

STUDIES IN THE BIOLOGY OF *POA SUBCAERULEA* SM.

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ABSTRACT

Poa subcaerulea has a widespread distribution in Great Britain, being common in the hill country of Scotland and Wales, and in sand dunes along the British coast. It is essentially a plant of moist habitats.

There is considerable variation within populations but all show taxonomic characters of great constancy. *P. subcaerulea* panicles are usually small, with a low number of spikelets, a tendency to two branches at the lowest node and glumes with three nerves. The rhizomes spread extensively and normally have one tiller per tillered node. Leaves are broad and may be hairy.

Pollen diameter is from 30.6–37.5 μ and fertility is high. Seeds are long. Polyembryony has been found in all samples collected.

Chromosome numbers varied between $2n = 54$ and $2n = 109$. Autopolyploidy is widespread and chromosome number varies within populations. Apomixis may be the main method of seed production, and together with vegetative reproduction by rhizomes gives considerable cloning.

Taxonomically *P. subcaerulea* is quite distinct from other species of the *P. pratensis* group occurring in the British Isles, but it is essential to consider vegetative as well as floral characteristics in classification. Transplant studies have shown the great constancy of these taxonomic characters.

INTRODUCTION

The critical nature of *Poa pratensis* L. *sensu lato* is now well appreciated and this, together with its economic importance, has attracted much study to this group which is usually classified either into distinct ecological form complexes (e.g. Åkerberg, 1942), or subspecies (e.g. Hiitonen 1933; Hylander 1941, 1953, 1955; Tutin 1952, 1957), or divided into several separate species (e. g. Lindman 1926, Roshevitz 1934; Hultén 1950; Hubbard 1954; Melderis 1955; Dandy 1958). The concept of the last-mentioned authorities is followed in this paper.

Lindman (1926), who was the first to be particularly interested in this group, divided it into five species: *P. pratensis* L. *sensu stricto*, *P. angustifolia* L., *P. alpigena* (Fr.) Lindm., *P. subcaerulea* Sm. and *P. irrigata* Lindm. Hylander (1941, 1953, 1955) has treated these entities as subspecies of *P. pratensis*, and has included *P. subcaerulea* in subsp. *irrigata* (Lindm.) Lindb. f. On the specific level the epithet *subcaerulea* published by Smith in 1802 is much earlier than *irrigata* given by Lindman in 1905. More recently Clausen & Hiesey (1958) have added *P. arctica* R. Br. to this group, as it forms intermediates with *P. alpigena* in Sweden (Nygren, 1950).

Three of these species, *P. pratensis* L. *sensu stricto* (*P. pratensis* L. subsp. *pratensis*), *P. angustifolia* L. (*P. pratensis* subsp. *angustifolia* (L.) Lindb. f.) and *P. subcaerulea* Sm. (*P. irrigata* Lindm., *P. pratensis* subsp. *subcaerulea* (Sm.) Hiitonen. *P. pratensis* subsp. *irrigata* (Lindm.) Lindb. f., *P. pratensis* subsp. *alpigena* auct. flor. brit.) are present in Britain. Both the other species, the low-arctic *P. alpigena* (Fr.) Lindm. (*P. pratensis* subsp. *alpigena* (Fr.) Hiitonen) and arctic-alpine *P. arctica* R. Br. have a circumpolar distribution, but neither occurs in the British Isles.

Melderis has reviewed the taxonomic interest of *P. pratensis*, *sensu lato*, and with regard to *P. subcaerulea* has pointed out that no work has been carried out on this species in Britain, though Löve (1952) has investigated Icelandic populations and Åkerberg a limited number of Swedish plants. Since then data on Welsh populations have been recorded (Barling 1957, 1959).

It would appear from Åkerberg that *P. subcaerulea* is itself taxonomically very variable, for he describes a shore and a forest form, which hybridise with other forms of *P. pratensis*. Indeed the reticulate relationship of the various forms of *P. pratensis*, *sensu lato*, is well known and a similar pattern appears to exist between many Poae (Gustaffson 1947, Stebbins 1950; Nygren, Melderis, Clausen & Hiesey).

The variety of taxonomic opinions on *P. subcaerulea*, together with the knowledge of hybridisation with other species of the *P. pratensis* group, not to mention the ecological specialisation of species, makes this group a necessary study for a fuller understanding of the complex relationships within the Poae. The present paper is an account of more extensive studies on populations and transplants of British origin.

