LEAF MEASUREMENTS AND EPIDERMIS IN *POA ANGUSTIFOLIA*

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Abstract

In *Poa angustifolia* and *P. subcaerulea* leaf-blade length on fertile tillers increases and then decreases to the flag leaf. The third leaf-blade down from the panicle is usually longest. Leaf sheaths increase progressively to the flag leaf. Total leaf length is greatest in the leaf below the flag leaf. The per cent. contribution of sheath in the leaf increases to the flag leaf and sterile tillers show the reverse. Individual tillers may show modified patterns. The leaf blade epidermis of *P. angustifolia* was studied, and the lower of sterile tiller leaves contained none or very few stomata and were of a xeromorphic type, whilst the leaves of the fertile tiller showed stomata increasing in quantity to the flag leaf. Inflorescence initiation is in December–January when the leaves showing the above patterns on fertile tillers are all in the primordial stage.

Introduction

The leaves are of taxonomic importance in the *Gramineae*, for where floral characteristics of closely related species are very similar, vegetative features are commonly used as aids to identification. There is considerable variation in leaf dimensions in grass species both in the vegetative tiller (Langer 1958), and also in the fertile tiller (Borrill 1959 and 1961a). Leaf blade length is known to be affected by temperature, daylength and other factors (Langer 1954, Stuckey 1942), particularly in the sterile tillers. The variation in fertile tillers was suggested by Evans (1949) to be the result of apical dominance (Meyer & Anderson 1939). Borrill (1959) has suggested that it is due to the development of inflorescence primordia when the longest leaf blade has emerged and that subsequent leaf blades are shorter due to decrease in cell extension, not number. This work has done much to clarify the factors associated with varying leaf blade dimensions in the grasses. The culms of grasses also show considerable variation in internode length with increasing length up the shoot (Evans 1927, Cooper 1956, Barling 1959). Sørensen (1953) has used epidermal characters with species of *Puccinellia* found in Greenland and so have Burr & Turner (1933), Tutin (1955), Melderis (1955), and Borrill (1961b) in other species, whilst Prat's (1932 and 1948) work has thrown much light on the epidermal characteristics of the grasses.

The data presented here are chiefly from transplants of *Poa angustifolia* and *P. subcaerulea* grown in 8-in. pots of calcareous loam immersed in washed gravel at Cirencester (lat. 51° 43′ N., long. 1° 57′ W.) at an elevation of 440 ft. (130 m), under natural daylength.

Sterile tillers

The contribution of leaf blade and sheath to total leaf length in *P. subcaerulea* (Table 1) is typical. In the early part of the season the relative proportion of blade increases up the tiller. This trend may be reversed in leaves formed in the autumn when the blades shorten probably as a result of decreasing photoperiod. The sheaths may also decrease in length later in the season. The blade is always asymmetrical, with a marginal indentation near the apex.

Fertile tillers

The leaf measurements from transplants of *P. angustifolia* and *P. subcaerulea* have shown a characteristic and similar pattern in the relative development of leaf blade and sheath as well as in total length (Table 2). The third leaf blade down from the panicle is usually the longest with progressively shorter blades above and below. However, the

TABLE 1. *P. subcaerulea:* % contribution of blade and sheath to leaf length in early (E) and late (L) growth of sterile tillers.

Origin		*Time*	*Leaves in ascending order* 1.	2.	3.	4.
Slapton	Sheath	E	55·56	38·04	28·48	22·73
	Blade		44·44	61·96	71·52	77·27
Craig-y-Llyn	Sheath	E	66·51	25·30	22·73	—
	Blade		53·49	74·70	77·27	—
Bwllfa wall	Sheath	L	30·46	25·32	22·73	23·23
	Blade		69·54	73·68	77·27	66·67
Montrose	Sheath	L	80·65	64·10	37·50	28·53
	Blade		19·35	35·90	62·50	61·47

TABLE 2. Average values of leaf and internode lengths for *P. angustifolia* and *P. subcaerulea* (mm.).

		Blade	*Sheath*	*Total*	*Internode*
P. angustifolia	F	32·86±2·35	102·29±4·10	135·15±6·81	199·57± 9·20
(transplants 1958)	2	69·43±3·10	93·43±3·25	162·86±6·63	127·71± 6·71
	3	81·57±3·90	67·29±3·20	148·86±6·90	70·43± 6·80
	4	70·29±3·40	33·71±2·91	104·00±9·50	14·57± 1·21
P. angustifolia	F	36·39±2·65	121·74±4·97	162·44±6·63	323·78±11·70
(wild plants)	2	71·13±3·30	114·65±3·98	185·65±6·44	164·70±7·40
	3	92·87±4·21	75·39±3·77	164·09±7·00	73·00±7·01
	4	61·00±6·30	51·78±3·25	112·91±9·09	18·22±0·77
P. subcaerulea	F	35·50	96·43	131·93	149·86
(transplants 1958)	2	70·50	81·50	152·00	79·79
	3	75·64	53·57	129·21	28·71
	4	72·07	41·64	113·71	15·29

