VARIATION IN *MELAMPYRUM PRATENSE* L.

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ABSTRACT

Melampyrum pratense is morphologically extremely variable in Britain and this variability has been found to occur at three levels. There is geographical variation brought about by climatic selection from a basic pattern. Superimposed upon this geographical variation is ecological variation caused by selection in different habitats. The third level of variation is brought about by the random isolation of particular genotypes in individual populations leading to minor but detectable differences between populations in similar ecological habitats.

It was found that there are two morphologically separable groups within *M. pratense* which differ also ecologically in Great Britain and these have been given subspecific rank: subsp. *commutatum* is restricted to base-rich habitats in southern England; the remaining British populations belong to subsp. *pratense*.

INTRODUCTION

Melampyrum pratense is an annual hemiparasitic member of the subfamily Rhinanthoideae of the Scrophulariaceae. The plant is found throughout most of Great Britain and Ireland, and in Britain usually occurs as small isolated populations of up to about two hundred plants. In this account only British plants are dealt with, as insufficient material from Ireland was seen.

PARASITOLOGY

Melampyrum pratense, in common with other members of the Rhinanthoideae, parasitises host plants by means of root haustoria. This parasitic habit appears first to have been noted by Decaisne (1847) and the nature of the parasitic attachment has been studied in considerable detail by subsequent authors.

Little is known of the physiology of the parasitism of the Rhinanthoideae but from field observations of *M. pratense* it is possible to suggest what some of these physiological requirements might be. In Britain, the seeds of *M. pratense* germinate about December and develop an extensive root system, but little vegetative growth takes place beyond the production of cotyledons until March. If the roots become attached to a suitable host during this period rapid growth commences towards the end of March and flowering begins within six to eight weeks. If no contact with a host is made the cotyledons expand and two or three pairs of very diminutive stem leaves are produced, after which growth ceases. During May and June these undeveloped plants gradually wither away. Plants of *M. pratense* do not appear to be able to parasitise one another, unlike species of *Euphrasia* (Yeo 1961).

Plants of *M. pratense* are able to thrive on soils which are exceedingly low in nutrients. Growth of other vascular plants in such habitats is extremely slow in comparison with *M. pratense* which reaches its full size in a matter of a few weeks. It seems that this can only be by the acquisition of nutrients from the host plants and it is evident that, in nutrient-deficient habitats at least, the species obtains a considerable proportion of its nutrients from the host.

It has been suggested by J. L. Harper (personal communication) that the requirement is for growth substances and that these are responsible for the rapid burst of growth mentioned above. It is difficult to conceive of this occurring without the acquisition of nutrients

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from a host, particularly on poor soils, so that whilst it may be possible that growth substances are necessary, these are not the sole requirement.

The ability to parasitise also appears to be important in connection with water relations. During a dry period in the summer of 1959 a perfectly healthy population of *M. pratense* was seen in a wood on Keston Common, Kent, in which other herbaceous plants were dead or severely wilted. In this locality *Melampyrum* was presumably growing on the roots of tree species. A similar situation was noted in an experimental plot at Oxford when, after a period of drought during which weeds were dead or dying, young plants of *M. pratense* parasitic on *Betula* and *Calluna* were growing vigorously. *M. pratense* is a shallow rooted species but is evidently able to obtain a fully adequate water supply from the host species and is thus independent of soil water.

Host plants

It is frequently assumed that *M. pratense* parasitises herbaceous plants but all the evidence suggests that the hosts are woody plants. Although it is rare for populations to occur without any associated herbaceous species, *M. pratense* is never found away from trees or shrubs and, in parts of northern Britain where large woody plants are absent, it is associated with *Calluna, Erica, Myrica* or combinations of the three.

It is extremely difficult in the field to trace root connections and it has not been possible to determine whether *M. pratense* parasitises herbaceous plants, but from the fact that it never occurs solely with these plants, this is unlikely. In several populations examined, connections have been traced between *M. pratense* roots and those of *Quercus robur, Corylus avellana* and *Betula pubescens*. In cultivation experiments the plant has been successfully grown on *Betula pubescens, Calluna vulgaris* and *Rubus fruticosus*, but not on herbaceous plants. From field observations it is clear that *Fagus sylvatica, Sorbus aucuparia, Quercus petraea, Vaccinium myrtillus, V. oxycoccus, Erica tetralix* and *Myrica gale* are also host plants.

Whilst it is evident that *M. pratense* can parasitise a number of woody species—it is not clear whether particular populations are host-specific. Bog populations in northern Scotland do not spread to neighbouring birch woods where the plant might be expected to grow. In the New Forest, Hampshire, it is always associated with trees, although in certain other parts of the country it grows on *Calluna, Erica* or *Myrica*, all three of which occur in the New Forest.

ECOLOGY

M. pratense shows considerable ecological diversity and populations from different types of habitats tend to be morphologically different. The three main types of habitat in Britain are (i) calcareous scrub and woodland, (ii) acid woodlands and (iii) bogs. These habitats are subdivisible as follows:

(i)　*A.*　chalk and limestone habitats.
(ii)　*B.*　acid woodland in the New Forest, Hampshire.
　　　C.　other acid woodland habitats in southern England (neogenic region).
　　　D.　acid woodland habitats in south-west England (palaeogenic region)
　　　E.　acid woodland habitats in northern England
　　　F.　acid woodland habitats in Scotland
(iii)　*G.*　bogs in northern Scotland
　　　H.　bogs in northern England

The most commonly associated species in each habitat are listed in Table 1. Those of types *E* and *F* are so similar that they are listed together. The acid woodland habitats were grouped into four types because of geographical differences and likewise the two bog types. Neogenic and palaeogenic regions of southern England were considered separately as it was thought that plants from these areas of different origin might differ morphologically.

TABLE 1. Commonly associated species from the different ecological types

Ecological type	A	B	C	D	E & F	G	H
Acer campestre	+	—	—	—	—	—	—
Anthoxanthum odoratum	—	—	—	—	+	—	—
Betula spp.	—	—	+	+	+	—	—
Calluna vulgaris	—	—	—	—	—	+	—
Corylus avellana	+	—	+	—	—	—	—
Crataegus monogyna	+	—	+	—	—	—	—
Deschampsia flexuosa	—	—	—	—	+	—	—
Drosera spp.	—	—	—	—	—	+	—
Erica tetralix	—	—	—	—	—	+	+
Eriophorum spp.	—	—	—	—	—	+	+
Hedera helix	+	+	—	—	—	—	—
Holcus lanatus	—	—	+	—	—	—	—
Ilex aquifolium	—	+	+	+	—	—	—
Myrica gale	—	—	—	—	—	+	+
Molina caerulea	—	—	—	—	—	+	—
Narthecium ossifragum	—	—	—	—	—	+	—
Potentilla erecta	—	—	—	—	+	+	—
Potentilla palustris	—	—	—	—	—	—	+
Pteridium aquilinum	—	+	+	+	+	—	—
Quercus robur	+	+	+	+	+	—	—
Quercus petraea	—	+	+	—	—	—	—
Rubus fruticosus	+	+	+	—	—	—	—
Solidago virgaurea	—	+	—	—	—	—	—
Teucrium scorodonia	—	+	—	—	—	—	—
Thelycrania sanguinea	+	—	—	—	—	—	—
Trichophorum caespitosum	—	—	—	—	—	+	—
Vaccinium myrtillus	—	+	—	+	+	—	—
Vaccinium oxycoccus	—	—	—	—	—	—	+
Viburnum lantana	+	—	—	—	—	—	—

In southern England, populations occupy two very different habitats; chalky or lime-stone soils with a pH of 6·8 or more, and acidic soils with pH values of up to about 5·5.

On the chalk of Kent, Surrey, Hampshire and Oxfordshire, *M. pratense* usually occurs on the edge of scrub and chalk grassland or as a hedgerow plant. Populations of *M. pratense* are also found in similar habitats on the oolitic limestone of the Cotswolds and the carboniferous limestone of the Wye Valley and associated species are much the same.

On acid soils in southern England *M. pratense* usually occurs at the edges of rides, paths or roads through woods, or in clearings, and in common with populations from calcareous habitats only thrives in light shade or in the open. Where shading becomes heavy the number and vigour of the plants is reduced.

Populations from woodland in the New Forest are quite characteristic in appearance and differ very much from other southern forms but are sometimes indistinguishable from plants from Scottish bogs. They differ from these, however, in always being associated with trees. As will be mentioned later, the New Forest populations of *M. pratense* form a disjunct feature in an otherwise more or less continuous picture of variation in southern England.

In south-west England and Wales *M. pratense* grows in habitats very similar to the acidic woodlands of southern England but populations also occur on shallow soils and on steep and often rocky banks. This type of habitat is the one most commonly found in northern England and parts of Scotland and plants from such habitats are morphologically similar. As *M. pratense* is an annual it is clear that in these places where the soil is so shallow and nutrient-deficient the ability to thrive is closely correlated with the parasitic habit.

All the habitats so far described are usually well drained, but there are two types of habitat where this is not so. These are blanket bogs in northern Scotland and bogs or mosses in northern England. In Ross, Sutherland and Caithness *M. pratense* was found growing in considerable quantity in boggy flushes and waterlogged peat.

In the only two known bog habitats visited in England, at Wybunbury Moss, Cheshire, and Brigham Moss, Cumberland, the associated species differ somewhat from the Scottish bogs and the plants of *M. pratense* are rooted in *Sphagnum* rather than in peat.

From an investigation of *M. pratense* in the field the following points were apparent:
(i) Plants from ecologically different habitats are frequently morphologically distinct.
(ii) Plants from habitats with a low nutrient status are generally smaller than those from richer soils.
(iii) The host plants from various habitats are not necessarily the same.

From these points two questions arise. First, whether morphological differences are phenotypic or genotypic, and secondly, whether the apparently different morphological races are host-specific. A series of cultivation experiments were carried out in an attempt to answer these questions.

CULTIVATION EXPERIMENTS

Although up to 50% of the seeds sown (with or without a host) germinated, only about 0·5% reached maturity and because of this the value of the results obtained from the cultivation experiments was much reduced.

Samples, each of twenty seeds all from one population, were sown in pots with forty-three of the most commonly associated species, but only two plants matured, one on *Betula pubescens* and one on *Rubus fruticosus*, and it was not possible to come to any conclusion concerning host range.

