group A: 4 satellited submetacentric chromosomes without any other constrictions.

Group B: 4 satellited submetacentric chromosomes with a secondary constriction in the long (unsatellited) arm.

Group C: 6 metacentric chromosomes with a secondary constriction in each arm.

Group D: 12 submetacentric chromosomes, of which 10 have a secondary constriction in the long arm, and 2 have a secondary constriction in the short arm.

Group E: 58 approximately metacentric chromosomes, of which 14 are long (>3.5 µm), 32 are of medium length (1.75 - 3.5 µm) and 12 are short (<1.75 µm).

Group F: 26 submetacentric chromsomes, of which 8 are long (>3.25 µm), 8 are of medium length (2.75 - 3.25 µm) and 10 are short (<2.75 µm).

Group G: 6 short chromosomes with subterminal centromeres + 1 telocentric.

A diagrammatic representation of chromosome types is shown in Fig. 2:6 and a complete idiogram is presented in Fig. 2:7.

An acentric fragment was seen in one of the root-tip metaphase plates examined and one telocentric chromosome occurs in the karyotype which has been analysed. The latter chromosome is possibly part of a longer chromosome which has misdivided at the centromere. Chromosome fragments have previously been reported in this species (Flovik 1938).

The analysis of such a complicated karyotype as this must necessarily contain many inaccuracies. Matching of chromosomes in the human karyotype has been improved with the aid of

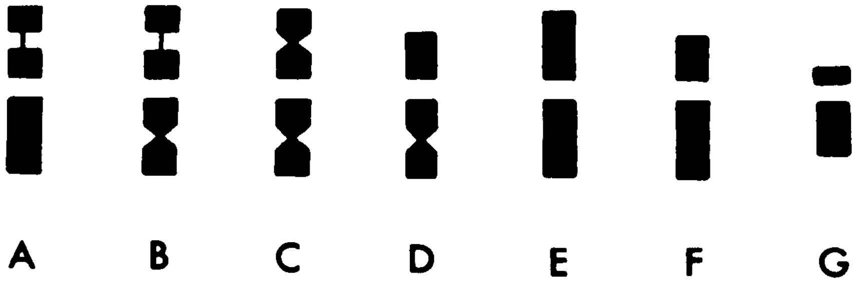


Fig. 2:6 Diagrammatic representation of chromosome types in the karyotype of Alopecurus alpinus Sm.

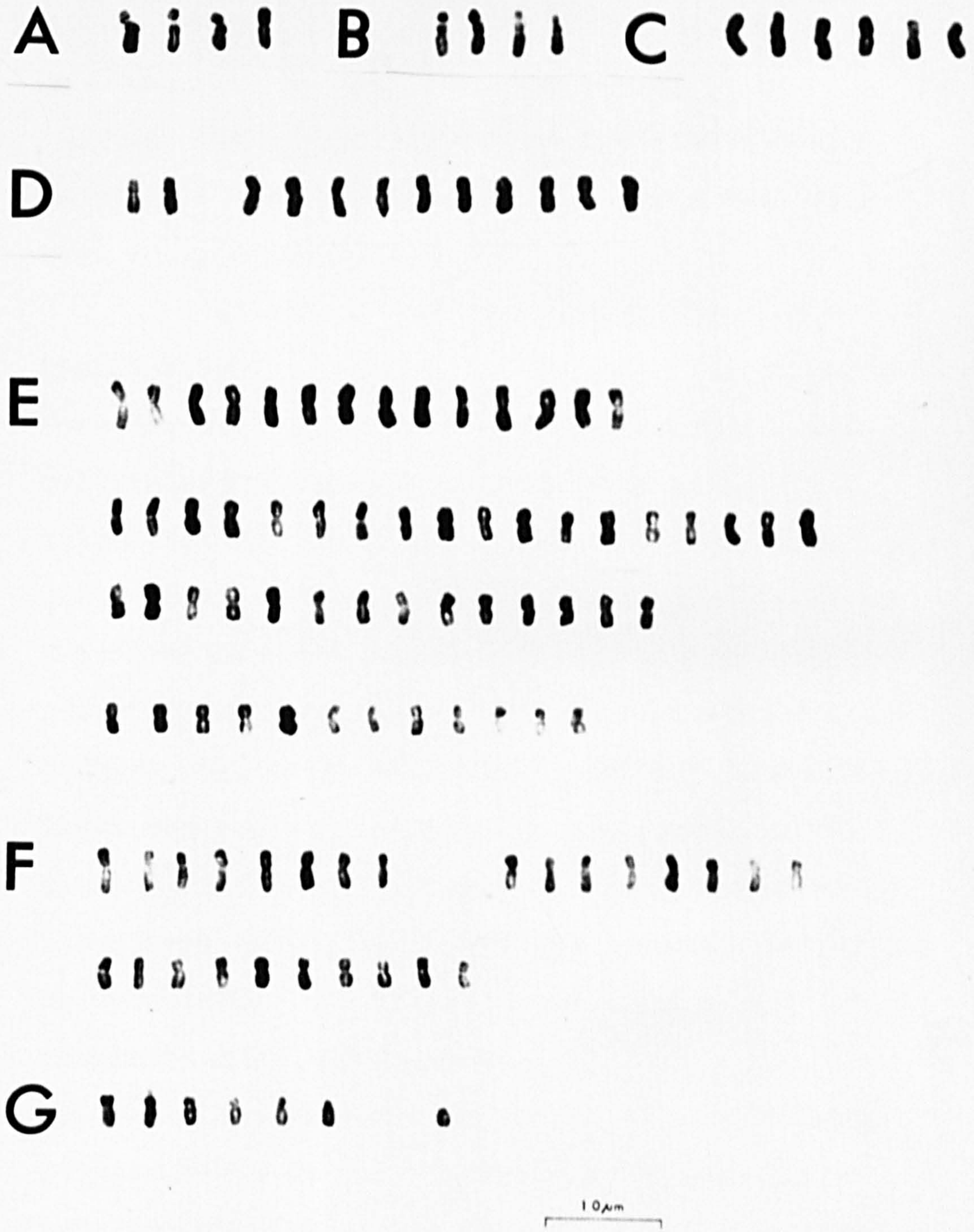


Fig. 2:7 Idiogram of *Alopecurus alpinus* Sm. from Glas Maol, Angus.

an electronic digital computer (Stewart and Killean, 1964) and this method could be adapted to analyse more complicated karyotypes such as that of *A. alpinus*.

Meiosis is fairly regular for such a highly polyploid species. The majority of chromosomes form bivalents at first metaphase, though a few multivalents have been seen as well as some univalents which remain outside the metaphase plate (Plate 2:27). These univalents and one or two bivalents are often excluded from the two nuclei resulting from the first meiotic division, and in general the second division is similar (Plate 2:28). These observations agree with those made on Greenland plants (Jörgensen, Sörensen & Westergaard 1958), but Flovik (1938) described the frequent occurrence of univalents, multivalents and lagging chromosomes in plants from Spitzbergen.

The presence of some irregularities in meiosis leads to the formation of genetically unbalanced pollen-grain nuclei, some possessing rather more and others rather fewer chromosomes than the haploid number. This does not seem to affect pollen fertility which is high (88%) and in conjunction with chromosome fragmentation is probably

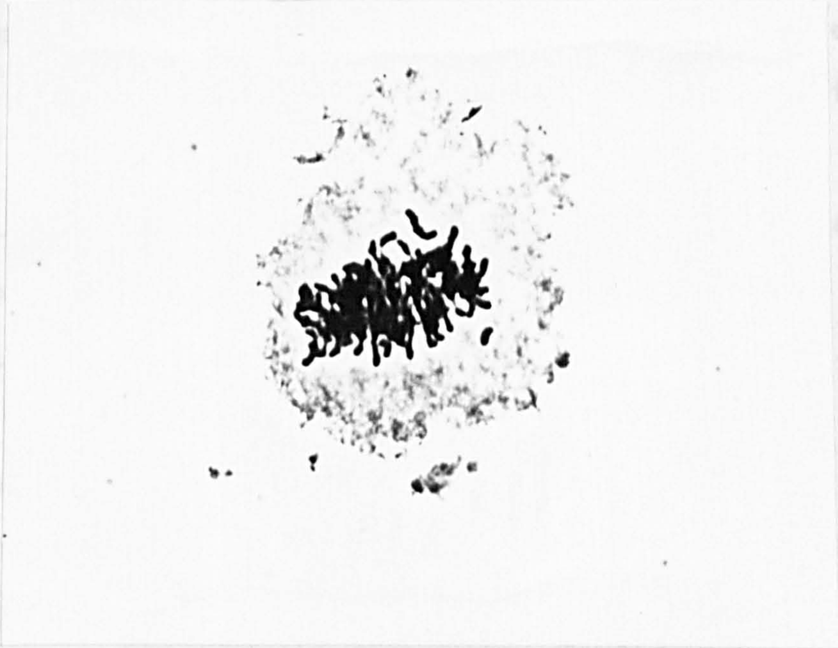


Plate 2:27 Metaphase I of <u>Alopecurus alpinus</u> Sm. with some chromosomes excluded from the metaphase plate.

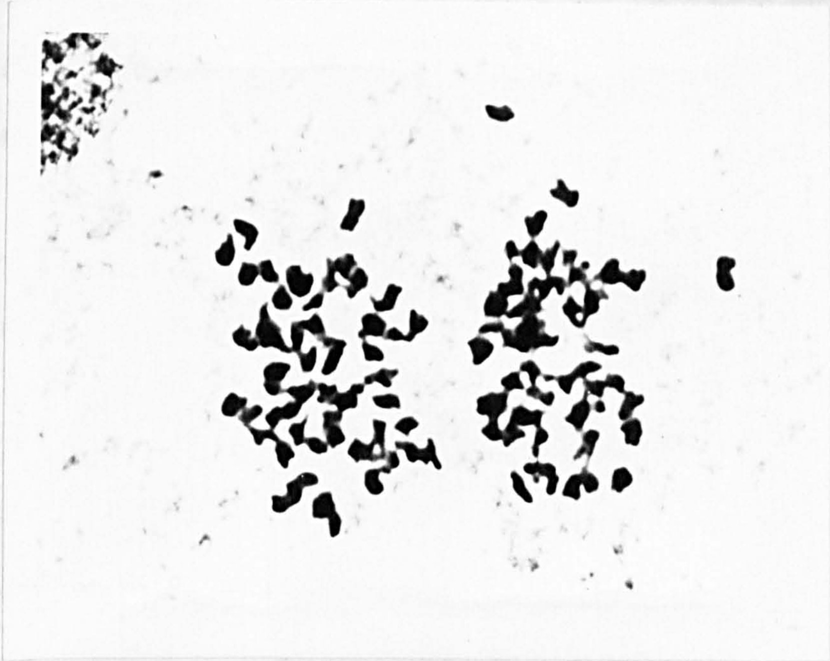


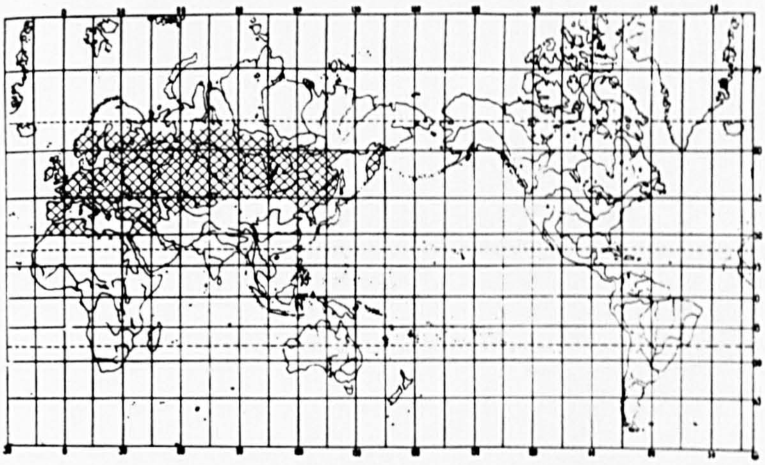
Plate 2:28 Metaphase II of <u>Alopecurus alpinus</u> Sm.

responsible for the variable chromosome number of this species, even amongst plants belonging to the same population. The limited information available suggests that the chromosome number may be constant within the two British populations examined although it varies between populations. Each of the British populations may, therefore, be composed of a single clone which has spread vegetatively. A. alpinus is very rare in Britain and in order to conserve the species, only a minimal number of plants were collected in the field.

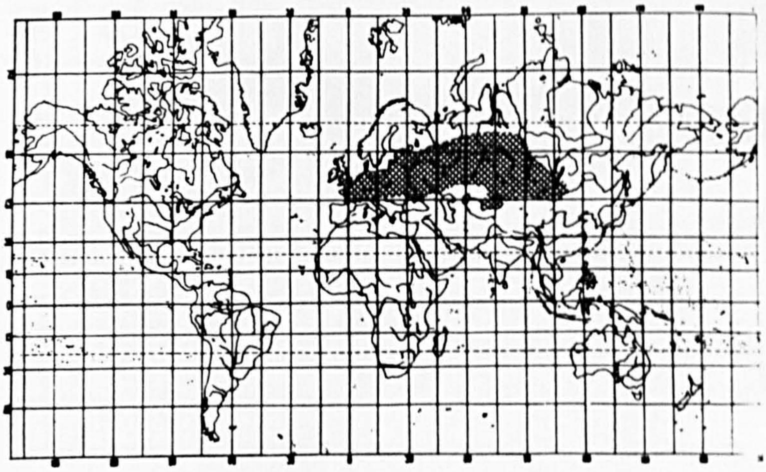
Examination of herbarium material shows that many populations of this species in Britain and in the Arctic include awned and awnless plants, though on close examination it has been found that many plants at first thought to be awnless have short awns which are not exserted from the inflorescence. The Teesdale and Glas Maol plants are, however, all awnless. When Teesdale plants were grown in a controlled environment growth room they retained shorter leaf blades and lacked the glaucous hue developed by the Scottish plants.

British plants do not generally flower well in the field and at least in Teesdale they do not seem to set seed. The reasons for poor flowering are not clear, as in 1969 plants especially those from Teesdale flowered well in a growth-room with a long day-length regime. All the plants were self-sterile and failed to set seed even when artificially selfed. It is possible that poor seed set in the field is due to the fact that the populations are small and isolated, many plants belonging to a single clone and which are thus unable to pollinate one another because of self-sterility.

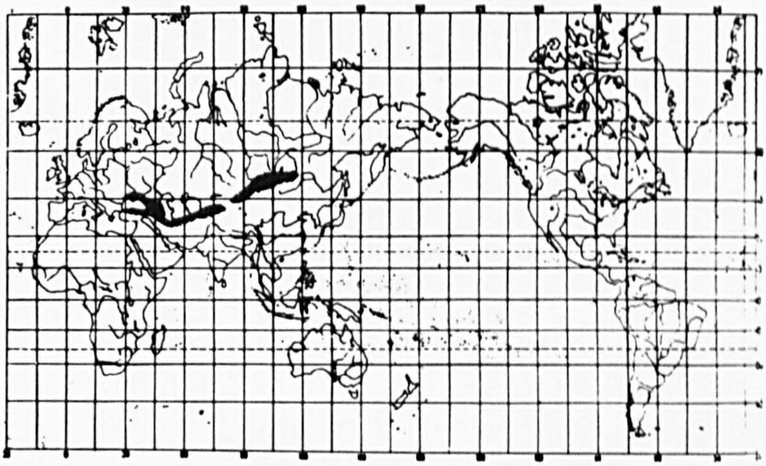
Strelkova (1936) has examined the geographical distribution of cytological groups within the genus _Alopecurus_ and has found that diploid (Annuae) and tetraploid (Ventricosae and Pratenses) groups have a wide distribution in Europe and Asia from the Mediterranean northwards to the Arctic Circle. The octoploid Vaginatae group is confined to the high mountain ranges of eastern Europe and Central Asia, while the high polyploid Alpinae (including _A. alpinus_) occurs mainly along the Arctic coasts of Canada and the U.S.S.R. (Maps 2:1 - 2:4). Several other authors have found a correlation between polyploidy and geographical distribution, highly polyploid groups usually occurring at high latitudes or in mountainous regions. Many hypotheses have been advanced to explain this and they are discussed in relation to the flora of Upper Teesdale in Chapter 5.



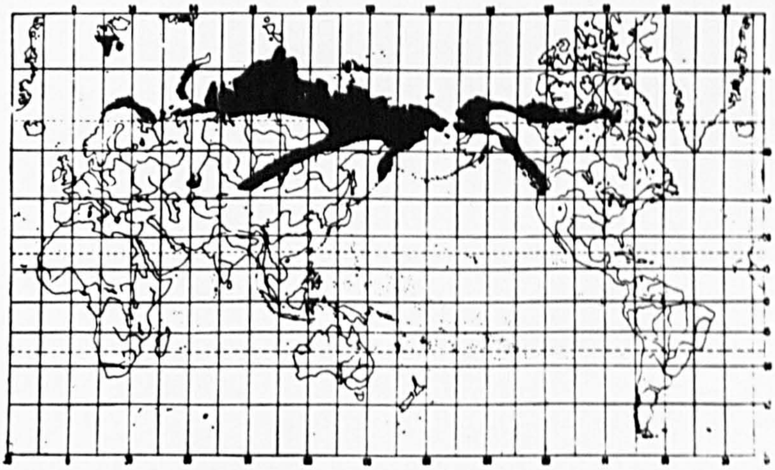
Map 2:1 **Area of distribution of the group Annuae (2n = 14 chromosomes)**



Map 2:2 **Area of distribution of the group Pratenses (2n = 28 chromosomes)**



Map 2:3 **Area of distribution of the group Vaginatae (2n = 56 chromosomes)**



Map 2:4 **Area of distribution of the group Alpinae (2n = 98 chromosomes)**

Chapter 3.

Vegetation and soils.

Vegetation and soils.

A vegetation survey has been made in Britain and the Alps of the species being investigated as part of the study of ecotypic differentiation. Also, previous workers (eg. Elkington 1963, 1964) have shown that species may become ecologically restricted towards the edge of their range. The majority of species under consideration are at or near their geographical limits in Teesdale and it is, therefore, of interest to try to determine the factors limiting their distribution.

Soil samples have been collected and analysed from as many sites as possible and the results are compared with the vegetational information.

I Materials and methods.

Vegetational descriptions were made at sites using a 0.5 m^2 quadrat. Cover and abundance were estimated by eye and recorded on the 10 point Domin scale. Additional species present in the community, but outside the area covered by the quadrat were also recorded (+). Slope, aspect, geology and soil depth were also noted at each site. Floristic lists have been prepared for each species from these field notes.

Soil samples were air dried, shaken through a 2 mm. sieve and stored in cardboard boxes in the laboratory before being analysed. All samples were analysed for selected exchangeable cations and certain samples in which the physical nature of the soil is of interest were also analysed mechanically.

Exchangeable cations were extracted by placing 5 gm. soil in 200 cc. normal neutral ammonium acelate solution and shaking on a mechanical shaker for 4 hours. The suspension was then filtered through a Whatman No. 50 filter paper and the filtrate made up to 250 cc. This method is similar to that used by Beckett & Nafady (1967) and numerous other authors, and is based on the principle that highly competitive ammonium ions replace the cations absorbed on to clay and humus particles, the cations therefore passing into solution. The major criticism of this quick and useful method is that free calcium carbonate dissolves in the ammonia solution and is therefore overestimated in highly calcareous soils, particularly those developed on chalk which have a low organic matter content and great care is necessary when interpreting such results. Exchangeable potassium was measured directly by flame photometry, calcium magnesium and lead were measured by atomic absorption spectrophotometry. pH was measured electrometrically at approximately field capacity. Organic matter content was estimated by the loss in weight after removal by oxidation with 20 vol. hydrogen peroxide (Robinson 1927). This method has been criticised because oxidation, especially of woody material is incomplete, but the weight of ignited unoxidised material in these samples was insignificant. The ignition method was not used to estimate total organic matter as the majority of samples were thought to contain high proportions of clay and calcareous components which tend to decompose on heating thus giving inaccurate results. Carbonate content was determined by recording the weight loss of oven-dry soil (from which organic matter had been removed) after reaction with a normal solution of hydrochloric acid.

Mechanical analysis of particle size was carried out by means of sieving and gravimetric methods. The coarse sand fraction was determined by sieving 10 gm. samples through a 0.2 mm. sieve. Finer fractions (fine sand, silt and clay) were determined by the pipette sampling method based on Stokes' Law. This method has been reviewed by Day (1965).

II Vegetation survey of individual species. *Cochlearia alpina*.

In Britain this species grows in two completely different types of habitat. The first type comprises a group of sites in damp situations with floristically rich communities (Table 3:1, lists 1 - 5), while the second group consists of well-drained rocky spoil heaps of old lead mines in the Pennines. (Table 3:1, lists 6 and 7). Amongst the first group, *C. alpina* is most common in Yorkshire along the banks of rivers and streams which drain the Carboniferous Limestone hills of the Craven Pennines. Here *C. alpina* is associated with numerous grasses eg. *Anthoxanthum odoratum*, *Holcus lanatus* and herbs characteristic of damp ground eg. *Filipendula ulmaria*, *Geum rivale* and *Ranunculus acris* in a closed community. At higher altitudes, flushed areas and damp rock ledges of limestone or calcareous schist are characteristic sites. These are frequently in north-facing situations where the soil is continually moist. Bryophytes are plentiful and montane species eg. *Epilobium anagallidifolium*, *E. alsinifolium* and *Alchemilla alpina* are often present.

In Scotland McVean & Ratcliffe (1962) record *C. alpina* in several of the rock ledge communities eg. their Tall Herb Nodum and Saxifragetum aizoidis association which are fragmentary representatives of herb and fern meadows. Some of these herb-rich communities are analagous with the hay meadows of Teesdale and Pigott (1956) mentions that *C. alpina* may be locally plentiful in these damp pastures. In western Ireland Braun-Blanquet & Tüxen (1952) record *C. alpina* growing on the northern slopes of Ben Bulben in rocky situations similar to those described by McVean & Ratcliffe (loc. cit.) in Scotland. These Irish communities have been placed in the alliance Cochlearion alpinae, named after the characteristic species, this alliance being placed within the order Potentilletalia caulescentis, a group of communities found on rocky calcareous soils, mainly in the Alps.

There are no records of C. alpina in communities from continental Europe, possibly because of taxonomic difficulties in this genus, but Nordhagen (1943) records a species of Cochlearia which may be the same as the British plant on damp rock ledges in Silkilsdalen, Norway where the vegetation is similar to that of the Saxifragetum aizoidis association in Scotland where C. alpina is plentiful.

The old lead mine spoil heaps on which C. alpina grows are very well-drained and in relatively exposed situations. The spoil heaps are composed mainly of small calcite chippings (approximately 10 mm^3) with abundant pieces of other minerals, such as barytes, galena and sometimes fluorspar. The plant cover is sparse, frequently less than 50% and the number of species present is low. Festuca ovina, Plantago lanceolata and Rumex acetosa are frequent associates, as are *Minuartia verna* and *Thlaspi alpestre*, two species characteristically found on ground contaminated with lead. This habitat is frequent in the Pennines, but rare elsewhere.

TABLE 3:1

Floristic lists from British localities
of *Cochlearia alpina*.

List No.	1	2	3	4	5	6	7
Site No.	70	83	45	49	42	46	41
Altitude (m.)	839	732	214	168	336	214	336
Aspect	NNW	SE	Nil	Nil	NNE	Nil	SE
Slope (degrees)	19	25	Nil	Nil	70	Nil	10
Soil depth (mm.)	20	150	300	300	10	300	20
Cover (%)	100	100	100	100	60	90	30
Anthoxanthum odoratum	-	-	2	+	-	-	-
Arrhenatherum elatius	-	-	2	+	-	-	-
Briza media	1	-	-	-	-	-	+
Deschampsia caespitosa	5	+	4	-	-	-	-
Festuca ovina	3	-	4	+	5	2	1
F. rubra	-	2	-	-	-	-	1
Holcus lanatus	-	-	4	+	-	-	-
Cerastium holsteoides	1	-	-	-	1	-	3
Cochlearia alpina	3	5	2	+	2	3	1
Filipendula ulmaria	-	-	-	+	-	-	2
Geum rivale	-	-	2	+	-	-	-
Minuartia verna	-	-	-	-	-	4	3
Plantago lanceolata	-	-	3	+	-	2	+
Ranunculus acris	-	-	2	+	-	-	-
Rumex acetosa	2	-	2	-	3	3	+
Succisa pratensis	-	-	2	-	-	2	-
Bryum pallens	-	-	-	-	4	5	-
Cratoneuron commutatum	2	2	-	-	-	-	-
Pseudoscleropodium purum	-	-	2	-	-	1	-

Localities and additional species of low frequency.

1. Glas Maol, Angus, Grid Ref. NO/162772 *Sesleria albicans*, *Carex bigelowii*, *Alchemilla alpina*, *A. glabra*, *Epilobium anagallidifolium*, *Gnaphalium supinium*, *Montia fontana*, *Sagina maritima*, *Sibbaldia procumbens*, *Brachythecium albicans*, *Ceratodon purpureus*, *Mnium punctatum*, *Polytrichum urnigerum*, *Rhytidiadelphus squarrosus*, *Peltigera* sp.

2. Green Castle, Moorhouse N.N.R., Westmorland. Grid Ref. NY/715311 *Agrostis camna*, *Chrysosplenium oppositifolium*, *Epilobium alsinifolium*, *Cratoneuron filicinium*, *Philonotis calcarea*.

3. Streamside, Woodall, Wensleydale, Yorkshire. Grid ref. SD/987898 *Equisetum palustre*, *Angelica sylvestris*, *Trifolium repens*.

4. Streamside, Grassington, Yorkshire. Grid ref. SD/993645 *Centaurea nigra*, *Leontodon hispidus*, *Sanguisorba officinalis*, *Senecio jacobaea*, *Acrocladium cuspidatum*, *Mnium undulatum*.

5. Winnats Pass, Derbyshire. Grid ref. SK/136825 *Poa pratensis*, *Anthriscus sylvestris*, *Draba muralis*, *Geranium lucidum*, *G. robertianum*, *Mercurialis perennis*, *Polemonium coeruleum*, *Saxifraga hypnoides*, *Silene dioica*, *Amblystegium serpens*, *Barbula recurvirostra*, *Hypnum cupressiforme var. resupinatum.*

6. Streamside meadow, Woodall, Wensleydale, Yorkshire. Grid ref. SD/987898 *Carex nigra*, *C. panicea*, *Armeria maritima*, *Thlaspi alpestre*.

7. Dirtlow Rake, near Castleton, Derbyshire. Grid ref. SK/154821 *Arabis hirsuta*, *Cirsium vulgare*, *Erophila verna*, *Galium sterneri*, *Thymus drucei*.

The soils on which this species grows are rather variable, pH ranging from 5.6 to 7.4 and calcium content from 14.38 to 83.45 m.eq./100 gm. soil (See Table 3:2). The two samples from old lead spoil heaps have a higher percentage of exchangeable calcium than the other two samples and also have an extremely high exchangeable lead content, though a small amount of lead is also present in the other samples.

TABLE 3:2

Analysis of soil samples from British localities of *Cochlearia alpina*.

No.	Locality	pH	M.eq./100 gm. air-dried soil.			
			K	Ca	Mg	Pb
41	Dirtlow Rake, Derbyshire	7.4	0.15	83.45	0.04	3.93
46	Woodall, Wensleydale, Yorkshire	6.7	0.24	38.75	6.35	3.70
49	Grassington, Yorkshire	7.0	0.21	15.95	0.04	0.18
70	Glas Maol, Angus	5.6	0.34	14.38	2.92	0.10

Draba incana.

In common with *Cochlearia alpina*, *Draba incana* is a colonist of old lead mine spoil heaps, but it is also present in a series of natural habitats which are characterised by being in the main well drained and strongly calcareous. These range from sand dunes to montane pastures and rock ledges. In the northern Pennines, D. incana is not uncommon on the ledges of limestone "scars" where it is mainly associated with Festuca ovina, Sesleria albicans, Galium sterneri and Thymus drucei, also occasionally with montane species such as Sedum rosea. In Scotland it is present in similar communities on ledges of limestone or calcareous schist, but with the addition of more montane herbs such as Alchemilla alpina and Silene acaulis. McVean & Ratcliffe (1962) have described similar rock ledge communities and D. incana is recorded in the Tall Herb Nodum of their vegetation survey. In western Ireland D. incana grows in similar rocky communities together with Cochlearia alpina on the northern slopes of Ben Bulben (Braun-Blanquet & Tüxen 1952), but unlike that species, D. incana is one of the characteristic species of the Sedum roseum - Arenaria hibernica association.

D. incana can also be found in the closed turf of calcareous upland pastures in the Pennines. Unlike the rock ledge communities, these are grazed, sometimes heavily, by sheep, so that the vegetation is only about 2 cm high. A wider variety of herbs and bryophytes is present in this community than on the ledges, though many of the ledge species are also present.

On the north and west coasts of Scotland, *D. incana* is quite a common colonist of sand dunes, together with other northern species such as *Dryas octopetala*, *Oxytropis halleri* and *Saxifraga hypnoides*. (Gimingham 1964) It also grows on calcareous dune soils on the coast of Denmark (Böcher, Christensen & Christensen 1946) in association with a number of other calcicolous species eg. *Pulsatilla vulgaris*, *Ctenidium molluscum*. In Teesdale, *D. incana* grows on what may almost be described as inland sand dunes, on Widdybank Fell and Cronkley Fell, but here the "sand" is composed of the eroded and windblown particles of sugar limestone. These are extremely dry and bare habitats and at Thistle Green on Cronkley Fell, *D. incana* and *Festuca ovina* are virtually the only colonists of a wide area of eroded ground. (Plate 3:1)

The lead mine spoil heaps on which *D. incana* occurs are similar to those which *Cochlearia alpina* has colonised, though the two species have not been found growing together. Though the vegetation is much more open, many of the associates present in the limestone pastures grow here and *Minuartia*

Plate 3:1 Draba incana colonising bare, eroded ground at Thistle Green, Cronkley Fell, Teesdale.

verna is particularly abundant.

In the Alps, D. incana (usually known here as D. stylaris) has a very scattered distribution and is not a very common species. In the Ober - and Unter - Engadin it occurs in the Potentilla Caulescens association (Braun-Blanquet & Rübel 1933), an alpine community on calcareous, stony ground where rosette species, especially of Draba and Saxifraga are particularly abundant. In more exposed sites with a slightly acid soil it is present in a community dominated by Elyna myosuroides.

In Scandinavia D. incana occurs in sub-alpine meadow communities, some of which have been placed by Nordhagen (1943) in the Festucetum rubrae sub-alpine association. This association has no direct British equivalent, though it contains several species, eg. Anthoxanthum odoratum, Deschampsia caespitosa, Festuca rubra, Galium boreale, Polygonum viviparum and Potentilla crantzii which are present in the calcareous upland pastures and rock ledge communities of the northern Pennines and in Scotland.

TABLE 3:3

Floristic lists from British localities of *Draba incana*.

List No.	1	2	3	4	5	6	7	8	9	10	11
Site No.	81	82	47	24	55	69	50	51	63	5	6
Altitude (m)	747	747	503	542	534	598	473	473	481	191	222
Aspect	SE	SE	SW	Nil	NE	SE	SW	NW	NNE	NW	N
Slope (degrees)	10	35	30	Nil	40	Nil	5	10	10	20	25
Soil depth (mm)	40	40	50	50	60	10	30	25	30	Nil	Nil
Cover (%)	60	60	100	30	70	40	70	65	100	70	60
Agrostis tenuis	-	-	+	-	2	-	-	-	-	-	-
Festuca ovina	4	3	7	4	6	2	6	5	5	+	-
Koeleria cristata	-	-	2	3	2	-	4	-	3	-	-
Sesleria albicans	4	-	5	+	3	-	2	2	+	-	-
Carex capillaris	-	-	-	-	+	-	-	1	-	-	-
C. caryophyllea	-	3	2	-	-	-	-	-	-	-	-
Arabis hirsuta	-	-	2	-	-	-	-	-	-	1	+
Bellis perennis	-	-	-	-	2	-	-	-	+	-	-
Campanula rotundifolia	-	-	1	+	3	1	-	+	2	2	2
Cerastium holosteoides	-	1	2	-	1	-	-	-	-	+	-
Draba incana	2	2	2	1	3	1	3	3	3	3	2
Euphrasia sp.	3	2	-	-	-	-	-	-	1	-	-
Galium sterneri	3	1	2	+	3	-	-	-	2	2	-
Hieracium sect. vulgata	-	-	-	-	-	-	-	-	-	+	1
Leoutodon hispidus	-	-	-	-	-	-	-	-	-	+	1
Linum catharticum	-	-	2	-	2	-	1	3	3	-	-
Minuartia verna	2	1	2	1	2	-	3	3	4	1	2
Plantago lancedata	-	-	-	+	1	-	-	-	3	-	-
Prunella vulgaris	-	-	-	-	3	-	-	-	1	-	-
Rumex acetosa	-	-	-	-	-	-	-	-	-	1	+
Saxifraga hypnoides	-	+	-	-	-	2	-	-	-	+	-
Scabiosa columbaria	-	-	1	-	-	-	-	-	-	2	-
Sedum acre	-	-	-	-	-	-	1	1	-	3	-
Succisa pratensis	-	-	-	-	-	-	-	-	-	2	2
Taraxacum sp. (sterile)	-	-	-	+	2	-	-	-	1	-	-
Thymus drucei	5	4	3	1	5	1	2	3	4	+	2
Trifolium repens	-	-	3	-	1	-	-	-	3	-	-
Veronica officinalis	-	-	3	-	-	-	-	-	1	-	-
Viola riviniana	-	-	1	-	3	-	-	-	3	-	-
Bryum pallens	-	-	-	-	1	1	-	-	-	-	+
Climacium dendroides	-	-	-	-	4	-	-	-	2	-	-
Ctenidium molluscum	2	2	-	-	1	5	-	3	+	-	-
Ditrichum flexicaule	-	-	-	-	2	-	-	2	-	-	-
Encalypta streptocarpa	-	-	-	-	2	-	-	-	-	+	-
Hypnum cupressiforme	-	-	3	-	1	-	-	-	-	-	-
Rhacomitrium lanuginosum	1	1	1	-	2	-	1	2	2	-	-
Rhytidiadelphus squarrosus	-	+	1	-	+	-	-	-	1	-	-
R. triquetrus	-	-	-	-	1	-	-	-	1	-	-
Tortella tortuosa	2	+	1	-	3	-	+	+	2	?	-
Cetraria islandica	-	-	-	-	+	-	-	-	2	-	-
C. rangiferina	-	-	-	-	+	-	-	-	1	-	-
Cornicularia aculeata	-	-	-	-	+	-	-	-	1	-	-
Peltigera aphthosa	-	-	-	-	+	-	-	-	+	-	-

Localities and additional species of low frequency.