MATERIAL AND METHODS

Populations of *P. subcaerulea* from centres distributed through most of its latitudinal range in the British Isles have been studied as follows:— v.c. 3, Slapton Sands and Dawlish Warren (sea level); v.c. 34, Hazel Hill and Five Acres (800 ft.); v.c. 41, Cwmdare: Lluestai Llwydion (900 ft.), Tir-Evan-Bach-Traws (600 ft.), Pwll Rhys (600 ft.), Tir Morris (750 ft.), Cefn-y-Gyngon (1,100 ft.), Windber (950 ft.), Bwllfa (950 ft.); v.c. 41, Pen Rhys (800 ft.), Craig-y-Llyn (1,900 ft.), Limeslade (sea level), Jersey Marine (Sea level); v.c. 42, Pontpren (600 ft.), Penderyn (600 ft.); v.c. 44, Pendine (sea level); v.c. 45, Maenclochog (800 ft.), Rosebush (800 ft.), Wolf's Castle (300 ft.); v.c. 46, Ffair-Fach (1,000 ft.); v.c. 60 St. Annes (sea level), Bispham (sea level); v.c. 69, Grange-over-Sands, (sea level), Windermere (800 ft.), Kirkstone Pass (1,500 ft.), Knock Fell (2,200 ft.); v.c. 70, Dunmail Raise (2,000 ft.); v.c. 77, Bailliesmuir (300 ft.); v.c. 90, Montrose (sea level); v.c. 92, Balmoral (800 ft.); v.c. 98, Glenbeg (800 ft.).

The transplants were grown in 8 in. pots immersed in a washed gravel bed situated at Cirencester (Lat. 51° 43' N., Long. 1° 57' W.), at an elevation of 440 ft. The soil used was a calcareous loam derived from the Great Oolite.

DISTRIBUTION AND ECOLOGY

P. subcaerulea was described by Smith (1802) from specimens gathered by Rev. H. Davies in Anglesey. In his *English Flora*, Smith (1824) mentioned that this species occurs in mountainous situations in Wales, Anglesey, Westmorland, Cumberland and Scotland. According to Hubbard, *P. subcaerulea* has a widespread distribution in the British Isles, though it is more common in the north than in the south. It is found in a variety of habitats: moist mountain grasslands, stream sides, dune slacks and sea shores, and the last environments have resulted in its distribution along the south coast of England.

Outside the British Isles, this species has been recorded from Fennoscandia, Denmark, the northern part of the European U.S.S.R. and Iceland (cf. Hylander 1953). It seems that this species is common in N.W. Europe, from at least 50°N. to slightly within the Arctic Circle, overlapping over much of this territory with other species of the *P. pratensis* group. An excellent map showing the distribution of *P. subcaerulea* in N.W. Europe is given by Hultén. It is probably at its southern limits in the British Isles and is replaced to the south by the *P. pratensis* complex. This may account for its ecological prevalence in the hill or mountain areas as opposed to lowlands of the British Isles.

Its distribution in the British Isles is incompletely known. Habitats, particularly in South Wales, are as follows:—

1. *Permanent grasslands*. The plant was found in enclosed and open hill grasslands, particularly where *Agrostis tenuis* or fine-leaved fescues (*Festuca rubra* and *F. ovina*) were dominant. In these pastures the plants are not very obvious, their long rhizomes and single tillers giving a very diffuse appearance. It is most noticeable in flower, or where conditions may lead to local concentration as on pathways.

It has been recorded in tussocky swards of *Molinia caerulea*, usually as isolated plants with very long culms and rather poor vegetative development, and also amongst swards where *Juncus effusus* is prominent.