In another experiment seeds were collected from seventy-five wild populations as follows:—

Acid woods	50 samples
Scottish bogs	15 samples
Calcareous habitats	9 samples
Wybunbury Moss, Cheshire	1 sample

Twenty seeds were sown from each sample under the following conditions:
(i) Acid ground (pH 4·5) with *Betula pubescens* as host in a forestry nursery bed at Bagley Wood, Berkshire.
(ii) As (i) but with *Calluna vulgaris* as host.
(iii) Calcareous ground (pH 8–8·2) with *Betula pubescens* as host at the Botany School, Oxford.

Of the seeds sown on *Betula pubescens* one or more plants from five samples reached maturity as follows:

Four plants of sample 90 from an acid woodland from which *Betula pubescens* was absent. Although the soil in Bagley Wood was much richer than that from which the seed had been collected, morphologically the plants were indistinguishable from the wild population.

One plant from sample 80 and two from sample 84, both from Scottish bogs. Again *Betula pubescens* was not present in the original locality, and soil conditions were very different. The plants were morphologically indistinguishable from those of the populations from which the seeds were collected, apart from the plant from sample 80 which was shorter.

Two plants from sample 100 and one from 103, both from calcareous habitats. The plants from sample 100 were very stunted and died as soon as flowering started, but the plant from sample 103 was normal although growing in acid soil.

Only three of the seeds sown on *Calluna* reached maturity. Two of these came from and were indistinguishable from the sample collected from Wybunbury Moss, Cheshire, despite the very different habitat.

The other plant was from sample 107 and grew perfectly satisfactorily on *Calluna vulgaris* which was absent from the original calcareous habitat.

It is evident from these experiments that whilst seeds of *M. pratense* germinate freely,

even in the absence of a host, establishment on a host appears difficult. In a wild population examined near Oxford in May, a number of undeveloped seedlings like those described previously were found, although not in the great proportions (about 99%) found in cultivation. It is evident that the plant is difficult to grow successfully but the reasons for this are not apparent as plants that did grow had come from a variety of very different habitats.

Although the cultivation experiments were not successful as a whole, certain conclusions can be drawn from them in combination with field observations.

M. pratense does not necessarily appear to be host-specific beyond being confined to woody species. That there is a lack of specificity for any particular woody species, in some populations at least, is shown by the ability to grow on *Betula* or on *Calluna* when not previously associated with these species. However, as mentioned earlier, *M. pratense* does not appear to be able to spread from one habitat with certain associated woody species to a neighbouring habitat in which different species are present.

Plants grown in cultivation under very different conditions from those appertaining in the wild did not differ morphologically (with the exception of height in sample 80 and the stunted plants of sample 100) from the populations from which they originally came. It would seem, therefore, that for these populations at least, population differences are genotypic rather than phenotypic.

MORPHOLOGICAL CHARACTERS

A large number of morphological characters have been used by previous authors for the discrimination of various subspecific taxa. Attempts to name forms using descriptions of Ronniger (1914), Beauverd (1916), Soó (1928), Britton (1943) and Jasiewicz (1958) frequently failed, either because of the inadequacy of the descriptions, or because the plants in question did not fit any prescribed taxon. Many of the taxa are based on different numbers of parts or ranges of size and when a large number of specimens are examined it is often found that variation in the particular characters is continuous. Some of the subspecies and varieties are based on minor morphological variants and two or more can often be found in the same population.

The most recent account dealing with British forms is that of Britton (1943) in which some eleven subspecies, seventeen varieties and ten forms of *M. pratense* are described.

From examination of herbarium material it was evident that morphological variation in *M. pratense* is to some extent correlated with geographical distribution and, in order to investigate this further, 140 random samples of 25 plants each were collected from four main areas of Britain (southern and northern England, and central and northern Scotland). These areas were selected as being those in which the species is most abundant.

On attempting to group the populations objectively by eye it was found that there were several morphological groups, linked by intermediates which had an ecological basis. It was also clear that the ecological groups corresponded with those described earlier. Similar results were obtained using scatter diagrams. As it was not possible to separate all the samples into discrete groups, either by eye or by the use of diagrammatic methods, it was decided to classify populations on the basis of geographical distribution and habitat in order to analyse the variability biometrically.

The characters selected for examination are listed below and were selected either because they had been regarded as important by previous authors or because they were considered to be amenable to statistical analysis.

1. Length of hypocotyl.
2. Height.
3. Number of sterile nodes and total number of nodes
4. Number of pairs of cauline and intercalary leaves.
5. Branching habit.

6. Number of sterile and fertile branches.
7. Presence or absence of cotyledons at maturity.
8. Shape and size of cauline leaves.
9. Number of pairs of entire and toothed bracts.
10. Degree of toothing of bracts.
11. Calyx length.
12. Corolla length and colour.
13. Anther and anther-appendage length.
14. Pollen size.

For conciseness the ecological types are referred as *A, B, C*, etc., as described on page 337. Type *H* has been omitted as there were only two samples of this type.

STATISTICAL ANALYSIS OF MORPHOLOGICAL CHARACTERS

A biometric analysis of certain of the listed characters was carried out to obtain comparative information on the morphology and also on the degree of genetic variability in the different ecological types and to see if any of the morphological differences were of taxonomic significance. Twelve selected populations were also compared. Seven of these populations were from bogs in Sutherland and five from chalk habitats in Kent. These were selected in order to compare two groups of populations differing widely ecologically and geographically from the point of view of morphology and genetical variability.

Morphological differences and genetic variability in plant populations can be investigated by means of analyses of variance of means and standard deviations. The method used for *M. pratense* was based on that described by Day & Fisher (1937) for the analysis of populations of *Plantago maritima*.

In the analysis of genetic variability it is necessary to make an allowance for the wide diversity of some of the mean values (Day & Fisher 1937), e.g. mean heights vary from about 6 to 37 cm. Differences in means might be expected to be accompanied by similar differences in the standard deviations. If this were so, analysis of variance of the standard deviations would supply little further information than the analysis of the means.

It is possible to compare variabilities by dividing the standard deviation by the mean and obtaining a 'coefficient of variation.' This method would be satisfactory if an increase in the mean carried with it a proportional increase in the standard deviation. In biological material this is not always so (Day & Fisher 1937).

To eliminate the effect of widely differing means when comparing variabilities, an analysis of covariance of the means and the standard deviations of the populations must be carried out.

An analysis of covariance of means and standard deviations was carried out on characters 2, 8, 11, 12 and 13 and an analysis of variance on 3, 4, 9 and 10.

Where differences among types or populations are significant, the least significant difference is estimated using the Student-Newman-Keuls' test (Steel & Torrie 1960). This method is used because the estimation of the least significant difference using the usual *t*-test is suitable only for independent comparisons involving two means. When more than two means are compared the comparisons are non-independent and the *t*-test is not a truly valid criterion. The Student-Newman-Keuls' procedure takes into account the number of means.

As the number of populations from each ecological type was not equal (numbers varying from six to twenty), the least significant difference was estimated using the following formula:

$$q \; \alpha(p,n) \; s \; / \; \tfrac{1}{2} \left(\frac{1}{r_i} + \frac{1}{r_j} \right)$$

where $q \; \alpha$ is a value read from a table (Table A8, Steele & Torrie 1960) and

p = number of means
n = number of degrees of freedom of the error variance
α = 5 % or 1 % level of significance
s = error variance
r_i, r_j = number of observations in means for desired comparison.

Tables 2, 3, 4 and 5 show the significant differences between means and variabilities of the ecological types and selected populations.

TAXONOMIC VALUE OF MORPHOLOGICAL CHARACTERS

(i) *Length of hypocotyl*

Hypocotyl length was not treated statistically as from field observations it was clear that length varies very much with density of surrounding vegetation. Length also varies with the depth of burial of the seed and this is important in view of the seeds being dispersed by ants. Although hypocotyl length has been used by Britton (1943) as a taxonomic character it cannot be regarded as having any value.

(ii) *Height*

All measurements of height refer to the length of the main axis from the cotyledonary node to the stem apex. Total height is unsatisfactory because of the variable length of the hypocotyl. Height decreases markedly northwards (Fig. 1), but as can be seen from
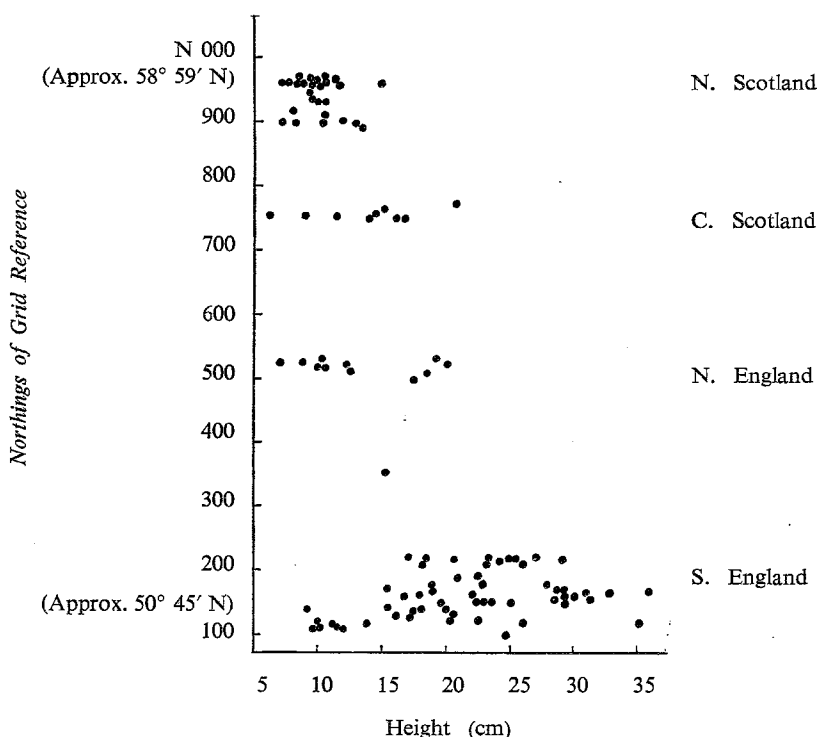
Fig. 1. Geographical scatter diagram of height showing diminution of height of populations northwards.

Fig. 2, variation is almost continuous so that there are no clear groupings based on height alone, although in combination with characters such as leaf shape, ecological types *A* and *G* form two groups only partially merging with other populations. Height has been widely used in the delimitation of subspecies and varieties but its unsuitability is seen from the description of the subsp. *vulgatum* (Pers.) Ronn. in which height is said to vary from 10 to 50 cm. This covers almost the whole range of heights of all other forms of *M. pratense*.