1. Green Castle, Westmorland (cliffledge). Grid ref. NY/713312 *Cystopteris fragilis*, *Oxalis acetosella*, *Sedum rosea*, *Pseudoleskea catenulata*.

2. Green Castle, Westmorland (scree). Grid ref. NY/713312 *Cardamine pratensis*, *Myosotis alpestris*, *Plagiochila asplenioides*.

3. Askrigg, Wensleydale, Yorkshire. Grid ref. NY/961926 *Helictotrichon pratense*, *Luzula campestris*, *Achillea milleforium*, *Senecio jacobaea*, *Dicranum scoparium*.

4. Thistle Green, Cronkley Fell, Yorkshire Grid ref. NY/843284.

5. Cronkely Fell, Yorkshire. Grid ref. HY/841280 *Briza media*, *Alchemilla glabra*, *Polygala amarella*, *Polygonum viviparum*, *Mnium longirostrum*.

6. Creag an Lochan, Ben Lawers, Perthshire. Grid. ref. NN/595397 *Carex pulicaris*, *Alchemilla alpina*, *Sagina maritima*, *Silene acaulis*, *Thuidium tamariscinum*.

7. Old lead mine spoil heap, Widdybank Fell, Co. Durham. Grid ref. NY/812302 *Carex flacca*, *C. panicea*.

8. Old lead mine spoil heap, Widdybank Fell. Co. Durham Grid ref. NY/812302 *Scapania aspera*.

9. Widdybank Fell, Co. Durham. Grid ref. NY/813303 *Brentelia chrysocoma*, *Pleurozium schreberi*, *Rhodobryum roseum*, *Cladonia pyxidata*.

10. Millers Dale, Derbyshire. Grid ref. SK/163729 *Festuca rubra*, *Zerna erecta*, *Hieracium pilosella*, *Rubus saxatilis*, *Saxifraga tridactylites*, *Teucrium scorodonia*.

11. Millers Dale, Derbyshire. Grid ref. SK/161727

Draba incana grows on soils similar to those from *Cochlearia alpina* localities, except that they have a higher pH and exchangeable calcium content than some of the samples from *C. alpina* sites (See Table 3:4) and they are usually drier. Samples from lead mine spoil heaps have a high lead content, though not as high as that of some of the *C. alpina* soil samples from similar sites. One reason why these two species are not found growing together may be that *C. alpina* is tolerant of a higher amount of lead in the soil than *D. incana*. Soil samples from natural habitats of both species, however, all contain a certain amount of lead and and it is possible that there are individuals tolerant of high amounts of lead amongst populations in natural habitats and that from these plants, highly lead tolerant populations can be built up and colonize the highly contaminated soil of old spoil heaps. A similar mechanism for the evolution of heavy metal tolerant populations of *Agrostis tenuis* has been proposed by Bradshaw et al. (1965), and by Kruckeberg (1951) for the evolution of populations of *Achillea borealis* tolerant of serpentine soils in the U.S.A.

TABLE 3:4

Analysis of soil samples from British localities of *Draba incana*.

Sample No.	Locality	pH	M.eq./100gm. air-dried soil			
			K	Ca	Mg	Pb
51	Spoil heap Widdybank Fell, Co. Durham.	7.2	0.7	71.25	0.52	0.47
54	Cronkley Fell, Yorkshire.	7.1	0.30	121.88	1.25	0.22
24	Thistle Green, Cronkely Fell, Yorkshire.	7.3	0.40	86.25	0.52	0.16
81	Green Castle, Moorhouse N.N.R., Westmorland.	7.1	0.44	81.25	1.67	0.05
47	Askrigg, Wensleydale, Yorkshire.	7.0	0.48	80.00	1.50	0.11
6	Miller's Dale, Derbyshire.	7.3	0.15	68.75	0.25	1.85

Polygala amarella.

This species is restricted to three calcareous areas in Britain, these being Upper Teesdale, the Craven District of Yorkshire and the North Downs of Kent. In Continental Europe it is more widespread but there too is restricted to calcareous soils.

In Britain it grows in a different type of habitat in each area, but in France and Switzerland it can be found in various situations. It shows no preference for slope or aspect either in Britain or in the Alps and several populations are on flat ground (Fig. 3:1).

All the British localities are unshaded, but P. amarella was found growing on stony ground amongst light woodland at several localities in France and Switzerland. Where it is growing in turf, it is very noticeable that on steep slopes, such as Dib Scar and Mastiles Lane in Yorkshire and at Crundale Downs in Kent, P. amarella plants occur in the small bare patches caused by soil creep (Plate 3:2) and seedlings are clustered around the parent plants in such situations.

In Teesdale P. amarella is restricted to closely grazed limestone turf along the outcrop of "sugar" limestone, on Widdybank and Cronkley Fells. Though there is a heavy rainfall in this area, the very porous nature of the soil ensures that it is always well-drained and never becomes waterlogged. Common associate species include Briza media, Sesleria albicans (syn. S. coerulea), Carex capillaris, Galium sterneri, Gentiana verna,

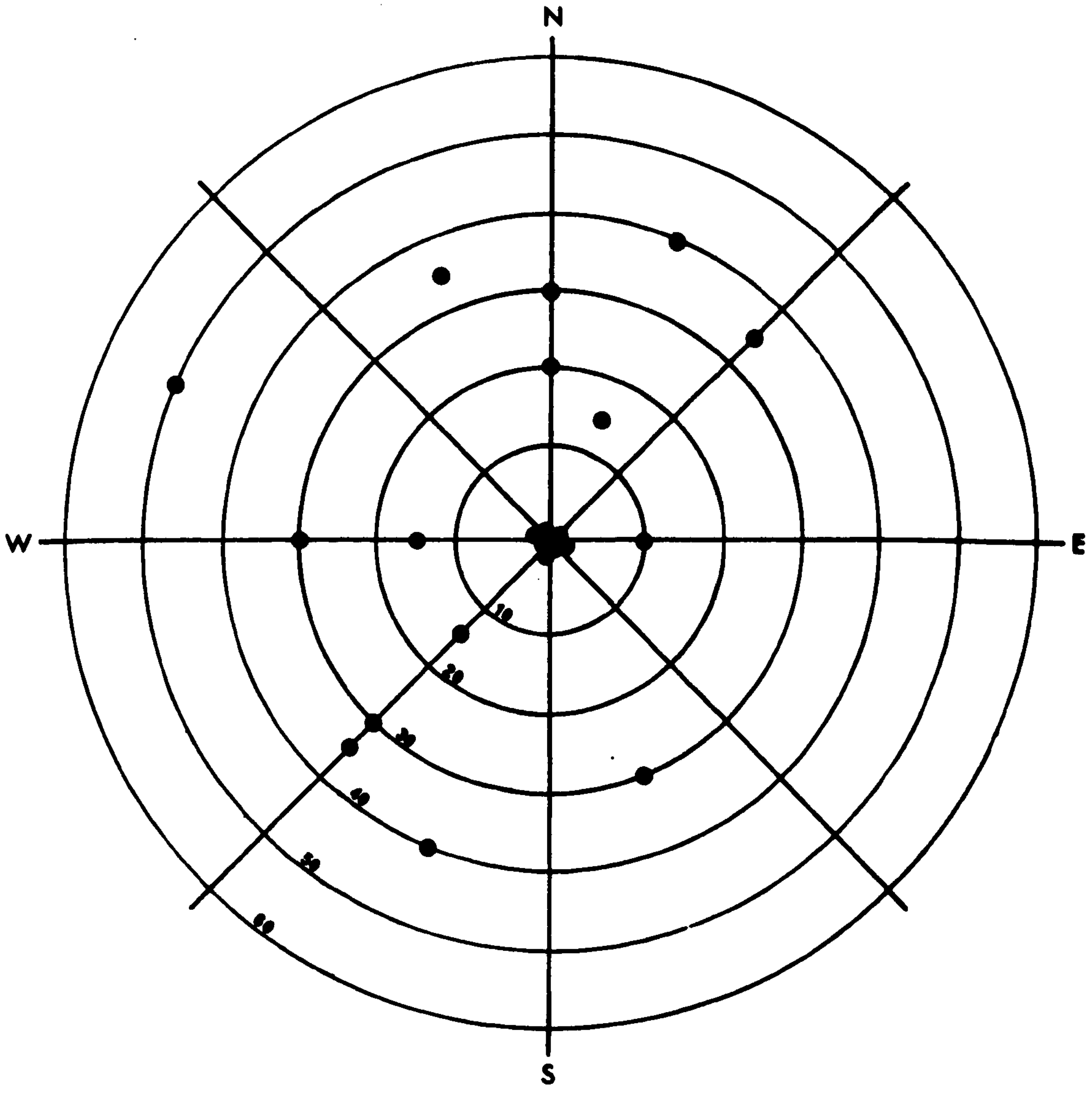


Fig. 3:1 The distribution of Polygala amarella in relation to slope and aspect.

Plate 3:2 Polygala amarella growing in a patch of stony ground, on a steep bank at the side of Mastiles Lane, Yorkshire.

Plate 3:3 Tufa hummocks in a calcareous mire, near Malham, Yorkshire.

Thymus drucei, *Viola riviniana* and *Rhacomitrium lanuginosum*.

In parts of the Craven district, e.g. by Mastiles Lane, *P. amarella* grows on similar well-drained limestone slopes and old records suggest that the species was quite common in such situations at the end of the last century, until avid collectors of herbarium specimens almost caused it to become extinct. *P. amarella* is now more characteristic of calcareous mire communities in this area, particularly around Malham, where it occurs on tufa hummocks which have been deposited from the highly calcareous spring water (see Plate 3:3). *P. amarella* plants are most frequent on the sides of the hummocks, avoiding the tops where the soil has been leached and has often become acid, as indicated by the presence of species such as *Calluna vulgaris*. Hummock species associated with *P. amarella* include *Molinia coerulea*, *Sesleria albicans*, *Parnassia palustris*, *Primula farinosa*, *Succisa pratensis* and *Valeriana dioica*. Plant cover between the hummocks is less dense, only about 20% as opposed to 100% on the hummocks, and consists mainly of sedges and bryophytes such as *Carex lepidocarpa*, *C. panicea*, *C. hostiana* and *Drepanocladus revolvens*, a type of community which McVean and Ratcliffe (1962) regard as being related to the Carex panicea - Campylium stellatum nodum they have described in Scotland. At present these areas of rather open vegetation are maintained by cattle trampling, though it is probable that water erosion has also helped to form the mosiac of vegetation.

In Kent, *P. amarella* grows in a very different type of habitat and is found in very dry chalk turf, especially where the soil is very thin around the margins of old chalk pits. Several of the associated species, eg. *Briza media* and *Linum catharticum* are also found in the drier sites in Yorkshire, but others, eg. *Zerna erecta*, *Cirsium acaulon*, *Hieracium pilosella* and *Lotus corniculatus*, some of which are characteristic species of the Cirsio - brometum, a common chalk grassland association, are constant associates only in south-eastern England.

In each of the three main areas of occurrence, *P. amarella* sites have been found which are intermediate between the main vegetation types, for instance at Dib Scar in Craven the community includes some species eg. *Parnassia palustris* and

Primula farinosa which are characteristic of the calcareous mines and others eg. *Briza media* and *Helianthemum nummularium* which are characteristic of the drier sites. Evidence has already been quoted showing that *P. amarella* was formerly much more widespread, at least in the Craven district and it is probable that all the present British localities represent habitats which are unsuitable for farming and which were less accessible to the 19th century botanists. The ecological distribution of this species in Britain today is therefore of a relict nature.

In France and Switzerland *P. amarella* is found in a very diverse group of habitats. It is a sub-alpine plant and is replaced in alpine pastures by *P. alpina*. Many of the sites are on very dry stony unstable slopes where percentage cover is low and where herbs form a major component of the vegetation. Two sites visited (Table 3:6, lists 6 and 7) were in damp situations, one a roadside ditch and one in a very floristically rich fen, showing that in Continental Europe as well as in Britain, *P. amarella* can colonise either very dry or very damp sites. In the fen *P. amarella* plants are restricted to low hummocks of Molinia and this site is in many respects similar to the calcareous mires near Malham. It may be added that several other localities were visited where P. amarella was reputed to grow in marshy habitats, but the majority of them had been drained, or filled in with rubble for building purposes.

The dry communities in which P. amarella grows in the Alps are too heterogeneous to be classified phytosociologically, but in northern France, the communities on dry chalk grassland are similar to those in south-eastern England and probably belong within the alliance Mesobromion erecti. Fens dominated by Molinia coerulea and Schoenus nigricans have been placed within the alliance Molinion (Braun-Blanquet & Rübel 1932). In Scandinavia P. amarella is also found in both damp and dry habitats. Nordhagen (1943) mentions it as one of the species which occurs occasionally in high level bryophyte springs and flushes in the mountains of southern Norway, but it also occurs in the dry alvar vegetation of the island of Öland (Elkington, personal communication). In Denmark, the species is rather rare, but occurs in rather mesic sites on north-facing calcareous slopes in northern

Jutland (Böcher, Christensen & Christensen 1946) together with other calcicolous species such as *Briza media*, *Carex flacca*, *Cirsium acaulon*, *Linum catharticum*, *Camptothecium lutescens* and *Ctenidium molluscum*.

TABLE 3:5

Floristic lists from British localities of Polygala amarella.

List No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Site No.	34	35	36	40	39	56	89	54	55	65	25	27	29	30
Altitude (m)	366	374	374	229	351	488	503	534	534	534	168	92	137	137
Aspect	Nil	Nil	Nil	NNW	SW	W	SW	NNE	NNE	Nil	W	SSE	E	NNW
Slope (degrees)	Nil	Nil	Nil	35	20	30	14	15	40	Nil	15	30	10	30
Soil depth (mm)	75	150	50	40	25	100	100	75	150	115	60	25	50	25
Cover (%)	100	80	70	80	80	100	100	100	70	100	90	100	80	60
Selaginella selaginoides	1	-	+	-	-	+	-	-	-	1	-	-	-	-
Agrostis tenuis	-	-	-	-	-	-	-	1	2	-	-	-	-	-
Briza media	-	-	-	1	3	3	3	2	3	3	4	-	2	2
Festuca ovina	6	4	4	4	4	6	6	7	6	7	4	2	6	4
Koeleria cristata	-	-	-	-	-	-	+	-	2	-	-	-	-	-
Molinia coerulea	2	2	+	-	-	-	-	-	-	-	-	-	-	-
Sesleria albicans	2	+	2	9	8	5	5	4	3	-	-	-	-	-
Sieglingia decumbens	-	-	-	-	-	1	+	-	-	-	-	-	-	-
Zerna erecta	-	-	-	-	-	-	-	-	-	-	6	7	2	6
Carex capillaris	-	-	-	-	-	+	+	3	+	4	-	-	-	-
C. caryophyllea	-	-	-	-	-	3	1	-	-	-	-	-	-	-
C. flacca	-	-	-	3	4	-	-	1	-	-	2	-	2	2
C. hostiana	-	+	3	-	-	-	-	-	-	-	-	-	-	-
C. panicea	5	8	5	-	-	2	-	-	-	-	-	-	-	-
C. pulicaris	+	2	+	-	-	+	-	-	-	-	-	-	-	-
Alchemilla glabra	-	-	-	-	-	-	-	-	+	+	-	-	-	-
Antennaria dioica	-	-	-	-	-	-	-	+	-	1	-	-	-	-
Anthyllis vulneraria	-	-	-	-	-	-	1	-	-	-	-	1	-	-
Aphanes arvensis	-	-	-	-	-	-	-	-	-	-	+	1	-	1
Bellis perennis	-	-	-	-	-	-	-	+	2	+	1	-	+	-
Betonica officinalis	-	-	-	-	-	-	-	-	-	-	+	+	-	-
Blackstonia perfoliata	-	-	-	-	-	-	-	-	-	-	+	-	+	+
Campanula rotundifolia	2	-	1	-	-	+	+	2	3	-	-	-	-	-
Carlina vulgaris	-	-	-	-	1	-	-	-	-	-	-	1	1	1

Table 3:5 continued.

Centaurea nigra	-	-	-	+	-	-	-	-	-	-	-	-	+	-
Cirsium acaulon	-	-	-	-	-	-	-	-	-	-	4	1	1	-
Euphrasia sp.	+	-	-	+	2	1	3	-	-	-	-	-	-	-
Fragaria vesca	-	-	-	-	-	-	-	-	-	-	-	2	+	
Galium sterneri	-	-	-	-	-	2	3	2	3	2	-	-	-	-
Gentiana verna	-	-	-	-	-	3	2	+	+	-	-	-	-	-
Gentianella amarella	-	-	-	-	+	-	1	+	1	+	+	+	-	-
Helianthemum nummularium	-	-	-	+	2	3	4	4	-	-	-	-	-	
Hieracium pilosella	+	-	-	-	-	+	-	2	-	-	2	3	3	
Leontodon hispidus	-	-	-	1	2	-	-	-	-	-	3	2	-	
Linum catharticum	+	-	-	-	2	1	2	2	2	2	2	2	2	-
Lotus corniculatus	+	-	1	-	3	-	-	1	-	-	2	3	5	
Minuartia verna	-	-	-	-	-	2	-	+	2	-	-	-	-	-
Parnassia palustris	+	-	1	+	-	-	-	-	-	-	-	-	-	-
Plantago lanceolata	1	-	+	-	-	1	+	3	1	-	+	-	-	-
Polygala amarella	1	1	1	2	3	1	1	2	1	3	1	1	1	
P. vulgaris	-	-	-	-	-	-	-	-	-	+	1	1	+	-
Polygonum viviparum	-	-	-	-	-	-	-	2	+	1	-	-	-	-
Potentilla erecta	1	1	1	-	-	1	-	1	-	2	-	-	-	-
Poterium sanguisorba	+	-	-	+	+	-	-	-	-	-	-	2	3	
Primula farinosa	3	1	2	2	-	-	-	-	-	-	-	-	-	-
Prunella vulgaris	+	-	-	-	-	-	-	-	3	-	-	2	-	-
Ranunculus acris	+	+	+	-	-	-	-	-	-	-	-	-	-	-
R. bulbosus	-	-	-	-	-	-	-	-	-	-	2	1	-	-
Scabiosa columbaria	-	-	-	1	+	-	-	-	-	-	-	-	-	-
Succisa pratensis	1	2	2	1	-	-	-	-	-	-	-	-	-	-
Taraxacum sect. Erythrosperma	-	-	-	-	-	-	-	-	2	-	-	1	2	-
Thymus drucei	-	-	2	-	-	4	2	4	5	3	-	1	-	1
Trifolium pratense	-	-	+	-	-	-	-	-	-	-	+	-	+	-
T. repens	-	-	-	-	-	-	-	-	1	-	1	1	+	-
Valeriana dioica	+	+	1	1	-	-	-	-	-	-	-	-	-	-
Veronica officinalis	-	-	-	-	-	-	-	-	-	-	-	3	+	-
Viola hirta	-	-	-	-	-	-	-	-	-	-	1	+	-	-
V. odorata	-	-	-	-	+	-	-	-	-	-	-	-	2	-
V. riviniana	-	-	-	-	-	3	1	1	3	3	-	-	-	-
Camptothecium lutescens	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Ctenidium molluscum	1	+	-	2	4	3	1	-	1	-	+	-	-	-
Dicranium scoparium	-	-	-	1	-	-	1	-	-	-	-	-	-	-
Ditrichum flexicaule	-	-	-	-	-	-	2	-	2	-	-	-	-	-
Hypnum cupressiforme	-	4	-	-	-	-	1	+	1	+	-	-	-	-
Pseudoscleropodium purum	-	-	-	-	-	-	-	4	-	-	-	-	-	2
Rhacomitrium lanuginosum	5	-	4	-	-	3	2	1	2	1	-	-	-	-
Rhytidiadelphus squarrosus	-	-	1	-	-	-	-	1	+	-	-	-	-	-
R. triquetrus	-	-	-	-	-	-	-	2	2	2	-	-	-	-
Tortella tortuosa	-	-	-	-	-	5	-	-	3	-	-	-	-	-
Cetraria islandica	-	-	-	-	-	-	1	+	+	1	-	-	-	-
Cladonia furcata	-	-	-	-	-	-	1	-	1	+	-	-	-	-
C. rangiferina	-	-	-	-	-	-	2	2	+	4	-	-	-	-
Cornicularia aculeata	-	-	-	-	-	-	1	+	+	-	-	-	-	-
Peltigera sp.	-	-	-	-	-	2	-	-	+	-	-	-	-	-

Localities and additional species of low frequency.

1. Near Gordale Beck, Malham, Yorkshire. Grid ref. SD/910655 *Equisetum variegatum*, *Carex dioica*, *C. lepidocarpa*, *Luzula campestris*, *Pinguicula vulgaris*.

2. Great Close Mire, Malham, Yorkshire. Grid ref. SD/907664 *Calluna vulgaris*, *Anthoxanthum odoratum*.

3. Ha Mire, Malham, Yorkshire. Grid ref. SD/898667.

4. Dib Scar, near Grassington, Yorkshire. Grid ref. SD/990662 *Populus tremula*, *Pimpinella saxifraga*.

5. Mastiles Lane, near Grassington, Yorkshire. Grid ref. SD/961649.

6. Widdybank Fell, Co. Durham. Grid ref. NY/817294.

7. Widdybank Fell, Co. Durham. Grid ref. NY/818294. *Plantago maritima*, *Viola rupestris*, *Frullania tamarisci*, *Cladonia pyxidata*.

8. Cronkley Fell, Yorkshire. Grid ref. NY/841280 *Dryas octopetala*.

9. Cronkley Fell, Yorkshire. Grid ref. NY/841280 *Cerastium holosteoides*, *Draba incana*, *Climacium dendroides*, *Encalypta vulgaris*, *Mnium longirostrum*.

10. Cronkley Fell, Yorkshire. Grid ref. NY/843279 *Empetrum nigrum*, *Cirsium vulgare*.

11. Magpie Bottom, near Shoreham, Kent. Grid ref. TQ/547609 *Aceras anthropophorum*, *Chrysanthemum leucanthemum*, *Filipendula vulgaris*, *Trifolium striatum*, *Eurhynchium swartzii*, *Fissidens cristatus*.

12. Purple Hill, near Bredhurst, Kent. Grid ref. TQ/814622 *Asperula cynanchica*, *Centaurea scabiosa*, *Hippocrepis comosa*, *Polygala calcarea*, *Veronica chamaedrys*.

13. Crundale Downs, near Wye, Kent. Grid ref. TR/076485 *Bromus commutatus*, *Dactylis glomerata*, *Deschampsia caespitosa*, *Holcus lanatus*, *Gymnadenia conopsea*, *Achillea millefolium*.

14. Crundale Downs, near Wye, Kent. Grid ref. TR/074487 *Thelycrania sanguinea*, *Viburnum lantana*, *Hypericum perforatum*.

TABLE 3.6

Floristic lists from localities of *Polygala amarella* in France & Switzerland.

	1	2	3	4	5	6	7
Site No.	03	04	019	024	025	017	014
Altitude (m)	836	717	1027	[illegible]	61	892	36
Aspect	SW	Nil	N	N	NE	Nil	Nil
Slope (degrees)	35	Nil	20	30	34	Nil	Nil
Soil depth (mm)	50	90	150	Nil	50	25	50
Cover (%)	40	70	90	50	70	50	100
Arrhenatherum elatius	-	4	+	-	-	-	-
Briza media	-	2	-	-	3	4	-
Carex flacca	+	-	-	-	2	+	-
Anthyllis vulneraria	-	+	-	4	-	-	-
Asperula cynanchica	-	-	1	-	2	-	-
Cerastium holosteoides	-	+	-	-	-	1	-
Chrysanthemum leucanthemum	+	2	-	2	-	-	-
Euphrasia sp.	-	-	-	3	1	-	-
Galium mollugo	-	-	-	-	+	1	-
Globularia cordifolia	+	-	1	-	-	-	-
Hieracium sect. Vulgata	-	1	-	3	1	-	-
Hippocrepis comosa	-	1	+	-	+	-	-
Leontodon hispidus	-	-	-	1	2	-	-
Linum catharticum	1	3	-	+	2	2	-
Lotus corniculatus	1	2	2	-	1	-	4
Medicago lupulina	-	2	-	-	-	1	-
Onobrychis viciifolia	-	+	-	+	-	-	-
Polygala amarella	1	3	2	3	1	2	1
Poterium sanguisorba	+	-	1	-	-	-	-
Prunella vulgaris	-	3	2	-	-	-	-
Scabiosa columbaria	+	-	-	-	1	-	-
Succisa pratensis	-	-	3	-	-	-	2
Taraxacum sect. Vulgaria	-	2	-	+	-	-	-
Tetragonolobus siliquosus	-	-	+	-	-	1	-
Thymus drucei	-	+	-	-	2	-	-
Tragopogon pratense	-	+	-	-	-	+	-
Trifolium repens	-	3	-	-	-	1	-
Valeriana officinalis	-	1	-	-	-	+	-
Vicia cracca	-	1	-	1	-	-	-
Bryum pallens	-	-	-	3	-	4	-
Ctenidium molluscum	-	-	8	-	8	-	-
Tortella tortuosa	1	-	-	1	-	-	-

Localities and additional species of low frequency.

1. Dry mountainside near Couvet, Jura, Switzerland. *Corylus avellana*, *Sesleria albicans*, *Anthericum liliago*, *Carex humilis*, *Cephalanthera longifolia*, *Coronilla emerus*, *C. vaginalis*, *Helianthemum nummularium*, *Thymus serpyllum*.

2. Flat ground by roadside, near Couvet, Jura, Switzerland. *Cytisus decumbens*, *Zerna erecta*, *Achillea millefolium*, *Anemone nemorosa*, *Centaurea scabiosa*, *Hieracium pilosella*, *Lathyrus pratensis*, *Plantago lanceolata*, *P. major*, *Ceratodon purpureus*.

3. Edge of pine wood near Seyne, Basses Alpes, France. *Pinus mugo*, *Festuca ovina*, *Koeleria brevifolia*, *Carex caryophyllea*, *C. ornithopoda*, *Plantago maritima*, *Polygala vulgaris*, *Potentilla tabernaemontani*, *Ditrichum flexicaule*, *Rhytidium rugosum*, *Thiudium abietinum*.

4. Steep slaty hillside, La Grave, Hautes Alpes, France. *Populus deltoides*, *Festuca longifolia*, *Euphorbia cyparissas*, *Linaria alpina*, *Oxytropis campestris*, *Pimpinella major*, *P. saxifraga*, *Tussilago farfara*, *Valeriana montana*.

5. Downs near Corbie, Somme, France. *Juniperus communis*, *Brachypodium pinnatum*, *Helictotrichon pratense*, *Koeleria cristata*, *Blackstonia perfoliata*, *Campanula rotundifolia*, *Carlina vulgaris*, *Filipendula vulgaris*, *Teucrium chamaedrys*, *Camptothecium lutescens*, *Cladonia rangiformis*.

6. Roadside ditch, Fugière, near La Mure, Isère, France. *Equisetum palustre*, *Agrostis stolonifera*, *Alopecurus pratensis*, *Carex lepidocarpa*, *C. otrubae*, *Juncus inflexus*, *Arabis hirsuta*, *Filipendula ulmaria*, *Ranunculus repens*, *Rhinanthus minor*, *Drepanocladus revolvens*, *Philonotis capillaris*.

7. Fen near Villeneuve, Vaud, Switzerland. *Frangula alnus*, *Molinia coerulea*, *Phragmites communis*, *Carex demissa*, *C. nigra*, *Dactylorchis majalis*, *Eriophorum latifolium*, *Gymnadenia conopsea*, *Schoenus migricans*, *Angelica sylvestris*, *Cirsium palustre*, *Parnassia palustris*, *Potentilla erecta*, *Serratula tinctoria*, *Thalictrum flavum*, *Campylium stellatum*, *Fissidens cristatus*.

The results of soil analyses for this species are shown in Tables3:7 and 3:8. Soils from British sites are all fine-grained with a high pH and a very high calcium carbonate content, each sample analysed having more than 100 m. eq. exchangeable calcium per 100 gm.soil. Some of these values, however, may be rather exagger~~r~~ated due to the effect of ammonium acetate on free calcium carbonate which was mentioned on p.101. On the whole, organic matter content is rather low and is very low in the chalky samples from Kent which are almost pure white in colour. Soils from the drier sites in the Pennines are thin, almost black rendzinas developed on Carboniferous Limestone, while those from the calcareous mires are similar, though damp, deeper and of a rather coarser nature.

The pH of French and Swiss samples is also high, often greater than 7.5 and exchangeable calcium content is again high. The fen soil (sample C.14) has a lower calcium content than the other continental samples. This is probably because only a low proportion occurs as free carbonate, most of it being adsorbed on to the humus particles in this highly organic soil, together with potassium and magnesium which also

TABLE 3:7

Analysis of soil samples from British localities of *Polygala amarella*.

Sample No.	pH	% of total						M.eq/100gm. air-dried soil			
		CO_3	Organic matter	Coarse sand	Fine sand	Silt	Clay	K	Ca	Mg	Pb
34	7.0	23.7	14.2	17.1	15.6	10.4	6.6	0.21	123.75	1.56	0
40	7.1	63.3	19.8	4.2	5.4	0.2	5.4	0.36	190.0	0.17	0.10
39	7.3	-	-	-	-	-	-	0.32	143.21	0.79	0.90
54	7.1	80.0	12.4	2.3	6.3	1.3	2.2	0.30	121.88	1.25	0.22
25	7.6	-	-	-	-	-	-	0.48	141.88	1.46	0.11
29	7.5	82.2	6.7	1.8	5.3	0.7	5.8	0.64	111.25	1.04	0.05

Sample No.	Locality
34	Gordale Beck, Malham, Yorkshire.
40	Dib Scar, Grassington, Yorkshire.
39	Mastiles Lane, Grassington, Yorkshire.
54	Cronkley Fell, Yorkshire.
25	Magpie Bottom, Kent.
29	Crundale Downs, Kent.

TABLE 3:8

Analysis of soil samples from French and Swiss localities of *Polygala amarella*.

Sample No.	pH	% of total		M.eq/100gm.air-dried soil.		
		CO_3	Organic matter	K	Ca	Mg
C3	7.7	84.0	4.0	0.20	94.81	4.17
C4	7.4	-	-	0.33	133.70	2.08
C14	6.8	10.0	66.8	0.77	63.75	5.42
C17	7.5	-	-	0.26	171.25	2.71
C19	7.7	55.4	4.5	0.19	357.50	3.75
C24	7.6	14.9	1.1	0.14	166.25	3.75
C25	7.8	-	-	0.17	80.63	0.43

Sample No.	Locality
C3	Near Couvet, Jura, Switzerland.
C4	Near Couvet, Jura, Switzerland.
C14	Villeneuve, Vaud, Switzerland.
C17	Fugière, near La Mure, Isère,France
C19	Near Seyne, Basses Alpes, France.
C24	La Grave, Hautes Alpes, France.
C25	Corbie, Somme, France.

have very high values in this sample. All the other samples analysed had a very low organic matter content. The majority of these soils were obviously skeletal, many of them on steep unstable slopes and in several cases eg. in localities near Couvet and La Grave are composed simply of clay and weathered rock fragments. Sample C.25 from chalk downs in northern France is similar to samples from the chalk downs of south-eastern England.

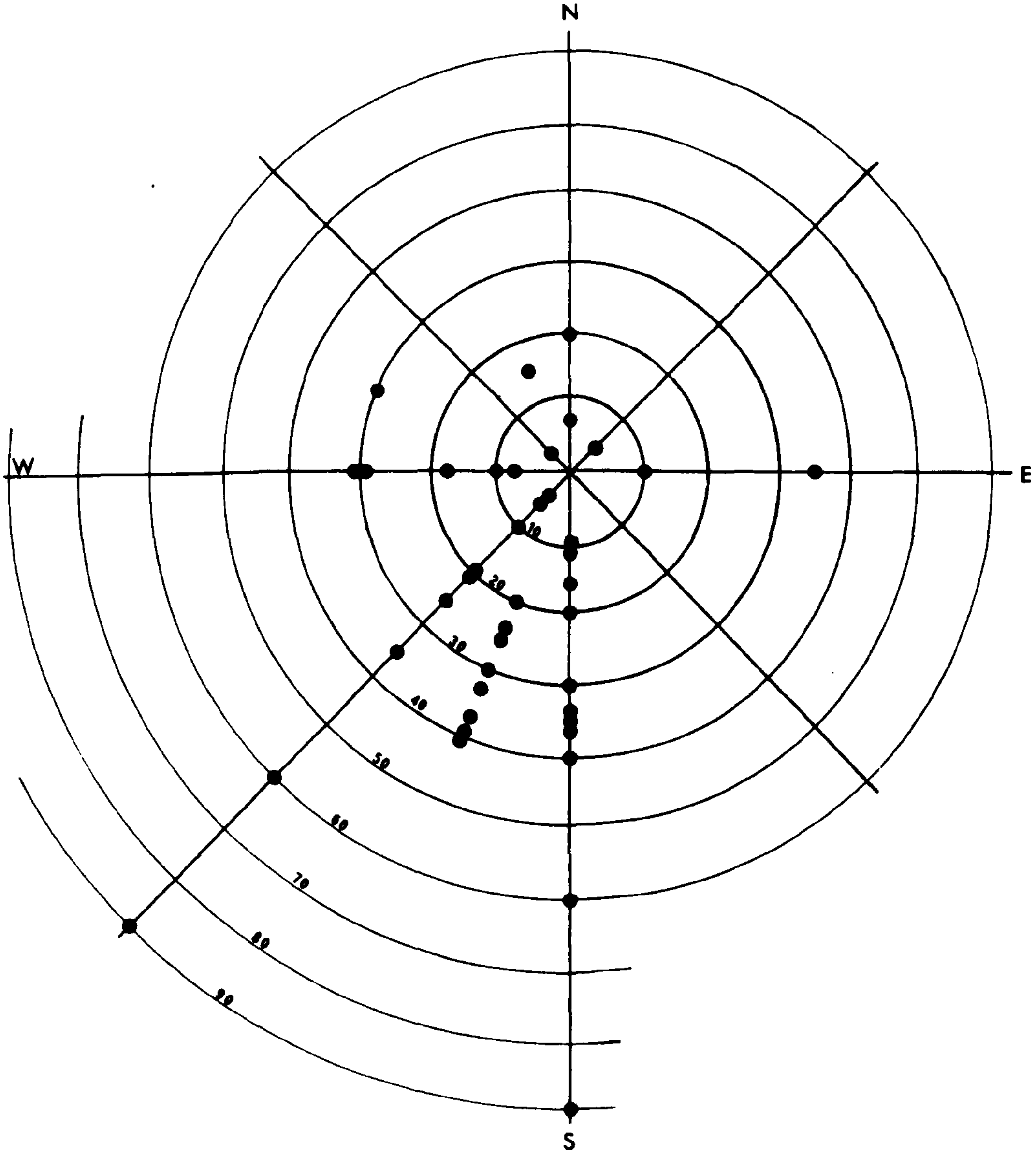
Soils from all localities of this species, both in Britain and in continental Europe are characterised by a high pH and a very high calcium content. These conditions are maintained by the constant flushing of basic minerals into the soil by the direct weathering of the rock underlying thin rendzina soils, by the downward movement of freshly weathered rock fragments of skeletal soils on steep slopes, or from highly mineralised ground water seeping into the organic soils of the mire and fen communities.