TABLE 1. Morphological data from wild populations in *P. subcaerulea*

<i>Origin</i>	<i>Habitat</i>	<i>Inflor. length</i> mm.	<i>Branches</i> <i>lowest node</i>	<i>Spikelets</i> <i>per panicle</i>	<i>Height of culm</i> mm.	<i>Tillers/tillered</i> <i>node</i>
Slapton Sands	Shore	36.46 ± 1.93	2.60 ± 0.12	31.35 ± 1.20	126.60 ± 9.65	—
Dawlish Warren	Fixed dune	52.67 ± 2.26	3.30 ± 0.14	50.40 ± 4.20	148.40 ± 7.17	—
Windber	Waste tip	27.35 ± 1.79	2.00 ± 0.00	23.17 ± 1.48	107.65 ± 8.09	—
Cefn-y-Gyngon	Sheep shelter	40.40 ± 2.47	2.47 ± 0.24	28.15 ± 2.21	100.46 ± 10.12	1.00 ± 0.00
Craig-y-Llyn	Road verge grassland	38.24 ± 4.78	2.18 ± 0.13	27.82 ± 2.59	137.77 ± 15.60	—
Penderyn	Grassland	45.20 ± 2.61	2.10 ± 0.10	33.04 ± 2.31	155.80 ± 13.05	1.00 ± 0.00
Five Acres, Forest of Dean	Grassland	52.10 ± 1.69	2.63 ± 0.14	46.73 ± 2.76	136.00 ± 7.10	1.00 ± 0.00
St. Anne's	Fixed dune	53.72 ± 1.89	2.72 ± 0.11	50.65 ± 2.19	198.43 ± 11.99	1.00 ± 0.00
Bispham	Cliff top	43.20 ± 0.97	2.60 ± 0.22	39.65 ± 2.65	82.95 ± 3.85	1.00 ± 0.00
Helvellyn	Grassland	38.72 ± 1.61	2.15 ± 0.06	29.31 ± 1.83	122.90 ± 6.01	1.06 ± 0.02
Kirkstone Pass	Grassland	47.14 ± 2.00	2.31 ± 0.08	36.14 ± 2.46	175.45 ± 11.25	1.00 ± 0.00
Montrose (Tay Fisheries)	Fixed dune	51.46 ± 2.08	2.20 ± 0.09	43.34 ± 2.72	284.48 ± 18.95	1.14 ± 0.04
Glenbeg	Grassland	32.07 ± 1.30	1.90 ± 0.12	27.40 ± 1.99	75.30 ± 5.23	1.04 ± 0.04
Balmoral	Road verge	45.85 ± 1.19	2.15 ± 0.10	37.03 ± 1.82	179.60 ± 6.74	1.00 ± 0.00

2. *Road-verge grasslands.* On the hill areas the fertilising effects of road dust has led to the formation of improved swards a few yards wide in what is often rough grassland dominated by *Nardus stricta* or *Molinia*, and on these areas *P. subcaerulea* is frequently found.
3. *Sheep shelters.* Where localised shelter or "camping" is taken by sheep, as under walls, banks or stunted hawthorn, then the heavy trampling and faeces concentration result in localised modification of the flora. On these small areas bare ground is obvious, and *P. subcaerulea* is frequently found, often in well developed mats, together with such species as *Agrostis tenuis*, *Poa annua* and *Stellaria media*. These modifications are often isolated amongst large acreages of rough grazings.
4. *Waste places and walls.* Plants have been found growing on walls at a variety of sites in north Glamorgan and south Breconshire. *P. subcaerulea* has been repeatedly found on tips of colliery waste, where the loose weathered shale allows the spread and development of long rhizomes and provides conditions similar to the sand dune environment. It is also found in swards developed on the stable areas of colliery tips where it may be accompanied by *Agrostis tenuis* and *Festuca ovina*.
5. *Sand dunes.* *P. subcaerulea* is frequently found on sand dunes, particularly on fixed dunes and slacks. In the present study plants have been collected from Dawlish Warren, Jersey Marine, St. Anne's and Montrose. Plants are sometimes found in the shifting sand and also in the turf of nearby golf courses. It is also common on walls, cliff top grassland, and gravelly shores in these areas. At Dawlish it is found on fixed dunes and also in slacks among such species as *Spiranthes spiralis*.
6. Other habitats in which the plant has been found include the ballast of railway tracks, roadside gutters, garden pathways and hedgerows.

PLANT CHARACTERS

Wild populations were selected from a wide range of geographical and ecological environments to provide representative data (Table 1). Plants follow a regular pattern with short inflorescences and a low spikelet number. There was usually one tiller per tillered node, and rhizomes were difficult to excavate in dense swards, and much rotting of rhizomes was found. However, long rhizomes easily excavated were characteristic of sand dunes, and the somewhat similar waste-tip areas.

Culms were short in grazed grasslands but where they were sheltered by unpalatable herbage, such as tufts of *Juncus effusus*, they might be very tall as at Cwmdare where heights of 510, 505, 460 and 425 mm. were found. The lengthening of fertile tillers is due to internode elongation which increases to a maximum in the node below the panicle. Two branches at the lowest node is common but 1-5 branches may be found in wild or transplant panicles. Data for transplants is found in Table 2. The number of panicle nodes seldom exceeds twelve (Barling 1959) and the glumes are both three-nerved.

