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FESTUCA RUBRA NEAR *CARDIFF*:

A TAXONOMIC, MORPHOLOGICAL AND ANATOMICAL STUDY OF THREE SUB-VARIETIES OF *FESTUCA RUBRA* L. SUBSP. *EU-RUBRA* HACK., VAR. *GENUINA* HACK., GROWING NEAR CARDIFF, S. WALES.

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[WITH FOURTEEN FIGURES IN THE TEXT.]

I.—INTRODUCTION.

THE present paper is the result of a morphological and systematic study of three forms of *Festuca rubra* L., which had been observed by Professor (now Principal) Trow of the University College of South Wales (Cardiff), and grown in his garden side by side, maintaining their distinctness for several years.

The interest of these forms was enhanced by their local economic importance (sward consisting of these grasses being in great request for bowling-greens, &c., and saleable at 6d. per square yard, or £121 per acre, as a standing crop to be removed at the cost of the purchaser): by the difficulty of assigning the three forms to their proper positions in the current scheme of taxonomy; and by the interesting ecological relations of the habitats affected by them.

II.—SYSTEMATIC.

It will be convenient to begin with a description of the forms included in Hackel's Section *Ovinæ* of the genus *Festuca* which correspond with the plants variously known to English authors as *Festuca ovina*, *duriuscula* and *rubra*.

1. *Section* OVINÆ, *Hackel.*

Radical sheaths not thickened at the base. Ligules very short, truncate, often biauriculate. Laminæ either all complicate or those of the culm more or less flat; vernation conduplicate. Spikelets elliptical or oblong-elliptical. Fertile glumes narrow, margins scarious, in fruit the margins very involute. Ovary

obovate-oblong, glabrous, rarely sparingly hispidulous, style exactly terminal. Caryopsis oblong, pale, with deep ventral furrow, glume closely adherent, and mark of hilum extending nearly the whole length.

This section Hackel divides into two sub-sections.

1. *Intravaginales*, characterised by their branches growing apogeotropically that is, they grow up inside the sheath which subtends them and emerge from the top of the sheath where the latter passes into the lamina. Each bears a dorsal prophyll followed by normal leaves (*i.e.*, having sheath and lamina). This includes nine species among which is *F. ovina*.

2. *Extravaginales* and *Mixtæ*. Branches either all, or only the lower ones, diageotropic, growing out through the base of the subtending sheath, and up external to it. Dorsal prophyll very small and with a gradual transition through various scale-leaves to normal foliage leaves. In the typical Extravaginales all the branches are extravaginal; the Mixtæ connect these with the Intravaginales. The three forms under investigation come in this intermediate group. Here Hackel places only two species, *F. rubra* L. sens. ampliss. and *F. Porcii* n.sp.

2. *Festuca rubra* L. sens. ampl.

Sheaths of the radical leaves all entire; ligules glabrous.

Further details which Hackel considers of importance in his description are: sheaths of the radical leaves on withering break up into irregular fibres, laminæ persist after death, ligules the same throughout, scarious margins not producing auricles, those of cauline leaves not equally biauriculate or nearly uniauriculate.

Following Hackel's key to the sub-species and varieties one is led to subsp. *eu-rubra* and var. *genuina*.

3. Subsp. *eu-rubra*.

About as many intravaginal as extravaginal branches. Laminæ obtuse; those of radical leaves obtusangled, 5 to 7 nerves, single sclerenchymatous strands corresponding to these on the lower surface, those of cauline leaves with motor cells clearly arranged.

Var. 1 (6) *genuina*. Loosely cæspitose, basal extravaginal branches creeping. Laminæ difformed: radical complicate, and angulate, obtuse-hexagonal in trans. sect., sclerenchymatous bundles separately arranged, motor-cells absent; cauline flat.

Seven sub-varieties of *genuina* are described:—

a vulgaris. Tall, radical leaves soft, setaceous (0·6—0·7 mm. diam.) dark-green; panicle loose (6—15 cm. long). Spikelets

small (7—8 mm. long), lanceolate or oblong, green or slightly grey-violaceous; fertile glumes 4—4·5—5 mm. long, mucronate or shortly aristate, glabrous.