(iii) and (iv) *Number of nodes and sterile nodes on the main axis and pairs of cauline and intercalary leaves*

These characters are taken together because the sum of pairs of cauline and inter-calary leaves is equal to the number of sterile nodes. Considerable importance has been attached by previous authors to the node at which the inflorescence commences (*i.e.* sterile
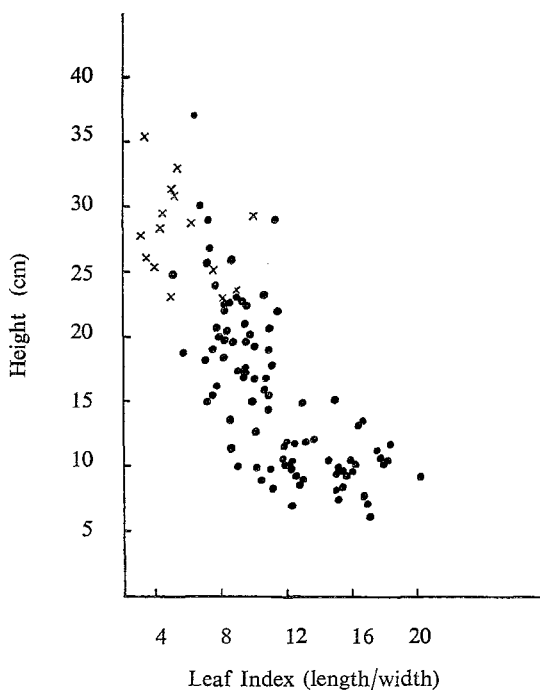
Fig. 2. Height plotted against leaf index. Crosses, populations from calcareous habitats; solid dots, all other populations.

node number plus one) and the relative numbers of cauline and intercalary leaves. Cauline leaves are those leaves with axillary branches, and intercalary leaves the leaves without axillary branches between the cauline leaves and bracts.

It is not always possible to distinguish between intercalary leaves and bracts as the lowest flower buds, in the axils of untoothed bracts, sometimes abort and fall off, especially if the plant is growing in deep shade. Further, in old plants dehisced fruits are also lost so that the number of intercalary leaves is not a satisfactory character. It is of interest to note, however, that populations of type *A* and type *G* do not differ significantly with

regard to intercalary leaf number but differ from all other populations. As type *A* is found in southern England and type *G* in northern Scotland, this upsets the south-north geographical cline in this character (see Fig. 3.).
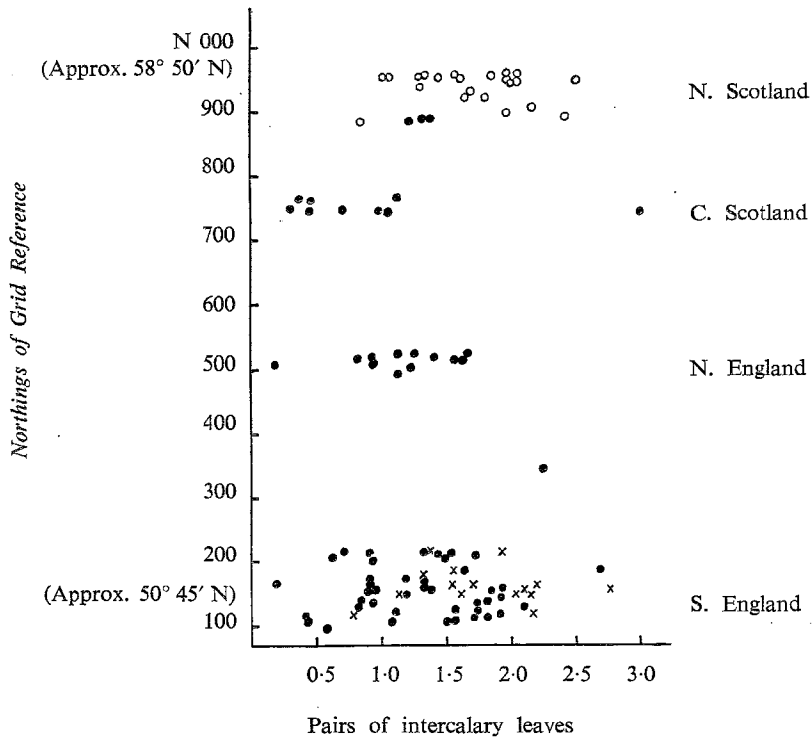

Fig. 3. Geographical scatter diagram of number of pairs of intercalary leaves showing similarity of northern bog populations (open circles) and populations from calcareous habitats (crosses).

    Britton (1943) separates six of his subspecies into two groups on the basis of cauline leaf number and the position of the inflorescence. Four subspecies are defined as having one pair of cauline leaves and the inflorescence commencing at nodes 2-3-(4). The other two are said to have 1–3 pairs of cauline leaves and the inflorescence commencing at nodes 4–5. Identification of forms so described is frequently impossible as there is considerable variation in the number of sterile nodes, cauline and intercalary leaves both within and between populations. There appears to be no correlation between number of parts and habitat in Britton's taxa and hence these taxa appear to be of little significance.

(v) *Branching habit*

    The angle of branching varies from horizontal to almost vertical and from cultivation experiments appears to be genetically controlled. The character was not analysed for two

reasons. Firstly, in pressed specimens the branches were distorted. Secondly populations where the main axis was prostrate had branches which were likewise horizontal but rose vertically at the tips and these were difficult to compare with other populations. The character might have proved of interest if analysed in the field.

(vi) *Number of sterile and fertile branches*

Although this character has been used taxonomically it is of little use, as the proportion of sterile to fertile branches decreases with age and unless all populations are sampled at the same time comparisons are not valid.
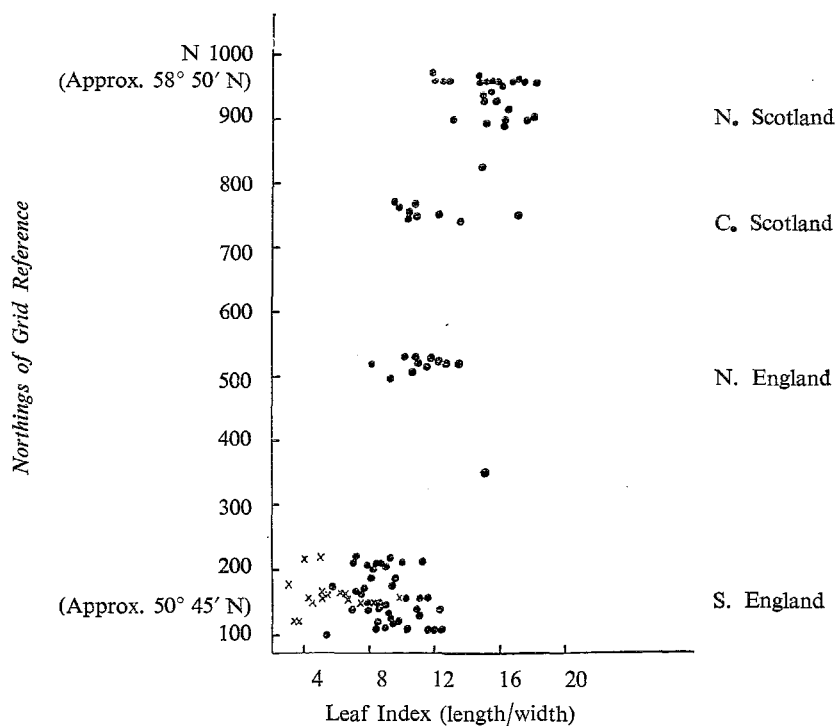
Fig. 4. Geographical scatter diagram of leaf index (length/width) showing narrowing of leaves northwards. Solid dots, populations from acid habitats; crosses, populations from calcareous habitats.

(vii) *Presence or absence of cotyledons at maturity*

This character is again affected by age, although in populations of small plants the cotyledons are frequently still present when flowering commences. With large plants the stems become woody at the base and the cotyledons are lost. As with the number of sterile and fertile branches, all populations would have to be sampled at the same time and allowance would have to be made for the effect of climatic differences on the rate of growth due to geographical distribution and altitude.

(viii) *Cauline leaves*

Leaf shape is one of the most conspicuously variable characters of *M. pratense* and a number of infraspecific taxa have been largely based on leaf shape. One of these, subsp. *commutatum* (Tausch) C. E. Britton (1943), is defined as having lanceolate to ovate leaves, all other forms having narrower leaves. From field observations, examination of herbarium

specimens and statistical analysis, this subspecies, corresponding with ecological type *A*, appears to be more distinct than any others described.

Leaf shape is closely correlated with geographical distribution and height, as can be seen from Figs. 4 and 2. A measurement of leaf shape is obtained from the length/breadth ratio of one of the uppermost pair of cauline leaves of each plant. Length is total length of the leaf and width is measured across the widest portion. In Fig. 5, where leaf length is plotted against leaf width, it is clear that there are two patterns of variation, one made by plants from calcareous habitats and the other from the remaining populations.

Plants from calcareous habitats, with the exception of some populations from Kent, are quite distinct with regard to leaf shape from all other populations, the leaves being ovate to ovate-lanceolate instead of lanceolate to linear-lanceolate. Despite some of the Kentish populations inter-grading in leaf shape with populations on non-calcareous soils in the same area, type *A* populations are significantly different from all other populations in leaf shape.

(ix) *Number of entire and toothed bracts*

This character does not appear to be of much use taxonomically, as the number of entire bracts is correlated with height, short plants having more entire bracts than tall plants.
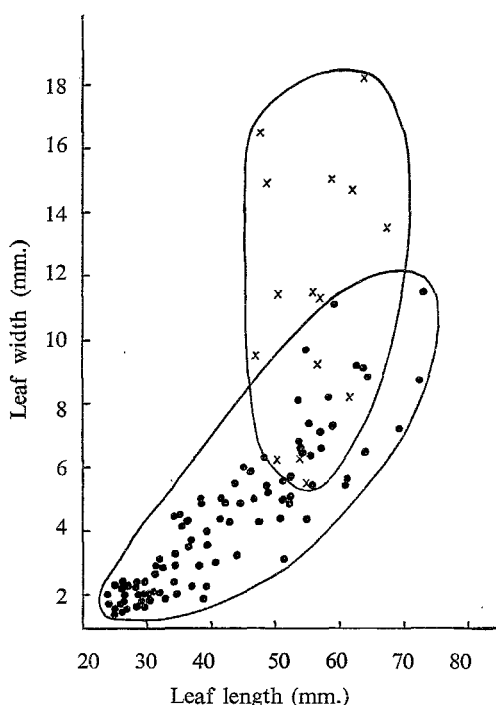

Fig. 5. Leaf width plotted against leaf length showing difference between plants from calcareous habitats (crosses) and other populations (solid dots).