Hippocrepis comosa.

This species is a characteristic herb of calcareous grasslands, in Britain and Europe. It is found particularly on dry sunny slopes and only rarely grows in shaded situations though it has been found in light woodland at low altitudes in the Alps. Sites are frequently on south to south-west facing slopes (Fig. 3:2) where there is high insolation, particularly in the afternoon when the sun is most effective in warming the ground. Sites with a northern aspect are few and only on gentle slopes so that cool damp situations are avoided. When the data for each region are considered separately (Fig. 3:3) it is seen that the north or north-east facing sites are mainly in southern England or in the Alps. Sites in northern and western Britain tend to be steeper south-west facing slopes, as do sites of diploid populations.

In south-eastern England H. comosa is a common constituent of undisturbed chalk downland turf. Tansley (1939) lists it as one of the exclusive species which are almost wholly restricted to chalk grassland. Amongst other pioneer species, it is one of the first colonists

Fig. 3:2 The distribution of *Hippocrepis comosa* in relation to slope and aspect



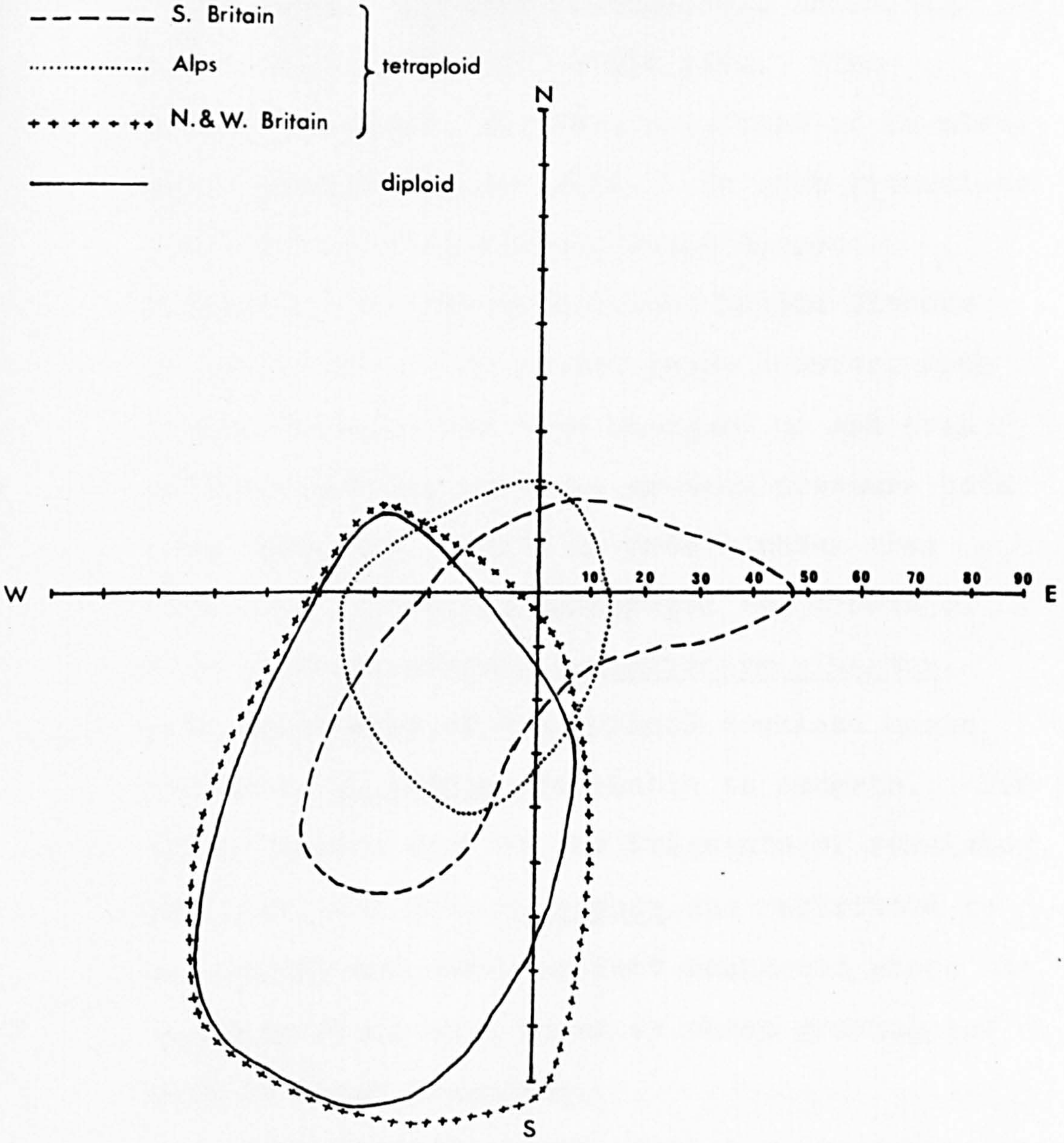


Fig. 3:3 The regional distribution of Hippocrepis comosa in relation to slope and aspect.

of extremely dry open communities, including the bare ground of old chalk pits. The largest colonies, however, are found on downland with a deeper organic soil. In such situations the species often forms a dense carpet, completely covered with golden yellow flowers in early June. In recent years however, much of the downland has been ploughed up and even on the remaining pastures grazing pressure both from sheep and rabbits is much lighter than formerly. This has encouraged the growth of tall grasses, notably Brachypodium pinnatum, with which many of the typical downland herbs including H. comosa are unable to compete. For these reasons many of the fragments of remaining downland turf with H. comosa are restricted to earthworks and other ancient monuments where the sward is still kept short by sheep grazing and also by human trampling.

Tüxen (1927) considers that most of the chalk downs of southern England can be classified as belonging to the Mesobrometum, an association of lowland calcareous grassland communities dominated by grasses of the genus Bromus and found in much of France and Germany. Species of high constancy in association with H. comosa in these communities include *Zerna erecta*, (syn. *Bromus erectus*), *Festuca ovina*, *Carex flacca*, *Campanula rotundifolia*, *Carlina vulgaris*, *Cirsium acaulon*, *Helianthemum nummularium*, *Lotus corniculatus*, *Poterium sanguisorba*, *Scabiosa columbaria* and *Thymus drucei*. (Table 3:9, lists 1 - 8). The discontinuous communities in the driest situations on skeletal soils, including some of the sites of diploid populations are probably referable to the Xerobromion. *H. comosa* has also been recorded from this alliance in the Jura Mountains (Pottier - Alapetite 1943).

In northern and western Britain, *H. comosa* grows on Carboniferous and Devonian limestones which unlike chalk are hard, well-jointed rocks which form prominent cliffs and crags. *H. comosa* can often be found growing on ledges or even apparently clinging to the bare rock of a vertical cliff, its long woody taproot penetrating deep into the cracks in the rock. On Cronkley Fell, where the limestone has been locally metamorphosed, the small population of *H. comosa* is growing in a piece of fairly closed turf, surrounded by bare patches of "sugar" limestone sand.

Nearly all sites in northern and western Britain are completely unshaded and have probably remained so throughout the Post-glacial period. Recent pollen analyses of deposits from Teesdale suggest that even at the time of maximum afforestation only light woodland was present here and there are Post-glacial pollen records of a number of species in the present Teesdale flora which are intolerant of shading, eg. *Helianthemum canum*, *Dryas octopetala* and *Plantago maritima*. The significance of this is discussed in Chapter 4.

The chalk downlands of southern England and the limestone grasslands of northern England have a number of species in common, but some of the southern associates, eg. *Zerna erecta*, *Carlina vulgaris* and *Cirsium acaulon* disappear in the north and are replaced by other species such as *Sesleria albicans*, *Helictotrichon pratense* and *Galium sterneri*. *Thymus drucei* is also much more abundant in northern England, though it is a constant associate of *H. comosa* throughout Britain. (Table 3:9, lists 11 - 14).

The communities in which *H. comosa* is present in northern England are dominated by the two grasses *Festuca ovina* and *Sesleria albicans* and show strong affinities with arctic-alpine communities belonging to the order Seslerietalia coeruleae. Sites on the Carboniferous limestone in Derbyshire (Table 3:9, lists 9 and 10) are somewhat intermediate between the Mesobrometum of southern England and the Seslerietum in the north. Shimwell (1968) has classified them within the Helictotricho - Caricetum flaccae, an association which differs from the typical Mesobrometum by the absence of *Zerna erecta*, *Brachypodium pinnatum*, *Cirsium acaulon* and *Asperula cynanchica* and from the Seslerietum by the absence of *Sesleria albicans*.

In France and Switzerland, *H. comosa* occurs in a variety of habitats and communities from dry stony hillsides to alpine and sub-alpine pastures. It is very abundant in Switzerland, especially on soils derived from glacial drift. In the lowland and sub-alpine regions of Europe, it is usually found in calcareous grasslands belonging to the alliances Mesobromion erecti or Xerobromion, which are both classified within the order Brometalia erecti. (Table 3:10, lists 1 - 5) In the high Alps, however, it is most abundant in three of the associations within the order Seslerietalia coeruleae, a group of dry, calcareous alpine meadows. (Braun-Blanquet & Jenny 1926). These are as follows:-

1. Caricetum firmae, a community found in exposed situations on thin stony soils with a high calcium content. *Carex firma*, *Saxifraga caesia*, *Sesleria coerulea*, *Anthyllis vulneraria* and *Dryas octopetala* are species of high constancy.
2. Seslerieto - semperviretum. This community replaces the Caricetum firmae on warm dry soils on sheltered slopes which are protected by a moderate covering of snow in winter. *Hippocrepis comosa* is found most frequently in this association (Table 3:10, lists 6 - 10). Common associates include *Carex sempervirens* (dominant), *Sesleria coerulea* v. *calcarea*, *Anthyllis vulneraria* v. *alpestris*, *Minuartia verna*, *Helianthemum alpestre*, *H. grandiflorum*, *Carex humilis*, *Festuca violacea* and *Dryas octopetala*. Ludi (1948) lists *Hippocrepis comosa* as one of the constant species in this association on the Schinigeplatte in the Bernese Alps.
3. Festuca violacea - Trifolium thallii association This is found on less base-rich or even base-deficient soils where the snow patches are slow to melt. *H. comosa* ascends to its highest altitude in this association. Associated

species other than the two after which the association is named include *Sesleria coerulea*, *Leontodon hispidus*, *Anthyllis vulneraria* v. *alpestris*, *Potentilla aurea*, *Poa alpina*, *Ranunculus montanus*, *Myosotis alpestris* and *Campanula scheuchzeri* (see Table 3:10, lists 11 and 12).

In addition *H. comosa* occasionally occurs in the association Festucetum halleri of the order Caricetalia curvulae (Braun-Blanquet & Jenny 1926), a group of communities which replace the Seslerietalia on non-calcareous rocks.

In the Pyrenees, *H. comosa* grows in communities which are similar to those in the Alps. It occurs most frequently in the Festucetum scopariae, an association which is the floristic and ecological equivalent of the Seslerieto - Semperviretum in the Alps, though less rich in species (Braun-Blanquet1948). It also occurs occasionally in rock ledge communities belonging to the Scabiosa velutina - Crepis blattarioides association. In the mountains of northern and central Spain, *H. comosa* is present in a number of sub-mediterranean communities on warm dry sunny slopes, but in truly Mediterranean communities it is replaced by other species in the genus.

TABLE 3:9

Floristic lists from British localities of *Hippocrepis comosa*.

List No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Site No.	8	26	28	32	33	98	97	54	43	44	48	37	17	95
Altitude (m)	53	153	92	122	137	60	60	61	275	275	168	229	15	534
Aspect	NE	SW	SSW	S	SW	NNW	SSW	S	WNW	S	S	SW	S	W
Slope (degrees)	5	20	20	10	5	14	23	36	30	60	10	5	15	18
Soil depth (mm)	150	30	40	80	50	100	50	70	40	60	60	30	35	60
Cover (%)	100	80	100	100	100	100	95	90	100	95	85	85	100	90
Crataegus monogyna	-	1	-	+	+	-	-	-	-	-	-	-	-	-
Brisa media	-	6	3	5	-	-	5	-	+	+	-	+	-	-
Dactylis glomerata	-	-	-	-	-	-	-	1	-	+	-	-	-	-
Festuca ovina	5	2	4	5	5	7	6	8	7	6	5	6	2	5
Helictotrichon pratense	2	-	-	+	1	-	2	-	-	3	1	3	4	-
H. pubescens	-	-	-	-	-	2	-	-	-	+	-	-	-	-
Koeleria cristata	3	-	-	1	4	2	-	3	+	1	-	3	-	1
Sesleria albicans	-	-	-	-	-	-	-	-	-	-	5	5	5	4
Sieglingia decumbens	-	-	-	-	-	-	-	-	-	-	-	-	+	1
Zerna erecta	7	6	6	6	6	-	-	1	-	-	-	-	-	-
Carex caryophyllea	+	-	-	3	-	3	-	-	-	-	-	+	+	-
C. ericetorum	1	-	-	3	-	3	-	-	-	-	-	-	2	-
C. flacca	2	3	-	3	-	2	4	-	1	2	+	2	3	-
Anthyllis vulneraria	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Aphanes arvensis	-	-	1	1	-	-	2	1	-	-	-	-	-	-
Asperula cynanchica	-	-	+	-	+	-	-	-	-	-	-	-	-	-
Betonica officinalis	-	-	-	-	-	1	-	-	-	+	-	-	-	-
Blackstonia perfoliata	-	1	+	-	-	-	-	-	-	-	-	-	-	-
Campanula rotundifolia	1	-	1	+	1	-	-	2	2	2	1	1	-	2
Carlina vulgaris	1	-	3	1	1	+	1	1	-	-	-	-	-	-
Centaurea nigra	-	-	2	+	-	-	-	-	1	-	+	-	2	-
C. scabiosa	-	1	1	-	-	-	-	-	-	-	-	-	-	-
Centaurium erythraea	-	-	-	-	-	1	1	-	-	-	-	-	-	-
Cerastium holosteoides	-	-	-	-	-	-	-	1	-	-	-	1	-	-
Chrysanthemum leucanthemum	-	-	1	-	-	-	-	2	-	-	-	-	-	-
Cirsium acaulon	-	1	-	1	1	1	+	-	-	-	-	-	-	-
Euphrasia sp.	-	-	+	-	+	2	+	-	-	-	1	3	-	-

Table 3:9 continued.

Filipendula vulgaris	-	-	1	+	2	3	-	+	+	1	-	-	+	-
Galium pumilum	-	-	-	-	-	1	1	-	-	-	-	-	-	-
G. sterneri	-	-	-	-	-	-	-	-	2	3	-	3	-	+
Gentianella amarella	-	2	-	-	-	1	-	-	-	-	-	-	-	-
Helianthemum canum	-	-	-	-	-	-	-	4	-	-	-	-	-	+
H. nummularium	2	1	2	4	4	-	-	3	5	5	2	4	3	1
Hieracium sect. Pilosella	+	-	2	3	2	2	2	4	-	-	3	1	-	-
Hippocrepis comosa	3	2	5	5	5	3	5	1	5	6	2	1	3	2
Leontodon hispidus	2	2	3	2	3	-	1	1	-	-	1	-	2	-
Linum catharticum	-	1	+	2	+	-	-	2	+	-	-	2	-	-
Lotus corniculatus	1	2	2	3	+	3	+	1	-	-	2	+	1	-
Ononis repens	-	+	-	-	-	-	1	-	-	-	+	-	-	-
Pimpinella saxifraga	-	-	-	-	-	-	-	-	-	+	2	-	-	-
Plantago lanceolata	-	2	-	1	-	3	2	+	-	1	+	+	2	-
P. media	-	-	-	1	+	-	-	-	-	-	-	-	-	-
Polygala calcarea	-	+	3	-	3	-	1	-	-	-	-	-	-	-
P. vulgaris	-	-	-	+	-	-	-	-	+	2	-	-	+	-
Poterium sanguisorba	2	2	3	2	3	3	3	2	4	+	1	1	1	-
Ranunculus bulbosus	-	+	1	1	1	-	-	-	-	-	1	-	-	-
Scabiosa columbaria	1	1	1	1	2	+	-	+	+	3	-	-	2	-
Taraxacum sect. Erythrosperma	-	+	-	+	1	-	-	-	-	-	1	3	-	-
Thymus drucei	-	-	+	+	+	2	2	3	2	-	3	2	+	5
Trifolium repens	-	2	-	1	-	-	-	1	-	-	+	-	-	-
Viola hirta	-	-	1	+	-	-	-	-	+	1	-	-	+	-
V. odorata	+	-	-	-	2	-	-	-	-	-	-	-	-	-
Barbula fallax	-	-	-	-	-	-	-	1	-	-	1	-	-	-
Camptothecium lutescens	1	-	-	-	1	-	-	-	-	-	-	-	-	-
Ctenidium molluscum	2	2	-	3	1	-	-	-	4	-	2	-	+	2
Eurhynchium swartzii	-	1	-	+	-	-	-	-	-	-	-	-	-	-
Fissidens cristatus	1	1	-	+	-	-	-	-	-	+	1	-	1	-
Hypnum cupressiforme	-	-	-	-	-	-	-	-	-	-	1	3	-	-
Neckera crispa	-	2	+	+	-	-	-	-	-	-	-	-	-	-
Pseudoscleropodium purum	1	1	-	-	9	-	-	-	2	8	-	-	-	-
Tortella tortuosa	-	-	-	-	-	-	-	2	-	-	-	2	-	+
Cladonia furcata	-	-	-	-	-	-	-	-	-	-	1	-	-	1

Localities and additional species of low frequency.

1. Devil's Ditch, near Newmarket, Cambridgeshire. Grid ref. TL/623612 *Astragalus danicus*.
2. Biggin Hill, Kent. Grid ref. TQ/409604 *Achillea millefolium*, *Bellis perennis*, *Hypericum perforatum*, *Rhinanthus minor*.
3. Purple Hill, Bredhurst, Kent. Grid ref. TQ/812622.
4. Wye Downs, Kent. Grid ref. TR/071465 *Aceras anthropophorum*, *Gymnadenia conopsea*, *Prunella vulgaris*.
5. Downs near Burham, Kent. Grid ref. TQ/727628 *Viola riviniana*.
6. Cliff top, Birling Gap, E. Sussex. Grid ref. TV/554958.
7. Cliff top, Durlston Head, Dorset. Grid ref. SZ/029771 *Spiranthes spiralis*, *Inula crithmoides*.
8. Great Orme's Head, Caernarvonshire. Grid ref. SH/771823 *Brachypodium sylvaticum*, *Cirsium vulgare*, *Sherardia arvensis*.
9. Topley Pike, Derbyshire. Grid ref. SK/105724 *Primula veris*.
10. Wye Dale, Derbyshire. Grid ref. SK/105727 *Festuca arundinacea*.
11. Ghaistrill's Strid, Grassington, Yorkshire. Grid ref. SD/992646 *Barbula vinealis*, *Encalypta vulgaris*.
12. Cave Hole Wood Scar, Yorkshire. Grid ref. SD/790662 *Luzula campestris*, *Galium verum*, *Camptothecium sericeum*.
13. Silverdale, Lancashire. Grid ref. SD/476768 *Anthoxanthum odoratum*, *Carex panicea*, *Fragaria vesca*, Hieracium sect. Vulgata, *Potentilla sterilis*, Rubus vestita, *Acrocladium cuspidatum*, *Mnium longirostrum*, *Rhytidiadelphus squarrosus*, *Rhytidium rugosum*, *Weissia controversa*.
14. Cronkley Fell, Yorkshire. Grid ref. NY/841283 *Ditrichum flexicaule*, *Rhacomitrium lanuginosum*, *Frullania tamarisci*, *Cornicularia aculeata*, *Squamaria crassa*.

TABLE 3:10.

Floristic lists from localities of *Hippocrepis comosa* in France & Switzerland.

List No.	01	02	015	016	018	03	05	06	012	013	011	023
Altitude (m)	168	412	854	671	854	836	1272	1678	1983	1987	2204	1922
Aspect	S	SSW	W	S	S	SW	E	SSW	W	S	W	SSW
Slope (degrees)	40	40	18	35	20	35	10	37	32	30	30	30
Soil depth (mm)	100	100	50	10	50	50	25	40	50	150	100	>150
Cover (%)	60	70	70	100	80	40	90	50	95	70	95	95
Daphne striata	-	-	-	-	-	-	-	-	-	1	4	-
Anthoxanthum odoratum	-	3	-	-	-	-	2	1	2	-	-	-
Arrhenatherum elatius	-	-	+	-	-	5	-	-	-	-	-	-
Brachypodium pinnatum	1	-	2	-	+	-	-	-	-	-	-	-
Briza media	-	1	+	+	-	-	-	-	2	-	-	3
Bromus arvensis	3	5	-	-	-	-	-	-	-	-	-	-
Festuca ovina	-	-	-	-	+	-	6	6	6	-	-	-
F. rubra	1	-	-	-	-	-	-	-	-	5	-	-
F. violacea	-	-	-	-	-	-	-	-	-	-	4	2
Helictotrichon pubescens	-	-	-	1	-	-	1	-	-	-	-	-
Koeleria cristata	1	-	-	-	-	-	4	-	3	-	-	-
Nardus stricta	-	-	-	-	-	-	-	-	-	-	-	7
Poa alpina	-	-	-	-	-	-	-	+	-	-	-	-
Sesleria albicans	-	-	-	-	-	4	-	-	4	+	5	2
Zerna erecta	-	-	1	7	1	-	-	-	-	-	-	-
Anthericum liliago	+	-	-	-	-	+	-	-	-	-	-	-
Carex flacca	1	2	+	-	-	+	-	-	-	-	-	-
C. sempervirens	-	-	-	-	-	-	1	-	2	4	7	2
Crocus albiflorus	-	-	-	-	-	-	2	-	-	-	-	1
Achillea millefolium	-	-	+	-	-	-	1	-	1	-	-	-
Alchemilla monticola	-	-	-	-	-	-	3	-	1	-	-	1
Anthyllis vulneraria	-	-	2	+	-	-	-	+	+	-	1	-
Asperula cynanchica	-	1	2	-	-	-	-	-	-	-	-	-
Carlina vulgaris	+	1	-	-	-	-	-	-	-	-	-	-
Centaurea nigra	+	1	-	-	-	-	-	-	-	-	-	-
Cerastium arvense	-	-	-	-	-	-	-	-	1	4	-	-
Chrysanthemum leucanthemum	-	-	-	-	-	+	-	-	2	-	-	-
Coronilla emerus	-	6	-	-	-	+	-	-	-	-	-	-
C. vaginalis	-	-	-	-	4	+	-	-	-	-	-	-

Table 3:10 continued.

Galium erectum	+	-	1	+	-	-	-	-	-	+	-	-
Gentiana verna	-	-	-	-	-	-	1	-	-	-	-	1
Globularia cordifolia	-	-	-	-	-	4	-	-	-	2	-	-
Helianthemum nummularium	1	-	-	-	+	+	1	-	3	+	+	1
Hieracium pilosella	3	3	-	-	-	-	2	-	3	-	-	-
H. sect. Vulgata	2	2	-	-	-	-	-	-	-	-	-	-
Hippocrepis comosa	7	1	5	7	7	5	2	6	4	2	3	2
Leontodon hispidus	1	-	-	-	-	-	-	-	-	-	-	2
Linum catharticum	1	-	+	1	-	-	-	2	1	-	-	-
Lotus corniculatus	+	2	1	+	-	-	2	+	2	+	-	2
Medicago lupulina	+	-	-	+	+	-	-	-	-	-	-	-
Onobrychis viciifolia	-	-	+	-	+	-	-	-	-	-	-	-
Ononis rotundifolia	-	-	-	1	2	-	-	-	-	-	-	-
Plantago lanceolata	-	-	1	-	-	-	1	-	-	-	-	-
P. maritima	-	-	-	-	-	-	-	-	2	3	-	2
P. media	-	-	+	-	-	-	3	-	-	-	-	-
Polygala alpina	-	-	-	-	-	-	3	1	1	2	1	1
P. vulgaris	-	-	2	1	-	-	-	-	-	-	-	-
Potentilla tabernaemontani	+	-	-	-	-	-	+	-	+	-	-	-
Poterium sanguisorba	1	2	2	1	-	1	2	-	-	-	-	-
Saussurea alpina	-	-	-	-	-	-	-	-	1	+	-	-
Scabiosa columbaria	2	-	3	-	-	+	-	-	-	-	-	-
Sedum reflexum	-	-	-	1	1	-	-	-	-	-	-	-
Sempervivum tectorum	-	-	-	-	-	-	-	-	1	-	1	-
Soldanella alpina	-	-	-	-	-	-	-	-	-	-	3	1
Taraxacum sect. Erythrosperma	-	-	1	-	-	-	1	-	-	-	-	-
Teucrium chamaedrys	1	2	-	+	+	-	-	-	-	-	-	-
Thesium alpinum	-	-	-	-	-	-	1	-	1	-	-	-
Thymus drucei	-	-	-	-	+	-	1	1	2	1	-	2
T. serpyllum	1	-	-	-	2	+	-	-	-	-	-	-
Trifolium montanum	-	-	-	+	-	-	-	-	1	-	-	-
T. thallii	-	-	-	-	-	-	3	-	2	-	-	3
Camptothecium lutescens	-	-	-	7	-	-	2	-	1	-	-	-
Ditrichum flexicaule	-	-	-	-	-	-	-	-	+	-	+	-
Thuidium abietinum	-	-	-	1	-	-	-	-	+	-	-	-
Tortella tortuosa	2	-	-	-	2	-	1	-	1	2	3	-
Squamaria crassa	-	-	-	-	-	-	-	1	-	-	1	-

Localities and additional species of low frequency.

1. Roadside bank near Lescheres, Haute Marne, France. *Epipactisatrorubens*, *Euphorbia platyphylla*, *Primula veris*, *Sanguisorba officinalis*, *Campylium hispidulum*.
2. Hillside in the Loue Gorge, Doubs, France. *Hypericum perforatum*, *Polygala calcarea*.
3. Hillside above Bex, Vaud, Switzerland. *Carex ornithopoda*, *Prunella vulgaris*, *Rhinanthus minor*, *Silene vulgaris*, *Barbula vinealis*.
4. Lower slopes of Mount Nivolet, Savoie, France. *Listera ovata*, *Orobanche caryophyllacea*, *Centaurea scabiosa*.
5. Mountainside near Quet - en - Beaumont, Isère, France. *Antirrhinum latifolium*, *Helianthemum appeninum*, *H. canum*, *Saponaria ocymoides*.
6. Stony mountainside, near Couvet, Jura, Switzerland. *Corylus avellana* (seedling), *Polygala amarella*.
7. Alpine meadow, Vue des Alpes, Jura, Switzerland. *Luzula campestris*, *Galium pumilum*, *Ranunculus montanus*, *Veronica chamaedrys*, *Bryum capillare*, *Rhytidiadelphus squarrosus*.
8. Rocks in the Oberalp Pass, near Andermatt, Uri, Switzerland. *Agrostis tenuis*, *Sempervivum montanum*, *Breutelia chrysocoma*.
9. Mountainside N.E. of Pontresina, Engadin, Switzerland. *Botrychium lunaria*, *Carex ericetorum*, *Astragalus aristatus*, *Campanula rotundifolia*, *Myosotis alpestris*, *Potentilla sterilis*, *Cladonia fimbriata*.
10. Mountainside near Hotel Chantarella, St. Moritz, Engadin, Switzerland. *Androsace villosa*, *Chrysanthemum alpinum*, *Dryas octopetala*, *Polygala chamaebuxus*,*Pulmonaria longifolia*.
11. Val dal Fain, Ober Engadin, Switzerland. *Juniperus communis*, *Rhododendron chamaecistus*, *Arabis pumila*, *Bartsia alpina*, *Draba aizoides*, *Homogyne discolor*, *Oxytropis campestris*, *Primula viscosa*, *Saxifraga paniculata*, *Cetraria islandica*.
12. Col du Lautaret, Hautes Alpes, France. *Ajuga pyramidalis*, *Fragaria vesca*, *Gentiana clusii*, *Potentilla aurea*, *Viola calcarata*, *Barbula cylindrica*.

Analyses of soil samples from British localities (Table 3:11) show that in this country the species is restricted to highly calcareous soils with a pH usually above 7. Exchangeable magnesium content is low, with the exception of the sample from Great Orme's Head where the Carboniferous limestone is locally dolomitised. <u>H. comosa</u> is totally absent from the belt of Permian magnesian limestone which outcrops in the east Midlands, and this was at first thought to be due to an intolerance of high concentrations of magnesium, but seedlings transplanted into this soil thrive just as well as those transplanted into a calcareous soil from Derbyshire with a low concentration of magnesium. Two of the Alpine samples also have a high magnesium content. Lead is present in small amounts in samples from the northern Pennines.

Most of the soil samples are very dark in colour or even black, due to the high humus content and are mainly rendzinas or protorendzinas. In the sample from Cronkley Fell, particles of "sugar" limestone are mixed with the humus. Continental samples are more variable in regard to colour and humus content.

TABLE 3:11

Analysis of soil samples from British localities of *H. comosa*.

Sample No.	pH	% of total		M.eq./100 gm. air-dried soil			
		CO_3	Organic matter	K	Ca	Mg	Pb
33	7.4	-	-	1.54	131.25	2.60	0
31	7.4	-	-	0.38	115.00	1.56	0
8	7.3	-	-	0.24	103.13	0.79	0
44	7.3	3.0	31.3	0.55	73.75	1.56	0
48	7.3	-	-	0.11	100.63	0.15	0.11
37	6.8	-	-	1.09	110.625	2.92	0
17	6.6	-	-	0.83	51.875	2.98	0.10
21	7.1	80.0	12.4	0.39	103.125	1.04	0.13
94	7.3	22.6	14.3	1.17	37.50	11.46	0
97	7.4	39.7	8.9	0.15	68.75	0.25	0

Sample No.	Locality.
33	Burham Downs, Kent.
31	Wye Downs, Kent.
8	Devil's Ditch, near Newmarket, Cambridgeshire
44	Wye Dale, Derbyshire.
48	Grassington, Yorkshire.
37	Cave Hole Wood Scar, near Settle, Yorkshire.
17	Silverdale, Lancashire.
21	Cronkley Fell, Yorkshire.
94	Great Orme's Head, Caernarvonshire.
97	Durlston Head, Dorset.

Cation Analyses of soil samples from continental Europe (Table 3:12) show that the species is less restricted to calcareous soils there than in Britain. Exchangeable calcium content varies from 1.98 to 327.5 m.eq./100 gm. soil and there is a pH range from 5.8 to 8.0 In the Alps, H. comosa was found growing on granite and schist, as well as on limestone. The wide range of ecological communities in which H. comosa occurs in the Alps is thus related to the wide edaphic tolerance of the species there.

These results are similar to those described by Elkington (1962, 1964) for Gentiana verna and Myosotis alpestris which are also examples of species becoming edaphically restricted towards the edge of their geographical range. In Britain, several continental species become calcicolous in the north and west where the climate is more oceanic. This can be attributed to the fact that only the addition of minerals to the soil from the weathering of basic substrates is able to keep pace with the leaching effect of heavy rainfall.

TABLE 3:12

Analysis of soil samples from French and Swiss localities of <u>Hippocrepis comosa</u>.

Sample No.	pH	% of total		M.eq./100 gm. air-dried soil		
		CO_3	Organic matter	K	Ca	Mg
C3	7.7	84.0	4.0	0.20	94.81	4.17
C5	5.8	-	-	0.41	43.75	2.60
C6	6.3	-	-	0.22	1.98	0.25
C11	6.8	13.7	53.5	0.92	3.13	18.75
C12	5.8	-	-	0.85	23.75	8.85
C13	7.0	7.0	26.5	1.05	86.25	16.25
C18	8.0	33.0	1.5	0.16	327.50	3.13
C23	6.2	-	-	0.34	19.38	3.13

<u>Sample No</u>.	<u>Locality</u>.
C3	Near Couvet, Jura, Switzerland.
C5	Vue des Alpes, Jura, Switzerland.
C6	Oberalp Pass, near Andermatt, Uri, Switzerland.
C11	Val dal Fain, Ober Engadin, Switzerland.
C12	Pontresina, Engadin, Switzerland.
C13	St. Moritz, Engadin, Switzerland.
C18	Quet-en-Beaumont, Hautes Alpes, France.
C23	Col du Lautaret, Hautes Alpes, France.

Juncus alpinus.

In Britain, Juncus alpinus is a rare species of base-rich flushed communities in montane regions of northern England and Scotland. The vegetation of these flushes varies from a species-rich closed sward to a very open species-poor type of vegetation in stony streams and springs. Pigott (1956) has described the first type of community as a "turfy marsh", while the second type he considers as a "gravel flush." Both types are well represented in Upper Teesdale. The Scottish equivalents of these communities have been described by McVean & Ratcliffe (1962). There the species-poor flushes are represented by their Cariceto-saxifragetum aizoidis association, while the species-rich flushes are mainly contained within their Carex panicea - Campylium stellatum nodum.

The species-poor flushes (Table 3:13, lists 1 - 7) are found in stony areas around springs and shallow streams where the water is enriched with calcium from neighbouring rocks. Often these flushes form networks, the channels separated by oligotrophic hummocks with the vegetation composed mainly of Calluna, Molinia and Trichophorum. A good example of this has been described by McVean & Ratcliffe (1962) from Ardtulichan, Perthshire, but similar complexes can be found in other parts of Scotland, eg. on the north slopes of Shiehallion and in Glenshee, and also in Teesdale. On Widdybank Fell, a line of gravel flushes is present below the outcrop of "sugar" limestone. Though the underlying rock of the flushes is Whin Sill, an acid dolerite, the spring water is highly calcareous, having percolated down through the limestone.