TABLE 2
Inflorescence data in transplants of *P. subcaerulea*

<i>Origin</i>	<i>Culm height</i> mm.	<i>No. basal</i> <i>branches</i>	<i>No. spikelets</i>	<i>Panicle length</i> mm.
Lluestai llwydion grassland	350.18 ± 13.83	2.41 ± 0.13	41.13 ± 2.43	60.93 ± 1.92
Craig-y-Llyn	408.60 ± 17.08	2.42 ± 0.14	43.72 ± 3.89	70.17 ± 3.42
Cefn-y-Gyngon	319.29 ± 8.08	2.76 ± 0.08	42.96 ± 2.01	57.09 ± 1.80
Knock Fell	316.57 ± 10.39	2.48 ± 0.08	40.73 ± 2.84	62.87 ± 2.98

Rhizomes are produced as early as February and actively during March, April and May. Internode length measured has varied from 15.33 ± 0.59 mm. to 22.85 ± 2.45 mm., which is usually shorter than that found in *Poa angustifolia*, and the number of tillers per tillered node is also less (Table 3).

TABLE 3
Tillers/Tillered Node.

Origin	No. tillers/tillered node													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>P. subcaerulea</i>														
Windber														
a. waste tip	116	12	8	-	-	-	-	-	-	-	-	-	-	-
b. path	122	20	4	-	-	-	-	-	-	-	-	-	-	-
Jersey Marine	70	4	-	-	-	-	-	-	-	-	-	-	-	-
Slapton Sands	356	5	-	-	-	-	-	-	-	-	-	-	-	-
Dawlish	360	17	1	-	-	-	-	-	-	-	-	-	-	-
<i>P. angustifolia</i>														
Cirencester	-	-	5	14	7	8	11	7	9	8	2	3	2	2
<i>P. pratensis</i>														
Cirencester	26	21	19	4	1	1	-	-	-	-	-	-	-	-
Steadings	4	8	14	14	6	2	2	-	-	-	-	-	-	-

Roots are actively produced from the end of February to early May. Leaves are produced from March onwards and the number of green leaves found at Windber was 3.9 ± 0.3 in August, none in December and 1.48 ± 0.2 in March. Hairiness of the blade is frequently found and is a ready means of finding biotypes. Leaf blade length increases then decreases on fertile tillers.

Plants of *P. subcaerulea* that are kept in a heated greenhouse in autumn remain vegetative the next season, but if kept in the open and then placed inside during January they head in the greenhouse. Heading is usually accelerated by the higher temperatures. There is quite obviously a response to late autumn low temperature and daylength similar to that reported for *P. pratensis* by Peterson & Loomis (1949). Inflorescence primordia have been found in late December and January.

FLORAL BIOLOGY AND BREEDING MECHANISM

Anthesis in *P. subcaerulea* commences about two thirds of the way up the panicle at about the seventh or eighth node. Other spikelets flower above this node, and then at lower nodes, flowering at the lowest node last of all. The basal floret of a spikelet opens first and the top floret often does not open at all. Details of anthesis have been described elsewhere (Barling 1959) and it follows, essentially, that of typical cross-pollinating species.

Pollen grain size was measured as the greatest diameter, and for ten transplants had

TABLE 4
Seed production in enclosed and open pollinated panicles of *P. subcaerulea*.

Origin	No. selfings	Average seeds/panicle		Seeds set/spikelet	
		enclosed	open	enclosed	open
Lluestai llwydion 1	3	68	66	2.1	2.6
Lluestai llwydion 3	3	47	60	1.2	3.0
Tir-Evan-Bach-Traws 1	5	66	70	2.6	2.8
Tir Morris 1	3	49	68	1.7	2.4
Windber 1	3	96	95	3.8	3.9
Bwlfa Farm	3	372	391	3.9	4.0
Penderyn 5	5	124	165	2.7	3.5

a mean of 34.66 μ with a range of 26–45 μ , whilst 4 wild plants had a mean of 33.38 μ and a range of 27.5–40 μ . Pollen fertility, determined by staining, was a mean of 89% in the transplants and 81.75% in the wild material.

The seed production of open-pollinated and selfed panicles was determined for a number of plants (Table 4). The yield of many of the selfed panicles compares favourably with that found under open pollination of transplants or field material.