(x) *Degree of toothing of bracts*

The number of teeth per bract varies very greatly from population to population. The various British taxa are described as having few to many teeth per bract, with teeth small and blunt to long and acuminate. Usually the number and size of bracts and the extent of toothing is correlated. If the bracts are few in number they tend to be small with

blunt teeth and, if numerous, are larger with long acute teeth. Because of the great variability in toothing of bracts, both within and between populations, and because the nature of the teeth depends upon the number of bracts, the toothing of bracts is not a good character.

(xi) *Calyx length*

The calyx of *M. pratense* is four-lobed, with the two upper lobes frequently longer than the lower. The calyx becomes enlarged in fruit and all measurements were made on the oldest flower of a stem or branch. The length of the calyx tube is relatively constant throughout the country but total calyx length, measured from the base of the calyx to the apex of the longest tooth, was found to be very variable.

The mean calyx length of populations examined varies from about 3·5 mm to 7·8 mm, and there is a higher proportion of populations with long calyces in the north of Britain than in the south.
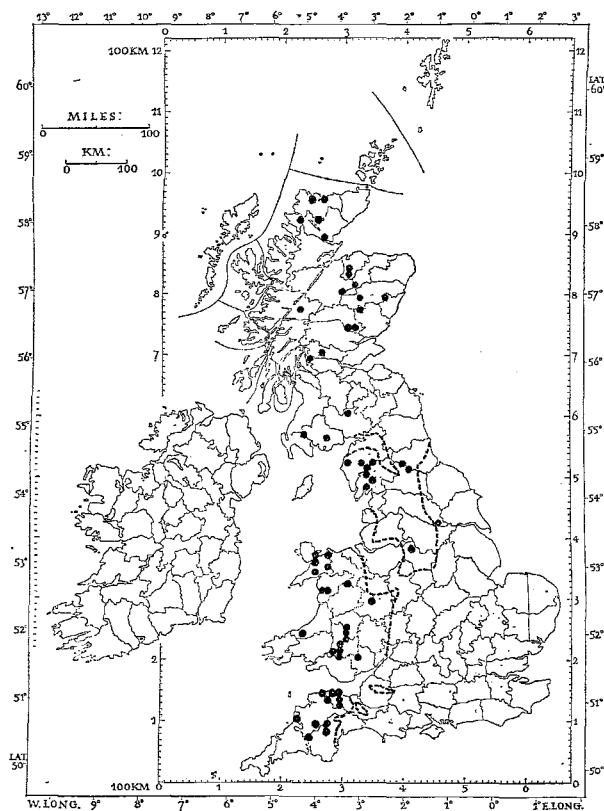

Fig. 6. Distribution map of the golden-yellow flowered form of *M. pratense* (var. *hians* Druce). The dotted line roughly divides the western palaeogenic regions of Britain from the south-eastern neogenic regions.

(xii) *Corolla length and colour*

Variation in corolla colour is a conspicuous character and there are three distinct colour forms which do not merge. The first type has a whitish or pale-yellow corolla tube with a pale-yellow mouth. This is widespread throughout Britain. The second type of flower is uniformly golden-yellow, sometimes verging on orange. This occurs as pure populations and apart from an unconfirmed record from Sussex appears to be restricted to palaeogenic regions of Britain (Fig. 6). It also occurs in Ireland but there are insufficient

data to gain an adequate idea of its distribution. It appears to be very rare or absent on the Continent. The golden-yellow form was first described by Druce (1884) as var. *hians* and was raised later to subspecific rank but, apart from flower colour and geographical distribution, there is nothing to distinguish it from other forms of *M. pratense*.

The third colour form which is limited to northern Britain has a pale-yellow or whitish corolla tipped with crimson and usually occurs mixed with plants with pale corollas. It is found in Scandinavia and in mountainous areas of other parts of Europe. It does not normally occur in pure populations in Britain and does not show any particular geographical distribution other than tending to be northern and montane.

In the first important monograph on the genus *Melampyrum* (Beauverd 1916) great stress is laid on the colour of the corolla after anthesis in *M. pratense* and the two subspecies are based on this. In subsp. *eu-pratense* Beauv. the corolla is said to become purple to pale red after anthesis and in subsp. *vulgatum* Pers. the corolla becomes blackish. Britton (1943) follows Beauverd and, although he recognises more subspecies, these are in two groups corresponding to the original two subspecies of Beauverd. It is not clear either from Beauverd or from Britton whether anthesis means (correctly) opening of the flower or (incorrectly) shedding of pollen.

In many of the populations examined, the flowers became slightly to markedly pinkish as they began to wither. The anthers usually burst just after the flowers open but there is no change in colour until the flowers begin to wither. No blackish corollas were seen other than decaying ones that had not fallen off. From vegetative characters a number of the populations could be allocated to varieties of either of Beauverd's subspecies when flower colour was ignored. If, however, flower colour was taken into consideration it was impossible to name many of the populations simply because none had blackish corollas. It is impossible to identify pressed specimens using either Beauverd's or Britton's descriptions as corolla colour is lost on drying and identification can only be made by comparison with specimens named by Beauverd or Britton. It is considered that corolla colour either
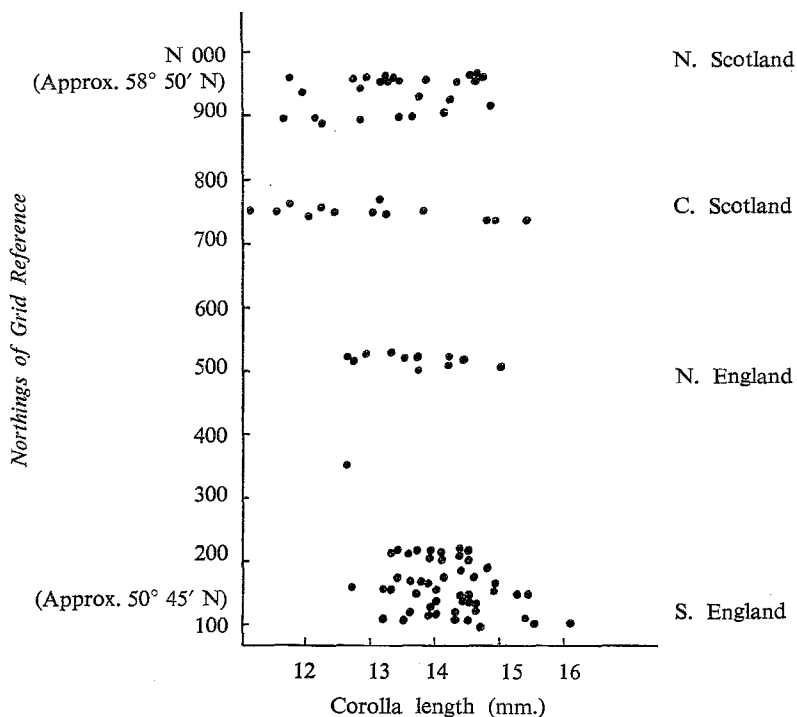

Fig. 7. Geographical scatter diagram of corolla length.

after anthesis or pollen shedding is a useless character and Beauverd's two subspecies are worthless and that Britton's identifications are based on invalid criteria.

Corolla length is variable, population means varying from 11·1 to 16·1 mm and individual corollas from 11 to 18 mm, and there are literature records of corollas up to 20 mm. There is a higher proportion of populations with short corollas in the north of Britain than in the south (see Fig. 7). There is no correlation between corolla and calyx length.

(xiii) *Anther and anther-appendage length*

Until recently anther length has not been used as a taxonomic character, although Beauverd (1916) used the relative length of the basal hairs of the anthers and the length of the anther appendages. The uselessness of this is seen in that different 'taxa' distinguished on this character sometimes occur in the same population and even on one plant.

Whilst attempting to find a character to separate badly pressed specimens of *M. sylvaticum* from depauperate forms of *M. pratense* it was found that there was great variation in the anther length of *M. pratense* and that anther length was of no use in separating the two species.

Anther length (length of loculus plus appendage) varies in Britain from about 2 to 3·5 mm. Populations with anthers 2·5 to 3·5 mm are widespread throughout the country but those with anthers less than 2·5 mm long are limited to northern and montane areas (see Fig. 8). There is no correlation between anther, corolla and calyx lengths. Observations on Continental material revealed that average anther length decreases northwards and Jasiewicz (1958) remarks that plants with small anthers are montane in Poland.
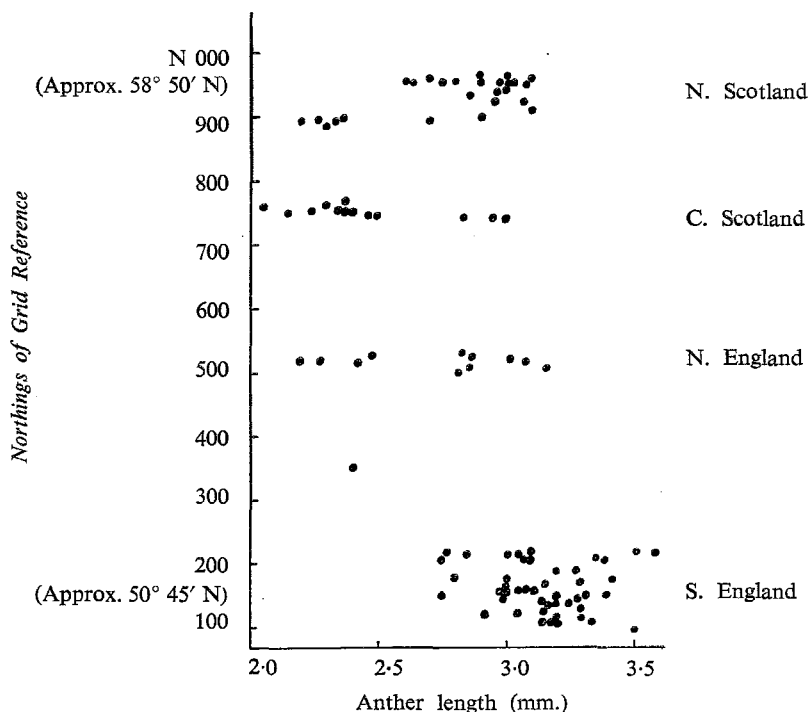

Fig. 8. Geographical scatter diagram of anther length.