The vegetation of the species-poor flushes is very open, cover never being more than 80% and often less than 50%. The majority of species are either monocotyledons or bryophytes, dicotyledonous herbs being very poorly represented. Associate species of high constancy are Carex demissa, C. lepidocarpa, C. panicea, Eleocharis quinqueflora, Juncus articulatus, Pinguicula vulgaris and Scorpidium scorpioides. In many respects, and particularly in the constancy of S. scorpioides this type of community is similar to those described by Poore (1955) in Breadalbane and which he placed in the Carex hostiana - C. demissa and C. demissa - C. panicea noda. McVean & Ratcliffe (1962) regard Poore's noda as being somewhat intermediate between their Carex panicea - Campylium stellatum nodum and their Cariceto - saxifragetum aizoidis association, but probably having a closer affinity with the latter.

Juncus alpinus also occurs in species-rich communities (Table 3:13, lists 8 - 13) around the margins of gravel flushes and especially on the low banks of streams which are flooded periodically with base-rich water. Pigott (1956) has described how gravel and silt derived from calcareous boulder clay is deposited on the inner banks of meanders of some of the small streams or "sikes" in Teesdale and forms damp base-rich habitats for a number of the Teesdale rarities. J. alpinus occurs frequently in such situations along Sand Sike and Slapestone Sike.

In parts of Teesdale and in several sites in Scotland, J. alpinus also occurs in the more closed vegetation surrounding the stony gravel flushes. The vegetation of the species-rich communities, though still dominated by sedges includes a much higher percentage of grasses and dicotyledonous herbs than the species-poor flushes and the vegetation is much less open, cover being almost 100% in most cases. Constant species include Carex demissa, C. panicea, Juncus articulatus, Succisa pratensis and Bryum pseudotriquetrum, as well as a number of other species characteristic of damp base-rich habitats, eg. Leontodon autumnalis and Parnassia palustris.

In Scandinavia Juncus alpinus grows in sedge and bryophyte-rich communities similar to those in Britain. Nordhagen (1928, 1943) records it in two of the alliances belonging to the order Caricetalia goodenowii, a group of mesotrophic-eutrophic mire communities. In Sikilsdalen it is a member of the alliance Caricion atrofuscae-saxatilis and in Sylene it is also found in the alliance Caricion canescentis-fuscae. Both of these communities share many species in common with the montane mesotrophic-eutrophic mires in Teesdale and Scotland, but on the whole the percentage cover is higher in the Norwegian mires.

In the Alps, J. alpinus grows in a variety of spring and mire communities. Braun-Blanquet & Rübel (1932) record that it is present in south-eastern Switzerland in the Cardaminetum amarae, a weakly acid spring community, but in other alpine regions it is more common in mire communities. In the French Alps (Braun-Blanquet 1954) it is a characteristic species of the

Scheuchzerio-Caricetea fuscae, a class comprising several different types of alpine mire. Within this class J. alpinus grows in acidophilous communities which belong to the alliance Caricion fuscae and also in sedge-rich eutrophic mires belonging to the Caricion davallianae, an alliance which is also found in the Pyrenees (Braun-Blanquet 1948).

Floristically, the British communities of which J. alpinus is a constituent are more similar to those of Scandinavia than those of the Alps.

TABLE 3:13

Floristic lists from British localities of *Juncus alpinus*

List No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Site No.	74	75	76	77	96	60	61	78	79	80	93	91	92
Aspect	NW	E	NE	NE	Nil	Nil	SW	NNE	Nil	Nil	S	Nil	Nil
Slope (degrees)	5	7	8	8	Nil	Nil	5	8	Nil	Nil	15	Nil	Nil
Soil depth (mm)	100	130	150	150	150	130	130	150	150	70	150	130	80
Cover (%)	20	60	60	60	30	20	30	90	100	100	95	90	100
Calluna vulgaris	-	1	-	1	-	-	-	-	+	-	-	-	-
Erica tetralix	-	2	-	1	-	-	-	-	-	-	-	-	-
Salix repens	-	-	-	-	-	-	-	+	-	-	2	1	-
Equisetum palustre	-	-	-	-	1	+	-	-	-	-	-	-	-
E. variegatum	-	-	-	-	-	-	-	-	1	-	-	2	1
Briza media	-	-	-	-	-	-	-	-	-	+	-	2	+
Deschampsia caespitosa	-	-	-	-	-	2	-	-	-	-	-	1	-
Festuca ovina	-	-	-	-	-	-	1	-	-	6	3	-	-
Molinia coerulea	1	+	-	-	-	-	-	-	-	3	1	-	-
Carex demissa	-	2	-	-	+	1	4	3	3	2	-	-	2
C. dioica	-	3	-	+	-	-	-	-	-	-	1	-	-
C. echinata	-	1	+	-	-	-	-	-	1	-	-	-	-
C. flacca	-	1	-	-	-	-	-	-	-	-	3	2	2
C. lepidocarpa	+	3	3	3	1	-	-	-	-	-	-	-	-
C. nigra	-	-	3	1	-	-	-	-	+	1	-	-	-
C. panicea	3	2	1	1	3	+	1	3	3	3	3	2	+
C. pulicaris	-	-	3	-	-	-	-	-	-	-	1	-	-
Eleocharis quinqueflora	-	3	-	3	3	-	-	3	3	-	-	-	+
Eriophorum angustifolium	+	-	+	-	-	-	-	-	-	-	-	-	-
Juncus alpinus	1	3	1	2	2	2	2	2	3	3	3	2	2
J. articulatus	2	2	2	-	1	-	-	3	2	2	2	-	2
J. kochii	-	-	2	1	-	-	-	+	1	-	-	-	-
J. triglumis	-	-	-	-	+	2	-	-	-	-	-	-	-
Kobresia simpliciuscula	-	-	-	-	-	1	4	-	-	-	-	-	-
Tofieldia pusilla	+	-	-	1	-	-	+	-	1	-	-	-	-
Triglochin palustre	-	1	-	-	-	-	+	-	-	-	-	-	1
Bellis perennis	-	-	-	-	-	-	-	-	-	+	-	-	+
Euphrasia officinalis agg.	-	-	-	-	-	-	-	-	-	3	3	+	3
Leontodon autumnalis	-	-	-	-	-	-	-	-	-	2	-	1	1
Lotus corniculatus	-	-	-	-	-	-	-	-	-	-	-	1	1

Table 3:13 continued.

Parnassia palustris	-	-	-	-	-	-	-	-	-	+	+	-	1
Pedicularis palustris	+	-	-	-	-	-	-	-	-	1	-	-	-
Pinguicula vulgaris	-	+	1	1	-	+	+	1	2	1	+	-	1
Plantago lanceolata	-	-	-	-	-	-	-	-	-	-	-	1	1
P. maritima	-	-	-	-	-	+	+	-	-	-	-	-	1
Potentilla erecta	-	-	-	-	-	-	-	1	1	2	+	-	-
Primula farinosa	-	-	-	-	-	-	-	-	-	-	+	-	+
Prunella vulgaris	-	-	-	-	-	-	-	1	-	2	-	3	3
Ranunculus acris	-	-	-	-	-	-	-	-	-	+	+	1	1
Saxifraga aizoides	1	+	-	-	+	-	-	+	-	-	-	-	-
Succisa pratensis	-	-	-	-	-	-	-	2	2	2	2	1	+
Taraxacum officinalis agg.	-	-	-	1	-	-	-	-	-	-	-	-	1
Trifolium repens	-	-	-	-	-	-	-	-	-	-	-	1	3
Acrocladium cuspidatum	-	-	-	-	-	-	-	+	-	-	-	2	-
Bryum pseudotriquetrum	-	-	-	-	-	-	-	-	1	1	1	1	2
Campylium stellatum	1	-	+	-	-	-	-	2	3	-	4	-	-
Cratoneuron commutatum	-	-	-	-	-	-	-	-	-	3	+	4	-
Ctenidium molluscum	-	-	-	-	-	-	-	1	-	-	+	-	-
Drepanocladus revolvens	+	-	-	1	-	-	-	1	-	-	-	-	-
D. uncinatus	-	-	-	-	-	-	-	-	3	-	-	-	1
Fissidens adianthoides	-	-	-	-	-	-	-	1	-	1	-	-	1
Mnium punctatum	-	-	-	-	-	-	-	-	-	-	-	1	1
Philonotis calcarea	-	-	-	-	-	-	-	-	-	-	-	5	1
Scorpidium scorpioides	1	2	5	6	5	-	-	-	-	-	-	-	-
Aneura pinguis	-	-	1	3	-	-	-	+	-	-	-	-	-
Lophocolea bidentata	-	-	-	-	-	-	-	-	-	-	-	+	1

Localities and additional species of low frequency.

1. Creag Odhar, Blair Atholl, Perthshire. Grid ref. NN/878637 Amblystegium varium, Campylopus fragilis.
2. Ben Vrackie, near Pitlochry, Perthshire. Grid ref. NN/943613.
3. Shiehallion, Perthshire. Grid ref. NO/722560.
4. Shiehallion, Perthshire. Grid ref. NO/722560 Drosera rotundifolia, Blindia acuta.
5. Widdybank Fell, Co. Durham. Grid ref. NY/818295.
6. Widdybank Fell, Co. Durham. Grid ref. NY/817295.
7. Widdybank Fell, Co. Durham. Grid ref. NY/815297 Armeria maritima.
8. Morrone, near Braemar, Aberdeenshire. Grid ref. NO/142906 Nardus stricta.
9. Devil's Elbow, Glenshee, Angus. Grid ref. NO/144764 Juncus squarrosus, Polygonum viviparum.
10. Branxholme Wester Loch, Roxburgh. Grid ref. NT/423110 Anthoxanthum odoratum, Holcus lanatus, Orchis mascula, Angelica sylvestris, Caltha palustris, Filipendula ulmaria, Ranunculus flammula, Climacium dendroides.
11. Cetry Bank, Co. Durham. Grid ref. NY/843298 Carex hostiana, Juncus acutiflorus.
12. Winch Bridge, Co. Durham. Grid ref. NY/905279 Festuca vivipara, Carex disticha, Isolepis setacea, Trifolium pratense, Dicranum scoparium, Rhacomitrium aquaticum.
13. Sand Sike, Langdon Beck, Co. Durham. Grid ref. NY/838310 Selaginella selaginoides, Agrostis stolonifera, Festuca rubra, Cerastium holosteoides, Minuartia verna, Tussilago farfara, Viola riviniana.

Analyses of soil samples from localities of this species are shown in Table 3:14. Results of the mechanical analysis show that J. alpinus always grows on coarse soils with a high proportion of coarse and fine sand, whether the floristic composition of the vegetation is species-rich or not, though on the whole, organic matter content is higher in samples from species-rich communities. pH is approximately neutral. Exchangeable calcium content is lower in Scottish soils, most of them being developed from calcareous schist rather than limestone, and particles of mica form quite a large proportion of the sand fraction. Lead is absent from nearly all the Scottish samples.

TABLE 3:14

Analysis of soil samples from British localities of *Juncus alpinus*.

Sample No.	pH	% of total						M.eq./100 gm.air-dried soil			
		CO_3	Organic matter	Coarse sand	Fine sand	Silt	Clay	K	Ca	Mg	Pb
60	7.3	16.3	3.0	16.7	33.9	10.4	10.1	0.09	105.63	0.04	0.43
92	7.0	9.6	15.1	23.6	31.1	5.7	2.0	0.23	64.08	0.79	0.11
93	6.6	6.1	17.6	22.5	19.9	5.0	3.5	0.26	23.13	0.15	0.10
91	7.1	-	-	-	-	-	-	0.10	10.0	0.90	0.18
74	7.3	-	-	-	-	-	-	0.08	21.25	0.10	0
75	7.1	1.6	1.8	53.9	32.4	1.0	1.7	0.17	6.25	0.13	0.10
76	6.2	2.9	12.8	40.8	15.7	3.9	5.7	0.15	15.63	1.56	0
78	6.7	1.8	10.9	35.4	34.5	2.5	4.7	0.18	17.83	0.15	0
80	6.1	-	-	-	-	-	-	0.51	29.38	5.21	0

Sample No.	Locality
60	Widdybank Fell, Co. Durham.
92	Sand Sike, Teesdale, Co. Durham.
93	Cetry Bank, Teesdale, Co. Durham.
91	Winch Bridge, Teesdale, Co. Durham.
74	Creag Odhar, Perthshire.
75	Ben Vrackie, Perthshire.
76	Shiehallion, Perthshire.
78	Braemar, Aberdeenshire.
80	Branxhome Wester Loch, Roxburghshire.

Carex ericetorum.

Carex ericetorum grows in three main areas in Britain: the Carboniferous limestone of the northern Pennines, the Permian magnesian limestone belt of the east Midlands and the chalk heaths of East Anglia. The associated vegetation is distinct in each area and vegetation lists from sites in each of these areas are shown in Table 3:15. A few species eg. *Festuca ovina* are constant associates throughout the British range, and the rather rare moss *Rhytidium rugosum* occurs sporadically. Most sites are on level or gently sloping ground and there is no aspect preference.

In the northern Pennines, constant associates include *Briza media*, *Sesleria albicans*, *Linum catharticum* and *Thymus drucei* with *Rhacomitrium lanuginosum* on higher ground, all species which are characteristic of calcareous grasslands in this district. In Teesdale *C. ericetorum* is a common constituent of *Sesleria* turf, on both Cronkley and Widdybank Fells but it is so heavily grazed by sheep and rabbits that inflorescences are often bitten off and it frequently passes unnoticed, or is confused with *C. caryophyllea*, a species which in the vegetative state is very similar to *C. ericetorum*.

In the east Midlands, the species is found in semi-natural turf, often in old limestone quarries and here too it was overlooked until fairly recently. *Zerna erecta* is the most commonly associated grass, but many of the other associates in the northern Pennines also occur here together with species of a more eastern distribution in Britain such as *Brachypodium pinnatum* and *Astragalus danicus*.

In East Anglia, *C. ericetorum* is frequent on the heaths of Breckland. Here the soil is often quite acid and calcifuges such as *Pteridium aquilinum* and *Calluna vulgaris* appear, though *C. ericetorum* is absent from the most strongly acid sites (Watt 1940). A number of "steppe" species are also present, including *Silene otites*, *Thymus serpyllum* and *Veronica spicata*, as well as *C. ericetorum* itself. The most constant associates in East Anglia are *Luzula campestris*, *Galium verum*, *Thymus serpyllum*, *Dicranum scoparum* and *Pleurozium schreberi*.

TABLE 3:15

Vegetation lists from British localities of *Carex ericetorum*.

List No.	1	2	3	4	5	6	7	8	9
Site No.	16	17	18	19	21	23	59	64	87
Altitude (m)	0	15	153	198	534	534	488	488	503
Aspect	S	S	SE	W	Nil	Nil	SSE	WNW	SW
Slope (degrees)	5	15	21	5	Nil	Nil	20	14	5
Soil depth (mm)	50	40	50	40	50	110	80	135	90
Cover (%)	95	100	100	80	90	100	90	100	100
Calluna vulgaris	-	-	-	2	-	-	-	-	-
Crataegus monogyna	1	-	-	-	-	-	-	-	-
Dryas octopetala	-	-	-	-	1	+	-	-	-
Rubus vestita	+	+	-	-	-	-	-	-	-
Ulex europaea	2	-	-	-	-	-	-	-	-
Anthoxanthum odoratum	+	+	-	-	-	-	-	-	-
Brachypodium pinnatum	-	-	-	-	-	-	-	-	-
Briza media	-	-	1	2	3	-	+	2	1
Festuca ovina	5	2	5	6	5	7	6	7	5
Helictotrichon pratense	3	4	4	3	-	-	+	+	-
Koeleria cristata	1	-	-	-	-	-	1	3	2
Sesleria albicans	6	5	6	7	4	7	6	5	4
Sieglingia decumbens	+	+	2	2	-	-	1	+	+
Zerna erecta	-	-	-	-	-	-	-	-	-
Carex caryophyllea	-	+	-	2	-	-	4	-	-
C. ericetorum	2	2	2	4	5	2	3	2	3
C. flacca	-	3	+	-	-	-	-	-	-
C. panicea	-	+	-	-	-	-	3	-	-
Luzula campestris	1	-	-	-	-	-	-	-	-
Achillea millefolium	-	-	-	-	-	-	-	-	-
Anthyllis vulneraria	-	-	4	-	-	-	-	-	+
Asperula cynanchica	-	-	-	+	-	-	-	-	-
Astragalus danicus	-	-	-	-	-	-	-	-	-
Campanula rotundifolia	1	-	2	2	1	1	-	-	-
Carlina vulgaris	-	-	2	-	-	-	-	-	-
Centaurea nigra	-	2	-	-	-	-	-	-	-
Cerastium arvense	-	-	-	-	-	-	-	-	-
Euphrasia sp.	+	-	3	1	-	-	2	-	3
Galium sterneri	-	-	+	-	+	-	-	-	-
G. verum	-	-	-	-	-	-	-	-	-
Gentianella amarella	+	-	-	-	+	+	-	-	2
Helianthemum canum	-	-	-	-	4	+	-	-	-
H. nummularium	-	3	2	-	-	-	1	2	2
Hieracium sect.Pilosella	-	-	-	2	-	-	-	-	-
Hippocrepis comosa	-	3	-	-	-	-	-	-	-
Leontodon hispidus	-	2	+	+	-	-	-	-	-
Linum catharticum	1	-	+	1	2	1	3	3	-

TABLE 3:15 continued.

List No.	1	2	3	4	5	6	7	8	9
Lotus corniculatus	-	1	4	-	-	-	-	-	-
Minuartia verna	-	-	-	-	2	1	1	1	+
Myosotis hispida	-	-	-	-	-	-	-	-	-
Plantago lanceolata	-	2	2	+	-	-	-	-	-
Polygala vulgaris	+	+	-	-	-	-	-	-	-
Potentilla erecta	-	-	+	+	-	-	-	-	-
Poterium sanguisorba	-	1	-	-	-	-	-	-	-
Prunella vulgaris	-	-	-	-	-	-	-	-	-
Ranunculus bulbosus	-	-	-	-	-	-	-	-	-
Rumex acetosella	-	-	-	-	-	-	-	-	-
Scabiosa columbaria	-	2	+	-	-	-	-	-	-
Senecio jacobaea	+	-	-	-	-	-	-	-	-
Taraxacum sp.(vegetative)	+	-	-	-	-	-	-	+	-
T. sect.Erythrosperma	-	-	-	-	-	-	-	-	-
Trifolium repens	-	-	-	-	-	-	-	-	-
Thymus drucei	6	+	1	3	2	3	3	3	2
T. serpyllum	-	-	-	-	-	-	-	-	-
Viola hirta	-	+	+	-	-	-	-	-	-
V. riviniana	-	-	-	-	-	-	1	+	-
V. rupestris	-	-	3	-	-	-	2	2	2
Acrocladium cuspidatum	-	2	-	-	-	-	-	-	-
Barbula fallax	1	-	-	-	-	-	-	-	-
Bryum pallens	-	-	-	+	1	-	-	-	-
Camptothecum lutescens	-	-	-	-	-	-	-	-	-
Ctenidium molluscum	-	+	-	4	1	2	-	1	-
Dicranum scoparium	3	-	-	1	-	-	-	-	-
Ditrichum flexicaule	-	-	-	-	1	-	-	-	1
Encalypta streptocarpa	1	-	-	-	-	-	-	-	-
Fissidens cristatus	-	1	-	-	-	-	-	1	-
Hypnum cupressiforme	2	-	+	1	+	-	-	-	-
Mnium longirostrum	-	1	-	-	-	-	-	-	-
Pleurozium schreberi	-	-	-	-	-	-	-	-	-
Pseudoscleropodium purum	-	-	-	-	-	-	-	-	-
Rhacomitrium lanuginosum	-	-	-	4	3	2	4	1	2
Rhytidium rugosum	-	+	-	+	-	-	-	-	4
Tortella tortuosa	1	-	-	+	2	1	-	3	2
Lophocolea cuspidata	-	-	-	-	-	-	-	-	-
Cladonia furcata	-	-	-	-	+	-	-	-	+
C. pyxidata	-	-	-	-	+	-	1	-	-
C. rangiferina	-	-	1	-	-	-	2	-	-
C. rangiformis	-	-	-	-	-	-	-	-	-
Cornicularia aculeata	-	-	-	-	+	-	1	-	-
Squamaria crassa	+	-	-	-	1	-	-	-	-

TABLE 3:15

Vegetation lists from British localities of
Carex ericetorum.

List No.	10	11	12	13	14	15	16	17	18
Site No.	1	3	7	8	9	10	12	13	14
Altitude (m)	110	69	31	63	15	15	15	23	31
Aspect	NW	Nil	Nil	NE	NW	Nil	Nil	Nil	NW
Slope (degrees)	15	Nil	Nil	5	5	Nil	Nil	Nil	5
Soil depth (mm)	70	110	30	150	>150	>150	>150	>150	90
Cover (%)	90	100	95	100	100	100	100	100	100
Calluna vulgaris	-	-	-	-	-	+	+	-	+
Crataegus monogyna	2	+	-	-	-	-	-	-	-
Dryas octopetala	-	-	-	-	-	-	-	-	-
Rubus vestita	-	-	-	-	-	-	-	-	-
Ulex europaea	-	2	-	-	-	-	-	-	-
Anthoxanthum odoratum	-	-	-	-	2	-	-	-	+
Brachypodium pinnatum	6	-	7	-	-	-	-	-	-
Briza media	4	-	-	-	-	1	-	-	-
Festuca ovina	8	8	5	5	4	8	5	9	8
Helictotrichon pratense	2	3	-	2	3	4	5	-	+
Koeleria cristata	1	-	1	3	3	4	4	-	2
Sesleria albicans	-	-	-	-	-	-	-	-	-
Sieglingia decumbens	-	-	-	-	-	-	-	-	-
Zerna erecta	4	5	2	7	-	-	-	-	-
Carex caryophyllea	2	+	-	+	1	-	-	-	+
C. ericetorum	2	1	5	1	2	3	2	2	4
C. flacca	2	3	-	2	-	-	-	-	-
C. panicea	2	-	-	-	+	-	-	-	-
Luzula campestris	-	-	-	-	3	+	1	+	+
Achillea millefolium	-	1	-	-	-	-	-	-	3
Anthyllis vulneraria	-	+	-	-	-	-	4	-	-
Asperula cynanchica	-	-	-	-	-	-	1	-	-
Astragalus danicus	-	-	+	+	1	-	2	-	2
Campanula rotundifolia	2	2	2	1	-	-	-	2	-
Carlina vulgaris	-	3	-	1	-	-	-	-	-
Centaurea nigra	+	-	+	-	-	-	-	-	-
Cerastium arvense	-	-	-	-	2	+	+	-	-
Euphrasia sp.	-	-	-	-	-	-	-	-	-
Galium sterneri	-	-	-	-	-	-	-	-	-
G. verum	-	-	2	-	2	3	3	3	2
Gentianella amarella	-	-	2	-	-	-	-	-	-
Helianthemum canum	-	-	-	-	-	-	-	-	-
H. nummularium	2	2	2	2	-	-	-	-	-
Hieracium sect.Pilosella	+	2	2	+	5	+	4	-	5
Hippocrepis comosa	-	-	-	3	-	-	-	-	-
Leontodon hispidus	+	2	1	2	-	-	-	-	2
Linum catharticum	2	1	2	-	+	-	1	-	1

Table 3:15 continued.

List No.	10	11	12	13	14	15	16	17	18
Lotus corniculatus	1	2	2	1	2	-	+	-	2
Minuartia verna	-	-	-	-	-	-	-	-	-
Myosotis hispida	-	-	-	-	+	1	-	-	-
Plantago lanceolata	3	1	+	-	-	3	+	-	2
Polygala vulgaris	+	-	1	-	-	-	-	-	-
Potentilla erecta	-	-	-	-	-	-	-	-	-
Poterium sanguisorba	2	-	3	2	-	-	-	-	-
Prunella vulgaris	1	-	1	-	-	-	-	-	2
Ranunculus bulbosus	+	+	-	-	-	-	-	-	-
Rumex acetosella	-	-	-	-	-	+	-	2	-
Scabiosa columbaria	+	+	+	1	-	-	-	-	-
Senecio jacobaea	-	-	-	-	1	2	+	-	1
Taraxacum sp.(vegetative)	+	+	-	-	-	-	-	-	-
T. sect.Erythrosperma	-	-	-	-	1	1	+	-	1
Trifolium repens	+	-	-	-	3	4	+	-	+
Thymus drucei	2	2	2	-	-	-	-	-	+
T. serpyllum	-	-	-	-	2	2	1	-	2
Viola hirta	-	-	-	-	-	-	-	-	-
V. riviniana	+	-	1	-	-	-	-	-	-
V. rupestris	-	-	-	-	-	-	-	-	-
Acrocladium cuspidatum	-	1	-	-	-	-	-	-	-
Barbula fallax	1	-	-	-	-	-	-	-	-
Bryum pallens	-	-	-	-	-	-	-	-	-
Camptothecum lutescens	-	-	-	1	+	-	-	-	-
Ctenidium molluscum	2	1	-	2	+	-	-	-	-
Dicranum scoparium	-	-	-	-	+	4	3	2	+
Ditrichum flexicaule	-	-	-	-	-	-	-	-	5
Encalypta streptocarpa	-	-	1	-	-	-	-	-	+
Fissidens cristatus	1	-	-	1	-	-	-	-	+
Hypnum cupressiforme	-	-	-	-	+	-	-	-	+
Mnium longirostrum	-	-	-	-	2	4	-	-	-
Pleurozium schreberi	-	-	-	-	4	3	4	6	-
Pseudoscleropodium purum	-	-	3	1	-	-	1	-	+
Rhacomitrium lanuginosum	-	-	-	-	-	-	-	-	-
Rhytidium rugosum	-	-	-	-	3	-	2	-	2
Tortella tortuosa	1	-	4	-	-	-	-	-	-
Lophocolea cuspidata	-	-	-	-	-	1	1	-	-
Cladonia furcata	-	-	-	-	-	-	-	-	-
C. pyxidata	-	-	-	-	-	-	-	-	-
C. rangiferina	-	-	-	-	-	-	-	-	-
C. rangiformis	-	-	-	-	-	3	-	-	3
Cornicularia aculeata	-	-	-	-	-	-	-	-	-
Squamaria crassa	-	-	-	-	-	-	-	-	-

Localities and additional species of low frequency.

1. Jenny Brown's Point, Lancashire. Grid ref. SD/462733 Erica cinerea.
2. Silverdale, Lancashire. Grid ref. SD/476768 Filipendula vulgaris, Fragaria vesca, Potentilla sterilis, Rhytidiadelphus squarrosus, Weissa sp.
3. Arnside Knott, Lancashire. Grid ref. SD/457744 Brachypodium sylvaticum, Helictotrichon pubescens.
4. Scout Scar, Lancashire. Grid ref. SD/487902 Festuca rubra, Orchis mascula.
5. Whitewell Green, Cronkley Fell, Yorkshire (grazed). Grid ref. NY/841282 Frullania tamarisci.
6. Whitewell Green, Cronkley Fell, Yorkshire (ungrazed). Grid ref. NY/841282.
7. Slapestone Sike, Widdybank Fell, Co. Durham. Grid ref. NY/811304.
8. Slapestone Sike, Widdybank Fell, Co. Durham. Grid ref. NY/811302 Carex capillaris.
9. Widdybank Fell, Co. Durham. Grid ref. NY/821292.
10. Markland Grips, Derbyshire. Grid ref. SK/508744 Bellis perennis, Betonica officinalis, Primula veris.
11. Lindrick Common, Nottinghamshire. Grid ref. SK/547827 Plantago media.
12. Went Valley near Kirk Smeaton, Yorkshire. Grid ref. SE/503173 Hypochaeris radicata, Potentilla tabernaemontani.
13. Devil's Ditch, near Newmarket, Cambridgeshire. Grid ref. TL/623612 Viola odorata.
14. Icklingham, Suffolk. Grid ref. TF/764734 Aphanes arvensis, Erodium cicutarium, Saxifraga granulata, Climacium dendroides, Polytrichum juniperinum, Rhodobryum roseum.
15. Foxhole Heath, Suffolk (grazed). Grid ref. TL/739775 Carex arenaria, Crepis capillaris, Erophila verna.
16. Foxhole Heath, Suffolk (ungrazed). Grid ref. TL/741776 Pinus sylvestris, Silene otites.
17. Lakenheath Warren, Suffolk. Grid ref. TF/756803 Pteridium aquilinum, Agrostis canina.
18. Grimes Graves, Norfolk. Grid ref. TF/806903 Agrostis tenuis.

Studies on the vegetation of the Breckland heaths have been made for many years by Watt and these have included investigations on the effect of rabbit grazing (Watt 1957). In Teesdale the *Sesleria* turf containing *C. ericetorum* is also heavily grazed by both sheep and rabbits and in both areas enclosures have been erected so that the effect of excluding grazing animals can be compared. Results from within a rabbit-proof enclosure erected on the grazed turf of Lakenheath Warren have shown that after a number of years, grasses particularly *Festuca ovina* become dominant at the expense of small herbaceous species and that other species such as *Carex ericetorum* which are just about able to survive in a tall sward flourish mainly in the temporary gaps produced as the *Festuca* plants die. At another enclosure on Foxhole Heath, Watt found that lichens were much more abundant in the grazed turf and several were exclusive to it.

A similar situation has been found on Cronkley Fell where two vegetation lists were made within a few yards of one another, one of grazed sugar limestone turf and one within a wire mesh enclosure erected in 1966 by the Native Conservancy. (Table 3:15, lists 5 and 6). Both *Festuca ovina* and *Sesleria albicans* have a considerably higher cover within the enclosure, while *Carex ericetorum* and *Helianthemum canum* are less abundant and lichens are considerably reduced. It therefore seems that in Britain a certain amount of grazing is necessary to check the spread of grasses and decrease competition, so that the less competitive species such as *C. ericetorum* can survive.

The heaths of East Anglia are floristically very similar to the grass heaths of northern and central Europe which have developed on sandy glacial soils. *C. ericetorum* has been recorded as a species of high constancy of such heaths in Sweden (Du Rietz 1930), Denmark (Böcher 1943), Finland (Jalas 1950), East Prussia (Steffen 1931) and Poland (Juraszek 1928). These heaths are characterised by the high proportion of continental steppe species in the flora, though as in the East Anglian heaths, the oceanic species *Calluna vulgaris* is usually present, and lichens are abundant. In Southern Sweden *Carex ericetorum* occurs mainly on morainic banks which are lightly wooded with birch and lowscrub (Sterner 1922) and in Poland too (Juraszek 1928) light pinewood covers much of the heathland. In the early Post-glacial period, light woodland probably covered most of the British localities of C. ericetorum and comparison with these continental heaths suggests that the species could have survived under similar conditions in Britain.

In the Alps, C. ericetorum is a constituent of a number of alpine meadow communities, ranging from the calcareous grasslands of the order Seslerietalia coeruleae (which are analagous to the calcareous grasslands of the northern Pennines) to the acid meadows of the order Caricetalia curvulae (Braun-Blanquet & Jenny 1926) and it is often listed amongst the species indifferent to soil pH. In south-eastern Switzerland (Braun-Blanquet & Jenny 1926, Braun-Blanquet & Rübel 1932) it is most abundant in the Elynetum, an association related to the Seslerio - semperviretum, but in situations with a slightly more acid soil. Table 3:16 shows vegetation lists for a number of sites in the French and Swiss Alps.

TABLE 3:16

Vegetation lists from Alpine localities of *Carex ericetorum*.

List No.	1	2	3	4	5	6
Site No.	C7	C12	C8	C9	C20	C10
Altitude (m)	1983	1983	1891	1891	1861	2166
Aspect	NNW	W	Nil	Nil	SW	W
Slope (degrees)	16	32	Nil	Nil	15	23
Soil depth (mm)	65	60	150	>150	100	12
Cover (%)	100	95	100	95	85	95
Daphne striata	+	-	-	-	-	+
Vaccinium uliginosum	2	-	-	+	-	-
V. vitis-idaea	1	-	-	1	-	-
Botrychium lunaria	3	2	1	-	-	3
Agrostis alpina	2	-	4	-	2	-
Anthoxanthum odoratum	-	2	-	+	-	+
Briza media	-	2	-	2	2	3
Festuca ovina	8	6	-	-	6	7
F. rubra	-	3	-	-	5	-
Helictotrichon pratense	1	-	-	2	-	1
Nardus stricta	-	-	8	8	-	-
Poa alpina	-	-	3	-	1	-
Sesleria albicans	1	4	-	-	-	1
Carex ericetorum	2	2	3	3	3	4
C. sempervirens	3	1	+	-	2	+
Achillea millefolium	1	1	1	2	-	-
Alchemilla monticola	+	1	+	-	-	-
Anemone vernalis	-	-	-	1	-	3

Table 3:16 continued.

List No.	1	2	3	4	5	6
Antennaria dioica	1	-	-	1	+	3
Anthyllis vulneraria	1	+	-	-	-	-
Campanula scheuchzeri	1	+	-	-	-	-
Cerastium arvense	-	1	2	-	1	-
Chrysanthemum alpinum	2	2	-	-	-	-
Gentiana kochiana	1	-	-	1	-	3
G. verna	+	-	4	-	-	-
Geum montanum	+	-	-	-	-	+
Helianthemum nummularium	-	3	-	2	-	-
Hieracium sect.Pilosella	-	3	2	2	-	2
Linum catharticum	-	1	-	1	-	-
Lotus corniculatus	-	2	+	1	+	-
Myosotis alpestris	-	+	-	-	+	2
Plantago lanceolata	1	-	1	-	-	3
P. maritiana	-	2	3	-	4	2
Polygala alpina	+	1	1	-	1	-
Polygonum viviparum	-	-	-	1	-	3
Potentilla aurea	2	-	2	1	-	2
P. tabernaemontani	-	+	-	-	2	-
Primula auricula	1	-	-	3	-	+
Taraxacum sp.	-	-	1	-	1	-
Thesium alpinum	-	1	-	+	-	-
Thymus drucei	-	2	1	-	+	-
Trifolium alpinum	-	-	-	2	4	+
T. repens	2	2	3	2	-	2
Viola calcarata	+	-	-	-	1	-
Polytrichum alpinum	1	-	-	-	-	2
Thuidium abietinum	-	+	9	-	-	-
Tortella tortuosa	1	1	-	-	-	-
Cetraria islandica	1	-	-	-	1	1
Peltigera polydactyla	2	-	-	-	-	1
P. rufescens	-	-	1	-	4	-

Localities and additional species of low frequency.

1. Alpine pasture, Julier Pass, Albula, Switzerland. *Selaginella selaginoides*, *Carex ornithopoda*, *Leontodon hispidus*, *Primula farinosa*, *Soldanella alpina*.

2. Mountainside north-east of Pontresina, Engadin, Switzerland. *Astragalus aristatus*, *Hippocrepis comosa*, *Potentilla sterilis*, *Saussurea alpina*, *Sempervivum tectorum*, *Camptothecium lutescens*, *Ditrichum flexicaule*, *Cladonia fimbriata*.