SEED, GERMINATION AND POLYEMBRYONY, AND SEEDLINGS

Seed length was longer than found in *P. angustifolia*, and hand threshed samples from six wild populations gave an average mean of 3.30 ± 0.045 , mm. and from six transplant populations 3.25 ± 0.044 , mm.

Seed samples were collected from a wide range of sixteen centres in 1958 and were germinated on moist filter paper in petri dishes at room temperature and full illumination; twelve transplant samples were similarly sown. The wild samples totalled 1,485 seeds which gave 1,055 seeds with one seedling, 110 seeds with two, and 4 seeds with three seedlings. Polyembryony was present in all samples and amounted to 7.7%, with germination equal to 78.8%. The transplant seeds totalled 1,174 with 758 single, 114 twin and 11 triplet seedlings, having 10.7% polyembryony and 75.2% germination.

Selfed seed was obtained from various transplants and generally germinated well. However, some samples contained much light seed and a comparison with more normal-sized seed was made (Table 5).

TABLE 5
Germination data for selfed seed samples of *P. subcaerulea*.

Date	Penderyn (thin)					Slapton (full)					
	Seedlings/seed			% Poly-embryony	% Germ-ination	Seedlings/seed			% Poly-embryony	% Germ-ination	
	1	2	3	4		1	2	3			
10 Sept. 1958	(Seed sown)					(Seed sown)					
25 Sept. 1958	9	6	—	—	6	15	73	10	1	11	84
29 Sept. 1958	13	7	—	—	7	20	73	9	2	11	84
3 Oct. 1958	22	9	—	—	9	31	73	9	2	11	84
6 Oct. 1958	67	13	—	—	13	80	73	9	2	11	84
9 Oct. 1958	64	17	2	4	23	87	73	9	2	11	84

Fifty seeds of each known transplant of varied geographical origin were sown half an inch deep in John Innes Seed Compost, together with some from transplants of *P. angustifolia*. It was found that the first leaves of *P. subcaerulea* and *P. angustifolia* were very similar but that the second leaf was wider and generally shorter in *P. subcaerulea*. Width differences were quite clear to the eye in the second leaf stage (Table 6). The leaf blade colour of *P. subcaerulea* was of a darker or bluer green. Also in *P. subcaerulea* the first tiller was found exclusively in the axil of the first leaf whereas in *P. angustifolia* it was found in the second leaf in many cases. In *P. subcaerulea* the first tiller either penetrated the sheath of the first leaf giving typical extra-vaginal tillering, or emerged sideways or took a very small angle pushing the sheath and blade towards the soil, whilst the second tiller was normally found in the axil of the second leaf and was intra-vaginal. In *P. angustifolia* the tillering was exclusively intra-vaginal.

This early extra-vaginal tillering was the most obvious of all the features recorded and revealed the characteristic tendency to a creeping as opposed to a bunched habit. Although the measurements of leaf blade width offered some hope of quantitative discrimination it was felt that for rapid work and single seedling identification it was unreliable in itself, and should be backed by colour features if discernible, as well as tiller behaviour.

TABLE 6
Seedling data in *P. subcaerulea* and some *P. angustifolia*

Origin	1st leaf		2nd leaf	
	Width (mm.)	Length (mm.)	Width (mm.)	Length (mm.)
<i>P. subcaerulea</i>				
Cefn-y-Gyngon	0.82	36.25	1.44	46.00
Craig-y-Llyn	0.55	22.40	1.17	39.60
Knock Fell	0.68	20.14	1.02	36.40
Pontpren	0.76	29.40	1.38	44.50
Penderyn	0.60	22.00	1.26	34.20
Lluestai llwydion	0.66	36.20	1.13	32.00
<i>P. angustifolia</i>				
Deer Park 1	0.55	18.83	0.89	43.67
Deer Park 2	0.55	23.38	1.00	46.00
Deer Park 3	0.51	23.83	0.89	46.67

CYTOLOGY

In the present work mitosis has been studied in root tips and meiosis in pollen mother cells. The root tips were stained in aceto-orcein or Feulgen and then squashed and irrigated in the stain if necessary when the counts were being made. Metaphase plates invariably contained large numbers of small, densely arranged chromosomes. In some cases there was difficulty in determining the exact number, but counts were made of three cells for each plant. PMC smears were stained with aceto-orcein.

