

BIOLOGICAL STUDIES IN *POA ANGUSTIFOLIA*

By D. M. BARLING

Royal Agricultural College, Cirencester

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INTRODUCTION

The agronomic importance of *Poa pratensis* in north-west Europe and North America has stimulated its intensive study, and that of the genus *Poa* as a whole (Nygren, 1954 for references). The latter is now known to contain apomictic and sexual species, which frequently hybridise to give intermediate types, and the considerable taxonomic interest of this generic complex has been discussed by Gustafsson (1947), Stebbins (1950), Nygren (1954) and Melderis (1955). *P. pratensis* itself contains obligate and facultative apomictic forms (Tinney, 1940, Åkerberg, 1942), and the situation, as well as the complexity found within single plants, has been neatly described by Nygren (1951). The species is thus a polymorphic group with a wide range of chromosome numbers that form an aneuploid series, and is classified into sub-species, form-complexes or part populations by various workers (Nannfeldt, 1935, Åkerberg, 1942; Tutin, 1952; Gustafsson, 1947; Hylander, 1953); or separated into distinct species (Lindman, 1926; Hultén, 1950; Hubbard, 1954). The subspecies recognised in Sweden are subsp. *pratensis*, subsp. *angustifolia* (L.) Lindb. fil., subsp. *irrigata* (Lindm.) Lindb. fil. (including *P. subcaerulea* Sm.), and subsp. *alpigena* (Fr.) Hiit. According to Åkerberg (1942), they are linked by intermediate forms particularly where they overlap. The first three taxa are distributed in the British Isles. The more recent work at the Carnegie Institution (Clausen *et al.*, 1947-53) has emphasised the extreme complexity of *P. pratensis*, as well as its capacity to hybridise with other *Poae* and produce intermediate forms. This American work has thrown considerable light on the taxonomy of *P. pratensis* and resulted in several agronomically useful strains.

The present work is an attempt to study the autecology and taxonomy of *P. angustifolia*, chiefly in the Cotswold area, though observations on other areas have been made. A description of British *P. angustifolia* is given by Hubbard (1954). Åkerberg (1942) has made detailed studies of one Scandinavian strain and three plants intermediate with *P.*

pratensis; he gives chromosome numbers of 50-65, and demonstrates the presence of apomictic and sexual reproduction in wild plants.

It is thus apparent that the taxonomic opinions on *P. pratensis* are extremely complex, resolving themselves firstly into those of workers who consider it to be extremely polymorphic with four main subspecies grouped around focal types, and linked by intermediate forms, and secondly, those of workers who hold these subspecies to be sufficiently distinct to merit specific rank. In the present field-studies, populations have been found where *P. pratensis* is represented not only by the *P. angustifolia* complex, but where other shorter-culmed and broader-leaved forms* are present, and transplant studies have revealed phenological as well as morphological differences between them. It was thus important in sampling to select only those plants with narrow leaf-blades as typical of the *P. angustifolia* complex, and some of the reasons for this will be discussed later. It is intended to deal with the study of the more complex populations containing *P. angustifolia* and other forms of *P. pratensis* in a later paper.

DISTRIBUTION AND SYNECOLOGY

Hubbard (1954) states that the British distribution of *P. angustifolia* was incompletely known but that it was commoner in the south than in the north, and he also suggests (1948) that it should be common in Gloucestershire. Hultén (1950) gives the distribution in north-west Europe, showing it as common in southern Sweden and Norway, and also to the east of the Baltic and in Denmark. An approximate northern limit is given and it is noted that the species is found in dry lowland areas, but that the distribution is incompletely recorded. The species is classified as "Boreal-circumpolar lacking large gaps in its area." Active recording has been made by me since 1947, and a large number of stations have been recorded in Gloucestershire and neighbouring areas, and a well-scattered selection of these is given in Table 1., whilst four records are listed by Hubbard (1948).

Records are most common from three habitats: firstly from permanent grasslands, particularly rough swards; secondly from road verges and thirdly from the unploughed headlands of arable areas. The permanent grasslands of the Gloucestershire Oolites may be divided into two broad groups, the rough and the cultivated swards; *P. angustifolia* is usually present in the former, where *Brachypodium pinnatum* and *Bromus erectus* are sward dominants and the sward is rather open, with agricultural activities negligible. The cultivated grasslands are intensively grazed and mown, and may be dominated by *Lolium perenne* or *Festuca rubra*, and whilst *P. pratensis sensu lato* is very common, *P. angustifolia* is rare, being found in those which are continuously put to hay and where species such as *Helictotrichon pubescens* and *Bromus erectus* are common. Detailed observations of the rough areas, however, have revealed forms of *P. pratensis*, so that sympatric populations of *P. pratensis* and *P. angustifolia* are found. *P. pratensis* is also very common in trampled areas such as gateways (Bates, 1938), so that it is frequent at the entry to rough areas and on pathways through them; thus the two taxa may be brought together in this way. In the Cotswold area, road-verges are often wide and frequently dominated by *Bromus erectus* and *Brachypodium pinnatum*, and *P. angustifolia* is common. However, close trampling or mowing of verges may result in colonisation by *P. pratensis* and often in establishment of sympatric populations.

The unploughed headlands of fields are often narrow strips of old permanent pasture in which the species discussed above are common. One striking example of this was found near Little Hinton, Wilts., where a large stretch of downland had been wire-fenced into

*These forms have short culms, both glumes 3-nerved and pointed, usually single tillers per node under field conditions, and broad leaves on sterile tillers with hairs at the collar; they are therefore very similar to *P. subcaerulea*.

separate fields, and arable crops grown, so that the original grassland was found near the fences, and there *P. angustifolia* was common.

Thus it is clear that a study of *P. angustifolia* is bound to take considerable account of *P. pratensis* as a whole, for, apart from the critical taxonomic nature of the group, there is considerable sympatric distribution of forms in the Cotswold area. This association may amount to physical contact between tillers and rhizomes.

TABLE 1.

POA ANGUSTIFOLIA. Records in the Botanical Districts and vice-counties of Gloucestershire.

v.c. 33.	{	1. Broadway Hill. Chipping Campden
		2a. —
		2b.(north). Upton St. Leonards.
v.c. 34.	{	2b. (south).
		3. Churcham.
		4. —
		5. Didmarton. Pennsylvania. Cold Ashton.
		6. (south). Avening. Amberley. Minchinhampton. Frampton Mansell
v.c. 13.	{	6. (north). Brimpsfield. Bisley. Camp. Chalford. Cranham. Edgeworth. Painswick. Tunley. Sapperton. Miserden.
		7a. Aston Blank. Bourton-on-the-Water. Cleeve Hill. Great Barrington. Hampnett. Hazleton. Little Rissington. Sherborne. Stow-on-the-Wold. Turkdean.
		7b. Ampney Crucis. Birdlip. Cowley. Chedworth. Colesbourne. Duntisbourne Abbots. Elkstone. Aldsworth. Barnsley. Bibury. Fosse Bridge. Fosse Cross. Rodmarton. Tetbury. Bagendon. Coln St. Aldwyn. Quenington. Nr. Coln Rogers. Wistley Hill.

Records in adjoining vice-Counties.