3. Alpine pasture, Val Roseg, Engadin, Switzerland. *Galium verum*, *Gentianella campestris*.

4. Edge of larch wood, Val Roseg, Engadin, Switzerland. *Calluna vulgaris*, *Koeleria cristata*, *Euphrasia sp.*, *Bryum caespiticium*.

5. Alpine pasture, Col du Lautaret, Hautes Alpes, France. *Achillea nana*, *Alchemilla alpina*, *Androsace carnea*, *Cardamine resedifolia*, *Draba aizoides*, *Minuartia verna*, *Ranunculus pyrenaeus*, *Sempervivum arachnoideum*, *Vitaliana primuliflora*, *Rhytidiadelphus triquetrus*.

6. Alpine pasture near Piz Lagalb, Bernina Pass, Ober Engadin, Switzerland. *Luzula spicata*, *Ajuga pyramidalis*, *Pedicularis verticillata*, *Brachythecium velutinum*, *Bryum pallens*, *Squamaria crassa*.

In the Pyrenees *C. ericetorum* grows in another community, the Elynetum - Oxytropidetum foucaudi related to the Elynetum of the Swiss Alps, but it is more common in dry acid communities developed on siliceous rocks dominated by *Festuca supina* and *Hieracium* pumilum (Braun-Blanquet 1948).

In the mountains of southern Norway, *C. ericetorum* is much less common than in the Alps and Pyrenees, but here too it grows on acid soils in a community dominated by *Nardus stricta* and *Agrostis tenuis* (Nordhagen 1943).

The analyses of soils from *C. ericetorum* sites are shown in Tables 3:17 and 3:18. In general, results correspond with those of the vegetation survey. British samples from the northern Pennines and East Midlands are highly calcareous, and those from the East Anglian heaths are less calcareous to strongly acid. The heath soils are also very sandy and in physical characteristics are similar to the soils of Upper Teesdale, where the "sand" is composed of particles of "sugar" limestone. Several samples have a high exchangeable magnesium content, particularly those from the Permian limestone, and also the samples from Arnside Knott, Lancashire where the limestone is highly dolomitised.

Samples from Alpine sites are less calcareous than most of the British samples and have a much lower pH. Several workers have remarked that C. ericetorum is indifferent to the chemical content of the soil and Jalas (1952) has shown that in some regions it behaves as a calcifuge while in others it behaves as a calcicole. In general it seems to be present more frequently on acid soils in central Europe and on calcareous soils in north-west Europe, and is another example of a continental European species (cf. Hippocrepis comosa) which is restricted to calcareous soils at the north-western boundary of its geographical range.

TABLE 3:17

Analysis of soil samples from British localities of *Carex ericetorum*.

Sample No.	pH	% of total						M.eq./100 gm. air-dried soil			
		CO_3	Organic Matter	Coarse Sand	Fine Sand	Silt	Clay	K	Ca	Mg	Pb
8	7.3	-	-	-	-	-	-	0.24	103.13	0.79	0
10	6.1	0.6	3.5	49.8	18.2	0.4	2.9	0.17	4.70	0.10	0
13	3.7	-	-	-	-	-	-	0.15	2.50	0.94	0
14	7.3	2.1	2.2	59.1	18.4	3.4	2.7	0.19	21.88	0.08	0
7	7.2	-	-	-	-	-	-	0.37	42.50	10.42	0.10
1	7.3	52.3	13.2	8.9	9.8	4.7	8.0	0.59	32.50	15.63	0
17	6.6	-	-	-	-	-	-	0.83	51.88	2.98	0.10
18	7.4	-	-	-	-	-	-	0.90	51.88	23.13	0
21	7.1	80.0	12.4	2.3	6.3	1.3	2.2	0.39	103.13	1.04	0.13
87	7.5	91.1	3.2	2.5	0.4	0.9	4.2	0.13	71.25	0.69	0.11
*87	-	-	-	94.0	0.4	-	4.7				

* without removal of CO_3

Sample No.	Locality.
8	Devil's Ditch, Cambridgeshire.
10	Foxhole Heath, Suffolk.
13	Lakenheath Warren, Suffolk.
14	Grimes Graves, Norfolk.
7	Kirk Smeaton, Yorkshire.
1	Markland Grips, Derbyshire.
17	Silverdale, Lancashire.
18	Arnside Knott, Lancashire.
21	Cronkley Fell, Yorkshire.
87	Widdybank Fell, Co. Durham.

TABLE 3:18

Analysis of soil samples from French and Swiss localities of <u>Carex ericetorum</u>.

Sample No.	pH	% of total		M.eq./100 gm.air-dried soi		
		CO_3	Organic Matter	K	Ca	Mg
C7	5.2	1.6	21.8	0.20	24.38	7.77
C8	6.3	-	-	0.17	46.25	3.65
C9	5.0	1.8	18.2	0.38	21.25	2.71
C10	4.8	-	-	0.40	13.75	3.13
C12	5.8	-	-	0.85	23.75	8.85
C20	4.8	1.1	18.5	0.63	22.50	4.17

Sample No.	Locality
C7	Julier Pass, Albula, Switzerland.
C8	Val Roseg, Engadin, Switzerland.
C9	Val Roseg, Engadin, Switzerland.
C10	Bernina Pass, Ober Engadin, Switzerland.
C12	Pontresina Engadin, Switzerland.
C20	Col du Lautaret, Hautes Alpes, France.

Carex paupercula.

Carex paupercula is a rather uncommon species of oligotrophic mires. It generally occurs in Britain in the Sphagnum-filled hollows and channels between hummocks of *Calluna vulgaris* and *Erica tetralix* in complexes of mire and bog similar to those described by McVean & Ratcliffe (1962) on Rannock Moor and by Ratcliffe & Walker (1958) at the Silver Flowe, Kirkcudbrightshire. Though my vegetation lists only cover four sites (Table 3:19), in three of these *C. paupercula* occupies a marginal habitat on the edge of such a channel where it is embedded in a deep carpet of *Sphagnum papillosum*, avoiding the wettest parts which are occupied by different *Sphagnum* species. Fig. 3:4 shows the marginal situation of *C. paupercula* along a channel in The Weel, Cow Green, Teesdale.

All sites are very poor in species, though the one near Tyndrum has slightly more and all the species are characteristic of acid habitats. These associations show most affinity with the Scottish sub-alpine Sphagnum - Carex mire described by McVean & Ratcliffe (1962).

TABLE 3:19

Floristic lists from British localities of *Carex paupercula* (all species listed)

List No.	1	2	3	4
Site No.	52	53	68	72
Altitude (m)	487	487	221	297
Aspect	Nil	Nil	Nil	Nil
Slope	Nil	Nil	Nil	Nil
Cover (%)	100	100	100	100
Depth of Sphagnum (mm)	>300	>300	>300	>300
Calluna vulgaris	+	-	-	1
Empetrum nigrum	-	3	-	2
Myrica gale	-	-	1	-
Vaccinium oxycoccos	-	-	-	+
Equisetum palustre	-	-	+	-
Molinia coerulea	-	-	2	-
Carex echinata	-	-	3	1
C. pauciflora	-	-	3	-
C. paupercula	4	8	3	5
Eriophorum angustifolium	1	+	-	1
E. vaginatum	8	5	3	-
Narthecium ossifragum	3	-	2	-
Drosera rotundifolia	-	-	1	+
Menyanthes trifoliata	-	-	2	-
Polytrichum commune	-	-	-	1
Sphagnum acutifolium	-	-	-	5
S. papillosum	8	7	9	5
S. rubellum	4	-	-	-

Localities

1. The Weel, Cow Green, Westmorland. Grid ref. NY/811298.
2. The Weel, Cow Green, Westmorland. Grid ref. NY/811298.
3. Cononish River, Tyndrum, Perthshire. Grid ref. NN/330287.
4. Glengavel, Ayr - Lanark border. Grid ref. NS/682326.

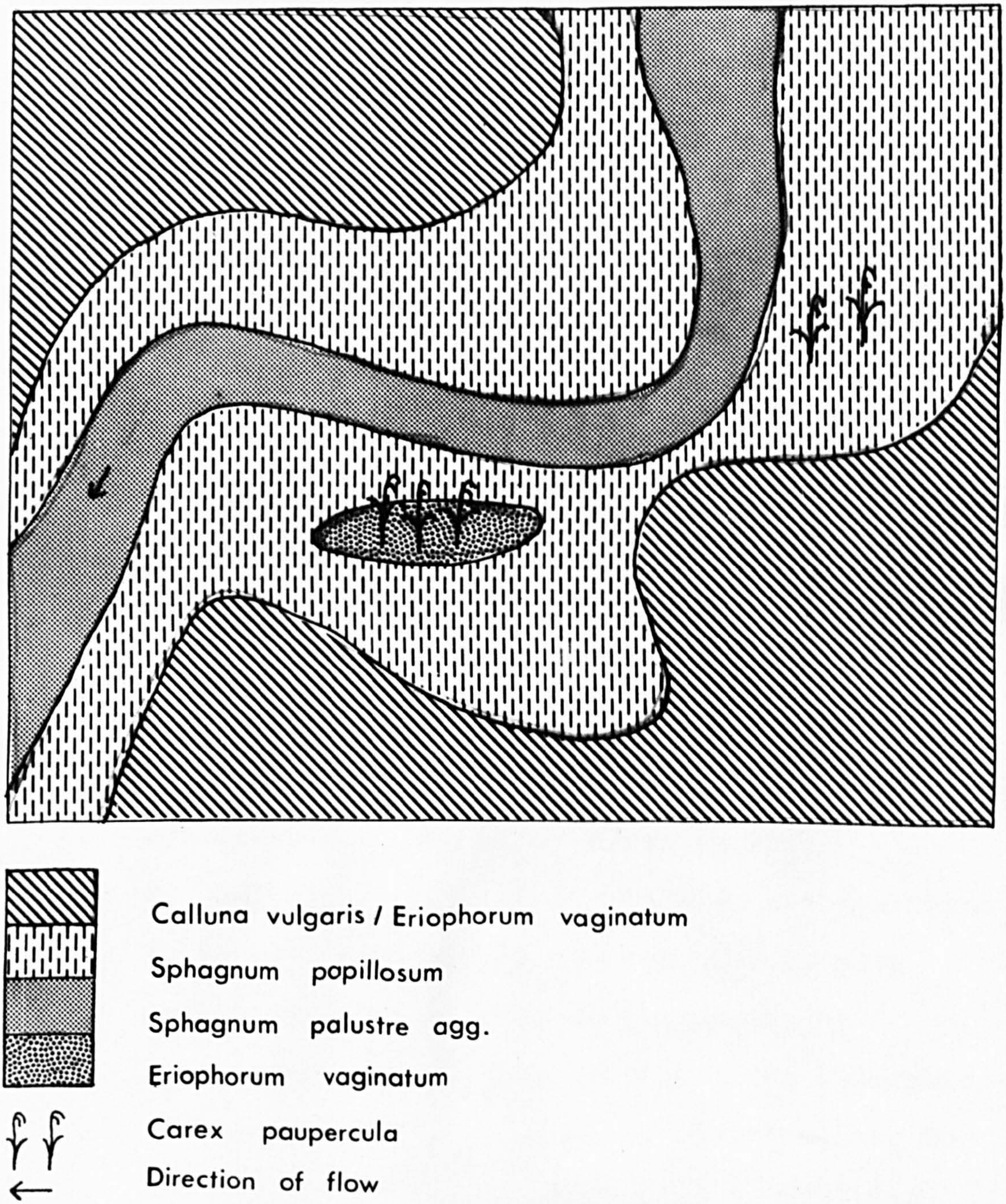


Fig. 3:4 Diagrammatic representation of the habitat of Carex paupercula in Teesdale.

In Scandinavia, *C. paupercula* occurs in similar habitats, but with the northern species *Sphagnum lindbergii* replacing *S. papillosum*. Nordhagen (1943) mentions its occurrence (as *C. magellanica*) in eutrophic - mesotrophic and mesotrophic - oligotrophic mires in Sikilsdalen, though it is slightly more common in the latter group, particularly where it is in association with *Sphagnum lindbergii* (dominant), *Andromeda polifolia* and *Eriophorum polystachyum*. In Rondane, Dahl (1956) has also found *C. paupercula* as a constituent of the Sphagnetum lindbergii association with a pH range of 4.0 - 5.4, and in Sylene, Nordhagen (1928) recognises a separate *C. paupercula* - rich facies of this association. The other mires in which *C. paupercula* grows in Sikilsdalen are dominated by sedges, and *Sphagna* are replaced by more mesotrophic mosses such as *Drepanocladus intermedius* and *D. exannulatus*. The eutrophic - mesotrophic mires in which it occurs belong to the alliance Caricion atrofuscae - saxatilis and the mesotrophic - oligotrophic communities belong to the alliance Caricion canescentis - goodenowii

In the Alps, C. paupercula is a characteristic species of a group of acid peat bogs, particularly those dominated by C. fusca (syn. C. goodenowii) and Eriophorum scheuchzeri (Braun-Blanquet & Rübel 1932), this type of community being analogous with the Caricion canescentis - goodenowii of Scandinavia. The Sphagnum-rich communities with C. paupercula are however absent from the Alps.

Notes accompanying herbarium specimens of C. paupercula from North America suggest that there too it grows in Sphagnum-dominated communities similar to those in Britain and Scandinavia.

The South American species C. magellanica which is very closely related to C. paupercula also grows in acid Sphagnum bogs (pH 4.0 - 4.8) in Tierra del Fuego, here dominated by S. magellanicum (Rovainen 1954) and seems very similar in ecology to its northern relative.

Alopecurus alpinus.

Alopecurus alpinus is a very local species in Britain, found in high altitude springs and flushes (Plate 3:4). Most of these are at above 850 m. on the upper slopes of mountains, often in hollows where the snow lies late. They are dominated by bryophytes, particularly of the genus Philonotis, these giving a bright green colour to the vegetation which can thus be recognised from a distance. Agrostis stolonifera, Montia fontana and Saxifraga stellaris are some of the commonly associated higher plant species. McVean & Ratcliffe (1962) have described similar bryophyte flushes in Scotland and suggest that they belong to the Philonoto - Saxifragetum stellaris association. The majority of these flushes are oligotrophic, but Ratcliffe & Eddy (1960) state that A. alpinus also occurs in more eutrophic sites. The vegetation of the sites on Little Dun Fell and on Cross Fell is similar to that of the richer Scottish flushes (Ratcliffe & Eddy 1960) and includes a number of calcicolous species eg. Sedum villosum, Cratoneuron commutatum and Philonotis calcarea. Ratcliffe & Eddy (1960) also record that A. alpinus occasionally grows in stands of Carex saxatilis and on wet rock ledges.

Plate 3:4 *Alopecurus alpinus* growing in a high altitude *Philonotis* flush on Glas Maol, Angus.

A. alpinus is absent from Scandinavia and the Alps but is a common and widespread species in coastal areas within the Arctic circle where it grows in wet tundra and by brooks and lake shores. It is a strongly nitrophilous species and forms a lush sward on manured ground around human habitations and under cliffs where seabirds nest (Porsild, 1957).

The related species *A. antarcticus* grows in similar damp habitats at high latitudes in the Southern hemisphere.

TABLE 3:20

Floristic lists from British localities of
Alopecurus alpinus (all species listed)

List No.	1	2	3
Site No.	84	85	71
Altitude (m)	808	808	938
Aspect	NE	NE	S
Slope (degrees)	7	7	12
Soil depth (mm)	150	150	80
Cover (%)	100	100	60
Equisetum palustre	2	-	-
Agrostis stolonifera	8	4	1
Alopecurus alpinus	2	2	2
Deschampsia caespitosa	-	+	2
Helictotrichon pratense	-	+	-
Carex bigelowii	-	-	1
C. curta	-	-	1
C. nigra	2	3	-
Eriophorum latifolium	3	-	-
Juncus triglumis	3	-	-
Triglochin palustris	+	3	-
Cardamine pratensis	2	2	-
Epilobium anagallidifolium	-	-	1
E. palustre	+	2	-
Montia fontana	-	+	2
Saxifraga stellaris	1	3	-
Sedum villosum	+	-	-
Bryum pseudotriquetrum	-	2	-
Cratoneuron commutatum	2	1	-
Dicranella squarrosa	-	2	-
Drepanocladus exannulatus	-	2	-
D. fluitans	-	-	4
Fissidens adianthoides	1	-	-
Hylocomium splendens	+	-	-
Mnium punctatum	1	-	-
Philonotis calcarea	-	3	-
P. fontana	-	-	6
Polytrichum commune	-	-	2
Aneura multifida	+	-	2
Nardia scalaris	-	1	-
Scapania undulata			

Localities

1. Little Dun Fell, Westmorland.
   Grid ref. NY/705332.
2. Little Dun Fell, Westmorland.
   Grid ref. NY/705332.
3. Glas Maol, Angus.
   Grid ref. NO/163761.

Only two soil samples were available for comparison, one from Little Dun Fell, Teesdale and one from Glas Maol, Angus. Both samples are dark peaty muds, but the Teesdale sample is considerably more base-rich than the Scottish sample. It contains four times as much exchangeable calcium and has a higher pH, though both samples are acid. From the geology of other localities where A. alpinus is said to grow, it is probable that the majority of sites have a rather acid soil, but Ratcliffe & Eddy (1960) have discovered A. alpinus in another mesotrophic flush on Cross Fell in the Pennines, and the species is probably indifferent to the base status of the soil in which it grows.

TABLE 3:21

Analysis of soil samples from British localities of Alopecurus alpinus.

Sample No.	pH	M.eq./100 gm.air-dried soil			
		K	Ca	Mg	Pb
84	6.2	0.33	34.38	3.13	0.10
71	4.8	-	8.75	2.29	0.16

Sample No.	Locality
84	Little Dun Fell, Moorhouse N.N.R., Westmorland.
71	Glas Maol, Angus.

Chapter 4.

Detailed studies of individual species.

PART I

Draba incana L.

Description

Sect. DRABAEA Lindm., Group HOLARGES D.C.

Biennial or sometimes perennial canescent herb with slender taproot; erect usually solitary simple or branched leafy stem elongating up to 35 cm. in the second year. Basal leaves in a loose rosette, sessile, lanceolate, up to 2.5 cm., entire or distantly toothed, densely covered with simple or stellately branched hairs, rarely almost glabrous; cauline leaves sessile, lanceolate-ovate, up to 1.5 cm., densely pubescent, rarely almost glabrous, their margins usually coarsely toothed. Stem and inflorescence branches covered with simple or stellately branched hairs. Inflorescence dense, elongating greatly in fruit, 8 - 40 flowered. Petals 2 - 4 mm., white, twice as long as sepals. Siliculae glabrous or pubescent with short stellately-branched hairs, oblong-lanceolate, 7 - 11 mm., often twisted when ripe, held erect on pedicels 2 - 9 mm. long. Style 0.1 - 0.7 mm. Seeds numerous, oval, orange-brown, approximately 1 mm. long.

General biology

Germination probably takes place mainly in spring and in the first year a vegetative rosette is formed. In the second year, i.e. after a cold period, a terminal inflorescence begins to develop in March. Flowering takes place on the main axes in May and June, but may continue throughout the summer on lateral branches. After flowering the main axis dies, but the plant may continue growth by the formation of lateral rosettes, which arise from the short stock near the base of the old rosette.

The flowers are small, white and homogamous. They have no special adaptations to attract insect pollen vectors and it is probable that most flowers are self-pollinated. The filaments of the stamens curve around the ovary so that the anthers are in close proximity to the stigma. When the flower opens the pollen is automatically transferred to the papillate stigmatic surface. Undisturbed plants set a high percentage of viable seed in an insect-proof greenhouse, showing that they are fully self-compatible. From these observations it therefore seems likely that *D. incana* is almost wholly inbreeding. Riley (1956) was able to show that even in Thlaspi alpestre, another morphologically similar though protogynous cruciferous species, only about 5% outbreeding occurs.

In order to determine percent outbreeding in D. incana an experiment has been set up in the Sheffield experimental garden. A central plant possessing the dominant marker character of pubescent siliculae was surrounded by 21 plants from a population with glabrous siliculae, the whole experiment covering an area of approximately 1,500 sq. cm. It is hoped that the marker gene from the central plant will appear in the progeny of the surrounding plants, but due to the biennial habit of the species, the results of this are not yet available.

Seed is produced abundantly from either selfed plants, or plants which have been artificially cross-pollinated after emasculation. There are up to 30 seeds per capsule and as a single plant may produce up to 40 capsules, the potential number of offspring is therefore around 1,200, though the number which survive to maturity is far less than this. The species is, however, well adapted by these features to rapidly colonise an area which is favourable to it.

When the capsules are ripe, stresses in the walls are built up presumably due to the differential drying out of the tissues and the capsules often become twisted and split open into the two valves. This is not a very efficient seed-dispersal mechanism as many seeds remain attached to the central septum and only gradually drop or are blown off. Seedlings have not been observed more than one metre away from their parents. By the time the seeds are ripe, the parent plants are dead, dry and light and it is probable that wind dispersal of whole detached plants is an additional method of seed dispersal.

Germination of seeds in Petri dishes in the laboratory is very variable and few conclusions can be drawn from the results. No cold period is necessary before germination can take place and seed will germinate as soon as it has been shed. In the field, germination in summer is probably prevented by the lack of sufficient moisture in the very dry, well-drained stony soils in which the species grows. From the limited results available it seems that light is necessary for germination. Germination is epigeal.

Variation

This species shows a large amount of inter-population variation, particularly with regard to height (of fruiting specimens) and pubescence of the leaves and siliculae. The pattern of variation is sharply discontinuous and is similar to that of many inbreeding species e.g. Capsella bursa-pastoris.

Height is very variable, some populations containing plants up to 20 cm. in the field, while other populations contain only dwarf plants, less than 3 cm. high in the field (See Table 4:1). Teesdale plants are dwarf and have been called var. nana Lindbl. in the past, but they are no smaller than plants from some of the other populations in the northern Pennines. Plants from Miller's Dale, Derbyshire are particularly tall, but examination of British herbarium material shows that other populations also include large forms. These height differences are maintained in cultivation.

TABLE 4:1

Variation in height of fruiting specimens of *D. incana*.

Population	Vice-county	Height in field (cm.)		Height after 1 year in cultivation (cm.)	
		Mean	Range	Mean	Range
Creag an Lochan	88	-	-	19.3	18.0 - 20.5
Widdybank Fell	66	4.6	3.7 - 6.0	9.3	7.5 - 12.0
Green Castle	69	-	-	4.5	2.5 - 6.0
Askrigg	65	3.8	3.0 - 4.5	3.5	3.0 - 4.5
Millers Dale	57	19.4	10.5 - 29.0	34.2	10.0 - 51.0

Both rosette and cauline leaves of plants from nearly all populations are densely pubescent, giving the species its English name, "Hoary Whitlow Grass". The type of pubescence is variable, individual hairs being simple, branched or stellate, stellate hairs being defined as having three or more branches. Different types of hairs are usually found on the upper and lower surfaces of both rosette and cauline leaves. The majority of British populations have simple hairs on the upper surface and stellate (or a mixture of stellate and simple) hairs on the lower surface. (See Table 4:2 and Plates 4:1 and 4:2). Population samples from Widdybank and Cronkley Fells, however, have a proportion of stellate hairs on both surfaces of the leaves (Plates 4:3 and 4:4). These two populations are the only British field samples to possess this pattern of variation, though two similar herbarium specimens from Ben Lawers have been found. Each population appears to be uniform with respect to the type of pubescence though plants from Derbyshire can be either glabrous or have simple hairs on the upper surfaces of the leaves. The presence of stellate hairs on the upper surface of the leaves is a dominant

TABLE 4:2

Variation in type of pubescence in British population samples of D. incana.

Population	Vice-county	Leaves		Siliculae
		Upper surface	Lower surface	
Creag an Lochan	88	simple	stellate	glabrous
Widdybank Fell	66	mixed	stellate	glabrous
Cronkley Fell	65	mixed	stellate	glabrous
Green Castle	69	simple	stellate	stellate
Askrigg	65	simple	mixed	stellate
Arnber Scar G.R. SD/937704	64	simple	stellate	-
Millers Dale	57	simple or glabrous	stellate	glabrous

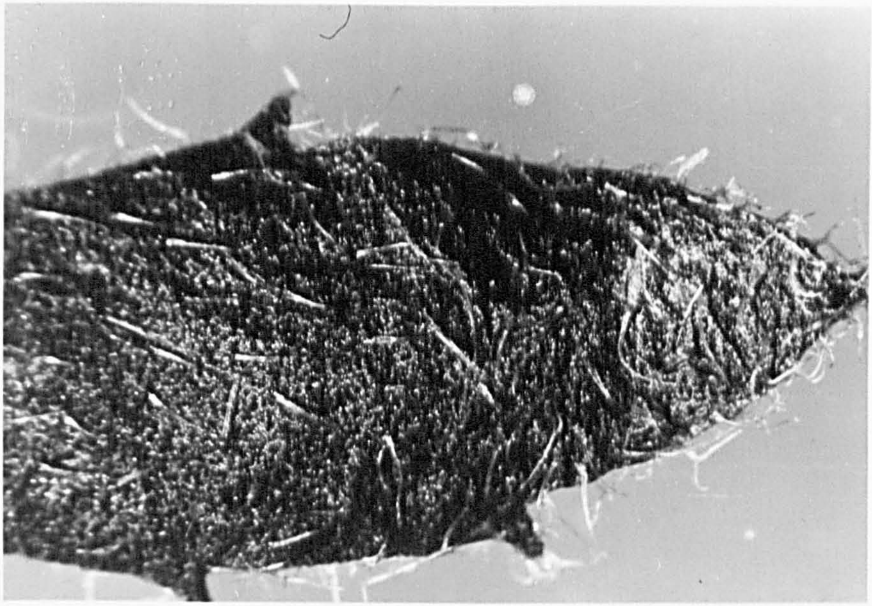


Plate 4: 1 Upper surface of Draba incana leaf from Arnber Scar with simple hairs.

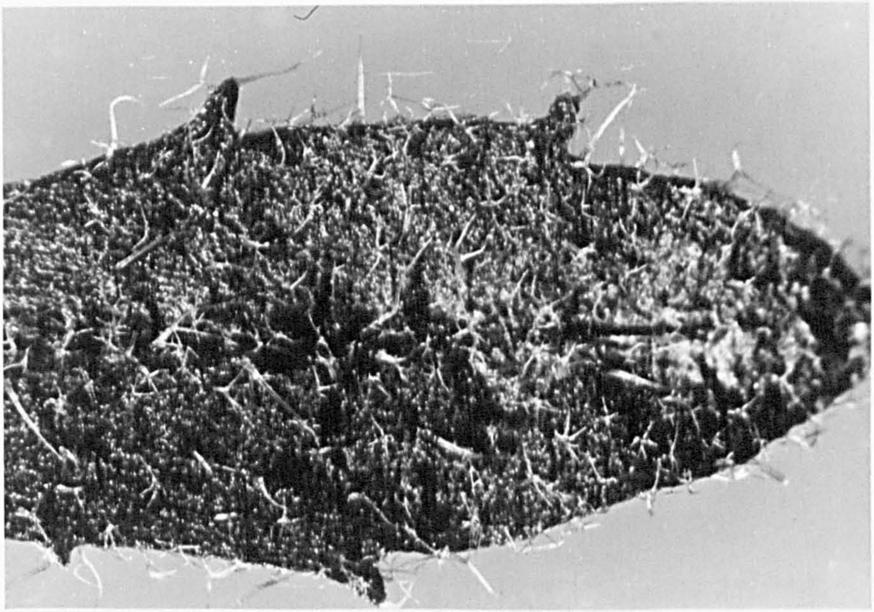


Plate 4:2 Lower surface of same leaf with stellate hairs.

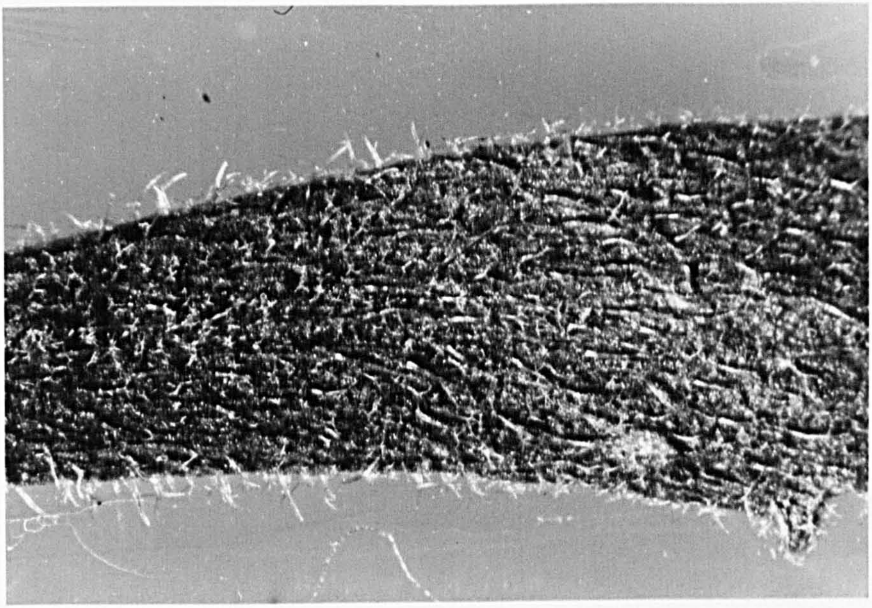


Plate 4:3 Upper surface of Draba incana leaf from Cronkley Fell, Teesdale with mixed simple and stellate hairs.

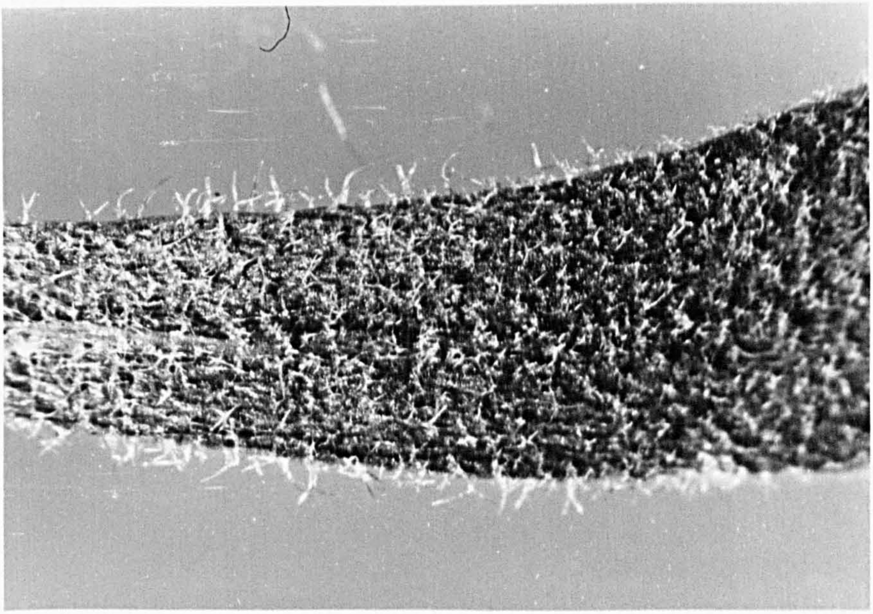


Plate 4:4 Lower surface of same leaf with stellate hairs.

character and appears in the F_1 hybrid when the stellately hairy plant is used as the pollen parent. The F_2 generation is not unfortunately available.

Continental European populations are also variable for this character. Herbarium specimens of plants from the Alps, Pyrenees and Scandinavia have been examined. All plants from the Pyrenees have only simple hairs on the upper surfaces of the leaves, while the majority of plants from the Alps have a dense covering of stellate hairs on both surfaces of the leaves and in this respect are similar to the British populations from Teesdale. (Plates 4:5 and 4:6) In Scandinavia, the situation is similar to that in Britain and only a low percentage of plants have stellate hairs on both sides of the leaves.

Some populations of D. incana consist wholly of plants with stellate hairs on the siliculae whilst in others all plants have glabrous siliculae. No plants have been found, either in the field or as herbarium material with simple hairs on the siliculae. In Britain only about 7% of the herbarium specimens examined have pubescent siliculae. Two of

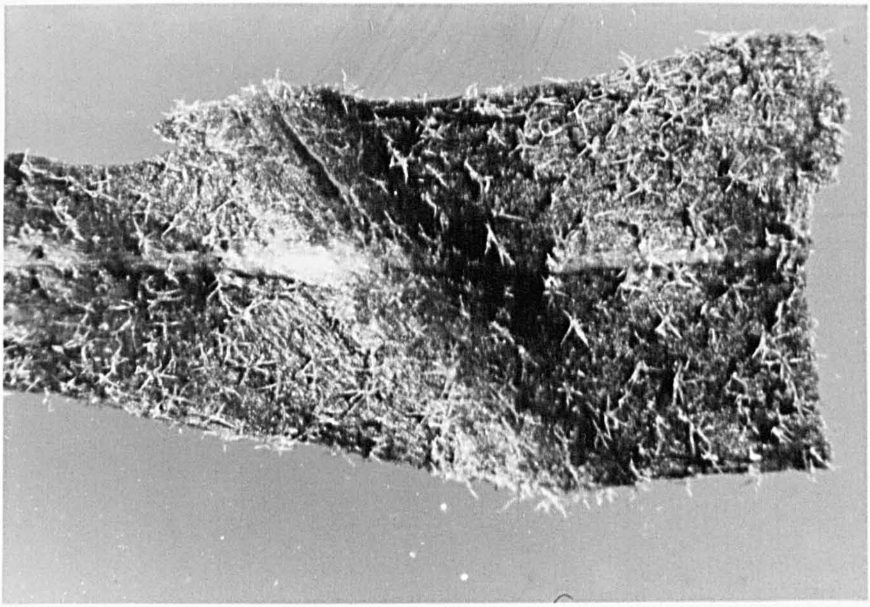


Plate 4:5 Upper surface of Draba incana leaf from Zermatt, Switzerland with stellate hairs.