Mitosis counts have given high numbers and it is possible to get widely different chromosome numbers within relatively small areas. Thus at Cefn-y-Gyngon, plants from different sheep shelters gave the different numbers of 70 and 98. Other numbers determined were Dawlish Warren 1, $2n = 92$; Dawlish Warren 2, $2n = 84$; Slapton Sands 1, $2n = 54$; Cwmdare, $2n = 65$; Lluestai llwydion grasslands 1, $2n = 72$; Lluestai llwydion tip, $2n = 90$; Tir-Evan-Bach-Traws, $2n = 105$; Bwllfa Farm, $2n = 56$; Limeslade, $2n = 92$; Penderyn 8, $2n = 83$; St. Anne's Airport, $2n = 109$; Grange over Sands, $2n = 98$; Knock Fell 1, $2n = 84$.

At meiosis univalents are commonly seen at first division when they usually lag at anaphase, they may divide and some are excluded from the interphase nuclei. Multivalents are common at first metaphase and segregation of chromosomes is clearly uneven in some mother cells. At second division lagging is again common and exclusion has been seen in some cells in the tetrad stage. The pattern is identical with that illustrated for north American *P. pratensis* by Nielsen (1945, Figs. 22-46). The number of univalents for various transplants was: Slapton Sands 2.90 ± 0.18 , Lluestai llwydion grassland 2.70 ± 0.20 , Penderyn 8, 1.85 ± 0.16 , Jersey Marine 1, 3.20 ± 0.27 , Knock Fell 2.80 ± 0.20 .

In Icelandic *P. subcaerulea*, Löve found chromosome numbers of $2n = 82-147$. Within an area of 10 metres diameter he found plants with $2n = 82, 84, 91, 105, 111, 112, 113$ and 119 chromosomes and provides the most detailed evidence of variation within populations. In addition, Åkerberg has given numbers of $2n = 87$ (for a form of *P. pratensis* which comes close to *P. subcaerulea*), 90, 90-95, for Swedish material.

TRANSPLANTS

Transplants have been much quoted already in the data on plant characters and it remains to mention the major features of genetic and taxonomic value derived from their study at Cirencester. An obvious factor was the genetic variation within and between populations. It would be difficult to show that the morphological variation revealed has

any adaptive value, but it shows that apomixis where present is not a barrier to variation.

The transplants have shown that many characteristics seen in the wild such as short culms, small spikelets and small panicles, are usually environmental effects. Thus greater values for the features measured have been recorded in transplants (Tables 1 & 2), and many of the extremes seen in the field are not seen under cultivation. When studied together the transplants from widely scattered localities show no great differences in gross morphology. It was not possible to detect differences according to altitude. Three-nerved acuminate glumes have been constant. Branching at the lowest panicle node has been variable within clones with a tendency to a greater number of branches than found in the wild. The number of spikelets, panicle length and number of panicle nodes all usually show much lower values than in *P. angustifolia*, but in some clones there are approaches in quantity to this species. These inherited tendencies are found within populations. The vegetative character of great constancy is the single tillering per node which has been recorded in all transplants. Hairiness of the leaf blade is a ready means of detecting population variability and it is inherited in clones. Hairs at the collar of the leaf blade are also constant in all transplants. Fig. 1 compares characters in *P. angustifolia* and *P. subcaerulea* transplants.