- v.c. 6. Swainswick, nr. Bath.
 v.c. 7. Kemble. Fox Hill, Little Hinton.
 v.c. 23. Burford. Fullbrook. Chadlington. Hill Barn. Milton-under-Wychwood. Shipton-under-Wychwood.
 v.c. 36. Ross-on-Wye. Tretire. Weston-under-Penyard.
-

PHENOLOGY

The seasonal development of established plants under field conditions is described below, and amounts, essentially, to the development of fertile tillers with broad leaves very early in the spring, followed by growth of sterile tillers with narrow leaves, and eventually the production of rhizomes and new roots. This culminates in the emergence and seed production of inflorescences, followed by negligible growth. The striking features of this development are, first, the early development of fertile tillers, and secondly, the later development of essentially vegetative growth, particularly rhizomes and roots. The differences of leaf-width may lead to difficulties in identification during the spring, and particularly so when the winter kill of autumn leaves is complete, though the emergence of the sterile tillers soon resolves this difficulty.

SEASONAL STAGES OF DEVELOPMENT IN *P. angustifolia*.

Stage 1. Winter period : remains of culms visible with foliage severely damaged by frosts; plants difficult to find after prolonged severe weather; only youngest leaves may be green and are surrounded by dead leaves. Inflorescence primordia found with difficulty.

Stage 2. Late February – early March : plants tufted; new growth on surviving tillers of the previous year consisting of broad short leaves; inflorescence primordia differentiated; basal axillary buds on the fertile tillers commencing to elongate.

Stage 3. Mid-March to early April : tufted, more densely tillered; tillering intra-vaginal, fertile tillers elongating and robust with broad leaf-blades; tillers from basal buds leafy with long, narrow, leaf-blades; panicles well developed inside the fertile tillers.

Stage 4. Mid-April to early May : panicles emerging and in some localities emerged; leaves of fertile tillers beginning to die back; basal sterile tillers now with very long and narrow leaf-blades; extra-vaginal tillers developing into rhizomes that are white and fleshy, or into short tillers that further increase the diameter of the tufts; length of rhizomes variable and up to 30 cm.; old brown roots being supplemented by the new adventitious roots from base of tillers; overall appearance tufted. Some tufts without fertile tillers are probably the products of the previous years rhizomes. Many culms dead owing to insect attack and straw coloured.

Stage 5. May to July : panicles fully emerged with some late ones emerging; anthesis, seed-setting and seed-ripening all occurring; tall culms with their broad leaf blades and often short flag-leaf, contrasted with the well developed sterile tillers with long narrow leaf-blades; shorter leaf-blades at base of the sterile tillers now withered; ripe seeds being shed in mid-July. Tips of rhizomes tillered but small. Many sterile tillers dead or withering.

Stage 6. August and autumn : all fertile tillers dead; seed more or less completely shed; sterile tillers now the main part of the plant; lower leaves dead; plants tufted often still connected by slender rhizomes, new small tufts establishing. Some tillering under less competitive conditions. Growth during August affected by rainfall.

Inflorescence primordia are found in January and very easily found in early March, and details of fertile tiller development are listed below with approximate dates.

Stage	Date and notes
1. Inflorescence primordia	December – January
2. Elongation of tiller	Commences 20th March
3. Spikelet primordia	Commences 12th March
4. Panicle emergence	Earliest 15th April
5. Meiosis in anthers	1st May
6. Pollen grains	15th May
7. Panicle branches open	26th May onwards
8. Anthesis	1st June onwards
9. Seed setting and ripening	23rd June onwards
10. Seed shedding	9th July onwards

Several workers have demonstrated the importance of photoperiod and low temperature on flowering responses in grasses (Evans, 1927; Cooper, 1951). In *P. pratensis*, Peterson and Loomis (1949) in their studies on North American material demonstrated that autumn conditions of low temperature and short day length are necessary for inflorescence initiation in the species, though they also point out that the same conditions are repeated in the early spring. In a comprehensive account of *P. pratensis* (Evans, 1949)

refers to this latter work and states that only autumn-formed tillers become fertile, and records much data on the phenology of *P. pratensis* in America, with correlations between photoperiod, temperature and seasonal development. At Cirencester the differentiation of inflorescence primordia in *P. angustifolia* was easily found in early spring, in late January both outdoors and in the greenhouse, and also in December, but with greater difficulty. Dissection of apical buds during early March showed varying degrees of bud differentiation within and between plants. The emergence of panicles was accelerated under greenhouse conditions of higher temperature (Table 2). Field emergence also varied from centre to centre in the Cotswolds, being earliest in sheltered areas with a southerly aspect, and so, presumably, being a temperature response. One of the most striking features of 1955 and 1956 was the fact that emergence of *P. angustifolia* preceded that of all other perennial grasses in the area of study, though the subsequent floral development was slow and far behind later-heading, but essentially early, species such as *Alopecurus pratensis*.

TABLE 2.
Panicle emergence in some greenhouse transplants.

Source	Date of emergence in greenhouse	Date of emergence in open
Deer Park 1.	4. 3.	3 to 9. 4.
Deer Park 2.	3. 5.	10. 5.
Deer Park 3.	4. 5.	10 to 14. 5.
Deer Park 4.	10. 4. to 4. 5.	21. 4. to 14. 5.

PLANT CHARACTERS

Populations. As an auxiliary to more detailed studies with a phenological bias, it was decided to sample several populations to compare morphological characters, for the populations as such are the effective breeding units, and are subjected to actual selection pressure so that they are the important sources of variability. Five areas were studied in the Cotswolds and one near Duddington in Northamptonshire, all centres overlying Oolitic Limestone formations. A single plant-unit was taken as a tuft of tillers clearly separated from any other by a distinct rhizome of a prior season. Considerable morphological variability was encountered in the populations, and as forms were frequently found that resembled poorly developed plants of the *P. pratensis* type, care was taken to collect only those with distinctly narrow leaf-blades on the sterile tillers as typical of the complex.

The data presented in Table 3 illustrate the variability within populations and also between areas. In all cases the number of fertile tillers was low, being highest in a more fertile enclosed and cultivated area near Cirencester.

Although the appearance of the inflorescence is similar, detailed data of length and branches from the basal node vary considerably, as do culm-height, and leaf-blade measurements. The differences between sterile leaf-blades and flag leaf-blades are increased by the fact that the former tend to lengthen with the advancing season, and the latter lengthen then shorten with the advancement of the culm. It is probable that the increasing photoperiod is associated with the former and panicle-competition for nutrients with the latter. Rhizome production was sporadic, and varied considerably from sample to sample, so that it is possible that intra- and inter-plant competition may have a profound influence, as was, in fact, found by transplant studies (Table 4). The study of competition in other Gramineae (Donald, 1954 ; Thomas, 1956) has shown that vegetative and reproductive capacities are affected. Hairiness was recorded from the upper leaf-blade surface on the sterile tillers and all plants were found to be hairy on this basis.

TABLE 3.
Population data on the morphology of *P. angustifolia*.