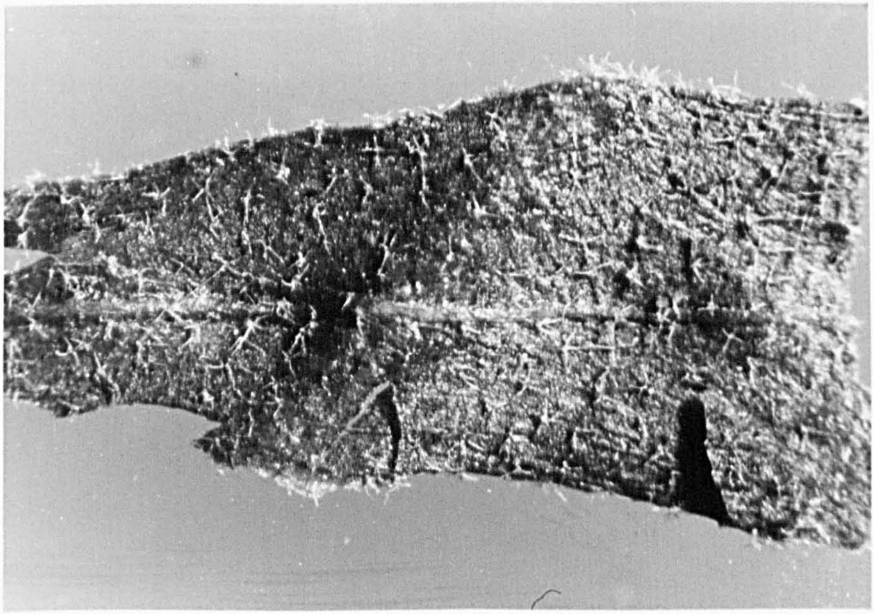


Plate 4:6 Lower surface of same leaf with stellate hairs.

the population samples collected from the northern Pennines, however, (See Table 4:2) have this character. It therefore seems that the form with pubescent siliculae may be more common in Britain than at first appeared. Crossing experiments carried out using a plant with pubescent siliculae as the female parent gave a generation of F_1 hybrids all with pubescent siliculae. This character is therefore dominant and is probably due to a single gene though the results of segregation in the F_2 generation are not yet available.

In parts of Continental Europe, a very high proportion of herbarium specimens of this species possess pubescent siliculae: in the Alps 82.9% and in Scandinavia 42.0%, though herbarium material from the Pyrenees has only glabrous siliculae. In the Alps, the presence of pubescent siliculae is correlated with the presence of stellate hairs on both surfaces of the leaves, plants with glabrous fruits only having simple hairs on the upper surfaces of the leaves. In Britain and Scandinavia there is no general correlation of this type, though the small proportion of Scandinavian plants which have stellate hairs on both leaf surfaces also have pubescent siliculae. (See Table 4:3)

Style length is also variable in D. incana. Style length of herbarium material was measured with a modified eyepiece micrometer under a low power stereo-microscope. It was found that the style length of British populations is less variable than that of Alpine or Scandinavian material. The majority of Alpine plants have longer stylesthan either British or Scandinavian plants which have a similar range of style length. In neither Britain nor Scandinavia is style length correlated with the presence of pubescent siliculae, but in the Alps, plants with pubescent siliculae in general have longer styles than those with glabrous siliculae which all have short styles. (See Fig. 4:1)

Taxonomy

The complex pattern of variation in this species is reflected in its complex taxonomy. The race commonly called D. incana L. or D. incana L. var. incana is the glabrous-fruited form found in Europe and N.E. Canada. The north-European and north American form with pubescent

TABLE 4:3

Variation of selected characters in herbarium material of *D. incana*.

	Britain	Alps	Pyrenees	Scandinavia
No. of plants examined	56	52	9	50
Mean style length (mm)	0.352	0.477	0.489	0.318
% plants with pubescent siliculae	7.1	82.9	0	42.0
% plants with stellate hairs on both leaf surfaces	17.9	82.9	0	8.0
% plants with pubescent siliculae and stellate hairs on both leaf surfaces	0	82.9	0	8.0
% plants with stellate hairs only on undersides of leaves	82.1	17.1	100	92.0

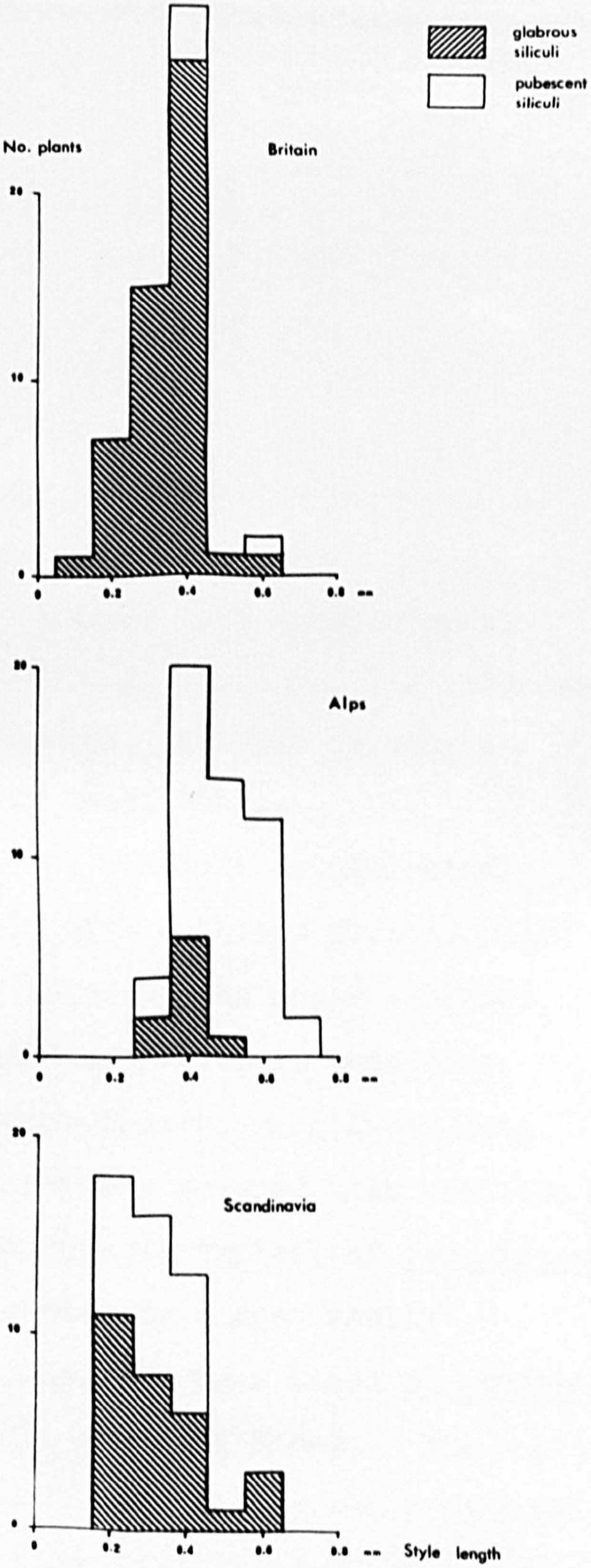


Fig. 4:1 Variation in style length and capsule pubescence in samples of <u>Draba incana</u> L. from three regions of Europe.

fruits has been distinguished as var. *confusa* (Ehrh.) Liljeblad. Until now, no taxonomist has noted the interpopulational variation in the pattern of leaf pubescence and it is usually simply referred to as "variable". The Teesdale form is distinct, being the only European population to possess the combination of glabrous fruits together with a proportion of stellate hairs on both surfaces of the leaves though there is possibly another such population on Ben Lawers. Teesdale plants have been referred to as *var. nana* Lindbl., but this is only a reflection of their dwarf habit.

In the Alps, two distinct morphological variants occur, one with glabrous fruits, short styles and simple hairs on the upper surfaces of the leaves, the other which is much more common with pubescent fruits, relatively long styles and leaves densely covered with stellate hairs. The first form is typical of *var. incana* while the second, which is almost wholly restricted to the Alps has been named *D. stylaris* Gay ex Koch (syn. *D. thomasii* Koch). The small proportion of Scandinavian plants which possess pubescent capsules and stellately-hairy leaves could also be referred to *D. stylaris*.

There is a great deal of confusion between the stellately-hairy Arctic species D. cinerea Adams and D. incana in Scandinavia where forms of both species are morphologically very similar. D. cinerea, is a hexaploid and both the pubescent and glabrous-fruited forms of D. incana are tetraploid. There may however be hybridisation where the two species are sympatric, but this can only be determined by cytological studies.

Another species closely related to D. incana is D. lanceolata Royle which is a perennial with rather narrow siliculae. Forms of this species occur in north America and in the mountains of central Asia. It is sympatric with D. incana in southern Greenland and the two species which are both tetraploid are reported to have hybridised there (Böcher 1966).

PART II

Polygala amarella Crantz

Description

Section Orthopolygala Chodat

Subsection Europaeae Chodat

Series Vulgares Chodat

Perennial herb 2-5 cm. Flowering stems solitary or numerous, usually unbranched, arising from the centre of a basal rosette. Leaves glabrous, fleshy, bitter. Basal leaves 5-25 mm., obovate ; obtuse or subacute. Cauline leaves 5-25 mm., lanceolate; acute, subacute or obtuse, widest near apex. Inflorescence a raceme with 7-25 blue, pink, white or lilac flowers. Inner (wing) sepals elliptic, enlarging to 3.2-5.0 (-5.4) mm. in fruit, with three rarely branched veins. Corolla 2-4 mm., not or scarcely articulated; crest of keel with 4-15 lobes. Capsule compressed, up to 4.4 mm., obovate to orbicular, almost as long as, but wider than the inner sepals. Seeds 1.8-2.4 mm., black, pubescent, with a white 3-lobed aril approximately one quarter of the length of the seed.

General biology

Seeds germinated in Petri dishes in early spring and transplanted to pots of garden soil kept outside develop into small rosettes which produce racemes of flowers the following June. Flowering has usually been completed by the middle of August. The structure of the flowers is such that self pollination probably occurs automatically in the majority of cases. The ovary possesses a short curved style and a lobed concave stigma which is enclosed within the keel of the corolla. The epipetalous stamens have very short filaments which are attached to the sides of the keel directly above the position of the stigma. The flowers are homogamous and when the anthers dehisce by means of an apical pore, pollen is shed on to the stigma where pollen tubes germinate, and the flowers are self-fertile. Venkatesh (1956) has observed similar features in Indian species of the genus and found no evidence of outcrossing in those species. In natural populations of P. amarella there is evidence that at least some outcrossing takes place. Occasionally, blue flowered and white flowered forms can be found growing together in the same population. Amongst these, a small proportion of pale blue or white flowered forms tinged with blue occur, indicating that crossing has taken place between the two colour forms. Insect visitors have not been observed, but it is possible that small flies effect cross-pollination. In the laboratory, blue flowered plants with acute leaf apices from Grassington in Yorkshire were crossed with a white flowered plant with obtuse leaf apices from Kent, but all the progeny of the Grassington plants were completely maternal for these characters. Seed of the reciprocal cross failed to germinate.

Seeds are ripe by late July or August and two seeds are usually present in each capsule. The capsule becomes dry and papery as it matures and finally splits at the edges. In the field there is considerable variation in the fertility of different populations. In 1968 and 1969 for example, less seed could be collected from the population on Dib Scar, where many of the flowers drop off before mature capsules are produced, than from the population on Mastiles Lane in the same area. Notes accompanying herbarium specimens from Dib Scar also state that the species seldom fruits there, though plants grown from seed in the experimental garden produced several capsules. The low number of seeds per capsule means that even under optimum conditions a plant with three racemes and 25 flowers in each will only produce 150 seeds, compared with an estimated number of 1,200 for Draba incana. In Britain optimum conditions for growth rarely occur. The flowers at the top of the raceme do not usually produce mature seed and the majority of plants from populations in Kent and Teesdale often produce only a single raceme per plant. As reproduction is wholly by seed the reproductive capacity of the species in Britain is therefore rather low. In continental Europe plants are often much larger and may produce 50 or more racemes per plant and therefore have a much higher reproductive capacity. When transplanted to the experimental garden at Sheffield, the number of racemes produced by continental plants was reduced to 2 or 3 after a year, indicating that these differences are not genetically controlled.

The seeds are black and pubescent with a short white aril. This aril does not appear to aid in seed dispersal as in natural populations the majority of seedlings occur within 5 cm of the parent. No chilling is necessary before germination can take place and the seeds will germinate as soon as they are shed. In Autumn, the pots in the experimental garden containing plants of this species are filled with young seedlings, but few of them develop beyond the cotyledon stage or survive the winter.

Seeds collected in August 1968 and stored dry in the laboratory were germinated in March 1969. There were considerable differences in the germination of seed collected from different populations, as shown in Table 4:4. Seeds from the Mastiles Lane population were the fastest to germinate, those from Dib Scar were the slowest and Teesdale seed was intermediate. Seedlings will only grow in a well-drained soil containing lime, though they are also highly susceptible to drought. In the absence of lime, the majority of seedlings do not develop beyond the cotyledon stage. In good conditions a small rosette forms after a few weeks.

TABLE 4:4

% Germination of *P. amarella* seed collected from different populations. Seed sown on damp filter paper in Petri dishes on the laboratory window ledge.

Population	Days after sowing.							
	0	8	13	14	15	17	20	28
Mastiles Lane	0	64.7	100	100	100	100	100	100
Dib Scar	0	0	0	0	5.6	5.6	22.2	38.9
Widdybank Fell	0	0	7.7	15.4	23.1	30.8	76.9	76.9
Cronkley Fell	0	0	19.4	42.9	47.6	47.6	81.0	85.7

Variation

Variation in this species was studied mainly by means of population samples collected in the field. Some plants were transplanted into the experimental garden at Sheffield and some were grown from seed collected from wild populations so that the amount of genetic variation could be determined. In order to conserve the species, which is now very rare in Britain, only a minimal number of plants were transplanted into the experimental garden from the field. These however proved difficult to grow and seedlings also tended to die after one season.

One of the most noticeable types of variation is in the height and general size of individual plants. In general, as previously mentioned, plants in British populations are smaller and have fewer inflorescences than those belonging to populations in continental Europe. The size of individuals is partly related to degree of exposure, and as early as 1906, John Cryer, a Yorkshire botanist exhibited a range of specimens at the Linnean Society collected from different altitudes and degrees of exposure in the neighbourhood of Grassington. Plants from sheltered sites were shown to be large and bushy, whereas plants from exposed sites at higher altitudes had a dwarf condensed habit with few inflorescences, but he did not know if there was any genetic basis for these different forms. Unfortunately the species has been over-collected from this area and only exists now at a few sites, so that it is not possible to obtain experimental evidence from this area or elsewhere as it only occurs now within a restricted altitudinal range.

Plants transplanted into the experimental garden at Sheffield, or grown from seed are always smaller than those from the same population in the field (Table 4:5). Plants from the populations in northern England show less reduction in height than plants from the Alps. Those grown from seed collected in Teesdale are even smaller than in the wild. In Alpine plants, as well as a reduction in size there is also a reduction in the number of inflorescences per plant. In the field 6 plants in the population at La Grave had a mean number of 8.3 inflorescences per plant, but after a year in cultivation at Sheffield 4 plants from this population produced a mean of only 2.0 inflorescences per plant. The species has been shown to grow in very specialised ecological conditions (see p.134). A combination of unsuitable soil conditions together with an unfavourable climate may therefore be responsible for this loss of vigour in cultivated plants. P. amarella is most unusual in this respect, as the majority of species grow much more vigorously in cultivation than they do in the wild. However, there

TABLE 4:5

Variation in height of *P. amarella*.

Population	Country	Height of population in field (cm.)			Height of plants after 1 year in cultivation (cm.)		
		Sample No.	Mean	Range	Sample No.	Mean	Range
Widdybank Fell, Co. Durham	England	12	2.5	1.4- 4.7	* 6	1.2	0.8-1.4
Dib Scar, N.W. Yorkshire	England	12	6.5	3.2- 9.0	* 3	3.5	3.4-3.6
Crundale Downs, Kent	England	12	8.9	4.0-13.0	1	2.5	(1 plant)
Couvet, Jura	Switzerland	8	10.9	8.0-13.0	1	4.0	(1 plant)
La Grave, Hautes Alpes	France	6	9.6	5.0-14.0	4	3.2	2.0-4.0

* Plants grown from seed.

appears to be a genetic component to variation in size, since plants from Teesdale retain their dwarf habit and condensed inflorescences in cultivation.

Another type of variation in this species is flower colour. In continental Europe the majority of populations have either blue or white flowers, though a few mixed populations were discovered in the Alps. Herbarium specimens show that several populations in southern Sweden consist of pink flowered forms, although the majority are blue.

In Britain, three main colour variants exist. In Teesdale it was thought for many years that only the pink flowered form was present (Plate 4:7) (cf. Pigott 1956), but when the population on Widdybank Fell was rediscovered it was found to have blue flowers and in the summer of 1968 two small populations of blue flowered plants were also found on Cronkley Fell (Plate 4:8). Reference to old herbarium specimens has shown that the blue form was previously known on Cronkley Fell but it seems to have been overlooked for a number of years. The plants are rather erratic in their flowering and may easily be missed in unfavourable years,

Plate 4:7 Pink-flowered form of Polygala amarella Crantz, Cronkley Fell, Teesdale.

Plate 4:8 Blue-flowered form of Polygala amarella Crantz, Cronkley Fell, Teesdale.

especially if botanists are searching for plants with pink flowers. In 1968 more blue than pink flowered plants were seen on Cronkley Fell, but in the following year the situation was reversed.

In the Craven Pennines all the populations known at present have blue flowers, but according to herbarium material blue, pink and white flowered forms have existed there in the past, the blue form being the most common. It seems that plants with the rarer flower colours may have become extinct through the activities of overenthusiastic botanists. The population at Orton in Westmorland also has blue flowers.

In Kent the majority of plants have flowers with peculiar greyish-lilac wing sepals and white corollas. This particular colour variant seems restricted to Kent and northern France (F. Rose, personal communication). At one locality near Wye, the population consists of a range of flower colours from white, through pale pink to the greyish-lilac of the other Kent populations.

In the past, plants from Kent have been distinguished as P. austriaca Crantz and one of the characters used to differentiate these southern populations from the northern ones is the shorter length of the wing sepals. In the present investigation it was found that wing sepals of Kent and Teesdale plants have the same mean and a similar range of length (Table 4:6) and that plants in both these areas have shorter wing sepals than the Craven populations and most plants from continental Europe (Table 4:7). Results from transplants and plants grown from seed indicate that this variation is genetically controlled (Table 4:6)

TABLE 4:6

Distribution of wing sepal length of *P. amarella* in three areas of Britain.

WILD POPULATIONS

Length (mm.)	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	Sample No.
Kent	-	-	1	13	21	-	-	-	35
Craven	-	-	-	-	6	9	26	2	43
Teesdale	-	-	3	11	18	3	-	-	35

CULTIVATED PLANTS

Length (mm.)	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	Sample No.
Kent	-	-	1	-	-	-	-	-	1
Craven	-	-	-	-	1	1	-	-	2
*Craven	-	-	-	-	1	2	1	-	4
*Teesdale	-	2	2	-	-	-	-	-	4

* Grown from seed.

TABLE 4:7

Distribution of wing sepal length of P. amarella in wild populations from continental Europe.

Length (mm.)	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	Sample No.
Population									
C3 Couvet, Switzerland.	-	-	-	-	1	3	8	-	12
C4 Couvet, Switzerland.	-	-	-	-	8	7	1	-	16
C17 Fugiere, France.	-	-	-	-	8	6	1	-	15
C19 Seyne, France.	-	-	-	3	9	-	-	-	12
C24 La Grave, France.	-	-	-	-	3	15	2	-	20
C25 Corbie, France.	-	-	-	-	11	7	-	-	18
* Öland, Sweden.	-	-	2	4	13	1	-	-	20
* Jämtland, Sweden.	-	-	-	4	10	5	1	-	20

* Data from herbarium specimens.

It is important to choose wing sepals of comparable age as they enlarge as the fruit capsules mature and where possible this was done.

Wing sepal length breadth ratio is another variable character. Measurements of wing sepals from samples of a number of British populations have shown that Teesdale plants have short broad wing sepals, plants from the Craven Pennines have long narrow wing sepals and that Kent plants are intermediate in this respect. There is very little intra-area variation in this character in British populations (Table 4:8), though the population at Gordale in the Craven region is rather anomalous. Population samples from continental Europe vary continuously in this character (Table 4:9) but none are as extreme as the wild plants in the Teesdale population in Britain. Comparison with results from material grown in the experimental garden suggests that variation is at least partly genetic although it was only possible to grow small numbers of plants.

Shape and size of the fruit capsule varies in wild populations and in Britain this variation is discontinuous (Tables 4:10 and 4:11). Plants from populations in the Craven district have significantly longer, narrower capsules than

TABLE 4:8

Variation in the wing sepal length/breadth ratio of British populations of *P. amarella*.

Population	Area	Mean	Standard Deviation	Sample No.
Crundale I	Kent	2.2312	0.2345	20
Crundale II	Kent	2.1208	0.1411	10
Bredhurst	Kent	2.0744	0.1374	5
Dib Scar	Craven	2.5290	0.2283	20
Mastiles Lane	Craven	2.5214	0.1962	20
Gordale	Craven	2.0748	0.1670	10
Widdybank	Teesdale	1.7481	0.1031	10
Cronkley P_1	Teesdale	1.6408	0.1539	15
Cronkley P_2	Teesdale	1.7723	0.1676	10
Plants in cultivation for 1 year.				
Crundale I	Kent	2.142	-	1
*Dib Scar	Craven	2.315	-	4
Mastiles Lane	Craven	2.500	-	1
*Widdybank Fell	Teesdale	2.031	-	4

* Grown from seed.

TABLE 4:9

Variation in the wing sepal length/breadth ratio of populations of *I. amarella* from continental Europe.

Population	Country	Mean	Standard Deviation	Sample No.
C3. Couvet	Switzerland	2.1150	0.1838	12
C4. Couvet	Switzerland	2.0286	0.2000	16
C17. Fugiere	France	2.2424	0.1389	15
C19. Seyne	France	1.9919	0.1562	12
C24. La Grave	France	2.0285	0.0728	20
C25. Corbie	France	1.9020	0.2289	18
* Öland	Sweden	1.9950	0.2490	20
* Jämtland	Sweden	1.9680	0.2857	20
Plants in cultivation for 1 year				
C24. La Grave	France	2.4490	-	7

* Data from herbarium specimens.

plants from either Kent or Teesdale. In capsules of transplanted plants and in those grown from seed the variation between areas in Britain is much less (Table 4:10) and this variation is probably due to phenotypic plasticity.

TABLE 4:10

Variation in capsule length/breadth ratio of British populations of P. amarella.

Population	Area	Mean	Standard Deviation	Sample No.
Crundale I	Kent	1.0322	0.0155	15
Crundale II	Kent	0.9803	0.0300	6
Bredhurst	Kent	1.0360	0.0762	6
Dib Scar	Craven	1.3070	0.0625	12
Mastiles Lane	Craven	1.2111	0.0985	18
Widdybank	Teesdale	1.0898	0.0949	12
Cronkley P_1	Teesdale	1.0704	0.0387	7
Cronkley P_2	Teesdale	1.1608	0.0927	11
Plants in cultivation for 1 year				
Crundale I	Kent	1.000	-	1
*Dib Scar	Craven	1.198	-	6
Mastiles Lane	Craven	1.067	-	1
*Widdybank Fell	Teesdale	1.210	-	4

*Grown from seed.

TABLE 4:11

Variation in capsule length/breadth ratio of populations of P. amarella from continental Europe.

Population	Country	Mean	Standard Deviation	Sample No.
C3 Couvet	Switzerland	1.1045	0.5563	10
C4 Couvet	Switzerland	1.1208	0.2828	16
C17 Fugiere	France	1.0737	0.0625	15
C19 Seyne	France	1.0213	0.0566	12
C24 La Grave	France	1.2135	0.1578	18
C25 Corbie	France	1.0391	0.0633	18
* Öland	Sweden	1.2070	0.1612	20
* Jämtland	Sweden	1.2350	0.0854	20

* Data from herbarium specimens

Plants in cultivation for 1 year				
C27 La Grave	France	1.2310	-	5

Leaf shape varies considerably in P. amarella. The apices of both cauline and basal leaves may be acute or obtuse and the leaf length/breadth ratio varies considerably between one population and another, particularly in Britain. Plants from both the northern areas in Britain and also all the continental populations have well developed basal rosettes, but many of the plants in Kent completely lack a rosette (in summer at least) and possess at most two or three basal leaves. (In this investigation a rosette is considered to consist of at least four basal leaves.)

Populations in Kent have obtuse or sub-acute cauline leaves and obovate basal leaves. The plants of Teesdale populations have basal leaves very similar to those of plants from Kent, but the cauline leaves of Teesdale plants are always extremely acute. Both cauline and basal leaves of most plants in the Craven populations and also the population at Orton in Westmorland are acute, though there are a proportion of plants with obtuse or sub-acute rosette leaves in some populations. These differences are maintained in cultivation (Figs. 4:2 and 4:3). In addition plants from the Craven district can also be distinguished by the presence of dark red anthocyanin pigment in the

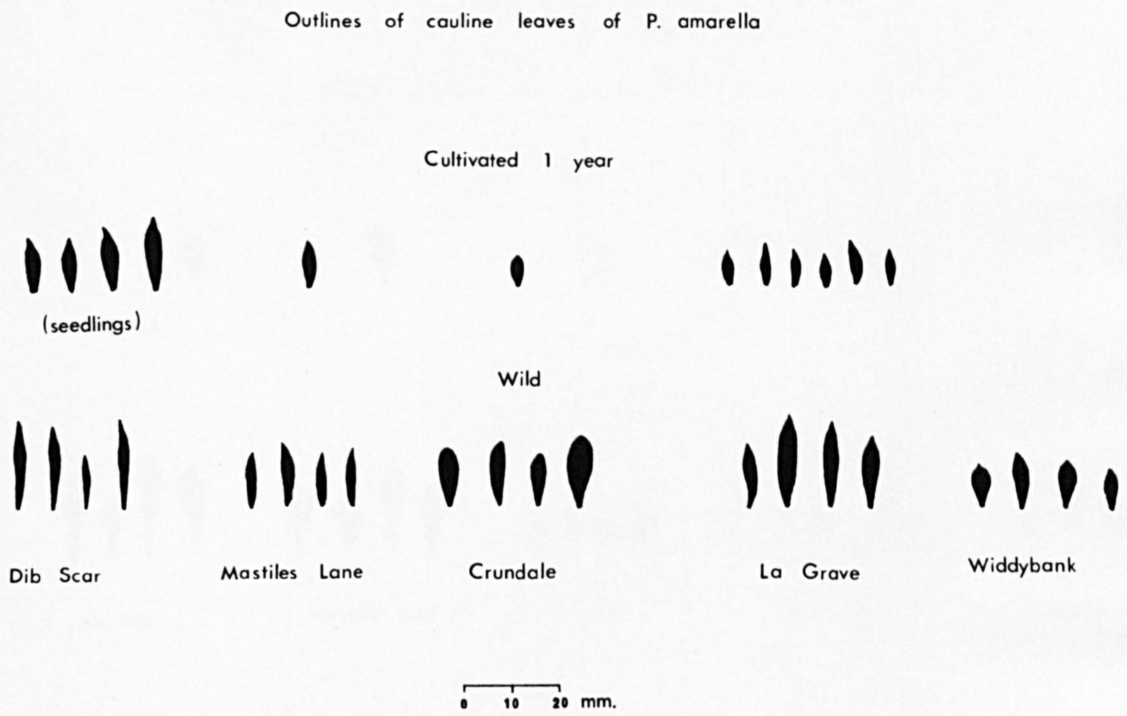


Fig. 4:2 Outlines of cauline leaves of Polygala amarella Crantz from populations in different regions of Britain and the Alps.

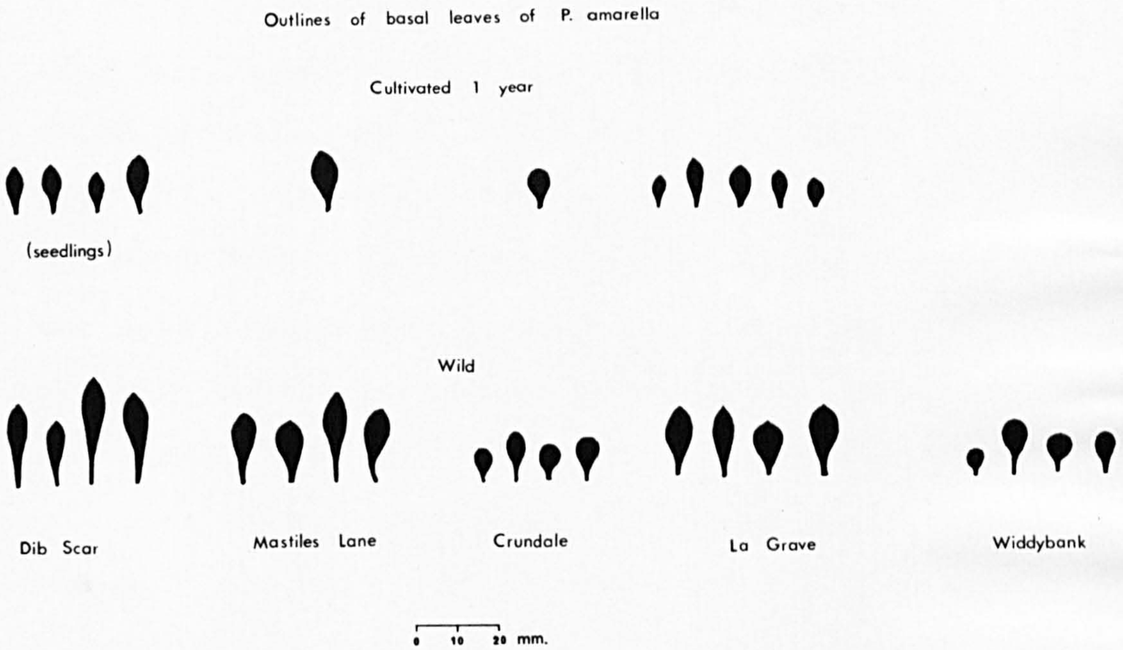


Fig. 4:3 Outlines of basal leaves of <u>Polygala amarella</u> Crantz from populations in different regions of Britain and the Alps.

leaves which is even more noticeable in cultivated than wild plants. In Britain the most similar populations in these respects to those in the Alps are the ones in the Craven Pennines. The population at Corbie in northern France has obtuse cauline leaves similar to the Kent populations in England, though the rosette leaves of the French plants are slightly more acute.

In continental Europe the length-breadth ratio of the basal leaves varies continuously but in Britain the majority of plants in each area are distinct from those in other areas (Tables 4:12 and 4:13). The Kent population has a lower mean length-breadth ratio than any of the continental populations and two of the Teesdale populations also have a low mean value. There is however considerable intra-area variation in this character in Britain particularly in the Craven district. Unfortunately, there was insufficient material in cultivation to confirm that this intra-area variation is genetic.

TABLE 4:12

Variation in the length/breadth ratio of basal leaves in British populations of *P. amarella*.

Population	Country	Mean	Standard Deviation	Sample No.
Crundale I	Kent	2.0778	0.3479	20
Crundale II	Kent	1.9952	0.7217	10
Bredhurst	Kent	1.3942	0.7460	5
Dib Scar	Craven	3.9253	0.4705	20
Mastiles Lane	Craven	2.8903	0.8012	20
Gordale	Craven	2.5604	0.5303	10
Widdybank	Teesdale	1.8260	0.2506	10
Cronkley P_1	Teesdale	2.2146	0.3409	15
Cronkley P_2	Teesdale	2.5316	0.4585	10
Plants in cultivation				
Crundale II	Kent	1.741	-	1
*Dib Scar	Craven	2.664	-	4
Mastiles Lane	Craven	2.187	-	1

* Grown from seed.

TABLE 4:13

Variation in the length/breadth ratio of basal leaves in populations of P. amarella from continental Europe.

Population	Country	Mean	Standard Deviation	Sample No.
C3 Couvet	Switzerland	2.4796	0.2742	12
C4 Couvet	Switzerland	2.6861	0.7225	16
C17 Fugiere	France	2.7836	0.3806	15
C19 Seyne	France	2.5412	0.8134	12
C24 La Grave	France	2.6242	0.4636	20
C25 Corbie	France	2.4557	0.5317	18
*Öland	Sweden	2.6400	0.5079	20
*Jämtland	Sweden	2.8680	0.7122	20
Plants in cultivation for 1 year.				
C24 La Grave	France	2.3090	-	7

* Data from herbarium specimens.

The relationship between wing sepal and basal leaf variation is shown in Fig. 4:4. This shows that the Teesdale and Kent populations are more similar to one another in these respects than to the Craven populations, although the population from Gordale in the Craven district is rather anomalous.

Cauline leaf length-breadth ratio shows a parallel pattern of variation to that of the basal leaves. Means and standard deviations of British populations are shown in Table 4:14 and of continental populations in Table 4:15. Comparison with measurements of cultivated plants shows that at least part of this variation is due to phenotypic plasticity. For example, plants grown from seed collected at Dib Scar have cauline leaves with a lower length-breadth ratio than the plants in the field (Fig. 4:2). Populations in the Craven district are far more variable than either Kent or Teesdale populations for this character as well as for basal leaf length-breadth ratio.

Analyses of variance show that differences between wild plants from the three areas of Britain are highly significant (Table 4:16) and also that most of the measureable differences

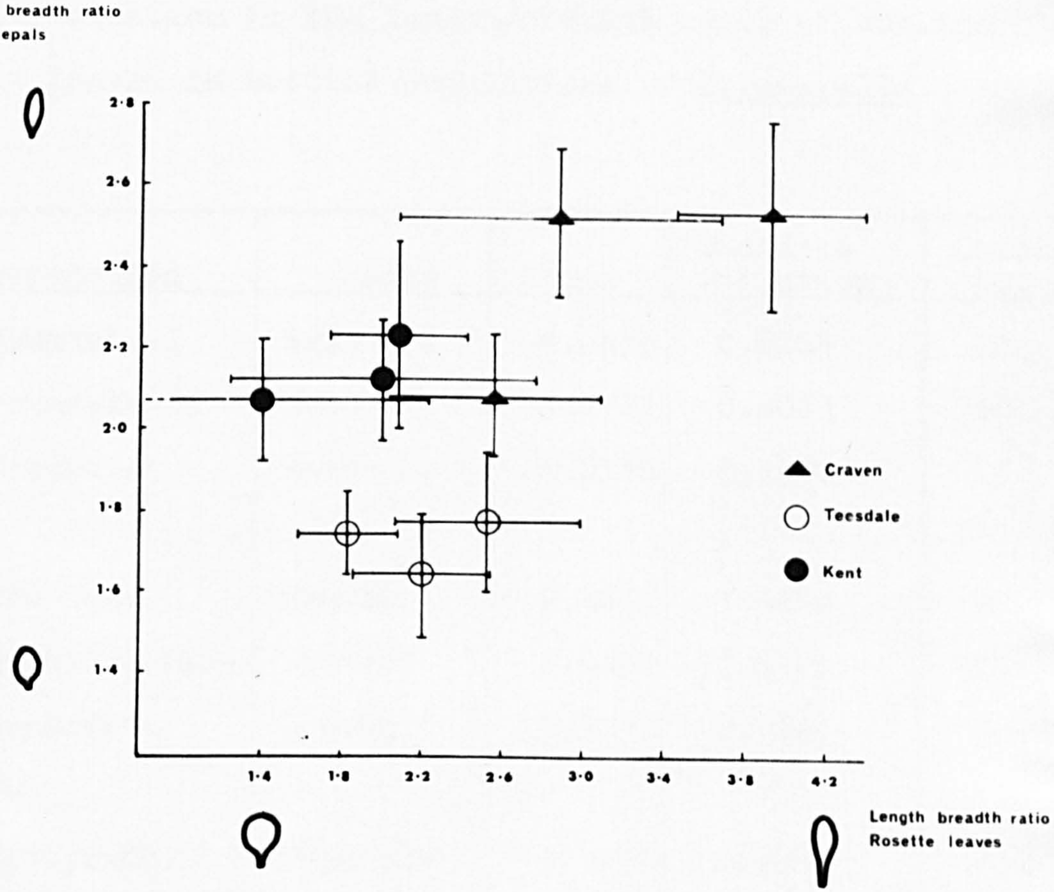


Fig. 4:4 Scatter diagram showing the relationship between basal leaf length/breadth ratio and wing sepal length/breadth ratio of Polygala amarella Crantz. Means and twice standard deviations plotted.