β. grandiflora. As the preceding, but spikelets large, 10 mm. and more long; fertile glumes 6—7 mm. long, with long awns.

γ. glaucescens. As α, but leaves glaucous-green, with spikelets often pruinous.

δ. juncea. Creeping at length. Laminæ of radical leaves juncaceous (0·8—1·2 mm. diam.), rigid, glaucescent, strengthened with stout sclerenchymatous strands; panicle somewhat loose, large, spikelets large (9—10 mm. long) glabrous, reddish hue.

ε. barbata. As α or β but spikelets shortly pubescent.

ζ. arenaria. Creeping at great length. Leaves rigid, sub-juncaceous, culm leaves generally subcomplicate. Panicle large; spikelets large, elliptic-lanceolate, 9—10 mm. long and more, densely hispid or villous.

η. dasyphylla. Celakovsky Prodr. d. Fl. Boehm. IV, 723 (1881).

4. *Position in Hackel's scheme of the three forms under investigation.*

The first form I have investigated, which is dark-green in colour, and which occurred as a weed in Professor Trow's garden, agrees with *β. grandiflora* and compares well with herbarium specimens of this in the British Museum. The second form is yellow-green and was found near Chepstow. While possessing the large spikelets of *grandiflora* it agrees fairly closely in other respects with *γ. glaucescens.* Herbarium specimens so named at South Kensington are rathermore glaucous and have smooth rachides. The third form is glaucous-green and came from the Barry pebble-ridge. It undoubtedly falls under var. *genuina*, but does not correspond with any of the sub-varieties described. One specimen only at the South Kensington Museum appears to agree with it (No. 1570, *Festuca* 504[3] Sp. 6 *rubra*). This was collected by Augustin Ley, June 25th, 1879, from "banks just above tidal mud under Wynd Cliff, Mon., Alluvial." The position and locality further suggest an agreement, but the specimen, if this is the case, is not a typical one, since it has a creeping habit. This might, however, be a fault easily committed by a collector unacquainted with the special habit of the plant. It is described as follows: "*Festuca repens*=*F. rubra* sp. pl.=*F. cambrica* Huds." "A variety of *duriuscula*" (Rev. Hugh Davies). "Doubtless under this as a super sp. . . . Another form of *F. rubra*" (A. Bennett).

The spikelets agree with those of *β. grandiflora*, but it differs in form of panicle, fineness of leaves and stoloniferous habit, as well as in other details which will be described later. It has therefore, been ranked as a new sub-variety of *genuina* under the name *tenuifolia*.

For the present, at any rate, it is just as well to keep to Hackel's analysis of the group as the basis for comparison of our British forms; otherwise there is much confusion. Boswell Syme's description (2, p. 145) of *Festuca rubra* subsp. *duriuscula*, "Linn.," Sm., includes the three forms A, B and C and Hackel's *α*, *β* and *δ*. He is inclined to think that *F. duriuscula*, Fries, also really represents the shortly stoloniferous plant which he supposes to be *F. duriuscula*, Linn.; but Fries, (4, p. 6), Koch (8, p. 705), and Babington (1, p. 440) place the forms of this *F. duriuscula* with longer stolons under *F. rubra*. Watson (13, p. 220) also regards *F. duriuscula* as "not strictly cæspitose; more shortly stoloniferous than *F. rubra*, with usually plane stem leaves; distinguished from *F. ovina* by larger panicles and more awned pales." In his records of distribution he confesses to great confusion between *F. duriuscula* and *F. ovina*, and between *F. rubra* and *F. duriuscula*. In his "Flora of Hampshire" Townsend (11, p. 423) regards *F. rubra* L., Bab., Gren. and God. as equivalent to *F. duriuscula* Sm.,?Syme; whilst J. W. White (14, p. 664) in his "Flora of Bristol" describes under "*F. rubra* L., *F. duriuscula* auct. angl., hard Fescue grass, the slightly creeping sub-cæspitose form which has commonly borne the name of *F. duriuscula* in this country." Druce's description (3, p, 245) of *F. duriuscula* applies to *β. grandiflora* of Hackel and does not include the forms *tenuifolia* and *glaucescens*. Whilst one might perhaps accept all three forms as *duriuscula*, this name does not go far enough, and it becomes necessary to distinguish between them. The differences are emphasised in the following diagnoses:—

5. *Description of the three forms.*

A. *Festuca rubra* subsp., *eu-rubra*, var. *genuina*, subvar. *β. grandiflora* Hackel, Monogr. Fest. Europ., 1882, p. 139.
F. rubra diversifolia β. Gaud.! (Fl. helv. I, 288) and *F. rubra megastachys* Gaud.! (l.c. 287).