Centre and Sward Type	No. sterile Tillers	No. fertile Tillers	No. New Rhizomes	Length of Panicle mm.	Height of Culm mm.	No. Branches at lowest panicle node	Flag Leaf mm.		Sterile Leaf mm.		% Hairi- ness
							Width	Length	Width	Length	
Deer Park	6.45	1.65	0.65	81.40	398.04	3.72	2.42	36.35	1.55	225.1	100
<i>Festuca rubra</i>	±	±	±	±	±	±					
<i>Bromus erectus</i>	0.43	0.15	0.10	2.75	4.08	0.11					
Royal Agricultural College	6.95	1.80	0.80	102.40	575.70	4.14	3.12	44.50	1.69	200.2	100
<i>Bromus erectus</i>	±	±	±	±	±	±					
	0.63	0.27	0.14	3.01	25.10	0.19					
Two Mile Lodge	3.64	1.32	0.88	88.45	546.60	3.81	2.58	29.66	1.50	147.0	100
<i>Brachypodium</i>	±	±	±	±	±	±					
<i>pinnatum</i>	0.36	0.16	0.16	3.36	13.23	0.14					
V.W.H. Kennels	8.45	2.85	1.35	113.05	584.00	3.94	3.13	43.32	1.64	258.0	100
<i>F. rubra-Lolium</i>	±	±	±	±	±	±					
<i>perenne</i>	1.00	0.46	0.20	2.81	14.60	0.15					
Three Mile Bottom	4.70	1.10	0.40	81.20	531.10	3.80	2.43	31.00	1.34	172.4	100
<i>Bromus erectus</i>	±	±	±	±	±	±					
	0.45	0.07	0.21	4.08	17.67	0.01					
Duddington	4.85	1.30	1.35	80.25	428.60	4.25	2.58	36.60	1.68	193.8	100
Nr. Stamford	±	±	±	±	±	±					
<i>Bromus erectus</i>	0.47	0.18	0.27	3.29	12.40	0.17					

As many data of phenological interest were found, the details are considered below for the different parts of the plants.

Population densities vary considerably and only one centre (Deer Park) has been recorded because of its unusually high count of 2.4 tufts per sq. foot.

TABLE 4. *Morphological characters of wild and transplanted individuals from Deer Park.*

Type	No. fertile tillers	No. sterile tillers	No. of rhizomes	Ht. of culms	Secondary fertile tillers	Length inflorescence	Branches lowest node
Wild	1.65	6.45	0.65	398.04	2.0%	81.40	3.72
	±	±	±	±		±	±
(1956)	0.15	0.43	0.15	4.88		2.75	0.11
Trans-plants	6.40	20.40	3.00	588.70	33%	100.00	4.44
	±	±	±	±		±	±
(1956)	0.11	1.90	0.50	8.50		3.21	0.12

Tiller and Root Development. There are three tiller types to be found in the complex, namely the sterile and fertile tillers and the rhizome. The sterile tillers are actively formed during the spring by the tillering of the fertile shoot, and these new tillers augment those that overwinter on the weaker of the previous season's rhizomes, and are later further augmented by the tillering of the rhizomes developed later in the spring. These sterile tillers can be readily recognised by their narrow leaf-blades and fine appearance. The longevity of these sterile tillers varies; some, produced in the spring of one year, flower and eventually die in the following season, thus persisting for up to fifteen months. Some sterile tillers may be killed before their first winter by insect or animal attack and so have an intermediate existence, often being found dead in late May. Where conditions are poor, some of the tillers do not develop inflorescence primordia and so may persist a little longer and usually do not flower before their death, others may produce late inflorescences. Tillers weakly developed at the apices of rhizomes often, under competitive conditions, survive from June of one year to the end of the following season in a sterile condition and exceptionally may gain overwinter.

The development of the fertile tiller from the sterile condition involves a complete change in the length and width of the leaf-blade; this is also accompanied by a slightly greater width of the tiller.

Rhizomes are produced by extra-vaginal tillering either during or just after the emergence of the panicles, and so can easily be found in May. The rhizomes are white and fleshy in appearance, with the scale-leaves a little longer than the internodes, and are of varying length. In some cases they are exceptionally short and later, after the death of the subtending leaf, appear like any other tiller in the tuft, often forming a second tuft up against the original one; in transplants they may be up to 40 cm. long, but are somewhat shorter under field conditions. The rhizomes root at the node and may branch from axillary buds, but are of the determinate type as described by Oakley & Evans (1921). The older rhizomes are harder and brown in colour with variable internode-length and diameter (Table 5).

A study of root development in *P. pratensis* by Sprague (1933) found considerable seasonal differences. New roots were formed in the spring, amounting to half of the roots being regenerated, and a decrease in root-weight occurred at the period of heavy tillering and stem-growth, being followed by a gradual recovery when tiller-growth was less.

TABLE 5.
Rhizome Measurements at Different Centres.

Centre	Internode Length (mm.)	Diameter (mm.)
Deer Park	9.68 \pm 0.67	1.003 \pm 0.0497
Duddington	9.10 \pm 0.904	0.780 \pm 0.0427

New roots are first found in *P. angustifolia* during the spring period, the first being found in late April, they become abundant in May, and usually appear just before the rhizomes. During the season as a whole they are but few in number and not of the prolific nature found in such species as *Lolium perenne*. Thus, until these appear, the old roots of the previous development are responsible for absorption during the period of elongation of the fertile tillers and the production of sterile tillers, and are probably functional for several seasons. Thus, in general, there is a distinct lag in development of vegetative as opposed to fertile tillers in *P. angustifolia*, and it thus differs from that found in the *P. pratensis*-complex.

Leaves: The sterile tillers of *P. angustifolia* have narrow but long leaf-blades, and this is one of the outstanding taxonomic features of the complex; the longest measured are as follows:—

SOURCE	WIDTH	LENGTH	RATIO
Duddington	1.95	560	1 : 287.18
Three Mile Bottom	1.80	522	1 : 290.00
Trent Lodge	1.60	418	1 : 261.25
Jackaments Bottom	1.80	481	1 : 267.22

However, the successive leaves of the sterile tillers differ in length and width, and similar differences are found in the fertile tillers (Table 6). During this work, a ratio of leaf-width to length was calculated, the width being measured microscopically just above the ligule, and the length to the nearest millimeter.

TABLE 6.
Leaf Blade measurements from fertile and sterile Tillers of *P. angustifolia* (mm.)

Centre	Fertile Tiller								Sterile Tiller				
	Old Leaves		New Leaves						Leaves				
	1	2	1	2	3	4	5	6	1	2	3	4	5
(A) Width	1.6	1.6	1.4	1.9	3.0	4.2	3.9	—	1.2	1.5	1.5	1.8	1.8
Length	—	350	65	67	116	149	101	—	60	140	141	168	266
Ratio	—	218.7	46.4	35.3	38.7	35.5	25.9	—	50.0	93.3	94.0	93.3	147.8
(B) Width	1.64	1.6	3.08	3.28	3.4	3.8	4.2	4.0	1.32	1.56	1.6	1.72	—
Length	137	418	119	155	78	102	115	80	53	72	120	330	—
Ratio	83.5	261.2	38.6	47.2	22.9	26.8	27.3	20.0	40.1	46.1	75.0	191.8	—

(A) — Bartonbury.

(B) — Trent Lodge.

The fertile tillers of the very early growth are sterile tillers of the previous season. Under exceptionally favourable winter conditions, dead, or partially dead leaves may retain their structure sufficiently well to permit measurements, and then the previous autumn's long narrow leaves contrast markedly with the shorter leaves developed by the new fertile tiller (Table 6).

Duval-Jouve (1875) and Arber (1934) have indicated that asymmetry about the mid-rib is found in *P. pratensis*, and this has also been recorded in *P. angustifolia*, and measurements for the fertile and vegetative tillers are given in Table 7. The close examination of leaf-blades also reveals a feature that is frequently found in other Gramineae, namely a slight kinking of the blade near the apex that probably results from being temporarily compressed in the top of the leaf sheath below.

TABLE 7.

Asymmetry in leaf blades of P. angustifolia. Measured in mm. on either side of mid-rib.