pattern within individual tillers is not necessarily constant as sometimes the second or fourth leaf blade is longest. The leaf sheaths consistently increase in length up the culm and, like the blades, show considerable variation in length from plant to plant. The culm itself shows the usual pattern of increasing internode length up to the panicle. The sheaths of the lower nodes are often longer than the internodes above them, whilst those of the top node are normally shorter, though exceptions to the latter are common. The ratio of sheath : blade is lowest at the flag leaf and increases down the fertile tiller (Table 3). Whilst these characteristic patterns are seen in leaf parts, total leaf length is greatest in the leaf above the one with the longest blade (Table 2).

A conspicuous feature of *P. angustifolia* is the difference in leaf characters in a tiller that is sterile in one season and fertile in the next (Barling 1959). The sterile leaves are long and narrow and of a xeromorphic type, whilst those on the fertile tiller are shorter but much broader (Fig. 1).

TABLE 3. Ratio of sheath : blade, and % sheath in the four top leaves of fertile tillers.

	angustifolia		*subcaerulea*	
	ratio	%	*ratio*	%
F	0·32	75·68	0·37	73·09
2	0·74	57·36	0·87	53·61
3	1·21	45·20	1·41	41·45
4	2·10	32·41	1·73	36·61

LEAF-BLADE EPIDERMIS IN *P. angustifolia*

In *P. angustifolia* the lower epidermis of the leaf-blade from sterile tillers had cells with folded walls and cork cells throughout the inter-nerve area. The nerves had narrower cells and silica-suberose couples, though there was variation in cell size in the inter-nerve areas. The major feature of the lower epidermis was the absence or limited occurrence of stomata (Fig. 2 and Table 4). The upper epidermis had more or less smooth-walled cells with the stomata in rows and asperites prominent (Fig. 1). Long unicellular hairs or asperites were found in the inter-nerve epidermis.

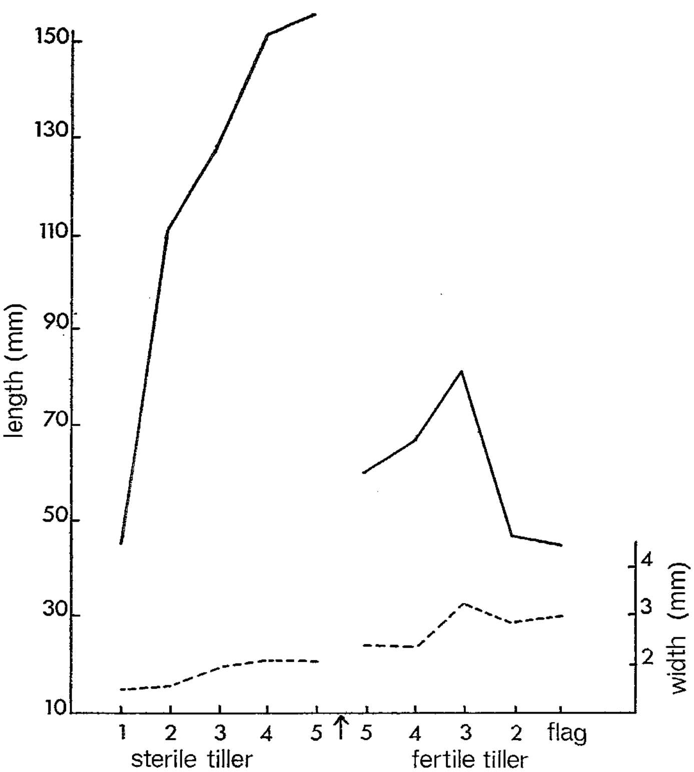

Fig. 1. Leaf blade length and width (broken line) sterile and fertile condition of a tiller of *Poa angustifolia*. ↑ Inflorescence initiation.