Jasiewicz (1958) divides *M. pratense* into two groups, the first mainly lowland with anther loculi (2·2–) 2·4 – 2·7 (–3·2) mm long and appendages (0·2–) 0·3 – 0·5 (–0·6) mm long and the second mainly montane with anther loculi (1·6–) 1·8 – 2·2 (–2·7) mm long and appendages (0·5–) 0·6 – 0·8 (–1·0) long. It is clear that the proportions between loculus length and appendage length are different in the two groups and are of importance in separating them.

Measurements of loculus length and appendage length of the anterior pair of anthers in flowers from each population sampled were carried out and it was found that appendage length was directly proportional to loculus length and that there were not two groups. The same was found of Continental material throughout the range of the species. Hence it seems unlikely that there are two types of anthers, as suggested by Jasiewicz, unless they are restricted only to Poland. Insufficient Polish material was seen to come to any conclusion about this.

(xiv) *Pollen*

For each sample, twenty-five pollen grains were measured from each of three plants, making seventy-five pollen grains per sample.

In most of the samples the pollen was 95–100% good, but about 2% of the plants examined had up to 50% of the pollen grains empty.

Pollen varied in diameter (18–) 19 – 22 (–24)μ. In some populations pollen grains were elliptical, measuring approximately 18 × 21μ, but in most the pollen grains were spherical. In a few populations there were occasional larger pollen grains, up to 27μ, these presumably being unreduced. Whilst the average diameter in populations was mostly 20 to 21μ, two samples had mean diameters of 23μ and 23·6μ and one had 18·5μ. It does not seem that variation in pollen size can be put down to differences in chromosome number as in all the samples on which chromosome counts were made, including the population with small pollen grains, the diploid chromosome number was eighteen.

Pollen of *M. sylvaticum* varies from 21–27μ in diameter and, hence, pollen size cannot be regarded as a reliable character for separating the two species.

GEOGRAPHICAL VARIATION

From Fig. 1 it is clear that height diminishes northwards and from Fig. 4 it can be seen that there is a decrease in leaf width in relation to leaf length northwards. In southern Britain there is also a slight decrease in height from east to west. There is an increase in calyx length northwards, brought about by the occurrence of some populations with longer calyces than those of the south. Similarly there is a slight decrease in corolla and anther lengths northwards, but the cline in these two characters is not smooth, as populations from central Scotland have shorter corollas and anthers than populations elsewhere in Britain. This is seen in Figs. 7 and 8.

VARIATION IN CONTINENTAL M. PRATENSE

As British material of *M. pratense* showed distinct geographical trends in certain characters it was thought that it might be informative to study the geographical variation of *M. pratense* on the Continent. To obtain a comparison with British material, British and Continental specimens were divided into the following groups which are designated by the prefixed letter or figures in the geographical scatter diagrams (Figs 9 to 11.).

i   S. England (v.c. 1–35, 51° N)
ii N. England (v.c. 60–70, 54° 15′ N)
iii Central Scotland (v.c. 88–89, 56° 20′ N)
iv N. Scotland (v.c. 105–108, 58° N)

NN	N Norway (68° 30′ N)	P	Poland (52° N)
SN	S Norway (61° 30′ N)	C	Czechoslovakia (50° N)
NS	N Sweden (62° N)	Ba	Bavaria (49° N)
SS	S Sweden (58° N)	T	Thuringia (51° N)
F	Finland (62° N)	LA	Lower Austria (48° 15′ N)
D	Denmark (56° N)	G	Geneva (46° 15′ N)
H	Holland (53° N)	I	Italy (northern) (45° N)
B	Belgium (51° N)	J	Jugoslavia (45° N)

Only areas from which more than twenty-five specimens were seen have been used in plotting the scatter diagrams. The countries or districts used do not represent the distribution of the plant but merely the areas in which it has most frequently been collected, or from which a sufficient quantity of material was seen. The herbarium at Geneva contains a collection of *M. pratense* from neighbouring French and Swiss provinces and hence the name of the city has been used to designate a geographical area.

Height

Whilst height decreases northwards the diminution is much more rapid in Britain than in north-west Europe. Plants from Scotland are markedly smaller than those from similar latitudes in Norway and Sweden and, even in the extreme north of Norway, the plants hardly approach the small stature of those of northern Scotland (see Fig. 9).
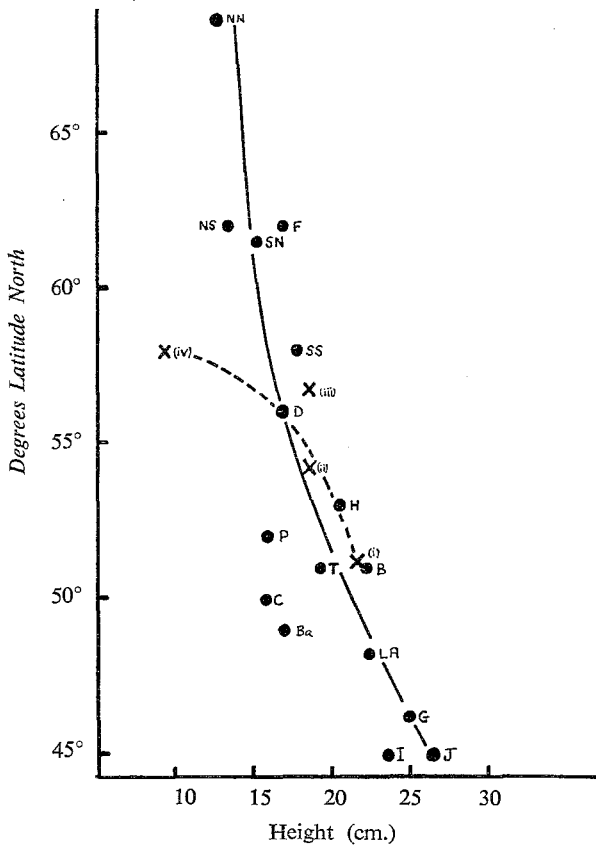
Fig. 9. Geographical scatter diagram of height showing differences between British material (crosses) and Continental material (solid dots). For interpretation of lettering see text.

Leaf index

The slight increase in leaf index from latitudes 45° N to 70° N on the Continent contrasts markedly with pronounced increase in that of British material, as can be seen from Fig. 10.

Number of branches

The number of pairs of branches of British plants does not differ noticeably from that of northern European plants although from the different trends in height this is unexpected.

Calyx length

In Britain there is a northward increase in calyx length and the trend appears more extreme than on the Continent.
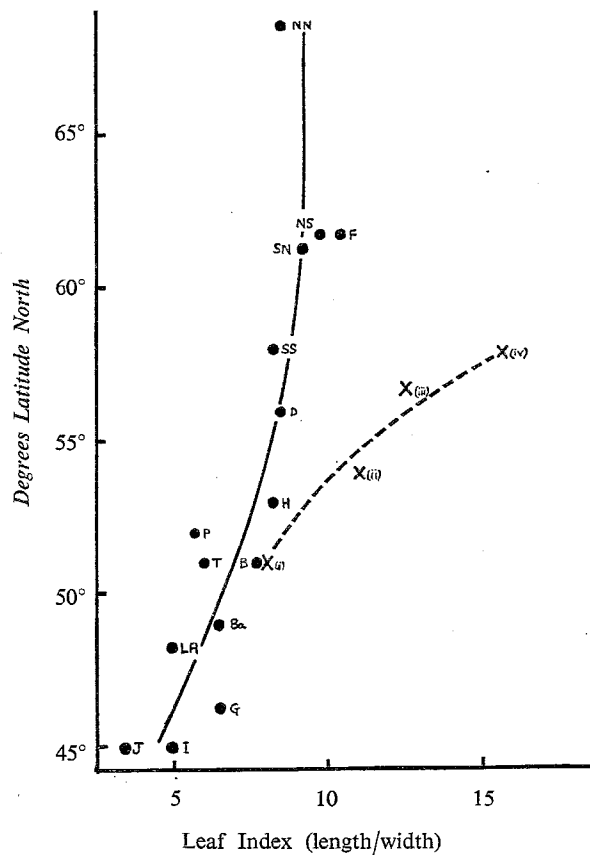

Fig. 10. Geographical scatter diagram of leaf index (length/width) showing differences between British material (crosses) and Continental material (solid dots). For interpretation of lettering see text.

Corolla length

Whilst there is a slight decrease in corolla length northwards in British plants, the variation in Continental material does not reveal any noticeable northerly trend.

Anther length

Except in central Scotland the anthers of British plants tend to be longer than those of Continental plants from similar latitudes and in Europe as a whole there is a steady decrease in length from south to north (Fig. 11).
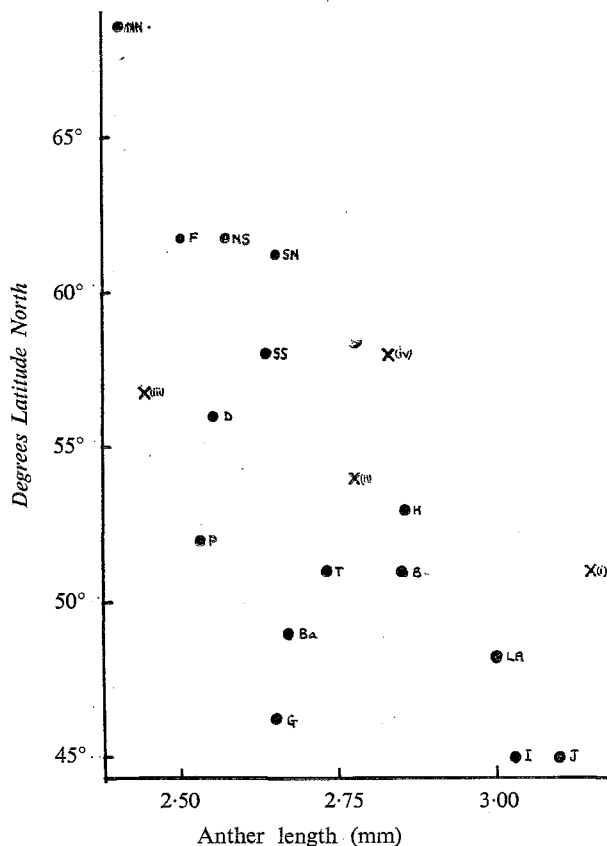

Fig. 11. Geographical scatter diagram of anther length. Crosses, British material; solid dots, Continental material. For interpretation of lettering see text.