Origin	Fertile Tiller					Sterile Tiller		
	1	2	3	4	5	1	2	3
Waterlane	1.8	2.2	2.52	2.52	—	1.04	0.88	0.88
	1.6	2.12	2.00	2.00	—	1.00	0.80	0.80
Kemble	—	—	1.64	1.92	2.32	0.88	0.76	—
	—	—	1.56	1.84	2.24	0.76	0.64	—
Kemble	—	—	1.56	1.60	1.28	0.64	0.68	—
	—	—	1.44	1.52	1.20	0.60	0.64	—

The leaf-ratio values have been intensively determined for sterile tillers in some populations. The sampling of tillers during the autumn has been found to be most suitable owing to the death of the shorter younger leaves by that time, for this means that the lowest green leaf on the tiller is very long and gives high values which contrast with the lower values given by the *P. pratensis* form if recorded in the same way. Values for clones and populations of *P. angustifolia* and *P. pratensis* are illustrated in fig 1. It will be seen that there is considerable variation between and within clones as well as within the populations, and it is intended to study this feature more fully in sympatric populations of the two taxa.

The number of leaves actually formed on tillers varies; on marked tillers that survive the winter and eventually flower the maximum recorded number is 11, and the minimum is 8. An intensive study of leaf-production has not been made, but the rate of leaf-production in the field is not high, and vegetative tillers with only 4 visible leaves between May and October have been recorded.

Several details of leaf-characters are of further interest. The width of leaf-blades of material classified as *P. angustifolia* has always been less than 2 mm. for sterile tillers, though this is exceeded in fertile tillers and sometimes in transplants. The winter burn of leaf by frost is severe and can be so complete as to make the location of plants virtually impossible.

Evans (1949) has given the average number of living leaves on tillers of *P. pratensis* as 3.4, and indicates that there is little variation from this mean. In the present work it has been found that the number of leaves on the tiller varies little at a given time but does

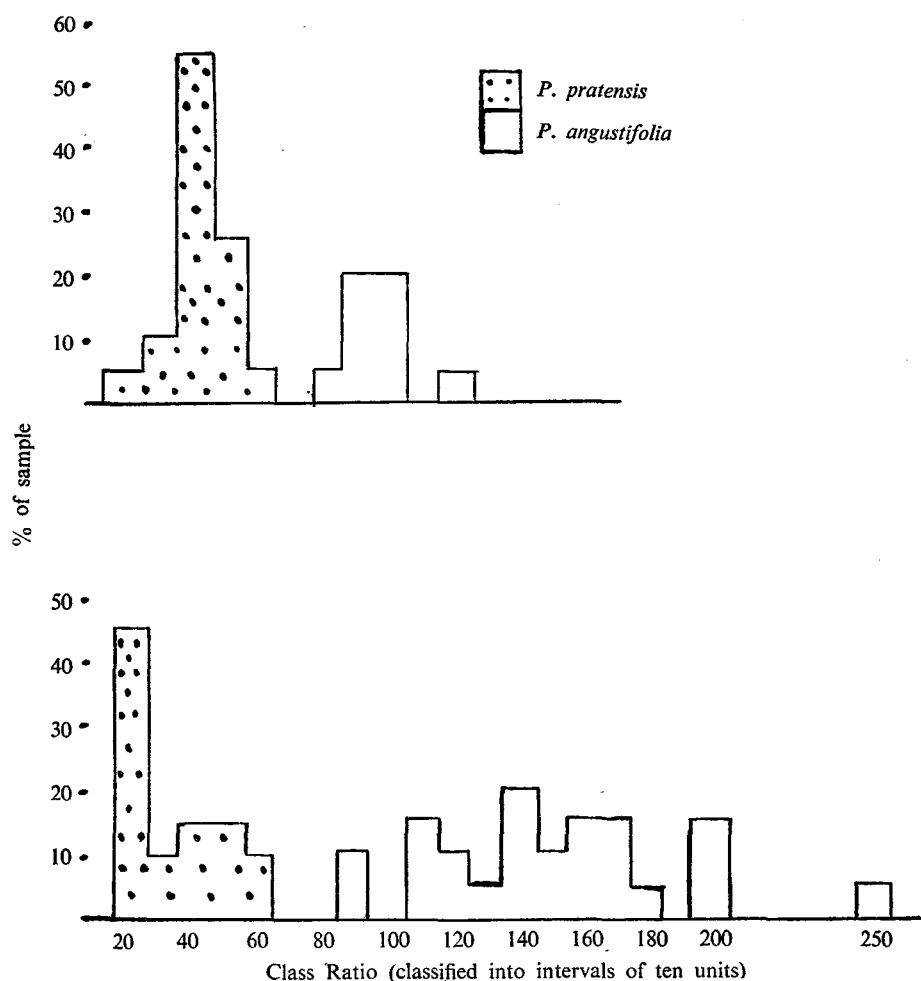


Fig. 1. Leaf Blade width : length ratios in clones and populations of *P. pratensis* and *P. angustifolia*.

so over the season as a whole (Table 8). Counts of leaves on the transplants showed a higher mean, and it is probable that lower competition and rate of leaf-death are responsible for this.

As the season advances, the sterile tillers of *P. angustifolia* produce new leaves at a slow rate and it is seldom that they become fertile during their year of origin. It is therefore,

TABLE 8.
No. of living leaves per tiller.

Centre	Date	No. of living leaves per tiller
Steadings Farm	18.6.56	1.88 \pm 0.098
Three Mile Bottom	18.6.56	1.90 \pm 0.078
Duddington	10.6.56	1.91 \pm 0.076
Deer Park	18.6.56	1.82 \pm 0.068
Deer Park	6.12.55	0.0*
Deer Park Transplants	18.6.56	2.82 \pm 0.064

* All expanded leaves with burned portions.

very difficult to obtain measurements of the actual stem at the base of the tiller, and in order to obtain some quantitative data on tiller size it was decided to measure the length of tillers from the base to the tip of the sheath of the uppermost expanded leaf. In Table 9, some populations and seasonal variations are given which show the rapid increase in length obtained in the early part of the season.

TABLE 9. Sterile tiller length at various centres.

Centre	Date	Mean length of tillers in mm.
Shooter's Hill	26.5.56	52.3 \pm 4.27
Royal Agricultural College	26.5.56	67.3 \pm 1.67
Duddington	10.6.56	46.25 \pm 2.70
Deer Park 1.	26.4.56	47.9 \pm 1.47
2.	26.5.56	59.5 \pm 1.78
3.	30.6.56	60.67 \pm 1.77
4.	26.7.56	61.28 \pm 1.39
5.	24.8.56	66.08 \pm 3.45
6.	15.10.56	62.05 \pm 5.01

Under greenhouse conditions the transplants may produce leaves well into November, whilst those outdoors have completed all visible growth, and these greenhouse leaves show a distinct shortening that is probably a result of decreasing day-length. Some measurements are recorded below.

Leaf-blade measurements of a greenhouse transplant ex Deer Park. D.P.1.

Month	Blade Length mm.	Blade Width mm.
September	211	2.04
	301	2.32
	250	2.48
October	176	2.32
	168	2.20
	150	2.20

The Culm and Inflorescence

The lengthening of the fertile tiller is due to internode-elongation. Measurements taken at different dates showed that elongation occurs in succession from the tiller-base, with each internode completing its elongation before there is any appreciable elongation of that above. Data, presented in Table 10, are similar to those recorded for various other Gramineae (Evans, 1927; Evans and Ely, 1941; Cooper, 1956), with internode-length increasing up the culm.

TABLE 10.
Elongation of fertile tillers at Deer Park. Internode length in mm.