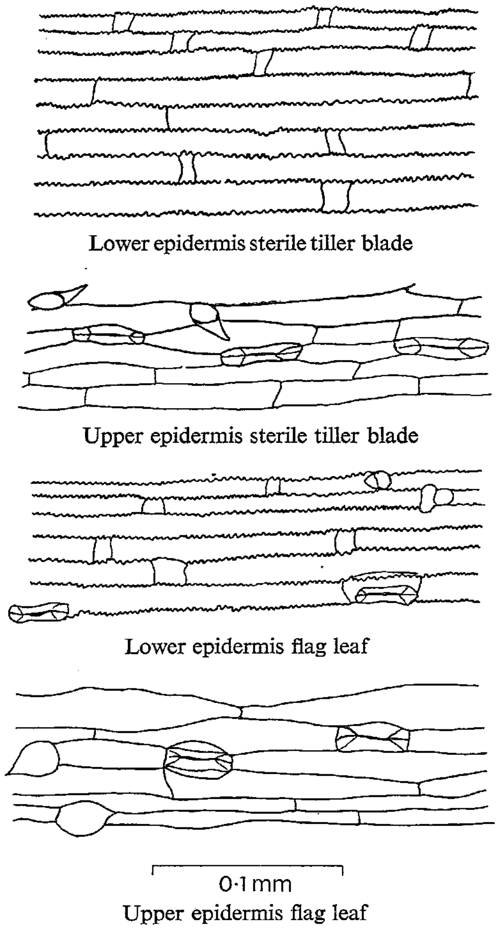

Fig. 2. *Poa angustifolia* leaf blade epidermis. Upper diagrams from sterile tiller leaves. Lower diagrams from flag leaf.

On the fertile tillers, by contrast, the lower epidermis of the flag leaf had numerous stomata (Table 4). The upper epidermis was of the type described for sterile leaves and the leaf margins showed asperites in all cases. As there was such a marked difference in the epidermal characters of the flag leaf blade and sterile tiller blades, this feature was investigated in all the leaves of the flowering tiller. The blade below the flag leaf showed stomata on the lower epidermis, but the third leaf down, which was longest, varied considerably. In some tillers there were abundant and well-distributed stomata, in others they were limited to the region near the mid rib. The fourth leaf down showed very few stomata on the lower epidermis in the majority of cases.

TABLE 4. Stoma density in *P. angustifolia* and *P. subcaerulea* transplants.

		Stomata/0·7 mm²	
		Upper epidermis	*Lower epidermis*
P. angustifolia			
Deer Park No. 1	Flag leaf	36·92±3·72	9·96±0·76
	Sterile tiller leaf	63·76±3·68	0·00±0·00
Daneway 18	Flag leaf	58·88±3·16	18·96±0·84
	Sterile tiller leaf	59·08±4·18	0·04±0·04
P. subcaerulea			
Cefn-y-Gyngon	Flag leaf	28·12±1·07	10·20±0·82
	Sterile tiller leaf	46·36±2·78	10·40±0·70

INFLORESCENCE INITIATION

In *P. angustifolia* the inflorescence primordia are first found in late December, but are easier to find in January and February. During this period the field populations tend to lose all foliage through winter burn, and the leaves that emerge on these fertile tillers in spring are to be found as primordia beneath the panicle primordium. The stages of primordial development in *P. pratensis* have been illustrated by Evans (1949). The stages in *P. angustifolia* show that the vegetative apex with its leaf primordia first elongates and develops large folds, whilst later these show deeper folds, the beginnings of branching. At this and subsequent stages the number of potential spring and early summer leaves can be counted and usual numbers are not more than five. Similar features are to be found in *P. subcaerulea.*

DISCUSSION

Borrill (1959) demonstrated the influence of the development of the inflorescence primordia on blade length in *Glyceria,* and noted that there is occasional disturbance by external factors. He found that the primordia developed as the longest leaf emerged, subsequent leaves being shorter, and in the species studied inflorescence initiation occurred in spring. In *P. angustifolia* there is winter initiation and at this time the leaves in the bud are usually four to five in number and are the ones that emerge on the extending culm in spring and early summer. These leaves show the same pattern as found by Borrill, although, unlike the leaves of *Glyceria,* they all emerge after inflorescence initiation.

Leaf-sheath length is closely correlated with increases in stem internode, but total leaf length shows no clear association with inflorescence initiation or internode length. It is also clear that the percentage contribution of the blade and sheath to total leaf length decreases and increases respectively in succeeding leaves. The annual species *Lolium temulentum* (Borrill 1961a) shows similar increases in sheath length, but total leaf length also increases to the flag leaf which is different from that found in the present species which are, of course, perennials. Probably differing patterns occur in different *Gramineae*, related to timing of inflorescence initiation and perenniality of species.

The epidermis of the lower surface of the narrow leaf blades shows an absence of or very few stomata, and it is reasonable to assume that this is a xeromorphic feature tending to increase its adaptability to dry areas, since the closure of the leaf by folding of the upper surface will effectively reduce water loss. On the fertile tiller, however, the narrow leaf blades with xeromorphic features change to broad leaf blades in which there is a progressive increase of stoma number in the lower epidermis. This reversal of xeromorphic characters is in striking contrast to many dicotyledons, and is possibly associated with the important part played by the leaves of the fertile tiller, particularly the flag leaf, in the filling of the caryopsis, as has been demonstrated in barley (Archbold 1945; Watson *et al.* 1958). Further, these broad leaves of the flowering tiller would be active in British conditions in the relatively moist periods of spring and early summer when water economy is not critical.

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