General comments

It might be expected that plants of *M. pratense* from west and north Scandinavia would resemble plants from northern Scotland, but this is not so. Northern Scandinavian plants are taller, have markedly broader leaves, slightly longer corollas and the same number of pairs of branches (or cauline leaves.) This gives the plants from these two areas a strikingly different appearance. These differences may be due to climatic and day-length differences in the two areas. Woodland plants from other parts of Scandinavia resemble more closely British plants though few are as small as those of many populations found in some parts of Britain. Plants collected from limestone areas in various parts of Europe from Gotland southwards closely resemble the forms from chalk and limestone in Britain. All plants from Belgium and Holland are very similar to plants of south and east acid-woodlands in Britain.

RESULTS OF STATISTICAL ANALYSES

In Tables 2 and 4 the means of particular characters for the populations of each ecological type are arranged in ascending order of magnitude. In Table 3 the means of variabilities (obtained by taking the logarithm of the standard deviations) are likewise arranged. In Table 5 again the means of variabilities (obtained by squaring the standard

TABLE 2

Significance of differences between means (in brackets) of ecological types *A* to *G*. Any two means *not* underscored by the same line are significantly different. Any two means underscored by the same line are *not* significantly different using the SNK test.

Character and level of significance	Ecological type and mean						
Height (cm) 5%	A (27·8)	C (22·4)	D (16·5)	E (12·8)	F (11·8)	B (11·2)	G (10·4)
1%	A	C	D	E	F	B	G
No. sterile nodes 5%	A (5·7)	C (4·67)	G (4·53)	D (3·79)	B (3·73)	E (3·63)	F (3·59)
1%	A	C	G	D	B	E	F
Total No. nodes 5% and 1%	A (11·6)	C (10·1)	G (8·18)	D (8·14)	B (8·01)	E (7·89)	F (6·91)
No. intercalary leaves 5% and 1%	A (1·79)	G (1·77)	C (1·24)	B (1·18)	D (1·06)	E (0·99)	F (0·93)
Leaf shape (l/b) 5% and 1%	A (5·53)	C (8·29)	D (9·44)	B (10·29)	E (11·11)	F (12·95)	G (15·67)
No. of entire bracts 5%	A (1·26)	C (1·73)	F (2·23)	D (2·28)	E (2·36)	G (2·56)	B (2·73)
1%	A	C	F	D	E	G	B
No. of teeth per bract 5% and 1%	A (6·52)	C (5·48)	E (3·41)	D (3·25)	B (2·81)	G 2·42()	F (1·85)
Calyx length (mm) 5%	C (5·1)	D (5·2)	A (5·25)	E (5·45)	F (5·5)	B (5·7)	G (6·35)
1%	C	D	A	E	F	B	G
Corolla length (mm) 5% and 1%	D (14·8)	A (14·4)	C (14·1)	B (14·1)	E (13·6)	G (13·6)	F (12·8)
Anther length (mm) 5%	B (3·25)	D (3·17)	C (3·16)	A (3·08)	G (2·88)	E (2·70)	F (2·42)
1%	B	D	C	A	G	E	F

deviations) are treated similarly. Although the variabilities in Tables 3 and 5 were obtained by different methods used in the original research, they are essentially similar since the log. of the square of the standard deviation (variance) is equal to twice the logarithm of the standard deviation. These variabilities represent the degree of genetic variability. The significance of differences between the means and variabilities have been analysed statistically as described on p. 341 at the 5% and 1% levels. Means or variabilities that are

TABLE 3

Significance of differences between variabilities of ecological types *A* to *G*

Character and level of significance	Type and variability mean						
Height 5% and 1%	Not significant						
Leaf shape 5%	F (1238)	C (1244)	A (1260)	E (1263)	B (1296)	D (1336)	G (1361)
1%	Not significant						
Calyx length 5% and 1%	Not significant						
Corolla length 5% and 1%	F (625)	E (701)	A (708)	B (710)	C (712)	D (783)	G (821)
Anther length 5% and 1%	Not significant						

not significantly different are underscored by the same line. Where differences are significant the means or variabilities are not underscored by the same line. This provides a pictorial method of comparing ecological types in any one of the characters analysed.

From Table 2 the following points can be seen: Type *A* is significantly different from all other types in five characters at the 5% level and four characters at 1%.

Types *C* and *F* are significantly different from all other types in two characters at the 5% and 1% levels.

Types *B* and *G* are significantly different from all other types in one character at the 5% level.

The morphological differences between type *A* and other types are greater than those between any of the other types. In view of the marked ecological difference as well, type *A* forms a distinct unit as will be mentioned later. It is evident that the various ecological types differ from one another to a greater or lesser extent. It is also clear, however, that the characters in which the differences occur are not necessarily the same for any two types.

From Table 4 it can be seen that there are significant differences between populations from Scottish bogs (type *G*, samples 70–80) with respect to the number of nodes and calyx and corolla length, and similarly with populations from calcareous habitats (type *A*, samples 101–109) in Kent. This suggests that, whilst there is selection for particular morphological forms in particular habitats, there are distinct genetical differences between closely sited populations in any one ecological type.

Tables 3 and 5 both indicate that there is relatively little difference in genetical variability between individual populations and between ecological types. The significance of this will be discussed later.

CYTOLOGY

Root-tips of pot-grown seedlings from fifteen samples were stained with feulgen and squashed in aceto-carmine. All had a diploid chromosome number of 18 and all except four had the chromosome morphology illustrated in Fig. 12a. In four samples there were additional pairs of satellites as illustrated in Figs. 12b to 12e.

The constrictions forming the satellites mark the position of nucleolar organisers and it has been suggested (K. Lewis, personal communication) that where chromosomes are

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TABLE 4. Significance of difference between means of 15 populations
(pops. 70 to 80 from northern Scottish bogs, type G; pop. 101 to 109 from calcareous habitats in Kent, type A)

Character and level of significance	Population and mean														
Height (cm) 5%	71 (7·8)	75 (9·2)	76 (9·5)	77 (9·8)	73 (10·1)	80 (10·3)	74 (10·4)	72 (10·4)	78 (14·9)	101 (23)	106 (23·6)	107 (25·3)	108 (28·4)	109 (29·5)	103 (31·3)
1%	71	75	76	77	73	80	74	72	78	101	106	107	108	109	1·3
No. of nodes 5%	70 (7·6)	75 (7·7)	71 (7·8)	76 (8·1)	77 (8·4)	80 (8·5)	73 (8·5)	106 (8·6)	72 (8·8)	109 (9·7)	101 (10·7)	78 (10·8)	108 (11·5)	107 (11·8)	103 (12·6)
1%	70	75	71	76	77	80	73	106	72	109	101	78	108	107	103
Leaf shape 5% and 1%	70 (18·2)	80 (17·7)	71 (16·7)	77 (16·1)	76 (16·0)	72 (15·9)	75 (15·6)	73 (15·1)	78 (12·8)	106 (8·7)	101 (8·1)	107 (7·3)	103 (5·0)	109 (4·4)	108 (4·2)
Calyx length (mm) 5%	77 (7·8)	72 (6·97)	71 (6·95)	80 (6·56)	101 (6·50)	78 (6·48)	70 (6·40)	76 (6·07)	75 (5·99)	73 (5·96)	107 (5·64)	106 (5·48)	109 (5·15)	103 (4·98)	108 (4·97)
1%															
Corolla length 5%	80 (11·7)	75 (12·8)	76 (13·2)	73 (13·6)	77 (13·7)	101 (13·7)	108 (14·0)	70 (14·1)	72 (14·2)	106 (14·4)	107 (14·5)	78 (14·6)	71 (14·8)	103 (14·9)	109 (15·4)
1%	80	75	76	73	77	101	108	70	72	106	107	78	71	103	109

TABLE 5.   Significance of difference between variabilities of fifteen populations (as in Table 4)

| Character and level of significance	Population and variability mean														
Height 5%	101 (1·4)	103 (6·6)	109 (7·4)	77 (9·2)	73 (10·7)	80 (10·8)	106 (10·9)	75 (11·3)	76 (11·6)	72 (11·7)	107 (11·9)	78 (12·4)	71 (13·7)	70 (16·3)	108 (24·0)
1%	Not significant														
No. of nodes	Not significant														
Leaf shape	Not significant														
Calyx length 5% and 1%	72 (9·2)	80 (11·9)	76 (43)	78 (48)	107 (66)	70 (71)	75 (80)	106 (82)	101 (86)	73 (92)	109 (94)	103 (98)	108 (100)	71 (105)	77 (172)
Corolla length 5%	72 (13·8)	108 (15·1)	106 (15·9)	70 (21·0)	101 (31·6)	80 (32·0)	77 (32·2)	76 (37·0)	71 (41·9)	109 (42·8)	103 (44·5)	107 (45·2)	73 (46·1)	78 (55·9)	75 (91·3)
1%	Not significant														
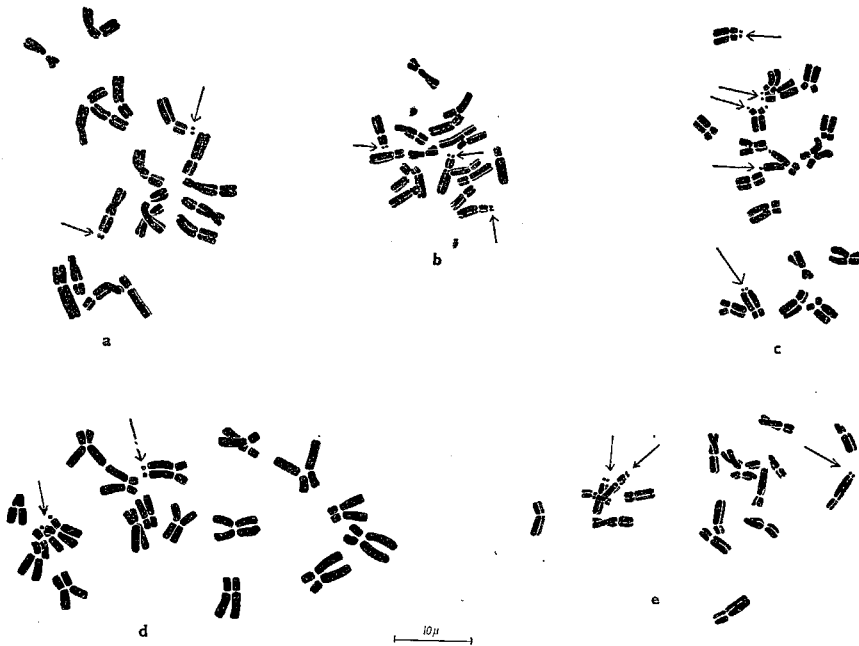
Fig. 12. Camera lucida drawings of root-tip chromosomes of *M. pratense*; (a), normal chromosome complement (sample 96); (b)—(e), abnormal chromosome complements with additional satellites and/or non-homologous chromosomes (samples 99, 26, 100 and 97 respectively).

non-homologous this might be due to the suppression of some of the nucleolar organisers by those remaining. The chromosomes are very heterochromatic and, because of staining in the resting nuclei, it is not possible to count the number of nucleoli.