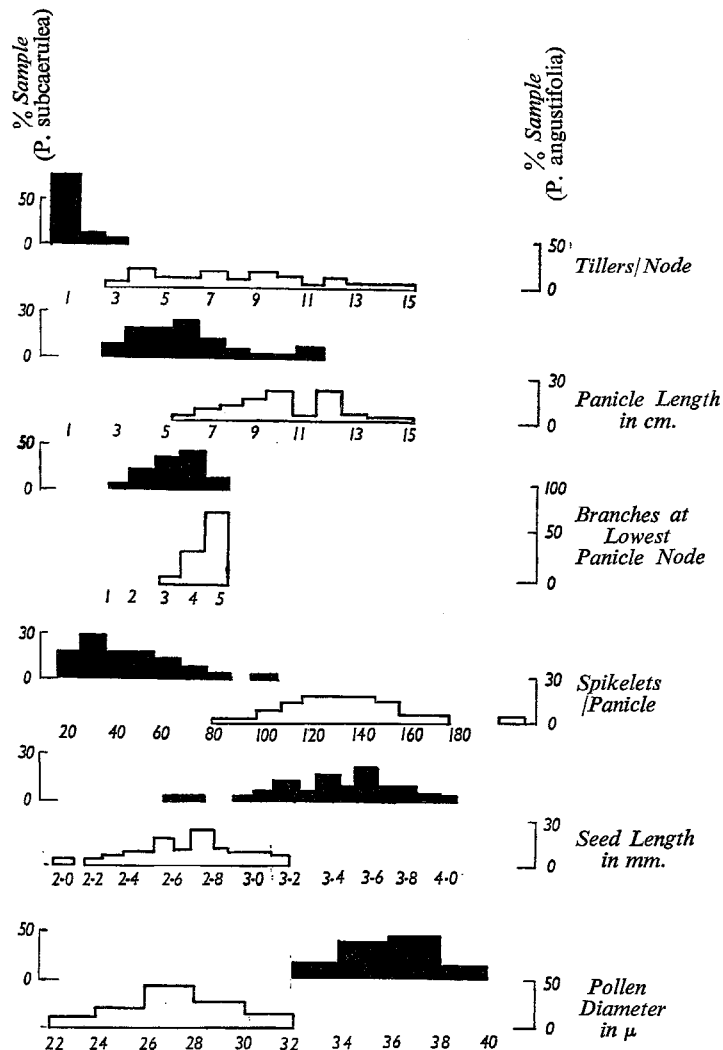


Fig. 1. Taxonomic characters in *P. subcaerulea* (solid black) and *P. angustifolia* (outline)

DISCUSSION

One of the obvious conclusions that can be made from these studies is that *P. subcaerulea* forms a morphological and ecological complex of widespread distribution in the British Isles, possessing characteristics of great similarity to related forms.

All the morphological features are important in the taxonomy of the group and are seen to rest on vegetative, inflorescence and seed characters. The outstanding vegetative feature is the production of single tillers on spreading rhizomes, which contrasts markedly with *P. angustifolia* (Barling 1959). Leaf blades may be hairy, a ready means of seeing variability in populations. The inflorescence is characteristically short, with a low number of spikelets and a tendency towards two branches at the lowest node. The number of nodes is also low and all these characters contrast with the values found in *P. angustifolia* (Barling 1959). Whilst these may be the general and focal features of taxonomy, the expected variability about these features is easily found. Panicles with spikelet numbers and branches similar to *P. angustifolia* may be seen though they are combined with the usual vegetative features of *P. subcaerulea*. Whilst these characters are more typical of related complexes, the decision to include such plants in *P. subcaerulea* is based on their presence within field populations of the group, their three-nerved acuminate glumes, and their conspicuous vegetative behaviour. The taxonomic difficulty is due to the retention of a basic type of inflorescence, long rhizomes, and hairy seed bases throughout the species of the *P. pratensis* group, in spite of the tremendous variability in ecological and physiological directions.

The cytology of the group shows high polyploidy and there is a wide range of numbers and variation within the same habitat, features found in other populations of *P. subcaerulea* (Löve, Åkerberg) and *P. angustifolia* (Barling, Åkerberg). If one considers the chromosome numbers of complexes in relation to their typical habitats, then the higher polyploids are of the wetter and more extreme climates. Such ecological variation within races has been reported by Winge (1940) and Jones (1958), amongst others. It is likely that increasing polyploidy in *P. pratensis*, *sensu lato*, has allowed some of its forms to survive in areas with more adverse conditions. However, the situation is far from clear as wide ranges of chromosome numbers have been reported from within each of the distinct taxa (see Melderis), and also from within populations (Löve). Thus it would be necessary to consider the average polyploidy of British populations on an altitudinal basis, and also to compare these with data from more northerly areas (Löve). Hagerup (1931) proposed that since the majority of polyploids have a better adaptability than diploids then an increase in polyploids could be expected in the flora of areas of more extreme climate. In this work no discussion of the degree of polyploidy, only its incidence, was undertaken. Löve & Löve (1958) have discussed this aspect and whilst supporting Hagerup's hypothesis, point out that the degree of polyploidy is only connected with distribution in exceptional circumstances. It appears that the apomictic Poae may present suitable material for studying the degree of polyploidy in relationship to environmental extremes, such as latitudinal and altitudinal distribution might involve. Thus the range of chromosome numbers reported by Löve for Icelandic material is greater than that found in the more limited work of the present study.