Stock perennial, loosely cæspitose. Extravaginal branches more numerous than, or equal to intravaginal ones; the former creep at length, diam. 0·8—1·0 mm., bear 5—6 (occasionally 9) scale-leaves, root at the nodes, older ones branch (Fig. 1).

Radical leaves 4—5 per shoot; sheath entire throughout, green at first, becoming more or less reddish-purple on drying, pubescent marcescent; ligule slightly bilobed; lamina almost appressed to shoot and in straight line with sheath, dark-green, lower surface with polished cuticle, complicate, length 33 mm., broadest diam. when closed 1·0 mm., fairly rigid (compared with B), 5 longitudinal ridges, 7 vascular bundles, 7 strands of sclerenchyma below abaxial surface (including margins) and a small strand along each ridge of adaxial surface.

Cauline leaves 3; sheath split throughout with overlapping edges, slightly pubescent or glabrous, generally slightly longer than the internode, base swollen, dark-coloured; ligule with broad, rounded sheath-lobe, abrupt transition from sheath to lamina; lamina as long as, or slightly longer than its sheath, highest with 9 longitudinal ridges, 9 vascular bundles and 11 strands of sclerenchyma abaxially, flat.

Haulm slightly curved at the base, then erect, terminated by panicle; length from base (including panicle) 76 cm., diam. varies between 1·8 and 1·0 mm. from base to apex; upper two-thirds naked, almost cylindrical, but 12—15 slight longitudinal ridges, more obvious on drying.

Panicle sub-secund, erect, length 18 cm., loose, open during anthesis, lower rhachillæ widely separated, internodes almost or quite smooth. Lower rhachillæ paired, unequal, with long stalks.

Spikelets large, 13 mm. long, green or slightly violaceous, 2 basal sterile glumes, 5—7 flowering glumes, axis jointed. Sterile glumes unequal, mucronate; lower smaller, 1-nerved, somewhat keeled; higher, larger, 3-nerved. Fertile glumes 5-nerved, all aristate, awns 3 mm. long; broadly lanceolate, 6—8 mm. long without the awn. Palea superior, 2-keeled, 2-nerved, pilose apex, Lodicules 2, massive, lower part becomes globular, upper unequally forked with blunt apices. Stamens 3. Ovary broadly ovoid or nearly globular, furrow glabrous, slight posterior; 2 nearly sessile terminal stigmas. The caryopsis has not been found to develop.

B. Subvar. *tenuifolia* (new subvar.).

Stock perennial, more densely cæspitose. Extravaginal branches about equal to intravaginal ones, the former generally short, gently curving upwards from their base, bearing 1—4 (6) scale-leaves, rarely rooting at the nodes and more rarely branched,

Radical leaves 4—5 per shoot; sheath-surface slightly rough hispidulous, due to minute downwardly directed reflexed hairs,

otherwise as in *grandiflora*; ligule slightly bilobed; lamina making a small angle with the shoot axis, dark glaucous green having the appearance of a "bloom," complicate, length 25 cm., broadest diam. when closed 0·8 mm., therefore more slender than in *grandiflora*, rather lax, 5 longitudinal ridges, 5—7 vascular bundles, 5—7 small strands of sclerenchyma below abaxial surface, absent from adaxial surface.

Cauline leaves 2—3; sheath split, quite smooth, only two-thirds length of internode, base swollen, green; ligule with lower (sheath) lobe raised into a definite auricle; lamina, usually shorter than its sheath, highest with 5—7 vascular bundles and 7—9 strands of sclerenchyma abaxially, flat or canaliculate.

Haulm, shorter and more slender than in *grandiflora*; length (including panicle) 52 cm.; diam. varies between 1·0 and 0·8 mm., upper half naked, almost cylindrical, but 10 slight longitudinal ridges, more apparent when dry.