Staining of the root tip chromosomes with feulgen and aceto-carmine was very satisfactory, but great difficulty was had in staining meiotic chromosomes in pollen-mother-cells. Aceto-carmine and aceto-orceine produced poor results with fresh material although the former stain was satisfactory with material fixed in 1:3 acetic alcohol. Best results were obtained by warming fresh anthers for about five minutes in a mixture of five drops each of aceto-orceine and aceto-lacmoid and three drops of normal hydrochloric acid. Examination of fresh material was desirable as in fixed material the chromosomes become very woolly in appearance.

It proved difficult to find dividing pollen-mother-cells but sucessful preparations were made from material from ten populations. In all these the results were identical and the chromosomes always showed the same pattern of behaviour.

At metaphase eight bivalents became arranged around the ninth on the metaphase plate as in Fig. 13a. At anaphase the eight bivalents appear to move to the wall of the pollen-mother-cell and fuse with each other at the ends to form a ring (Fig. 13b). That they fuse is suggested by the fact that when heavily squashed the dispersed chromosomes remain joined by bridges (Fig. 13d). The central bivalent becomes attached at its ends to the inside of the ring. In fresh material, however treated, the pollen-mother-cells always become orientated so that there appears to be only a single ring of chromosomes at anaphase. In fixed material orientation of the pollen-mother-cells is at random and it is clear in such preparations that there are two rings. At telophase (Fig. 13d) the chromosomes become separated but still have the same arrangement as at metaphase and this is retained until the later stages of the second division.

In *M. sylvaticum* there is the same phenomenon at anaphase but metaphase was not seen and the chromosomes were too woolly to count in the preparations made.
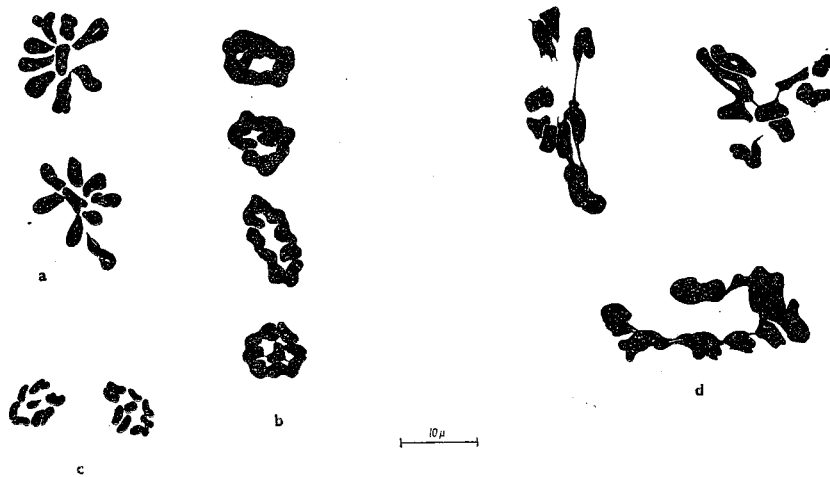
Fig. 13. (a)—(c), stages in meiosis of pollen mother cells of *M. pratense* ((a), metaphase; (b) anaphase; (c), telophase); (d) heavily squashed cells showing apparent bridges between chromosomes at anaphase.

The chromosomes of *M. pratense* are relatively large when compared with those of related genera such as *Rhinanthus* and *Euphrasia* and it may be that their peculiar behaviour is only a mechanical effect dictated by the lack of space for random orientation in the pollen-mother-cells. The bivalents are not sufficiently different morphologically to determine whether the same chromosomes always occupy the same position at anaphase.

Resting nuclei of both root-tips and pollen-mother-cells are very heterochromatic and the same situation is reported in *M. cristatum* (Hambler 1954). *Melampyrum* differs in this respect from *Rhinanthus*, the species of which have varying numbers of heteochromatic *B* chromosomes (Hambler 1954) which form stainable blobs in resting nuclei.

DISCUSSION

It is evident from the foregoing account that there are three types of variation in *M. pratense*, (i) geographical variation, (ii) ecological variation and (iii) variation from population to population.

(i) *Geographical variation*

In Britain there is a marked south-north cline in such characters as height and leaf shape. These clines can be explained on the basis of natural selection acting through climate. Such clines have been shown in *Alnus glutinosa* (McVean 1953).

With calyx, corolla and anther lengths the pattern differs. There is not a gradual change in size, but there is a change in the proportion of populations with floral parts of particular dimensions. It is difficult to conceive of a reason for this. If, for example, short anthers and long calyces are of selective advantage in the north then it might be expected that they would have been selected for in all populations in such areas. In northern Scandinavia there is a higher proportion of such populations than in Scotland and it may be that short anthers and long calyces (which are not necessarily selected for together in any one population) have a slight advantage under more extreme climatic conditions. This being so, selection for them would increase in a northerly direction and they might even be selected against in the south. In Britain this particularly applies to anther lengths, there being no populations with short anthers in the south. Similarly with calyx length there are very few specimens with long calyces from southern Europe.

Corolla colour is also a puzzling feature.   Taking first the golden-yellow form, this occurs in pure populations in palaeogenic regions of Britain and with the possible exception of a record from Wurttemburg is apparently absent elsewhere except in Ireland.   That it occurs in pure populations indicates that it is of selective advantage and when a mutation to this colour form occurs it spreads through the whole population.   If it was a normal mutant it would be expected to occur throughout the whole geographical range.   It is possible that the selective advantage of golden-yellow flowers is connected with a particular pollinator in certain areas.

The plants with crimson-tipped corollas are northern and montane and in Britain they mainly occur mixed with the normal form.   The situation on the Continent is unknown. As will be mentioned later *M. pratense* is usually self-pollinated so that these mixed populations are unlikely to be instances of balanced polymorphism, and the fact that pure populations of the crimson-flowered form are rare suggests that it is of no particular selective advantage.   As with the golden-yellow form its absence from a considerable part of the species' range is inexplicable.

(ii) *Ecological variation*

Whilst some characters show an almost continuous geographical cline, others, for a considerable part of their distribution, show a similar cline, but there are certain anomalies which appear to have an ecological basis.   The most conspicuous irregularity is in the cline of intercalary leaf number and is caused by the northern bog populations (see Fig. 3) which have a larger number of intercalary leaves than any other populations except those of type *A*.   Evidently plants with numerous intercalary leaves have been selected for in Scottish blanket bogs.

Plants from calcareous habitats might also be said to cause discontinuities in the leaf-shape cline (Fig. 4) though, as they all occur in southern Britain where leaves are broader than elsewhere, this is not obvious.   Leaf shape of the calcicolous forms is significantly different from all other forms, but otherwise the northerly change in leaf shape is more or less continuous.   It seems that the broad-leaf character has been strongly selected for in nearly all basic habitats, both in Britain and on the Continent.   Whether or not broad leaves are of selective advantage in calcareous habitats is not clear, but they may be an external manifestation of a physiological difference.

It was mentioned earlier that some chalk populations in Kent were indistinguishable from populations occuring in acid pockets in the same area.   There are two possible explantions for this.

The first is that there may originally have been two types of population, one calcifuge and narrow-leaved and the other calcicole and broad-leaved.   In Kent conditions on the chalk, where there are acid pockets of soil, would provide adjacent habitats for the two types.   Since they would be close together hybridisation and introgression would be possible.   None of the populations from chalk soils in Kent have such broad leaves as those from calcareous soils in Hampshire, Somerset and Gloucestershire where the populations appear to be more isolated.   This suggests that the narrower leaves of some Kent populations may be due to introgression.

The second possibility is that originally there was only one taxon composed of narrow-leaved plants and that there was selection for broad-leaved forms where populations developed on calcareous soils.   This selection would presumably be relatively slow and it might be that in Kent populations from acid soils might still be spreading to calcareous soils, giving forms with a variety of leaf shapes.

From each of the ecological types mentioned (i.e. *A* to *H*) plants of characteristic appearance have been collected (Fig. 14–19), although with the partial exception of type *A*, these various types intergrade to form a continuous series of morphological forms, i.e. they are a series of ill-defined ecotypes.   This ecotypic differentiation has been super-

imposed upon continuous geographical variation so that discontinuities in clines of certain morphological characters have been produced. One very marked exception to the pattern of variation in southern Britain, other than the calcareous plants, is the form found in the New Forest. The reason for this exception can be dealt with in considering variation in *M. pratense* in Britain as a whole.

It is possible that at the end of the last Ice Age the form of *M. pratense* found in southern Britain was like the form now found in northern Scottish bogs. As the ice retreated this form would have migrated northwards. As climatic and vegetation changes occurred it is possible that, beginning in the south, this bog form became more variable because of less rigorous climatic selection and diversification of habitats. In any one type of habitat particular gene combinations were probably selected for, resulting in the phenotypes characteristic of the particular habitats. The anomalous New Forest populations (type *B*) could be relicts of an earlier phase in the post-glacial period, as they much more resemble northern plants, especially those from blanket bogs, than other forms. This does, however, raise the question why this form of *M. pratense* has persisted in the New Forest whilst elsewhere in southern England there appears to have been selection for different and more vigorous forms. Furthermore this suggestion implies the existence of wet acid peat in southern Britain in the late-glacial and early Post-glacial periods. All the evidence suggests that the only boggy areas were base-rich shallow valley mires and fens, totally different types of habitats from the wet acid peat of northern Scotland and the dry acid podsols of the New Forest.

Fig. 14. Plant of type A (subsp. *commutatum*) from an oolitic limestone bank, Wotton-under-Edge, Gloucestershire (grid ref. ST 954940), × ¼.

There is an alternative and more likely explanation which will account for geographical variation of the species in Britain and also for the existence of the New Forest populations.

The New Forest plants and those from northern Scottish bogs differ markedly from Continental plants, but other forms of *M. pratense* in Britain, expecially those from southern England, resemble closely those forms from similar latitudes in western Europe.