In spite of this high polyploidy there is little disturbance at meiosis, and the occurrence of univalents and multivalents at metaphase of the first division appears to be insufficient to affect pollen fertility. There is good seed production when inflorescences are selfed and this, together with the constancy of polyembryony in seed from all sources, is probably indicative of apomixis. Åkerberg has shown sexual and apomictic forms in Swedish material and Löve apomixis in Icelandic plants. The effects of this on the breeding system are similar to those discussed for *P. angustifolia* (Barling 1959), and the opportunity may now be taken of discussing this feature in relationship to *P. pratensis* as a whole.

Löve has reported a range of chromosome numbers from $2n = 82-119$ in a sample area of ten metres diameter. A similar situation, on a less detailed basis, is found in the present work. There is no difference in visible taxonomic characters associated with this range, though certain features such as pollen diameter, height, etc., do show correlation

in Icelandic material. It seems that these taxonomic characters depend upon genes that are not lost by loss of chromosomes, and this is undoubtedly due to autopolyploidy of a high degree bringing about much repetition of basic hereditary material (multivalents at meiosis support this point). The same appears to hold for other forms of *P. pratensis*, *sensu lato*, and this autopolyploidy and its association with apomixis have been discussed in a thorough fashion by Darlington (1956).

There is obviously much ecological and physiological differentiation between these forms of *P. pratensis* which is of a genetic nature and this may have occurred at a much earlier period than the inception of the present levels of polyploidy, much nearer to the presumably diploid and sexual ancestors. The present differences in average polyploidy that seem to occur between *P. angustifolia* and *P. subcaerulea* are not the only reasons for their distinctiveness. If they have chromosomes in common they also have complex genetic differences, as their ecology shows.

P. subcaerulea is distributed widely in Britain in two major habitats of contrasting altitude, namely hill and mountain grasslands and dune slacks and shores. Both are essentially moist environments. Large gaps are nevertheless present in its distribution and these are probably the result of unfavourable habitat, though the under-recording that would arise from its critical nature may complicate the issue. The species is common in Icelandic grasslands and north west Europe, and is undoubtedly at the southern edge of its range, in much the same way as *Lolium perenne* is at its northern edge in the British Isles. This might account for its greater tendency, in the dense competitive grassland environment, to occur in hill areas, habitats of more extreme climate, and so behave as *P. pratensis*, *sensu stricto*, does in southern Europe and north Africa (Tutin) when it is at its southernmost points. The uncommonness of the form in the south of England (Hubbard), and its more or less restricted occurrence in the specialised maritime habitats, lend further support, and fits with many of Salisbury's (1932) generalisations.

Clausen & Hiesey suggest a latitudinal zonation of the forms of *P. pratensis*, with *P. arctica*, *P. alpigena*, *P. subcaerulea* and *P. pratensis* replacing one another from north to south. Whilst this is broadly true – for example *P. arctica* and *P. alpigena* are not known in Great Britain – it is not completely so since in many areas they are sympatric. Much overlap occurs in Sweden (Åkerberg) and certainly on a broad basis in the British Isles between *P. angustifolia*, *P. subcaerulea* and *P. pratensis*.

This tendency to geographical, coupled with ecological, specialisation in the polymorphic *P. pratensis* allows widespread colonisation and the development and maintenance of distinct physiological forms simultaneously. But the fact that the group is basically pastoral introduces a complexity of distribution since the variety of agricultural practices will lead to a modification of ecological barriers, and *P. pratensis*, *sensu stricto*, the main agriculturally useful form, will migrate to areas which, under more natural conditions, might be more suitable for others. Similarly, if there is a tendency for various pasture types to merge, there may be some areas in which the forms may be brought into very close contact, and even pollinating distance.

In conclusion it appears that in Britain *P. subcaerulea* is a species with a tendency to inhabit damp environments, hill grasslands and fixed dunes and shores. It is relatively easy to distinguish the typical panicles from other forms of *P. pratensis*, *sensu lato* but variation is such that panicle details may be similar to *P. pratensis* or *P. angustifolia* and so it is necessary to examine glume and vegetative characters. However, work in relationship to *P. alpigena* is much needed. A fuller and more detailed account of the distribution of *P. subcaerulea* in Great Britain would be of value in assessing the complex relationships of the other species of the *P. pratensis* group, and could indicate to what degree apomixis has permitted a fragmentation of distribution to small but suitable habitats. There is, even at this stage, much to suggest that *P. subcaerulea* and *P. angustifolia* are more or less extreme forms of *P. pratensis*, *sensu lato*, whether considered ecologically, cytologically or taxonomically.

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