TABLE 4:14

Variation in the length/breadth ratio of cauline leaves in British populations of _P. amarella_.

Population	Area	Mean	Standard Deviation	Sample No.
Crundale I	Kent	4.2973	0.6865	20
Crundale II	Kent	3.2722	0.4061	10
Bredhurst	Kent	3.0216	0.1906	5
Dib Scar	Craven	6.9269	1.5610	20
Mastiles Lane	Craven	4.6989	1.0220	20
Gordale	Craven	3.9012	0.5945	10
Widdybank	Teesdale	3.1410	0.6299	10
Cronkley P_1	Teesdale	4.1530	0.6429	15
Cronkley P_2	Teesdale	2.7930	0.5840	10
Plants in cultivation for 1 year				
Crundale II	Kent	2.385	-	1
*Dib Scar	Craven	4.217	-	4
Mastiles Lane	Craven	3.429	-	1

* Grown from seed.

TABLE 4:15

Variation in the length/breadth ratio of cauline leaves in populations of _P. amarella_ from continental Europe.

Population	Country	Mean	Standard Deviation	Sample No.
C3 Couvet	Switzerland	3.4962	0.8367	12
C4 Couvet	Switzerland	4.6841	0.7893	16
C17 Fugiere	France	4.3274	0.7307	15
C19 Seyne	France	4.0480	0.7608	12
C24 La Grave	France	4.9768	0.8827	20
C25 Corbie	France	3.7293	0.5083	18
*Öland	Sweden	4.4950	0.9047	20
*Jämtland	Sweden	4.4500	1.0160	20
Plants in cultivation for 1 year.				
C24 La Grave	France	3.3860	-	7

* Data from herbarium specimens.

TABLE 4:16

Inter-area variation in British samples.

Source of variation	d.f.	Mean square	F	P
Cauline leaf length/breadth ratio				
Between areas	2	36.708	27.280	< 0.001
Within areas	102	1.346		
Basal leaf length/breadth ratio				
Between areas	2	14.729	41.881	< 0.001
Within areas	102	0.352		
Wing sepal length/breadth ratio				
Between areas	2	4.323	51.463	< 0.001
Within areas	102	0.084		
Capsule length/breadth ratio				
Between areas	2	0.401	58.159	< 0.001
Within areas	87	0.007		

between populations in the same area of Britain (Tables 4:17 - 4:19) are highly significant. The one exception to this is the insignificant difference in wing sepal length-breadth ratio between samples in Kent and in Teesdale. Similar comparisons of continental population samples (Table 4:20) show that inter-population differences in capsule length-breadth ratio are not significant and differences in basal leaf length-breadth ratio are only significant at the one percent level.

TABLE 4:17

Intra-area variation in British samples.

I Kent

Source of variation	d.f.	Mean square	F	P
Cauline leaf length/breadth ratio				
Between populations	2	5.372	96.270	< 0.001
Within populations	32	0.056		
Basal leaf length/breadth ratio				
Between populations	2	0.929	9.940	< 0.001
Within populations	32	0.094		
Wing sepal length/breadth ratio				
Between populations	2	0.081	1.936	N.S.
Within populations	32	0.042		
Capsule length/breadth ratio				
Between populations	3	1.944	8.312	< 0.001
Within populations	26	0.234		

N.S. = not significant.

TABLE 4:18

Intra-area variation in British samples.

II Craven

Source of variation	d.f.	Mean square	F	P
Cauline leaf length/breadth ratio				
Between populations	2	29.112	21.226	<0.001
Within populations	32	1.372		
Basal leaf length/breadth ratio				
Between populations	2	6.060	15.83	<0.001
Within populations	32	0.383		
Wing sepal length/breadth ratio				
Between populations	2	0.709	17.473	<0.001
Within populations	32	0.041		
Capsule length/breadth ratio				
Between populations	1	1.084	35.585	<0.001
Within populations	28	0.028		

TABLE 4:19

Intra-area variation in British samples.

III Teesdale

Source of variation	d.f.	Mean square	F	P
Cauline leaf length/breadth ratio				
Between populations	2	5.081	13.170	<0.001
Within populations	32	0.386		
Basal leaf length/breadth ratio				
Between populations	2	2.256	17.678	<0.001
Within populations	32	0.128		
Wing sepal length/breadth ratio				
Between populations	2	0.064	2.785	N.S.
Within populations	32	0.023		
Capsule length/breadth ratio				
Between populations	2	0.027	3.792	<0.05
Within populations	27	0.007		

N.S. = not significant.

TABLE 4:20

Inter-population variation in French and Swiss samples.

Source of variation	d.f.	Mean square	F	P
Cauline leaf length/breadth variation				
Between populations	5	5.161	8.948	<0.001
Within populations	87	0.577		
Basal leaf length/breadth ratio				
Between populations	5	0.855	4.048	<0.01
Within populations	87	0.211		
Wing sepal length/breadth ratio				
Between populations	5	0.211	7.305	<0.001
Within populations	87	0.029		
Capsule length/breadth ratio				
Between populations	5	0.087	2.069	N.S.
Within populations	83	0.042		

N.S. = not significant.

When measurements of all British plants are pooled together and compared with measurements of continental plants there is no significant difference between the means, which is to be expected if they all belong to the same species. Comparisons of differences between pooled continental data and data from individual areas of Britain have not yet been attempted.

For each of the characters measured, the populations in the Craven Pennines show the most inter- and intra-population variation. This may be due to the diversity of habitats in the Craven district and differences in the selective value of various characters in different habitats. For example, the population on Dib Scar growing amongst tall grasses and in a habitat subject to drought in summer has higher length-breadth ratios for all the characters considered than the other populations in this area. The Gordale population is differentiated from both the Mastiles Lane and Dib Scar populations and this may be related to its calcareous mire habitat. The Craven populations are in general larger than any in Kent or in Teesdale, for example two of the populations visited in Kent consisted of less than six plants. It is in populations of this size that changes in the relative proportions of genes in the gene pool due to the Sewall Wright Effect are most likely to occur. The loss of the pink and white flower colour variants from the Craven area may be an example of this, though it is more likely to be due to the efforts of man. An alternative hypothesis to explain these local differences in gene frequencies is that they may merely be a reflection of chance differences existing at the time of establishment of the populations. The effects of inbreeding have served to reinforce this local differentiation of populations.

To summarise, morphological variation of P. amarella in Britain is discontinuous and plants from each of the three main areas of occurrence are differentiated from one another. Local variation between populations in the same area can also be detected. The variation of continental populations is continuous and the total range of variation for a number of quantitative characters includes that of the majority of the British plants, though the more extreme British forms, especially those from Teesdale and Kent lie outside this variation range.

The three British forms can be distinguished from one another as follows:-

1. <u>Teesdale</u>

   Plants 15-50 mm. Stems erect or ascending, usually solitary. Basal leaves 6-14 (-18) mm., obovate, forming distinct basal rosette. Cauline leaves 5-12 (-15) mm., lanceolate, acute. Inflorescence condensed with 7-17 (-24) blue or pink flowers. Wing sepals 3.2 - 4.6 mm. Capsule 3-4 (-4.4) mm., suborbicular.

2. <u>Kent</u>

   Plants 40-90 mm. Stems erect, slender, usually solitary. Basal leaves 7-18 mm., obovate, often not forming a distinct rosette. Cauline leaves 10-26 mm., lanceolate or narrowly obovate, obtuse. Inflorescence elongate with 10-30 grey-lilac or whitish flowers. Wing sepals

3.2 - 4.0 mm. Capsule 2.4 - 3.8 mm., suborbicular.

3. Craven

Plants (30-) 60-90 mm. Stems ascending, solitary to many. Basal leaves (6-) 12-27 mm., narrowly obovate to spathulate, acute, often with dark red pigment, forming distinct basal rosette. Cauline leaves (5-) 8-20 mm., lanceolate to linear-lanceolate, acute. Inflorescence elongate with 15-25 blue flowers. Wing sepals 4.2 - 5.4 mm., veins indistinct. Capsule 3.2 - 4.4 mm., broadly obovate.

The majority of these differences are maintained in cultivation though leaf length-breadth ratio tends to be less extreme than in wild populations.

Taxonomy

Until recently this species has usually been classified by British taxonomists as P. amara L. Crantz (1769) was the first to separate the small flowered race as a separate species, P. amarella Crantz from the large flowered race which retained the name P. amara L., though other authors have considered P. amarella Crantz to be a subspecies of P. amara L. Recent studies of morphological and cytological variation and also of geographical distribution suggest that the two should be retained as distinct species and this is the classification followed by McNeill (1968). Accordingly, British plants should now be classified as P. amarella Crantz.

The British populations have been split into different taxa in the past because of their discontinuous variation and distribution pattern. Teesdale plants have been named as P. uliginosa Reichenb. and Kent plants as P. austriaca Crantz, the name P. austriaca being retained in British floras until 1952 (Clapham, Tutin & Warburg, 1952). The present work indicates that the populations in all three British areas of distribution are morphologically and genetically distinct from one another when a number of characters are considered. When compared with the range of variation in continental Europe however, each of the three British forms falls partly within and partly outside that found in continental plants, though the Craven form is the most similar to the continental forms and cannot be easily distinguished from plants in the Alps or lowland Europe. Proctor (1957) has discovered a similar situation in Helianthemum canum (L.) Baumg. where races from disjunct stations in Britain are morphologically differentiated from one another. The Teesdale race is distinct and has been named ssp. laevigatum Proctor. It is now proposed that the British races of P. amarella should receive similar treatment.

The name P. uliginosa Reichenb. which has been applied to the Teesdale race was first applied (Reichenbach 1831) to a small flowered form growing in marshy ground in montane regions of Austria, Switzerland and Germany. This form is, however, morphologically indistinguishable from the majority of continental specimens of P. amarella. Fries (1835) has also applied the name to pink flowered Swedish plants. This name does therefore not distinguish the Teesdale race from other British or continental forms and a new one is therefore proposed. It is now suggested that Teesdale plants be classified as P. amarella Crantz ssp. backhousii G. Fearn.

P. austriaca Crantz was originally used to describe slender plants with basal rosettes, sparse inflorescences and small white flowers found in Austria (Crantz 1769). This description fits some, but not all of the Kent plants, though it does distinguish them from the forms in northern England. The present work however shows that the Kent race is incompletely separated from continental plants morphologically and more research is necessary to determine if separate taxonomic status is appropriate.

As the Craven populations are morphologically indistinguishable from the majority of continental forms, it is proposed that both these and the continental populations should be named P. amarella Crantz ssp. amarella.

PART III

Hippocrepis comosa L.

Description

Perennial herb, (1-) 5-30 cm.high, (4-) 10-60 (-100) cm.diameter, stems prostrate, ascending or erect, woody at base. Rootstock woody, tap-root up to 90 cm. Leaves (2-) 3-8 (-15) cm., imparipinnate; leaflets (2-) 4-8 (-16) x 1-5 (-8) mm., usually 3-8 pairs, obovate to oblong, subglabrous to densely pubescent beneath; stipules 1-3 mm., lanceolate, spreading. Heads 4-8 (-12) flowered, peduncles as long as or longer than the leaves. Flowers 5-10 (-14) mm., shortly pedicelled, yellow, the standard often veined red, its claw distinctly longer than the calyx. Calyx campanulate with 5 acute teeth. Stamens in a diadelphous arrangement, alternate filaments swollen at the top. Legume 10-30 mm., compressed, breaking into 3-6 horseshoe-shaped segments covered with short red-brown papillae. Seed 2.6-4.2 mm.

General biology

A short review of the biology of the species in relation to its role as a chalk grassland herb has been given by Salisbury (1952, p.70). He notes in particular that the species produces two different types of seed: "soft" seeds which germinate immediately and "hard" seeds which remain dormant. He also states that in winter, plants take on a prostrate habit, all the leaves and axillary branches lying in a horizontal plane. The following additional observations have been made by myself.

The main flowering period is in late May and June but some plants flower again in late August and September, though producing far fewer flowers in the autumn. The flowers are bright yellow and strongly scented, especially in warm weather and are visited mainly by bees which effect cross pollination while searching for nectar. The stamens and style are completely enclosed within the keel of the corolla, but the weight of an insect alighting on the flower activates a "trip" mechanism so that the stamens and style flick out, touching the insect's body, the anthers dusting it with pollen which can later be transferred to the stigma of another plant, thus effecting cross pollination. The flowers are self-sterile so that even if pollen is transferred to the stigma of the same flower no seeds result. (See below).

The seeds are enclosed in a long pod or legume, which becomes curved as it matures, individual segments which each contain one seed becoming horseshoe-shaped, thus giving the plant its common English name, the Horseshoe Vetch. The pods are shed about three months after the flowering period, but there is no special mechanism for the dispersal of seeds. When dry, the segments of the pod split lengthwise, liberating the seeds, but in a wet season, seeds are presumably only liberated after the legume wall has rotted.

When shed, many seeds are green and will not germinate. As mentioned above, Salisbury (loc. cit.) has noted the production of "hard" dormant seeds and "soft" seeds which are capable of immediate germination. The green seeds are certainly very hard and contain hard, green, though fully formed, embryos. When ripe, the seeds are yellow and much softer, especially after imbibition. The proportion of hard green seeds varies from population to population, plants from chalk downland in south-east England producing a higher proportion than those from northern England and the Alps. This appears to be genetically controlled and persists in wild plants cultivated in the experimental garden. It is possibly an adaptation by which populations can be built up rapidly in areas with a short growing season.

The green seeds gradually ripen throughout the winter to a yellow-brown colour and by April most seeds will germinate. Approximately 100% germination can then be obtained if the "soft" yellow seeds are chipped before imbibing in common with many other leguminous species. Seeds which have not been chipped beforehand give less than 5% germination immediately, though they germinate gradually after several weeks in soil. Green seeds will not germinate even after being chipped. Cold treatment is not necessary. Germination is epigeal.

Breeding system

Both diploid and tetraploid plants are self incompatible. Experimental crosses have been carried out in an insect-proof enclosure within a greenhouse. Any previously opened flowers were removed and hybridisations were carried out using flowers which had opened the previous day. Wing petals of the female parents were cut in half vertically and the keel slit with a fine needle to expose the style and stigma. Pollen was obtained from the male parent by gently squeezing the keel until pollen was extruded from its apex, catching it on the tip of a needle and transferring it to the stigma of the female parent. Pollinations were carried out on two successive days. To avoid contamination, needles were wiped with alcohol and dried between pollinations. This procedure was followed for artificially selfed plants, except that pollen was transferred from flowers on the same plant. Emasculation was unnecessary as none of the unpollinated or artificially selfed flowers (17 diploid and 35 tetraploid) set seed, though one selfed tetraploid flower did begin to produce a pod which was soon shed. Results of these crosses are shown in

Tables 4:21 - 4:23 . These show that crosses between plants of the same ploidy are on the whole successful, as are crosses between female diploid and male tetraploid plants, but only a single seed has been obtained from the reciprocal cross, female tetraploid x male diploid. All seeds obtained from interploid crosses are however only about half the normal size, are shrivelled and empty and fail to germinate. In the cross tetraploid female x diploid male, seed capsules start to develop, but are all shed approximately one week after pollination. In June 1970, a large proportion of capsules resulting from all crosses were shed at this time, possibly because of very hot conditions in the greenhouse, so that seed yield was generally low, but the 4X ♀ x 2X♂ cross was affected more seriously than any of the others indicating hybrid inviability. This is borne out by the previous year's results when none of the 4X ♀ x 2X ♂ crosses, which were carried out in better conditions, produced any seed at all.

Reciprocal differences have also been noted in many of the tetraploid x tetraploid crosses, seed yield varying according to which plant is used as the female parent even between plants from the same population, e.g. C1 from the

Marne Valley in France (See Table 4:22). From these results a series of "superiority" of female parents can be deduced viz. Durlston Head 1/6 > C6/1 > C1/2 > C1/1. Though more research is necessary to confirm this it is of note that in the two consecutive years in which crosses were made, plants from Biggin Hill consistently produced more seeds than plants from Bredhurst in reciprocal crosses.

TABLE 4:21

Crosses within and between diploid and tetraploid races of *Hippocrepis comosa*.

Date	Cross	Ploidy	No.of flowers pollinated	No. seeds obtained
June 1969	Durl Head ♀ x Topley Pike ♂	2X x 2X	5	11
	Biggin Hill ♀ x Bredhurst ♂	4X x 4X	3	3
	Bredhurst ♀ x Biggin Hill ♂	4X x 4X	3	0
	Biggin Hill ♀ x Silverdale ♂	4X x 4X	4	6
	Silverdale ♀ x Biggin Hill ♂	4X x 4X	9	24
	Durl Head ♀ x Bredhurst ♂	2X x 4X	4	11
	Topley Pike ♀ x Burham ♂	2X x 4X	6	21
	Biggin Hill ♀ x Durl Head ♂	4X x 2X	5	0
	Burham ♀ x Durl Head ♂	4X x 2X	3	0
	Bredhurst ♀ x Durl Head ♂	4X x 2X	3	0

TABLE 4.22

Crosses within and between diploid and tetraploid races of *Hippocrepis comosa*.

Date	Cross	Ploidy	No. of flowers pollinated	No. of seeds obtained
June 1970	Great Orme 1 ♀ x Durl Head ♂	2X x 2X	8	12
	Wye Dale 1/4 ♀ x Durl Head ♂	2X x 2X	4	0
	C6/1 ♀ x C1/2 ♂	4X x 4X	9	11
	C1/2 ♀ x C6/1 ♂	4X x 4X	8	7
	C1/2 ♀ x C1/1 ♂	4X x 4X	5	8
	C1/1 ♀ x C1/2 ♂	4X x 4X	5	0
	C6/1 ♀ x Durlston Head 1/6 ♂	4X x 4X	5	0
	Durlston Head 1/6 ♀ x C6/1 ♂	4X x 4X	6	4
	Biggin Hill 1/1 ♀ x Bredhurst 1/6 ♂	4X x 4X	7	12
	Bredhurst 1/6 ♀ x Biggin Hill 1/1 ♂	4X x 4X	6	3

Table 4:22 continued

Date	Cross	Ploidy	No. of flowers pollinated	No. of seeds obtained
June 1970	Overton 3 ♀ x C6/1 ♂	2X x 4X	4	2
	Overton 3 ♀ x C1/2 ♂	2X x 4X	4	0
	Overton 3 ♀ x C1/1 ♂	2X x 4X	3	0
	Wye Dale 1/4 ♀ x C1/1 ♂	2X x 4X	9	3
	Dovedale 1 ♀ x C1/1 ♂	2X x 4X	4	0
	Great Orme 2 ♀ x C6/1 ♂	2X x 4X	3	8
	Overton 2 ♀ x Streatly 1/2 ♂	2X x 4X	10	2
	C6/1 ♀ x Overton 3 ♂	4X x 2X	4	0
	C1/2 ♀ x Overton 3 ♂	4X x 2X	5	0
	C1/1 ♀ x Great Orme 2 ♂	4X x 2X	2	0
	C1/1 ♀ x Wye Dale 1/4 ♂	4X x 2X	9	1
	C1/1 ♀ x Overton 3 ♂	4X x 2X	3	0
	Streatly 1/2 ♀ x Overton 2 ♂	4X x 2X	9	0

TABLE 4:23

Crosses within and between diploid and tetraploid races of Hippocrepis comosa. (Summary of results)

Ploidy of Cross	No. of flowers pollinated 1969	1970	No. of seeds obtained 1969	1970
2X x 2X	5	12	11	12
4X x 4X	19	51	33	45
2X ♀ x 4X ♂	10	36	32	15
4X ♀ x 2X ♂	11	29	0	1

In order to investigate the mechanism of incompatibility in H. comosa observations were made on the growth of pollen tubes following compatible and incompatible pollinations, using a dye which causes the selective fluorescence of pollen tubes and their callose plugs in ultra-violet light. Styles were collected 24 and 48 hours after pollination and fixed in F.A.A. for at least 24 hours before maceration for 2 hours at 60°C in 8N Na OH solution and staining for a few minutes with methyl blue in 0.1N K_3 PO_4 solution. Styles were then mounted on microscope slides in "Univert" aqueous mountant, squashed and examined as semi-permanent preparations. This method is a modification of that used by Martin (1959).

In fully and partially compatible crosses (2X x 2X, 4X x 4X, 2X ♀ x 4X♂), pollen tubes quickly grow down the style and can be seen in the ovary 24 hours after pollination (Plates 4:9 - 4:11). Pollen tube growth is slower in incompatible crosses (2X selfed, 4X selfed, 4X ♀ x 2X♂) and the majority have not grown very far down the style 24 hours after pollination (Plates 4:12 & 4:13), though several pollen tubes have been seen in ovaries 48 hours after pollination. This mechanism is not therefore a very efficient method of preventing pollen tubes reaching the ovules, though in competition compatible pollen will reach the ovules first. In one cross (4X ♀ x 2X♂) the majority of pollen tubes fail to penetrate the stigma (Plate 4:14)

These observations of inhibition of incompatible pollen tubes and reciprocal differences in the success of 2X - 4X crosses suggest that incompatibility is at least partly due to a gametophytically controlled S allele system, as in several other genera of the Leguminosae, e.g. Trifolium. It is interesting that incompatibility does not break down in the tetraploid, as is usually the case. The origin of this tetraploid

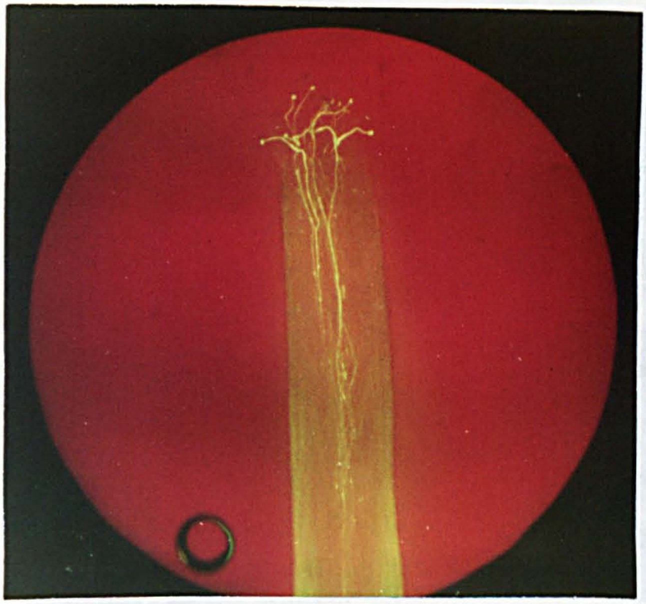


Plate 4:9 Pollen tubes in the style of a 2x x 2x cross, 24 hours after pollination.

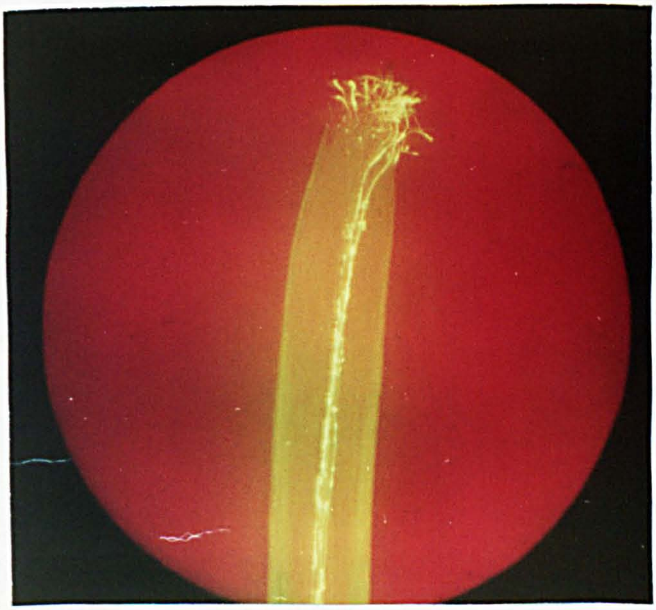


Plate 4:10 Pollen tubes in the style of a 4x x 4x cross, 24 hours after pollination.

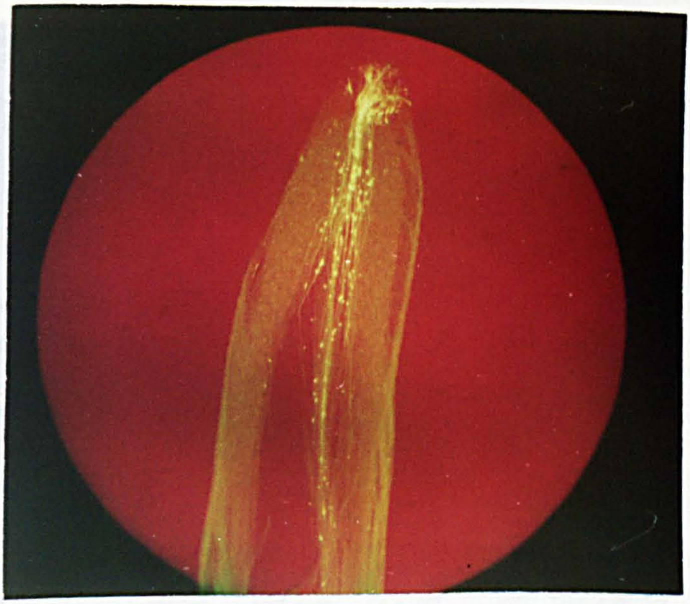


Plate 4:11 Pollen tubes in the style of a 2x♀ x 4x♂ cross, 24 hrs after pollination.

Plate 4:12 Pollen tubes clustered at the top of the style of a selfed 2x, 24 hrs. after pollination.

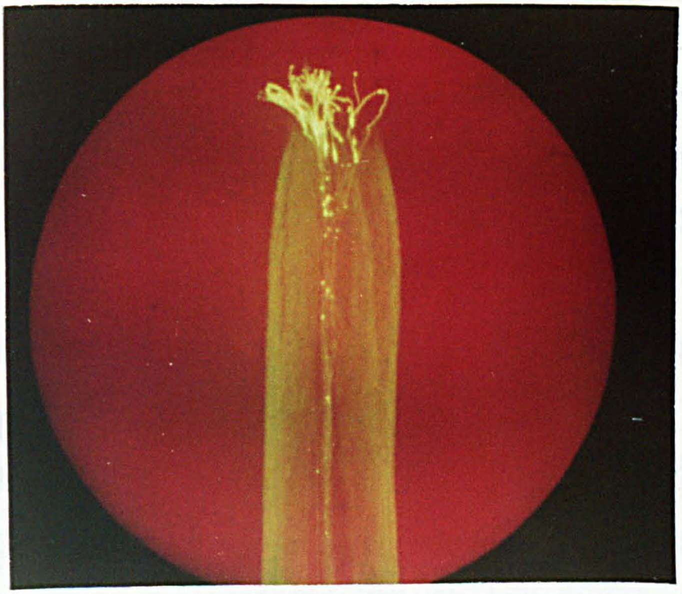


Plate 4:13 Pollen tubes clustered at the top of the style of a selfed 4x, 24 hrs after pollination.

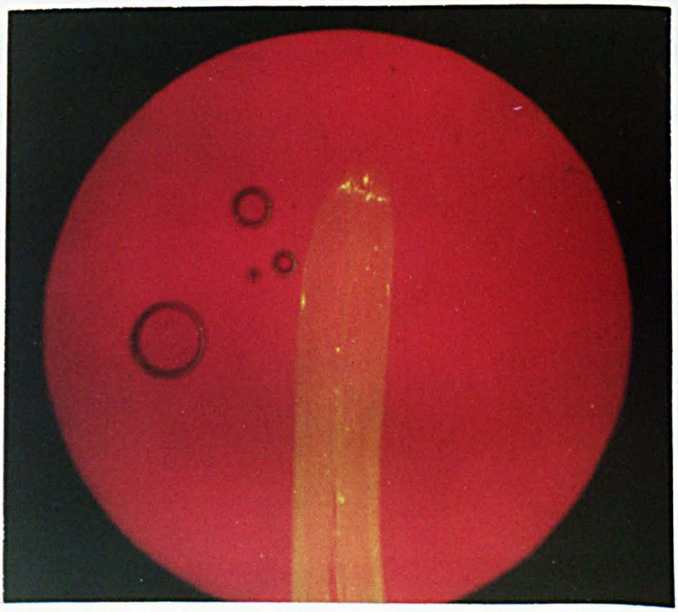


Plate 4:14 Pollen tubes failing to penetrate the stigma of a 4x ♀ x 2x ♂ cross, 24hrs after pollination.

is not yet known, but to be in accord with such a gametophytic system, it must be either of allopolyploid origin, or if it is an autopolyploid, then incompatibility must be dependent on alleles at more than one locus (Lewis 1956). Which of these is true cannot be determined until an artificial autopolyploid is produced from diploid H. comosa.

Besides the incompatibility system discussed above, there must also be a separate mechanism to account for the results of the 2X - 4X crosses in which some fertilisation must take place as pods start to develop, though they are prematurely shed with immature seeds. This is particularly the case in the 4X ♀ x 2X♂ cross. Mechanisms of hybrid inviability have been reviewed by Stebbins (1958) and it seems most likely that failure of complete seed development in interploid crosses of H. comosa is due to incompatibility between the embryo and the surrounding tissues, i.e. seed incompatibility. This is a widespread cause of hybrid inviability and has been the subject of a number of detailed studies, e.g. in Primula (Valentine 1955, Woodell & Valentine 1961, Valentine & Woodell 1963). In the majority of incompatible crosses in Primula the endosperm degenerates and gradually disintegrates followed by the breakdown of the embryo. Whether this is the case in H. comosa can only be determined by embryological preparations which it has not been possible to make yet.

In this species there are therefore two separate incompatibility mechanisms. One of these is active in the style and retards the growth of incompatible pollen tubes. This is not entirely reliable as incompatible pollen tubes may occasionally reach the ovary and at least in the 2X - 4X crosses may effect fertilisation. The other is a type of seed incompatibility which limits the development of embryos in interploid crosses, so that seeds, if formed, are empty. Crossing is therefore limited to plants of different genotypes within the same cytotype. Pollen incompatibility ensures that the species is completely outbreeding, thus theoretically leading to a high degree of heterozygosity and genetic flexibility.

Variation

H. comosa is a very variable species particularly with regard to leaf characters though there is also considerable variation in the production of anthocyanin which causes the red colouration in the veins of the flower petals. The wide range of variation in the tetraploid is partly due to biotic factors and partly due to the fact that the species is outbreeding.

The three most variable characters are leaf size, leaflet size and number of leaflet pairs per leaf. An analysis of this variation (see Table 4:24) shows that it is related to three main factors, ploidy level, grazing and place of origin.

Diploid populations differ from tetraploid populations in that they have so far only been found in habitats inaccessible to grazing animals. Plants are usually bushy and fairly erect with relatively large leaflets and a high mean number of pairs of leaflets per leaf. The diploid race is much less variable than the tetraploid race, especially with regard to leaflet length having a range of 4.0 - 6.5 mm., compared with

TABLE 4:24

No. leaflet pairs per leaf.

Ploidy	Origin	Grazing	Mean no. leaflet pairs/ leaf	Range	Standard deviation	No. of plants
2X	Britain	-	6.5	5.0 - 7.5	0.6781	20
4X	Britain	-	5.3	4.0 - 6.5	0.8970	20
4X	Britain	+	4.9	4.0 - 6.0	0.9216	20
4X	Alps	-	5.8	5.0 - 7.0	0.5736	20

Leaflet length.

Ploidy	Origin	Grazing	Mean leaflet length (mm.)	Range	Standard deviation	No. of plants
2X	Britain	-	5.0	4.0 - 6.5	0.8114	20
4X	Britain	-	5.3	4.5 - 9.0	1.1140	20
4X	Britain	+	3.8	2.5 - 6.0	0.9514	20
4X	Alps	-	6.7	4.5 -11.5	2.0600	20

Leaf variation in <u>H. comosa</u> plants which have been in cultivation for at least one year.

Fig. 4:5 Variation in leaves of Alpine tetraploid plants of <u>Hippocrepis comosa</u> L. after one year in cultivation.

4.5 - 9.0 mm. in ungrazed tetraploids from Britain. Plants from ungrazed British tetraploid populations are morphologically very similar to the diploid race, except that they have a mean value of only 5.25 leaflet pairs per leaf, compared with 6.53 in the diploid. Alpine tetraploids are extremely variable and retain this variation in cultivation. Leaf length varies from 3.0 - 15.5 cm. and leaflet length from 4.5 - 11.5 mm. (Fig. 4:5)

In addition to the variation mentioned above, a distinct ecotype has developed in tetraploid populations growing on calcareous pastures which are or have been heavily grazed by sheep and rabbits. Most of these pastures are on chalk downland in southern England, but also include the heavily grazed pastures on sugar limestone in Upper Teesdale. These plants have a prostrate habit throughout the year and small leaves and leaflets. The mean leaflet length of cultivated plants from grazed populations is only 3.8 mm., compared with 5.3 mm. for leaflets of tetraploids from ungrazed populations in Britain. These differences are even more marked in the field, showing that a certain amount of phenotypic plasticity is also involved.

The tetraploid population on Cronkley Fell consists of extremely dwarf plants with very small leaves and leaflets. A single plant from this population has been grown as a leaf cutting and after six months has retained the dwarf habit and has leaflets only 2 mm. long and a mean value of only 3.5 leaflet pairs per leaf. A longer period of cultivation will however be necessary in order to determine whether this population is genotypically distinct from others in Britain.

The prostrate, small-leaved form of the downland ecotype is clearly an adaptation to withstand the effects of heavy grazing. Any erect parts of the plant are bitten off as soon as they rise above the general level of herbage, so that plants with a prostrate habit including almost horizontal peduncles are at a selective advantage in an environment where the surrounding turf is maintained in a very short condition. Seedlings of this ecotype soon develop the prostrate habit (Fig. 4:6), producing branches and petioles which rest on the soil surface.