Date	1.	2.	3.	4.	5.
26.4.56	0.9	1.0	45.1	8.1	—
5.5.56	1.4	46.0	87.0	9.0	2.0
14.5.56	169.0	130.0	90.1	10.1	2.1
20.5.56	280.0	146.0	90.5	10.0	2.0
14.6.56	212.2	149.3	91.5	10.2	2.1

The early elongation of the fertile tillers of *P. angustifolia* results in the maximum culm-height being reached by the end of May or early June. Samples for further culm-measurements were then collected when the panicle-branches had opened (Table 11.), and culm-diameter was measured just below the panicle and just below the second node down from the inflorescence.

TABLE 11.
Culm internodes at various centres,

Centre	Internode length in mm. Nodes in descending order.						Diameter mm.	
	1	2	3	4	5	6	1	2
Trent Lodge	260.9	163.0	69.0	11.0	1.0	—	0.676	1.352
Steadings Farm	266.7	161.9	58.7	6.9	2.7	2.0	0.776	1.520
Deer Park	212.2	149.3	91.5	10.2	2.1	—	0.692	1.180
Shooter's Hill	227.9	141.0	77.2	9.2	1.7	—	0.648	1.356
Duddington	253.0	124.7	45.1	8.0	1.4	—	0.760	1.440

The inflorescence data recorded for various populations (Table 3) clearly show variability in length of panicle and number of branches at the lowest node. At Deer Park some additional observations showed the mean number of spikelets per panicle to be 115.20 ± 7.30 and the mean number of florets per spikelet as 4.03 ± 0.09 during the 1954 season.

The inflorescence of *P. angustifolia* is much branched, and in addition to recording the number of branches at the lowest node for various populations (Table 3), the number of branches at each node were counted in some cases (Table 12). The number of branches was higher at the first few nodes and decreased to one at the last few nodes ; the length of internodes decreased up the panicle and the number of nodes varied within and between plants.

TABLE 12.
Branches per node of the panicle at Deer Park.

Branches per node and node number.															
Plants	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Wild average	4.4	4.2	3.7	3.4	2.6	2.2	1.9	1.7	1.1	1.0	1.0	0.9	0.7	0.3	—
Transplant average	4.7	5.0	5.0	4.9	4.3	3.9	3.5	2.8	2.1	1.7	1.3	1.1	1.0	0.8	0.3
Variation in 3 panicles of transplant 1.	4	4	5	4	4	3	2	2	2	1	1	1	1	1	—
	5	5	5	5	4	4	3	3	2	1	1	1	1	1	—
	5	5	5	5	4	4	3	3	2	1	1	1	1	—	—

In the present work it was found that the truly narrow-leaved individuals had three nerves on the upper glume and one nerve on the lower glume, though slight differences were sometimes found within panicles.

FLORAL BIOLOGY

Anthesis in *P. angustifolia* has been studied under greenhouse and field conditions, and commences about two thirds of the way up the inflorescence, at the fifth to sixth node from the top. Further spikelets come into anthesis above this point and then downwards from this point occurring at the lowest node last of all. The occurrence along the branches is variable, usually the lowest spikelets opening first.

Basal florets of a spikelet open first, eventually followed by the others in ascending order, though the topmost floret may not open at all. The actual opening of the florets is variable: in some cases, stigmas spread first, and, in others in the same panicle, anthers may appear before the spread of the stigmas. The anthers are suspended clear of the pales on white, fine filaments, and eventually split along their length. The anthers are often tinged with purple and one may lag behind the others in elongation. In general, however, anthers and stigmas appear roughly together. Anthesis was first recorded in one plant at 10 a.m., in others as early as 6.30 a.m., B.S.T. Anthesis proceeded throughout the morning. One floret first opened at 10.0 a.m., stigmas were extended at 11.0 a.m., two anthers fully emerged at 12.30 a.m., and all three stamens fully elongated by 2.0 p.m. Observations at night showed florets open.

Pollen-fertility was determined for transplants and field material by making aceto-carmines squashes of anthers when adjudged fully ripe. Size of pollen grain was measured at the greatest diameter on shed pollen as the pollen grains were not all perfectly round. Fertility was always high and diameter variable (Table 13.).

In several plants pollination was studied in open and enclosed panicles. Whole ovaries were removed and stained in aceto-carmines and mounted in 45% acetic acid for observation. Permanent preparations were made in some cases by dehydration and mounting in Euparal. Pollen grains with smooth walls were readily seen and pollen-tubes could easily be seen where germination had taken place. Tube-cytoplasm was weakly stained but staining with either Iodine or Cotton Blue gave no better results, usually, in fact, less satisfactory ones. Pollen-tubes were never actually seen to penetrate the body of the ovary.

Pollen was readily shed by movement of the panicle and the general behaviour was typical of that of cross-pollinating grasses.

TABLE 13.
Pollen diameter and fertility in Deer Park wild plants and transplants.

<i>Plants</i>	<i>Pollen Diameter *</i> μ	<i>Range</i> μ	<i>% unstained **</i> <i>pollen</i>
Deer Park 6 Transplants	31.51	22.8 — 42.4	4.10
	28.46	24.0 — 33.6	8.60
	27.93	21.6 — 31.2	2.45
	28.05	19.2 — 31.2	6.70
	27.26	19.2 — 33.6	4.00
	29.90	19.2 — 45.6	8.80
Deer Park 4 Wild Plants	27.21	19.2 — 30.0	5.00
	26.93	22.8 — 33.6	6.80
	27.05	19.2 — 33.6	9.50
	23.40	21.6 — 32.0	8.60
Duddington Wild Plant	26.83	24.0 — 31.2	9.26

* 50 grains per plant

** minimum 300 grains per plant.

TABLE 14
Seeds/Panicle of selfed and open pollinated plants.

Plants		Open Pollinated	Self Pollinated
Deer Park transplants	1.	322	314
	8.	302	221
	5.	320	239
	3.	448	45
Trent Lodge		440	56
		386	330
Waterlane		421	382

Once the body of the ovary commenced to enlarge the pales closed. Removal of the ovary made little difference except that large numbers of ungerminated pollen grains might be found.

On ripening, seed was harvested from individual panicles, and open and self fertility data were estimated for transplants and field material. Open fertility was high, and self-fertility variable, being very high in some plants (Table 14).

Normal seed production in the field was determined from Deer Park in 1953 as 412.10 ± 29.30 per panicle. Seed-weight was also determined at Deer Park as 0.00025 grms.

CYTOLOGY

Apomictic and sexual reproduction has already been demonstrated in *P. angustifolia* by Åkerberg (1941), who also provides chromosome numbers of an aneuploid range of $2n = 50 - 65$. The chromosome studies in this work have all been on established material of wild origin. Root-tips have been stained in Feulgen and give small metaphase plates with high chromosome numbers. Owing to the density and the smallness of the chromosomes, accurate counting was not possible. The following numbers were calculated :—

Source	Number
Deer Park	c. 52
Deer Park	c. 60
Deer Park	c. 58
Bagedon	c. 61

Meiosis has only been studied in pollen mother cells. Feulgen staining gave variable results but some of the clearest views of metaphase and anaphase of the first division. Aceto-carmin squashes were useful but cytoplasmic staining was troublesome whilst aceto-orcin gave good results. However, pairing was regular and the number of univalents observed was small, being 3.9 ± 0.37 . This is in general agreement with the figures given by Nygren (1951) for the other *Poae*. The high pollen-fertility also indicates that this univalent formation is insufficient to disturb the efficiency of pollen formation. The univalents lag during anaphase, usually lying on the metaphase plate and dividing late. Cross-wall formation is often found, with these univalents or their products isolated from the haploid nuclei, and lagging is again found at the second division with univalents excluded at tetrad formation.