It is suggested that *M. pratense* migrated from southern Britain northwards after the last Ice Age, either as a periglacial survival or as an immigrant. As the migrant forms spread northwards there was a diminution in size, possibly because of a more rigorous climate, and a diversification of forms resulting from the colonisation of new habitats.

Fig. 15. Plants of type *B* (New Forest form) from Warwick Slade, near Lyndhurst, Hampshire (grid ref. SU 268065), × ¼.   *Cf.* Fig. 18.

If, as is suggested by McVean & Ratcliffe (1962), northern Scotland was until recent times wooded, suitable habitats for *M. pratense* would have been present.   When the woods were destroyed *M. pratense* could have survived on the subsequent blanket bog as a woodland relict.   This may also account for the absence of the species from raised bogs in England and Wales, since these may never have been wooded (*e.g.* Tregaron Bog, Borth Bog).   Plants on nutrient deficient soils, such as the acid peats of northern Scotland and the podsols of the New Forest, tend to be small and the similarity between New Forest plants of *M. pratense* and those from Scottish blanket bog may be entirely accidental.

Status of ecological variants of M. pratense

From Table 2 it can be seen that in types *E*, *F* and *G* for certain (and not necessarily the same) morphological features any one of the types is significantly different from the

others, indicating that there has been selection for a particular expression of a morphological character in a particular habitat. In none of these types, however, has selection proceeded sufficiently far to delimit well-defined ecotypes. From a taxonomic point of view all the types from northern Britain (*i.e. E, F* and *G*) can be regarded as a single taxon. Type *H* which was not dealt with statistically, can, from its morphology, be regarded as falling within this taxon.

In southern Britain the situation is different. Again referring to Table 2 it is evident that, ignoring type *B*, types *C* and *D* are indistinguishable except in the degree of toothing of the bracts and can be included in one taxonomic unit.

Type *A* differs considerably from all other types, in five characters at 5 % level and in four at the 1 % level. The situation here seems to be either that ecological selection has proceeded further than in other ecological types, or, as was suggested earlier, there were two distinct types of plant to start with. In Europe plants of *M. pratense* from calcareous habitats are usually distinct although in a few areas, e.g. Pas de Calais (F. Rose, personal communication), plants with narrower leaves like those from Kent are found in such habitats.

Fig. 16. Plants of type *C* from Fence Wood, near Newbury, Berkshire (grid ref. SU 511717), × ¼.

Even when the intermediate Kentish populations are included, the calcicolous forms are sufficiently well-defined to be regarded as a taxon distinct from that containing types *C* and *D*. Types *C* and *D* differ significantly from all of types *E, F* and *G* only in the number of nodes and toothing of bracts. Although types *C* and *D* tend to be larger in number and size of parts than the northern types there is a completely intergrading series, so that type *C* cannot be considered as distinct from the northern forms. There are a few New Forest populations tending towards the plants of type *C* and it is considered best to regard

the New Forest plants as a form of type *C*. Thus there are two taxa, one consisting only of type *A* and the other of types *B* to *H*. For convenience, nomenclature being dealt with later, these will be referred to as subsp. *commutatum* (plants from calcareous habitats) and subsp. *pratense* (plants from acid habitats).

Plants like those of type *C* are widespread throughout the geographical range of *M. pratense*. On the Continent there is a multiplicity of variant forms but from examination of herbarium specimens it seems that many of the Continental forms are of restricted distribution and that selection has produced different forms in similar types of habitat. The exact status of many of these forms is not clear as insufficient material has been seen, but it is suspected that the situation is as in Britain, i.e. that these forms are ill-defined.

With the exception of type *A* plants, all material seen from the Continent comes within the range of subsp. *pratense*.

Plants of subsp. *commutatum* are widespread being found in many of the areas where there is base-rich rock. It is clear that subsp. *commutatum* and subsp. *pratense* are ecologically and to a considerable extent morphologically distinct and hence the most suitable taxonomic status for them is that of subspecies.

Fig. 17. Plants resembling types *E* and *F* from Struan, Perthshire (grid ref. NN 806655), × ¼.

(iii) *Variation at the population level*

That there is variation between individual populations is evident from Table 4, but before considering this it is necessary to deal with the genetics of the species.

In Britain *M. pratense* usually occurs in small isolated populations. According to Knuth (1906–9), the plant is pollinated by bumble bees and failing this, it selfs. No observations were made of insect visitors, but in several samples when pollen grains were being
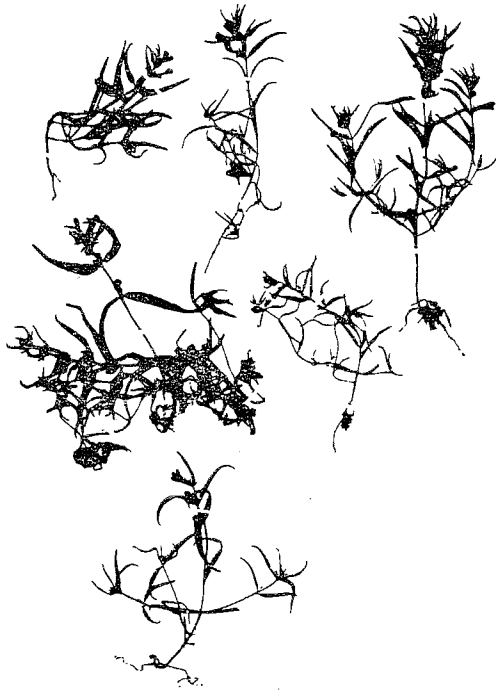
Fig. 18. Plants of type *G* from blanket bog near Meall Tuirslighe, Sutherland (grid ref. NC 654599), $\times \frac{1}{4}$

Fig. 19. Extreme form of plants of type *H* from Wybunbury Moss, Cheshire (grid ref. SJ 695502), $\times \frac{1}{4}$.

measured it was found that the anthers dehisced before the flowers opened. During the course of cultivation experiments at Bagley Wood, where *M. pratense* does not occur naturally, a solitary plant flowered about three weeks before any others and set seed, again suggesting that there is no self-incompatibility mechanism. Further, in Britain, many of the populations of *M. pratense* are so isolated as to form small inbreeding units and such populations could be expected to be more or less homozygous.

If the populations are homozygous it would be expected that the level of genetic variability both from population to population and from ecological type to ecological type would be relatively uniform. That this is so is indicated in Tables 3 and 5.

It was suggested earlier that *M. pratense* spread across Britain after the last Ice Age and it is probable that populations became isolated, either by fragmentation of large populations or the distribution of solitary or small numbers of seeds. Random assortments of genes would become fixed in individual isolated populations. This would account for the many minor but noticeable differences between individual populations in similar ecological habitats.

From the point of view of general inter-population variability *M. pratense* is morphologically much more diverse in southern Britain than in the north. This may be due to greater ecological diversity or to the less extreme climatic conditions of the south or a combination of both.

At present *M. pratense* is decreasing in wooded parts of Britain because of felling of some woods and the overgrowth of others. In northern Scotland it appears to be limited to waterlogged areas that do not get burnt in the periodical firing of heather that is carried out in connection with grazing.

Taxonomy of M. pratense

In past investigations of *M. pratense* solitary plants or small numbers of plants have been collected in different parts of Britain and the Continent. Because of geographical, ecological and population differentiation these plants have appeared to be distinct from one another and this has led to the description of many subspecies, varieties, subvarieties, forms and subforms, which do not have any validity when a large number of plants collected continuously over a geographical region are examined.

It has, however, been found that plants fall into two morphological groups that are sufficiently distinct to be considered as subspecies i.e. the subsp. *commutatum* and subsp. *pratense* mentioned earlier.

The specimen of *M. pratense* in the Linnean herbarium comes within the range of those plants which have for convenience been called subsp. *pratense* and which should therefore be called *M. pratense* L. subsp. *pratense*.

The plants with golden-yellow flowers belong to subsp. *pratense*. This form was first recognised as var. *hians* by Druce (1884) and later regarded as a subspecies by Beauverd (1914). The taxon is probably best regarded as a variety, being characterised by flower colour and a distinct geographical distribution. The correct name is therefore *M. pratense* L. subsp. *pratense* var. *hians* Druce.

The plants with crimson-tipped corollas cannot be regarded as having any taxonomic status since they do not occur in pure populations and have no distinct distribution, but can for convenience be called f. *purpureum*.

Plants resembling subsp. *commutatum* were distributed as *M. commutatum* Tausch by Tausch in 1832 but with no description. The original specimens distributed by Tausch have not been seen but from later-named specimens and descriptions it is clear that Tausch's plant was the one that for convenience has been called subsp. *commutatum*. Tausch's plant was described by Kerner in 1870 who said it should be regarded as a variety of *M. pratense*, and the correct citation would be *M. pratense* var. *commutatum* Tausch ex Kerner. The plant was raised to a subspecies by Britton in 1943 and, as this appears to be the correct taxonomic status, the valid name of the plant is *M. pratense* L. subsp. *commutatum* (Tausch ex Kerner) C. E. Britton.

Descriptions of the subspecies

M. pratense L. subsp. pratense: Plants (3–)9–25(–60) cm high (excluding hypocotyl). Uppermost cauline leaves (10–)20–80(–110) mm long, (1–)2–10(–20) mm wide, leaf length/

breadth ratio (5–)7–15(–20). Calyx 3.5–7(–12) mm long. Corolla tube whitish or pale yellow, mouth pale yellow, usually darker than the tube; or mouth crimson-streaked; or whole corolla golden yellow (var. *hians* Druce); (11–)12–14(–18) mm long. Anthers (2.0–) 2.4–3.2(–3.8) mm. Plants of acid soils in woodlands, hedgerows and bogs, widely distributed but rare in East Anglia, the Midlands and southern Scotland.

M. PRATENSE L. subsp. COMMUTATUM (Tausch ex Kerner) C. E. Britton: Plants (20–)25–45(–60) cm high (excluding hypocotyl). Uppermost cauline leaves (30–)40–70(–100) mm long, (4–)8–20(–27) mm wide, leaf length/breadth ratio (2–)3–8(–12). Calyx (3.5–)4.0–5.5(–6.0) mm long, corolla 13–15.5 mm, anthers 2.5–3.5 mm. Restricted to calcareous or base-rich habitats, usually a scrub or hedgerow plant, common in south-east England, rare in the south-west. Also recorded from Oxfordshire, Somerset and Lancashire but probably extinct in these counties.

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