A summary of the effects of ploidy and grazing on leaf variation is shown in Fig. 4:7.

Fig. 4:6 Variation in leaves of tetraploid *Hippocrepis comosa* L. from British chalk downland, showing (above) leaf outlines of plants after cultivation for 2 years and (below) the prostrate habit developing in seedlings.

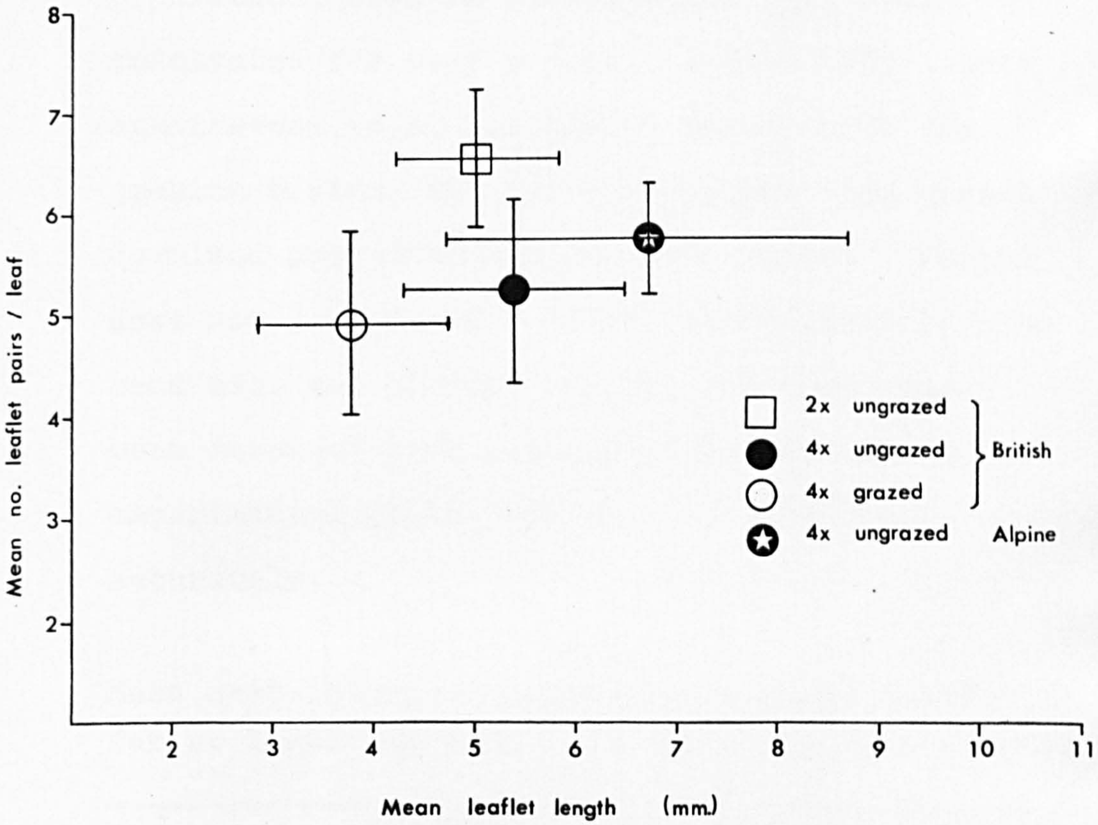


Fig. 4:7 Scatter diagram showing the effects of ploidy and grazing on leaf variation in cultivated plants of <u>Hippocrepis comosa</u> L. Means of samples of 20 plants and twice standard deviations plotted.

Seed size also varies from population to population, even in plants which have been cultivated for over a year. (Table 4:25) This again seems to be correlated mainly with the grazing factor, the two populations from grazed downland producing the smallest seeds. There does not seem to be a direct correlation between seed size and ploidy, but too few seeds have been obtained from diploid plants in the experimental garden for this to be tested accurately.

TABLE 4:25

Mean seed length of *Hippocrepis comosa* cultivated for at least one year. (except seed from Wye Dale)

Origin	Plant No.	Grazing	Ploidy	Mean seed length (mm)	No. seed measured
Durl Head	1/1	-	2X	4.12	5
Wye Dale	Field pop.	-	2X	3.09	20
Burham Downs	1/2	+	4X	3.23	20
Burham Downs	1/3	+	4X	3.71	20
Wye Downs	1/2	+	4X	2.61	20
Wye Downs	1/4	+	4X	2.47	20
Wye Downs	1/5	+	4X	2.63	20
Bredhurst	1/3	+	4X	3.30	20
Bredhurst	1/5	+	4X	3.13	20
Ayesgarth	1/1	-	4X	3.41	20
Seyne	C19	-	4X	3.12	20

Taxonomy

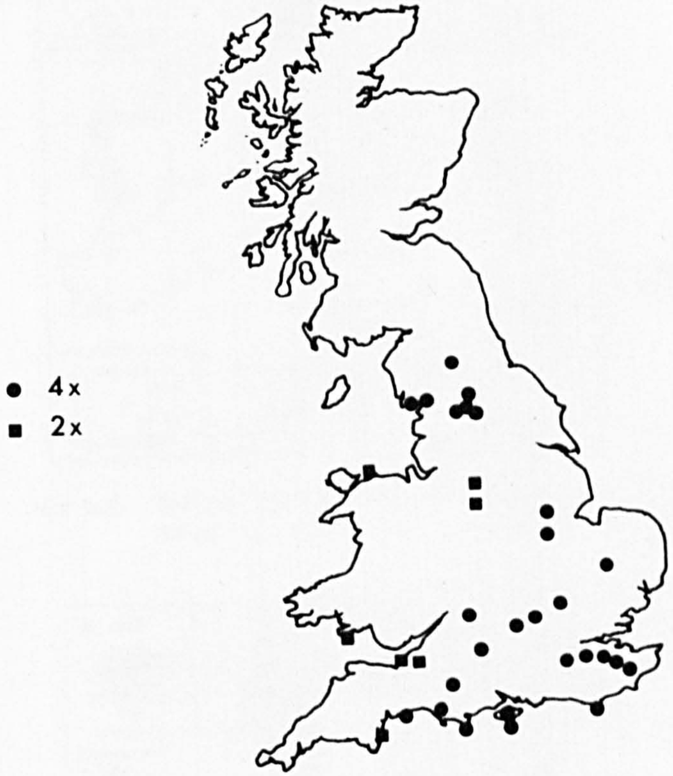
The taxonomy of the genus *Hippocrepis* has been revised by Hrabětová - Uhrová (1949) and more recently by Ball (1968). Hrabětová - Uhrová (loc. cit.) recognised the wide variation in *H. comosa* by splitting the species into three subspecies, seventeen varieties and numerous subvarieties and forms which seem to be of doubtful value. The three subspecies (ssp. *eu-comosa* Hayek, ssp. *Bourgaei* (Nyman) Hrabětová - Uhrová, and ssp. *glauca* Ten.) are distinguished mainly by the form and presence of papillae on the legume. ssp. *glauca* differs from ssp. *eu-comosa* in having very narrow hardly sinuous legumes with short white papillae, while ssp. *Bourgaei* has subarcuate almost glabrous legumes with deep sinuses and broad flattened areas between the seeds. Amongst the forms of ssp. *eu-comosa* var. *genuina* which she described are f. *gracilis* and f. *microphylla*, both of which include representatives of herbarium material from British chalk downland, showing that she recognised more than one taxon within the downland ecotype. However, she has also included herbarium material from Teesdale and from "Daddy's plain", Devon (two totally different races, both morphologically and probably cytologically) within ssp. *eu-comosa* var. *genuina*, thus showing that a taxonomic revision of this group based on herbarium material alone is impossible.

Ball (1968) in a more modern treatment elevates Hrabětová - Uhrová's subspecies to specific level, though he places *H. bourgaei* Nyman within the *H. scabra* D.C. group, which in view of the similarity between the form of legumes in this group and their distinctness from *H. comosa* and *H. glauca* seems a sensible arrangement. He states, however, that there is considerable variation in each species and that in certain areas specific differences break down and intermediate forms occur.

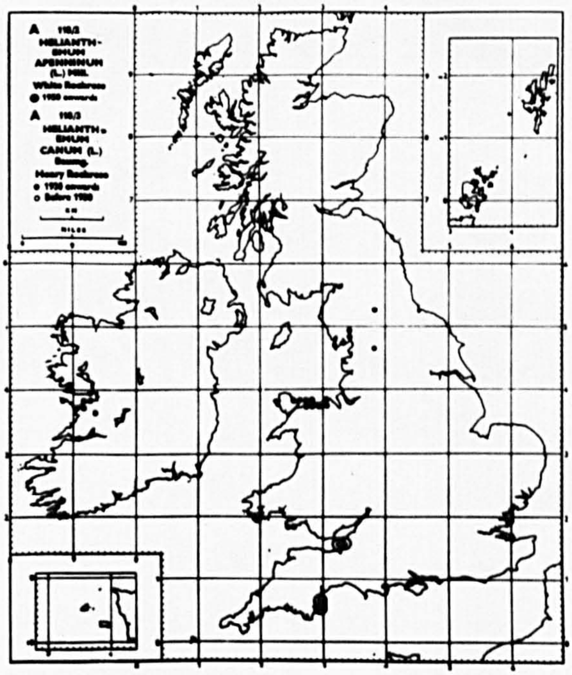
History of the distribution of cytotypes.

The three cytotypes of *H. comosa* have as far as is known very different world distributions. The tetraploid has by far the widest distribution and probably covers the whole of the world range of the species (Map 1:16p.31). Diploid populations are scattered within the range of the tetraploid, while the hexaploid race is confined to a small area of the Pyrenees.

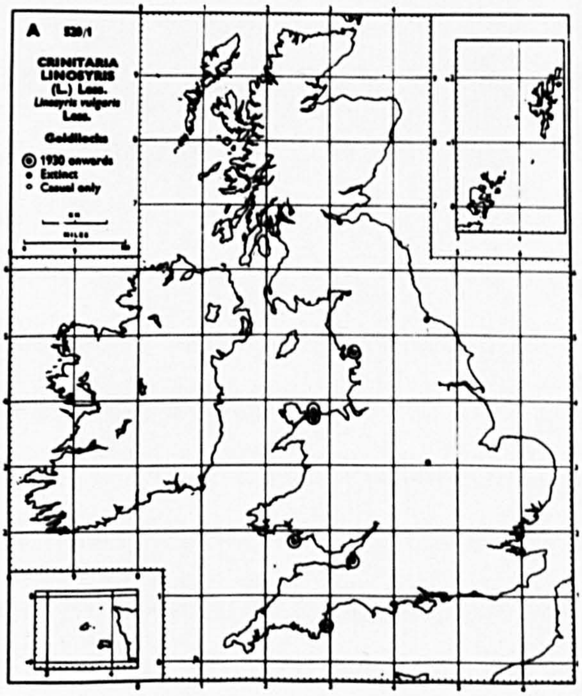
In France, diploid populations have a very irregular distribution, but in Britain they are restricted to certain areas. The British distribution of diploid and tetraploid populations which have been examined cytologically by myself or Monique Guern is shown on Map 4:1). Here the tetraploid race is again the most common and occurs mainly on chalk downland in southern England. It becomes less common in northern England where it grows on Carboniferous Limestone fells and cliffs, both in the Pennines and on the Lancashire coast, e.g. Cronkley Fell and Humphrey Head. In contrast the diploid race has a very disjunct distribution and grows only on Carboniferous or Devonian limestone cliffs, mainly in western Britain, but also in Derbyshire. The sites of diploid populations include a number of localities noted for their assemblages of rare relict species, e.g. Berry Head, Devon and Brean Down, Somerset. The distribution of the diploid cytotype of <u>H. comosa</u> shows a striking resemblance to the distribution of three relict species in particular. These are <u>Helianthemum canum</u>, <u>H. apenninum</u> (Map 4:2) and <u>Crinitaria linosyris</u> (Map 4:3). <u>H. canum</u> is a common associate of diploid <u>Hippocrepis comosa</u> in southern Britain and because of this it was thought possible that the population on Cronkley Fell might also be diploid, but it is in fact tetraploid in common



Map 4:1 The distribution of diploid and tetraploid populations of *Hippocrepis comosa* L. in Britain



Map 4:2 British distribution of <u>Helianthemum canum</u> (L.) Baumg. and <u>H. apenninum</u> (L.) Mill.



Map 4:3 British distribution of <u>Crinitaria linosyris</u> (L.) Less.

with all the other populations in northern England.

Several authors have noted the vicarious distribution of intraspecific chromosome races in other species in Britain. *Chrysanthemum leucanthemum* occurs as diploid and tetraploid races and as with *H. comosa* the tetraploid race is widespread and common, while the diploid race has a relict distribution, often occuring in coastal sites similar to those where diploid *H. comosa* populations grow. (Pearson, 1967). Another example is *Galium sterneri* where the diploid race has a relict distribution and is endemic to Britain. (Goodway, private communication). In *Campanula rotundifolia* (McAllister, 1969, unpublished) the tetraploid race is again the most widespread in Britain, while the hexaploid race is confined to northern and western districts including Teesdale.

As well as having differences in geographical distribution, diploid and tetraploid cytotypes of *H. comosa* also show differences in ecological distribution at least in Britain. The tetraploid race occurs in a variety of habitats, but is most common on grazed or formerly grazed chalk downland. The diploid race has never been found in the closed turf of grazed pastures and is restricted to open habitats, such as cliffs and rocky slopes on the older harder limestones where the plants are inaccessible to grazing animals and where competition from other plants is at a minimum. A summary of the habitats of diploid and tetraploid populations sampled is shown in Table 4:26. This Table does not represent a complete picture as a higher proportion of populations were sampled in northern England than in southern England. Hence, percentage occurrence of the tetraploid on inland cliffs is over-represented and the percentage occurrence on chalk downland is under-represented. The Table was compiled from 31 population samples with chromosome numbers counted by myself or by Monique Guern. The ecology of both cytotypes has been discussed in detail in Chapter 3.

There are several possible reasons for the restriction of diploid populations in Britain. One of these is related to differences in flower and seed production. Diploid plants produce far fewer inflorescences than tetraploids of comparable size in the experimental garden and have a mean value of only 5.5 inflorescences per plant as opposed to 42.3 for the tetraploids. Similar observations have been made in the field and as reproduction is mainly by seed, grazing will thus severely limit the reproduction of diploid plants.

TABLE 4:26

The habitats of diploid and tetraploid populations of *Hippocrepis comosa* in Britain.

Cytotype	Geology	Habitat	%occurrence
Tetraploid	Chalk	downland	39.1
Tetraploid	Chalk	earthwork	13.0
Tetraploid	Chalk	sea cliff	8.7
Tetraploid	Jurassic Oolite	roadside bank	4.3
Tetraploid	Jurassic Oolite	sea cliff	4.3
Tetraploid	Carboniferous Limestone	sea cliff	4.3
Tetraploid	Carboniferous Limestone	inland cliff	17.4
Tetraploid	Carboniferous Limestone	river bank	8.7
Diploid	Carboniferous Limestone	inland cliff	50.0
Diploid	Carboniferous Limestone	sea cliff	37.5
Diploid	Devonian Limestone	sea cliff	12.5

The diploid race does not extend as far north in Britain as the tetraploid race and all its known habitats are on warm slopes with a southern aspect mainly on the oceanic side of Britain. It is possible therefore that the diploid race may be less frost hardy and in accord with this no diploid populations were found in the Alps. Only tetraploids now occupy the areas which were covered by the last (Weichsel) Pleistocene ice sheets both in northern England (including Teesdale) and in the Alps. Tetraploids must therefore have migrated into these areas during the Post-glacial period and are therefore shown to be more aggressive than the diploids.

Manton (1934) has found a similar example in continental Europe where the tetraploid cytotype of Biscutella laevigata is abundant in glaciated alpine regions and the diploid cytotype is practically confined to unglaciated regions. There are also several other European examples with a vicarious distribution of intraspecific polyploid races related to glaciated regions. It is possible that the absence of glaciation in most of France is one of the reasons why diploid and tetraploid H. comosa populations are so irregularly distributed there.

In Britain, both cytotypes were possibly members of the late glacial steppe tundra flora in association with other species which are now either extinct or of a relict distribution, though even at that time the diploid may have been restricted to sheltered sites in western Britain. It is also possible that the tetraploid was a later immigrant from France before Britain was cut off from continental Europe at the end of the Boreal period. Since the species is shade intolerant, the majority of populations of both cytotypes would have been eliminated or severely reduced due to the development of the Post-glacial forest cover and could only have survived on cliff ledges or soils too shallow to support dense woodland. It was probably not until Neolithic and Bronze Age man began to clear the forest on the chalk that wide areas of treeless base-rich habitats became available again. These appear to have been colonised only by the tetraploid race, the diploid race, possibly because of its poorer seed production, remaining on the cliff ledges.

The tetraploid possibly arose at some time during the Pliocene period, but may not have spread widely until the Pleistocene when new ecological niches became available. As it appears to be more hardy than the diploid it would also have a selective advantage in the deteriorating climate of the cold periods. If it is an autopolyploid, it may possibly have had a polytopic origin, thus helping to explain its wide distribution and morphological variability. Alternatively, if it is an allo - or segmental allopolyploid its hybrid origin may have enabled it to colonise new and more widespread habitats. The diploid race in Britain now shows less morphological variation than the tetraploid race, possibly because of the restriction to a single type of habitat and a lower capacity for recombination. The hexaploid race probably arose relatively recently in the Pyrenees and has not yet had the time or opportunity to extend its range. It cannot be a relict race since it is necessarily derived from plants of a lower ploidy.

There are thus within this species three examples of the stages in plant colonisation described by Good (1947) in his Theory of Generic Cycles.

1. Juvenile species with a limited distribution. This is represented by the hexaploid race. As evidenced by its chromosome number it was the latest to arise.

2. Mature species with a wide distribution and wide variety of morphological types. This is represented by the tetraploid race.
3. Senile species with a limited distribution of a relict nature, scattered throughout the area it once occupied. This is represented by the diploid race which has the lowest chromosome number and which therefore was the first to arise.

Chapter 5.

General discussion.

General discussion.

The main aims of this project have been to investigate the evolution of a group of rare species selected from the flora of Upper Teesdale, as such species offer a good opportunity to study the effects of evolution on small isolated populations of plants. Associated problems have been those relating to the occurrence in Teesdale of certain species which are rare in Britain as a whole and the concentration of these species in Teesdale. In this work, investigations have been made into the variation and reproductive biology of a number of species and results from British populations have been compared with those from foreign populations in areas where the species are more common. From these results the evolutionary potential of rare species and reasons for their restricted distribution in Britain can be postulated. Suggestions are made for the conservation of such species.

A feature common to many members of the Teesdale flora, including those selected for investigation is that they reach the limits of their geographical distribution in Britain and are restricted to disjunct localities in this country. Some species such as Hippocrepis comosa are common in Continental Europe and south-eastern England but become disjunct towards the northern limits of their range. Polygala amarella and the diploid race of Hippocrepis comosa have been shown to have particularly disjunct distributions in Britain. It has also been shown that several species become ecologically restricted towards the edge of their range where the climatic regime becomes the major limiting factor in their distribution. Hippocrepis comosa for example which has a wide tolerance of edaphic conditions in Continental Europe is restricted to calcareous soils in Britain and Carex ericetorum which behaves as a calcifuge in parts of East Anglia also shows a calcicolous tendency in northern England. Pigott (1968) has shown that Cirsium acaulon which has a largely continental distribution in Europe exhibits a preference for south or south-west facing slopes in Derbyshire, near its northern limit in Britain, whereas in southern England and in Continental Europe it grows on slopes of almost any aspect. *Hippocrepis comosa* shows a parallel type of restriction and is more common on steep south-facing slopes in northern England, the Teesdale site being exceptional, while being less demanding in southern England and France.

All the species which have been investigated are restricted to treeless habitats in Britain where the vegetation cover is sparse and competition from other plants low. With the exception of *Carex paupercula*, they are also restricted to base-rich areas. Even in Continental Europe where they are more common, *Polygala amarella* and *Carex ericetorum* will only tolerate light shading. It has been suggested (Pigott & Walters 1954) that species now restricted to such habitats were members of a widespread Late-glacial Steppe tundra flora and have persisted throughout the Post-glacial period in continuously open base-rich habitats such as sand dunes, cliff ledges etc. during a period when most of the country was covered with dense forest or blanket bog. The present composition of the Teesdale flora suggests that a high proportion is relict from this Late-glacial vegetation. Recent results from pollen analyses of Teesdale peat deposits, particularly those from the Cow Green reservoir basin show a continuously high proportion of non-tree pollen in the Post-glacial record indicating that at least the tops of the fells have only been lightly forested throughout the Post-glacial period and that herbaceous species could have persisted in the semi-open conditions which prevailed. Though no pollen grains of the species investigated in this work have been identified, others eg. Dryas octopetala, Gentiana verna have been found in deposits of the period of maximum afforestation, indicating that such species have probably persisted in Teesdale since the end of the Pleistocene period.

The presence of subfossil remains of Arctic-Alpine species in Glacial and early Post-glacial deposits in southern England indicates that they formerly extended to the south of their present distribution. Remains of several Teesdale species eg. *Draba incana*, *Dryas octopetala*, *Potentilla fruticosa* have been found in Arctic beds in south-eastern England and in some cases remains from later deposits have been found in Ireland and northern England. These suggest that the range of these species has markedly declined during the Post-glacial period and that their present restricted distribution is of relatively recent origin. This restriction has been related partly to ecological and partly to climatic factors.

The present work has shown the importance of microhabitats in the establishment of populations of the selected species. Many of these species are pioneers of open habitats where the vegetation cover is sparse and competition from other plants is minimal. *Polygala amarella* seedlings only colonise the patches of scree and bare soil caused by soil creep on steep slopes. *Draba incana* is commonly found on bare sugar limestone "sand" or on old lead mine spoil heaps where the substrate consists of small calcite chippings which ensure that drainage is very free so that only a few plants able to withstand drought or tolerate heavy metals can grow. The open habitats on sugar limestone in Teesdale have recently been extended and erosion intensified by heavy grazing. Although overgrazing is deleterious to these plant communities, Watt's experiments in the Breckland (Watt 1957) show that under lowland conditions in the complete absence of grazing, tall grasses become dominant and the rare species are much reduced. Observations within an enclosure on Cronkley Fell where Sesleria albicans has become much more abundant suggest that this could also happen in Teesdale.

Biosystematic studies of several species in the Teesdale flora have shown that they are genotypically differentiated into a number of local races with a different race occurring in each of the disjunct areas. Examples such as Myosotis alpestris (Elkington 1964) and Potentilla fruticosa (Elkington & Woodell 1963) have already been quoted and now Polygala amarella and Draba incana can be added to these. Draba incana has a proportion of stellate hairs on both sides of the leaves in Teesdale plants, while in other parts of Britain it has only simple hairs on the upper surface of the leaves. There is also another morphologically distinct form which occurs in the Alps. *Polygala amarella* has a separate local race which is morphologically distinct in each area of distribution in Britain. In Teesdale the plants have small, relatively broad wing sepals, short obtuse basal leaves and acute cauline leaves. In plants from the Craven district wing sepals are long, relatively narrow and both the basal and cauline leaves have acute apices. Plants from Kent have small narrow wing sepals, short obtuse basal leaves and long, broad cauline leaves also with obtuse apices. In the examples of morphological differentiation in *Myostis alpestris*, *Potentilla fruticosa* and also of *Gentiana verna* (Elkington 1963) the differentiation is confined to one or at most two characters and no taxonomic recognition has been given to the Teesdale race. Proctor (1957) has investigated genotypic variation in *Helianthemum canum* and has found that several morphological races of this species occur in Britain. The Teesdale race differs in several characters from plants in other parts of Britain, as well as those in Continental Europe and he has accordingly given it the status of *ssp. laevigatum*. The variation of *Polygala amarella* has been treated in a similar way here and it is suggested that the Teesdale race be designated a new subspecies, though the Kent race which is incompletely distinct from continental forms is not worthy of separate taxonomic rank.

A survey of the plant communities in which Teesdale species grow has shown that in the case of northern species such as *Juncus alpinus* and *Carex paupercula* the communities in Teesdale are very similar to those containing the same species in Scotland and in Scandinavia. The communities in the Alps however tend to differ somewhat, for example *C. paupercula* is characteristic of Sphagnum bogs in northern Europe, whereas in the Alps it grows in more mesotrophic sedge-rich communities. The southern species *Hippocrepis comosa* grows in communities dominated by *Sesleria albicans* in the northern Pennines and in the Alps, but in southern England and in lowland Continental Europe it belongs to a different type of community dominated by grasses of the genus *Bromus*. An ecotype adapted to withstand heavy grazing has developed on chalk grassland and a similar ecotype seems to have evolved in Teesdale, either in response to this factor or as a climatic response. *Draba incana*, *Cochlearia alpina* and *Polygala amarella* also show ecotypic differentiation. *Draba incana* and *Cochlearia alpina* have both developed ecotypes which are adapted to withstand high concentrations of lead in the soil, while *Polygala amarella* shows ecotypic differentiation in each of its three areas of occurrence in Britain: in Teesdale it grows on damp but well-drained sugar limestone soils, in the Craven Pennines it is more common in base-rich mires, but at other localities in Craven and also in Kent it favours very dry, highly calcareous soils. The greater amount of morphological variation of this species in Craven and also the discontinuous variation between populations from different habitats there suggests that morphological variation in this species is adaptive, certain characters having a selective advantage in specific environmental conditions. In Continental Europe it also grows in a range of very dry to very wet base-rich situations, though it is becoming far less common in the latter as these are drained or infilled.

Morphological differentiation may have followed the fragmentation of a more or less continuous early Post-glacial distribution of these species into small isolated populations with limited gene flow and subject to genetic drift. Alternatively the present discontinuous variation may merely represent the remnants of more widespread polymorphic early Post-glacial populations. Bradshaw (1959) has shown that individual populations of species such as *Agrostis tenuis* which are widespread and common today can show a high degree of adaptive morphological differentiation so that it is not always necessary to invoke geographical isolation as an explanation for local race formation. The disoontinuous variation of *Polygala amarella* within the Craven district may well be the result of genecological differentiation, different leaf length/breadth ratios having a higher selective advantage in marshy or dry habitats. It would seem however that other characters in this species such as flower colour would have no direct adaptive significance and other explanations must be sought for such variation. Polygala amarella occurs in extremely small populations where chance loss of genes through gamete sampling error is probably operating and this may account for some of the discontinuities in morphological variation between adjacent populations. Both Polygala amarella and Draba incana are predominantly inbreeding species and this, superimposed upon the previous processes has further increased the chances of a high degree of homozygosity in populations of these species.

Stebbins (1942) has proposed the term "biotype depletion" to explain the low colonising ability of rare species by loss of alleles from populations but it seems unwise to invoke this as a complete explanation for the rarity of Teesdale species in Britain. The low colonising ability of *Polygala amarella* for instance, is due mainly to the small number of large heavy seeds produced by individuals. It is restricted to specialised habitats on the edge of its range and because of the presumed high degree of genetic homozygosity in the populations for reasons described above, does not now possess the ability to colonise new habitats should its present ones disappear due to some change in the environment. Allard (1965) has suggested that among predominantly inbreeding species, the successful colonisers are those with a high degree of genetic flexibility resulting from a low percentage of outbreeding within each population and the perpetuation of well adapted genotypes by inbreeding. Conversely the populations of unsuccessful colonisers are thought to consist of single biotypes which are unable to adapt to new habitats except by occasional recombination between adjacent biotypes and the perpetuation of better adapted genotypes in the progeny as new pure lines. The rarity of Polygala amarella can therefore be explained partly in genetic terms and partly in terms of low reproductive capacity.

Similar reasons can be suggested for the rarity of Draba incana, but unlike Polygala amarella this species has a higher reproductive capacity. Plants produce large numbers of small seeds which are more widely dispersed. This species is also tolerant of lead in the soil and along with Cochlearia alpina, another lead-tolerant species, has been able to take advantage of open man-made habitats, such as mineral spoil heaps. The convergence of previously isolated populations in artificial habitats in this way has presented the opportunity for a limited amount of outbreeding and a possible increase in the degree of heterozygosity.

Intraspecific polyploidy is a feature of several of the species investigated. Separate polyploid races or cytotypes of Cochlearia alpina, Hippocrepis comosa and Alopecurus alpinus occur in Britain, while Juncus alpinus and

Polygala amarella both have taxonomically closely related but cytologically distinct relatives in Continental Europe. Cytological variation in *Cochlearia alpina* is not correlated with any constantly occurring morphological differentiation and this has caused taxonomic confusion which can only be resolved by a detailed cytotaxonomic study. The two British cytotypes of *Hippocrepis comosa* have been shown to have different geographical and ecological distributions, the tetraploid being widespread especially on chalk downland and the diploid showing a relict distribution on coastal and inland cliffs on the western side of Britain. The respective distributions of the diploid and the tetraploid are discussed below in relation to historical factors and colonising ability.

Alopecurus alpinus is a high polyploid species and although the evidence is not conclusive, cytological comparisons of a Teesdale and a Scottish population suggest that these each have a different chromosome number and that the chromosome number within each population is fairly constant. Due to cytological irregularities at meiosis, the chromosome numbers of sexually produced progeny are likely to be different from one another and from their parents. That this is not the case suggests that these populations are reproducing solely by vegetative means. Self-incompatibility under growth room conditions and lack of seed production in wild populations supports the theory that the wild populations which have been examined each consist of a single clone. Harberd (1967) has shown that grasses in other genera eg. Holcus and Festuca are able spread clonally over wide areas and it seems probable that this is also the case in Alopecurus alpinus. The evolutionary potential of these populations is therefore extremely low.

The Arctic-Alpine element is well represented in the Teesdale flora and as it is known that Arctic floras possess a high degree of polyploidy, it seemed of interest to investigate the degree of polyploidy in the flora of Teesdale. All the species (excluding bryophytes and lichens) mentioned by Pigott (1956) in his description of the vegetation of Upper Teesdale were scored accordingly as being diploid or polyploid. Only species with known British and preferably Teesdale chromosome counts were used. On this basis it was found that 66.6% of 183 species in the Teesdale flora are polyploid. This figure corresponds closely to that of 65.8% for the flora of Iceland (Löve & Löve, 1953) and that of 64.0% for Kolguev Island in the Arctic Ocean (Sokolovskaya & Strelkova, 1941). It contrasts with calculated figures for lowland temperate regions such as Denmark (53.5%, Löve & Löve, 1949) and for Great Britain as a whole (53.3%, Tischler, 1955).

Several authors have noted the high percentage of polyploids in floras of Arctic or otherwise "unfavourable" regions. Sokolovskaya & Strelkova (1962) relate degree of polyploidy in grasses to distance from the centre of origin. As evidence for this they quote that the Mediterranean region where diploid species abound is generally assumed to be the centre of origin of the Gramineae and that most of the highly polyploid species occur in distant regions such as the Arctic. Other authors have attributed the high degree of polyploidy in Arctic regions to the greater hardiness of polyploids and in some cases such as Hippocrepis comosa this may be so, but Bowden (1940) found that the results of an experiment which he conducted on the winter hardiness of a large number of diploid species and their related tetraploids did not in general support this hypothesis. Hagerup (1927) and Sokolovskaya & Strelkova (1962) have suggested that low temperatures may upset cell division with consequent formation of polyploid gametes, but there is no evidence in favour of this. Flovik (1940) suggested that the increase in chromosome number increases potential diversity leading to the production of races which are able to colonise new and adverse habitats. Stebbins (1970) extends this theory and gives evidence to show that the highest proportions of polyploidy are found in the floras of areas which have been glaciated or disturbed by man and not necessarily in areas where the present climate is particularly cold. He attributes this to the superior aggressiveness of polyploids which are able to colonise new areas which their diploid predecessors cannot. In the present work, the tetraploid race of Hippocrepis comosa has been shown to be more aggressive than the diploid and has colonised glaciated areas in Britain and in the Alps, as well as chalk downland which was deforested by man during the Bronze Age. This greater aggressiveness can possibly be attributed to inter- or intra-specific hybridisation before polyploidy resulting in a high degree of heterozygosity. In the tetraploid, variability has been maintained by outbreeding within and between large populations, while the less variable diploid race is restricted to small, isolated, effectively inbreeding populations in habitats which probably escaped at least the final glaciation in Britain. The high percentage of polyploidy in the Teesdale flora can therefore be partly attributed to the effects of glaciation and partly due to the effects of man in causing disturbed and open habitats.

Any investigation of rare plants inevitably raises the problem of conservation. With the increasing effects of man's activities on the countryside, the habitats of wild species in general and rare species in particular are declining rapidly. It is essential that the few remaining populations of rare species should be preserved, partly simply to prevent their extinction and partly to maintain the size of the gene pool of the species. *Polygala amarella*, for example is differentiated into a number of morphological and ecological biotypes. If one group of habitats is destroyed, the gene pool of the species is correspondingly decreased in size and the species will become even more restricted ecologically. It is therefore necessary to retain the diversity of habitats to which different biotypes are adapted. *Polygala* amarella is particularly rare now in fen habitats in Continental Europe which have mainly been drained or infilled and its existence in Kent is also very precarious. It has become extinct at several sites recently, due to overcollection or changes in land use, the extent of grazed chalk downland having been greatly reduced in the last 50 years or so.

It is not enough simply to retain the habitats of rare species. They must be maintained in their present condition so that the normal succession from pioneer species to shrubs and trees does not take place, since these photophilic species would soon die out. It is unlikely that trees would become established on the fells in Teesdale, but it is probable that the growth of tall grasses may crowd out rare species of lower competitive ability in Teesdale and elsewhere. Controlled grazing is therefore necessary for the maintenance of rare species in chalk or limestone turf. Grazing in spring and early summer prevents the flowering and ripening of seed in erect species, so to be most effective, it would be preferable to limit grazing to summer and autumn. Alternatively, areas could be divided into plots which were grazed in alternate years.

Investigations into the reproductive biology of several species have suggested that their restricted range could be increased by human intervention. The grass Alopecurus alpinus appears to be unable to reproduce sexually in the small wild populations which exist today because of self incompatibility and clonal spread. The artificial pollination of plants with pollen from another population should increase heterozygosity and restore variability to this species and possibly increase its chances of colonising new habitats. Similarly, foreign pollen could be used to restore variability to the other inbreeding species such as Draba incana and Polygala amarella. There is a danger here, however, of disrupting the variation pattern, but it is thought that natural selection should stabilise this, so that after a few generations a new adaptive norm would be reached. In the absence of the conservation methods suggested above it is clear that the continual destruction of their specialised habitats by man will eventually cause these rare species to become extinct.

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