TRANSPLANTS

In a critical group such as *P. angustifolia*, it is essential to use transplants to study variation, and material has been collected from Deer Park, Kemble, Waterlane and Duddington, but only in the first has an extensive range been studied. Some data have already been discussed and the quantitative increases of characters noted (Table 4.).

Habit. Two main forms were found: first a tufted dense habit with erect tillers and slight rhizome development; and second, a looser, more open habit with suberect tillers and a greater rhizome production. The former was considered typical of *P. angustifolia* and the latter extreme.

Leaf Blade. On the sterile tillers these are narrow and long, though both short narrow-leaved and long wider leaved forms were found. The leaf-length varied up to 42 cm, and the width from 1.2 — 2.5 mm. under these transplant conditions.

Tillers. Tiller-width varied according to the width of the sterile leaves and rhizome length was also variable within and between plants.

Inflorescences. These varied in length within and between plants, similar variations being found in the number of nodes and the number of branches per node. The number of nerves of the upper glume was three, on the lower, one, though some variation was found within the panicles.

Phenology. The greatest variation was found in the time of panicle emergence and time of rhizome formation, there being:—(a) Variation in the emergence of the first panicles of the order of four weeks, resulting in the overlapping with forms of *P. pratensis* though these were always later on all stages of emergence and elongation of the culm. (b) Rhizomes were formed after panicle emergence and late appearance of the panicle was associated with later rhizome production. (c) Anthesis was variable but there was less difference between plants than found in the other stages; although forms of *P. pratensis* may produce panicles later there is much overlap of anthesis with *P. angustifolia*.

General Considerations. The transplant studies showed that there was considerable genetic variation within populations on a morphological and phenological basis, and in no certain way offered any means of avoiding subjective methods of classification. This variation could be arbitrarily classified into two groups as follows:—

(a) The tufted, early-flowering plants with very narrow leaf blades on the sterile tillers. These vegetative features were considered as the focal point of the *P. angustifolia* type and such plants were easily separated under field conditions, even where other forms of *P. pratensis* were present. Inflorescences had one-nerved lower and 3-nerved upper glumes.

(b) The more open, slightly creeping plants with a variable flowering time that had somewhat broader leaves under transplant and field conditions and formed a very small percentage of most populations. Blade-width was approximately 2.0 — 2.3 mm. under cultivation and about 2 mm. in the field. This group approached the *P. pratensis* group in its appearance and was considered to be an extreme form of *P. angustifolia*.

Whilst it must be emphasised that subjective techniques of classification are necessary in the group and therefore that the precise taxonomic limits are matters of opinion, the importance of the phenological data must also be stressed, for it has clearly shown that the very narrow-leaved forms are characteristically early spring forms and thus that *P. angustifolia* is a definite physiological form. This is all the more evident when comparisons are made with the *P. pratensis* group.

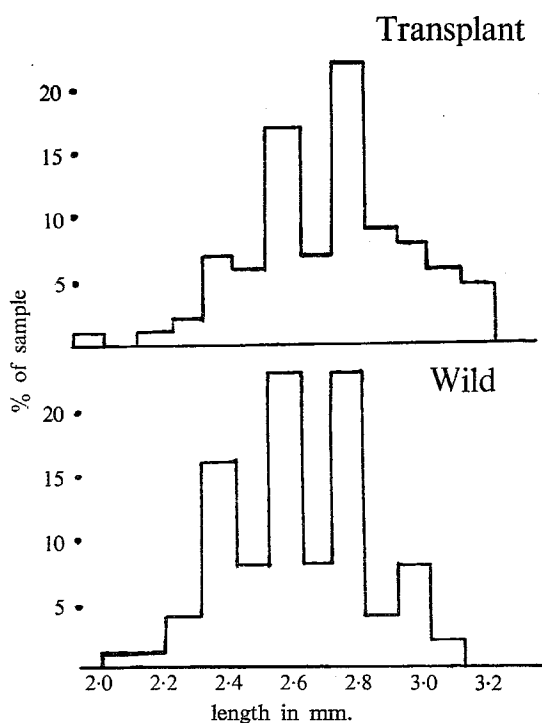
TABLE 15.

Germination and polyembryony in P. angustifolia.

Centre—or plant		Germination %	Seedlings/caryopsis				Polyembryony %
			1.	2.	3.	4.	
1955	Deer Park	87.5	313	60	4	—	8.0
	Hailey Farm	88.0	144	8	1	—	4.5
	General Sample	67.2	309	24	2	1	5.4
1956	Deer Park general	83.0	76	5	2	—	7.0
	Deer Park selfed	80.0	34	6	—	—	12.0
		86.0	41	2	—	—	4.0
		60.0	27	3	—	—	6.0
	Deer Park open	83.0	80	3	—	—	3.0
		86.0	82	4	—	—	4.0
		84.0	82	4	—	—	4.0

GERMINATION AND POLYEMBRYONY

Seed samples were collected from several centres during 1955 and a general bulk sample was also harvested from a wide area of the Cotswolds. All samples gave a high germination and in all cases there was a percentage of multiple seedlings (Table 15). Further data were collected for the 1956 season as well as for individual transplants. The polyembryony, that is evident for the various samples, is of well known occurrence in

Fig. 2. Seed length in wild and transplant *P. angustifolia* ex Deer Park.

P. pratensis, and, in the present work, the effect of competition on seedling size and development within multiple groups was obvious. The highest multiple association recorded was four, with twin seedlings the most common. Seed-length was measured in wild and transplant populations (Fig. 2).

SEEDLING MORPHOLOGY AND ESTABLISHMENT

Preliminary studies of morphology have been made on the following characters under greenhouse conditions; rate of germination, rate of leaf emergence, rate of tillering, leaf-blade width and length on the main tiller, tillering of secondary tillers and the appearance of rhizomes. Seed was collected from heads of *P. angustifolia* and sown in seed boxes and 3-inch whale-hide pots. In the boxes, seed was sown thickly in rows as well as spaced individual seed. Multiple seedlings were discarded.

The rate of germination was fairly even and sowing on 13.4.56 resulted in the emergence of the coleoptiles within ten days, the first leaf emerging 2 or 3 days later, the first tillers being recorded 30 days after sowing. No tillers were visible on the seedlings until at least 3 expanded leaves were developed, and two secondary tillers were obtained in the fourth leaf stage, whilst the third tiller was found in the fifth leaf stage. A small number of tillers developed from the axils of the coleoptiles, but, on the majority of plants in this series, the first tiller appeared in the axil of the second leaf often followed by the second tiller in the axil of the first leaf. The third tillers all arose in the axil of the third leaf.

Seedling competition in the present series was studied on thickly sown plants, and, 47 days after sowing, there were three more tillers on the pot-sown plants (Table 16).

There was a progressive increase in the length and width of successive leaves. Tillers arose from the secondary tillers when they had three leaves and were found in the axil of various leaves.

During these observations it was found that all the seedlings were not of the same habit type, that nearly all were hairy-leaved, and that a few plants were very broad-leaved. (3rd. leaf 3 mm.) and resembled seedlings of the *P. pratensis* complex.

DISCUSSION

The taxonomic complexity of *P. pratensis* (Gustafsson, 1947; Stebbins, 1950; and Melderis, 1955) suggests that the *P. angustifolia* complex can be regarded as one of at least four types that are linked by intermediate forms. This suggests two main problems, first, the field characteristics and general taxonomic limits of the group, and secondly, the means whereby these limits are maintained. As phenotypic variation within the populations is considerable, the use of transplants is a necessary part of these studies, and the wide range of sward types, in which the complex is found, necessitates sampling in as wide a range of areas as possible.

P. angustifolia is a colonist of poor grasslands, the rough swards of agricultural land, and road verges. However, the complexity of agricultural practices is such that all intensities of biotic pressure are to be found within limited areas, so that it is common to find the *P. pratensis* complex in the same or adjacent swards, and so within cross-pollination range. This introduces problems of taxonomic status in such populations, and makes it a necessary associated study of the *P. angustifolia* complex. The precise morphological limits of *P. angustifolia* in these, and all areas, are of immediate concern, and are made difficult by the fact that some populations, although containing a high percentage of typical narrow-leaved *P. angustifolia*, contain a very small number of types not satisfactorily included in that group. They exhibit various morphological and physiological differences which may indicate hybridisation with other sympatric complexes, and, owing to the

results of phenological studies of transplants, it was decided to collect only plants with narrow leaf-blades and well defined tufted growth as typical of *P. angustifolia*. It is therefore obvious that subjective techniques immediately enter the work, and, although these are often present in taxonomic work, they are somewhat sharpened in this case by the taxonomic difficulties of *P. pratensis* already fully discussed by Åkerberg (1942) and Nygren (1954), and made prominent by the work at the Carnegie Institution. It is not intended to reconsider these points here, but merely to indicate that, in this study, they are problems confined to single populations. Indeed the exploitation of the same habitat by what are regarded by some workers as subspecies of a polymorphic species, is one of the interesting features found in the Cotswold grasslands.

The opinion built up is that *P. angustifolia* is physiologically adapted not only to drier soils (Åkerberg, 1941; Hultén, 1950) but also to areas of low biotic pressure, the rough grasslands of agricultural areas. There is a marked absence in intensively managed areas where certain *P. pratensis* forms become prevalent and persistent. The phenology of the type, with its early and short period of vegetative growth followed by little growth in late summer and autumn, is well adapted to poorly managed areas. Detailed phenological studies show interesting features as follows:—(1) An early production of fertile tillers with broad leaves. (2) Elongation of fertile tillers accompanied by tillering of vegetative shoots with narrow leaf-blades from the base. (3) Early panicle emergence. (4) Rhizomes produced after panicle emergence, so that, in the early season an essentially tufted appearance is obtained above ground. (5) A poor period of vegetative growth in summer and autumn. The plants are early short season types, with almost complete die back in severe winter weather. Thus, whilst the group is taxonomically different in many ways from the *P. pratensis* complex, it can also be regarded as physiologically different in that it has earlier panicle emergence, poor post-emergence tillering, and negligible summer and autumn growth. In addition there is much genetic variation, as transplant studies have shown.

The chromosome numbers are difficult to count accurately (Åkerberg, 1942) and in the present work the following range has been recorded, $2n = c. 52 - c. 61$ and shows variation within populations. Meiosis in pollen mother cells has been studied and the presence of small numbers of univalents indicates aneuploidy, but it is insufficient to affect pollen-fertility as this is high. Floral biology suggests that cross-pollination is normal, but there is much evidence for apomixis as selfing gives high seed-yields in some individuals. Pollen is easily found on stigmas of self- and open-pollinated plants with the pollen tubes well developed, and aceto-carmin squashes of enlarging ovaries have been found in which there is no visible trace of pollen-tube penetration of the ovary body. This, however, does not preclude the presence of sexual reproduction, and both forms are reported on Swedish material by Åkerberg (1941). It is possible that apomixis is common as high self-fertility has been obtained, whilst the occurrence of polyembryony and aneuploidy support this view. In addition, progeny raised from randomly selected selfed seed of No. 1 Deer Park transplant, are, to the eye, identical in appearance, and are presumably the result of apomixis. Also, there is a considerable amount of rhizome production that would multiply the biotypes that establish in any sward, and do a great deal towards balancing any low establishment from seed.

At this stage it is worth considering the breeding mechanism of the complex at the population level, for it will considerably influence the genetics and taxonomy of the group. It has been recorded that seed-production per panicle is high both in the field and in transplants. However, when panicles are enclosed self-fertility is seen to vary considerably. It appears that in the majority of plants self-fertility is high but in a small proportion it is poor but does give a small yield, which may indicate the presence of a normal sexual reproduction. One of the obvious effects of this apomixis is an assured seed production,

which is accompanied by a reduced gene-exchange and reduced segregation of new genotypes. However, the presence of sexual reproduction in some plants would give an opportunity for the appearance of new gene-combinations that could be subject to ecological selection, and so endow the population with a versatility of breeding mechanism. Thus apomixis could rapidly multiply well-adapted forms, and the sexual process produce forms that might well be of value under different ecological conditions. In addition, the production of rhizomes would permit the easier spread of suitable biotypes in these dense and competitive grassland conditions than would be possible by seed.

The net effect would be to limit gene-exchange even within the relatively narrow limits of the population, and to limit also hybridisation with other ecological forms or subspecies of *P. pratensis* that, owing to the nature of agricultural activities, would be almost certain to be sympatric.

Thus apomixis coupled with the ecological specialisation of the complex would account for much of the taxonomic differentiation, whilst the possibility of sexual reproduction would permit the maintenance of variability by segregation following either hybridisation within the complex or with related and sympatric complexes. Clausen (1952) has reported that there is much variation between the survival rates of apomictic and sexual progeny in *P. pratensis*, and this might be very effective at the inter-complex level, and so reinforce the ecological specialisation. But this theoretical discussion can be only resolved by the detection of inter-complex hybrids by subjective field taxonomy or by their artificial production. There are seedling differences between the *P. angustifolia* and *P. pratensis* groups, and it may be possible to express these quantitatively, as Saeed (1956) has done in the agricultural strains of *Lolium perenne* at the seedling stage. Quantitative studies of the leaf-blade width : length ratios and other taxonomic details might supplement subjective taxonomic methods in sympatric populations, where the detailed and very wide hybridisations within the *Poa* reported by Clausen *et al.* (1947 - 1953), would lead to an expectation of inter-crossing.

Thus the extremely widespread distribution of *P. angustifolia*, and the presence of forms approaching the *P. pratensis* complex have shown characteristics that are well appreciated for other sections of the species (Åkerberg, 1941 ; Nygren, 1954), and at the same time introduced several eco-taxonomic problems of essentially local interest. Thus at the population level it has been obvious that there is considerable morphological and physiological variation within the taxon, and it has been necessary to resort to detailed transplant studies to obtain satisfactory analysis of the population variation where *P. pratensis* forms are present and intermediate types are suspected, and it is intended to give a further account of work on these sympatric populations. However the tufted nature of the centre parts of the plants and the narrow leaf-blades of the sterile tillers are, together with the early panicle emergence, the main characteristics of the complex. There is much therefore to confirm the view that *P. pratensis* is a polymorphic species consisting of several focal types or ecological population-complexes which may hybridise to give intermediate forms, but more detailed work is needed on the other Cotswold forms of the *P. pratensis* complex before a more reasonable assessment can be made. Thus a study of the other British subspecies of *P. pratensis sensu lato* and also the location and study of communities where they are sympatric may give a clearer picture of the eco-taxonomy of the complexes.

SUMMARY

Populations of *P. angustifolia* are of widespread occurrence in rough Cotswold pastures and on road-verges, being associated with such species as *Bromus erectus*. It is absent from hard grazed areas where *Lolium perenne* is abundant. The distribution mosaic of agricultural management results in considerable overlap with various forms (subspecies) of *P. pratensis* even within the same field.

P. angustifolia populations in rough swards show considerable variation and a small proportion of related forms are not satisfactorily included in the *P. angustifolia* complex. Transplant studies are being conducted on these variants which are very similar to *P. subcaerulea*. Variation in tillering, leaf-blade size and width, inflorescence and reproductive characters is found in *P. angustifolia*. Seed production is high but rhizome production is not great under field conditions.

Phenological studies show severe winter die-back and early spring development of fertile tillers with broad leaf blades in which panicle primordia are found in late February and early March. Elongation of the fertile tillers is accompanied by production of vegetative tillers with very narrow leaf blades. Panicle emergence occurs in April and early May, and culm elongation is the result of successive internode elongation with the topmost internode the longest. Rhizomes are produced after panicle emergence.

The sterile tillers increase in length in early spring and reach their maximum by mid-summer. The number of living leaves per sterile tiller is small, ranging from 1 to 3. The life of sterile tillers varies, sometimes being short, 2 or 3 months, but usually extends into the following season when fertile tillers develop from some of them. In these fertile tillers leaf-blade characteristics alter conspicuously as the leaf-blades are much broader on the culm. All leaf blades show asymmetry about the midrib. The plants or tufts are thus in a constant state of change from season to season having few truly perennial or completely persistent shoots.

Pollen-fertility is high and anthesis is typical of cross-fertilising species. Self-fertility is variable but usually very high. High chromosome numbers are found and P.M.C. meiosis shows occurrence of univalents. Polyembryony is common. There is evidence consistent with apomixis in some plants.

An account of seedling morphology is given and it is possible that there may be real quantitative differences between *P. angustifolia* and other forms of *P. pratensis* at this stage.

Transplant and field studies have emphasised the need for careful analysis of *P. angustifolia* where it is associated with other forms of *P. pratensis*.

P. angustifolia is essentially a colonist of well-drained soils subjected to low intensity of agricultural management, and its early but short season of active growth is well suited to such areas. It is therefore a distinct physiological type or ecological complex, within which a versatile breeding mechanism allows apomixis rapidly to multiply well-adapted biotypes whilst the sexual reproduction of other forms permits hybridisation and the segregation of new genotypes. Apomixis is probably the means whereby it maintains taxonomic distinctness in habitats in which other forms of *P. pratensis* may be in physical contact with it.

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REFERENCES

- ÅKERBERG, E., 1942, Cytogenetic studies in *Poa pratensis* and its hybrid with *Poa alpina*, *Hereditas*, **28**, 1-126.
ARBER, A., 1934, *The Gramineae*; Cambridge
BATES, G. H., 1938, Life forms of pasture plants in relation to treading. *J. Ecol.*, **26**, 452-54.
CLAUSEN, J., KECK, D. & HIESEY, W. M., 1947, Experimental taxonomy, *Carn. Inst. Wash. Y.B.*, **46**, 95-104.
———, 1948, Experimental taxonomy, *Carn. Inst. Wash. Y.B.*, **47**, 105-110.

- CLAUSEN, J., KECK, D., HEISEY, W. M., & GRUN, P., 1949, Poa investigations, *Carn. Inst. Wash. Y.B.*, **48**, 97-103.
- , 1950, Poa investigations, *Carn. Inst. Wash. Y.B.*, **49**, 104-107.
- CLAUSEN, J., GRUN, P., NYGREN, A. & NOBS, M., 1951, Genetics and evolution of Poa. *Carn. Inst. Wash. Y.B.*, **50**, 109-111.
- CLAUSEN, J., GRUN, P., HIESEY, W. M., & NOBS, M., 1952, New Poa hybrids, *Carn. Inst. Wash. Y.B.*, **51**, 111-117.
- CLAUSEN, J., HIESEY, W. M., GRUN, P., & NOBS, M., 1952, Survey of the range grass program. *Carn. Inst. Wash. Y.B.*, **51**, 107-111.
- CLAUSEN, J., HIESEY, W. M., & NOBS, M. A., 1953, The Poa program, *Carn. Inst. Wash. Y.B.*, **52**, 170-173.
- COOPER, J. P., 1951, Studies on growth and development in *Lolium* II, *J. Ecol.*, **39**, 228-270.
- , 1956, Developmental analysis of populations in the cereals and herbage grasses, 1. *J. Agric. Sci.*, **47**, 262-279.
- DONALD, C. M., 1954, Competition amongst pasture plants, 1. *Aust. J. Agric. Res.*, **5**, 585-597.
- DUVAL-JOUE, J., 1875, Histotaxie des feuilles de graminées. *Ann. Sci. nat.*, ser. 6, Bot., **1**, 294-371.
- EVANS, M. W., 1927, The life history of timothy, *U.S.D.A. Dept. Bull.*, **1450**.
- , 1949, Kentucky blue-grass, *Ohio Expt. Stn. Res. Bull.*, **681**, 1-52.
- EVANS, M. W., & ELY, J. E., 1941, Growth habits of Reed-Canary grass. *J. Amer. Soc. Agron.*, **33**, 1017-1027.
- GUSTAFSSON, Å., 1947, Apomixis in higher plants III, *Acta. Univ. Lund*, **43**, 183-370.
- HUBBARD, C. E., 1948, Gramineae, in Riddelsdell, H. J., Hedley, G. W., & Price, W. R., *Flora of Gloucestershire; Arbroath*.
- , 1954, *Grasses*, Penguin Books; London.
- HULTÉN, E., 1950, *Atlas of the distribution of vascular plants in N.W. Europe*; Stockholm.
- HYLANDER, N., 1953, *Nordisk kärlväxtflora*, **1**, Stockholm.
- LINDMAN, C. A. M., 1926, in Holmberg R., *Skandinavien Flora*, Stockholm.
- MELDERIS, A., 1955, Species problems in recent Scandinavian works on grasses, in *Species studies in the British Flora*, *Bot. Soc. Brit. Isles Conf. Rep.* **3**, 140-159.
- NANNFELDT, J. A., 1935, Taxonomical and plant geographical studies in the Poa laxa group. *Symb. Bot. Upsaliensis* **1** (5).
- NYGREN, A., 1951, Embryology of Poa, *Carn. Inst. Wash. Y.B.*, **50**, 113-115.
- NYGREN, A., 1954, Apomixis in the angiosperms, 2, *Bot. Rev.*, **20**, 577-649.
- OAKLEY, R. A., & EVANS, M. W., 1921, Rooting systems in Timothy, *J. Agric. Res.*, **21**, 173-178.
- PETERSON, M. L., & LOOMIS, W. E., 1949, Effects of photoperiod and temperature on growth and flowering of Kentucky Blue Grass, *Plant Physiol.* **24**, 31-43.
- SAEED, S. W., 1956, Recognition of Rye-grass species and strains in the seedling stage, *Emp. J. Exp. Agric.*, **93**, 27-36.
- SPRAGUE, H. B., 1933, Root development of perennial grasses and its relation to soil conditions, *Soil Sci.* **36**, 189-209.
- STEBBINS, G. L., 1950, *Variation and evolution in plants*; New York.
- THOMAS, W., 1956, Effects of plant population and rates of fertiliser nitrogen on average weight of ears and yield of corn in the south, *Agron. J.*, **48**, 228-230.
- TINNEY, F. W., 1940, Cytology of parthenogenesis in *Poa pratensis*, *J. Agric. Res.*, **60**, 551-560.
- TUTIN, T. G., 1952, Gramineae, in Clapham, A. R., Tutin, T. G., & Warburg, E. F., *Flora of the British Isles*; Cambridge.