Panicle subsecund, erect, total length 9 cm., much smaller than in *grandiflora*, somewhat dense, open during anthesis; lower rhachillæ paired, unequal, short-stalked, not widely separated, internodes flanked with upwardly directed hairs, slightly prickly to the touch.

Spikelets large, 12 mm. long, green or slightly violaceous, 2 basal sterile glumes and 5—7 (occasionally 8) flowering glumes; axis jointed. Sterile glumes as in *grandiflora*. Fertile glumes, lower mucronate, upper becoming aristate, awns 2·5 mm. long, narrowly lanceolate, 5—7 mm. long excluding awn. Palea superior, apex somewhat hispid. Lodicules 2, not so swollen below, unequally forked above, with acute apices. Stamens 3. Ovary ovoid. Caryopsis enclosed with persistent and closely adherent paleæ with portion of axis attached; 3 mm. long, 1 mm. broad, pericarp brown, with pronounced posterior furrow. Comes true from seed.

In accordance with the Vienna rules a diagnosis is given in Latin:

Subvar. *tenuifolia* (subv. nov.).

Elatior; folia innovationum mollia, setacea (0·8 mm. diam.), obscure glauco-viridia; vaginæ hispidulæ. Panicula densiuscula (9 c.m. lg.). Spiculæ magnæ (12 mm. lg.); glumæ fertiles 5—7 mm. lg., brevitus-longius aristatæ.

C. *Subvar. glaucescens.*

Stock perennial, fairly densely cæspitose. Extravaginal branches equal to intravaginal ones; the former may creep to a

distance, diam. 0·8—1·0 mm., bearing 8 scale-leaves, rooting at nodes and sometimes branching.

Radical leaves 5 per shoot; sheath perfectly glabrous; ligule slightly bilobed; lamina makes a slight angle with shoot axis, light yellow-green (glaucescent) complicate, fairly rigid, length 23 cm., greatest diam. when closed 0·8 mm.

Cauline leaves 2 (occasionally 3); sheath split, quite glabrous, only about half length of internode, base swollen green; ligule as in *grandiflora*, lamina very poorly developed and of short duration.

Haulm erect from near base, terminated by panicle; length including panicle, 46 cm., slender, upper half naked cylindrical, few striations visible when dry.

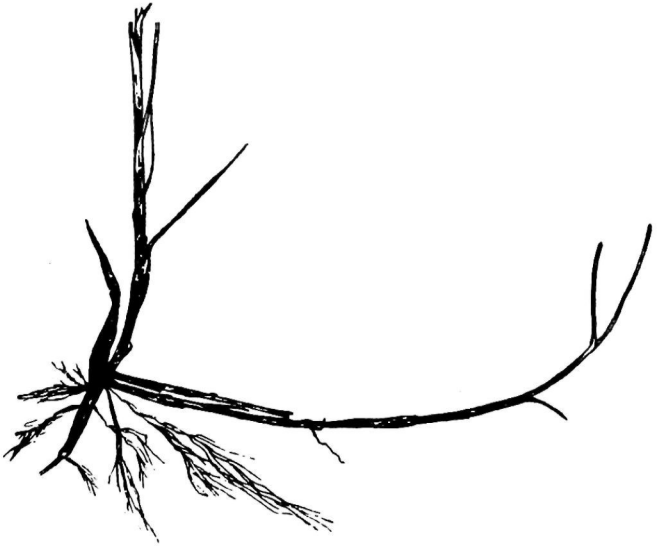

Fig. 1. Subvar. *grandiflora*. Base of shoot, nat. size.

Panicle sub-secund, erect, length 6 cm., fewer spikelets than B, densiusculous, open during anthesis, lower rhachillæ not widely separated, internodes as in *tenuifolia*.

Spikelets fairly large, 12 mm. long, distinctly violaceous and hispidulous, having a "bloom"; 2 basal sterile glumes; 4—6 (occasionally 7) flowering glumes, axis jointed. Sterile glumes as A. Fertile glumes all aristate, lanceolate, length 9 mm., excluding awn, awns 3 mm. Palea superior as in B, but more hispidulous. Lodicules, stamens, ovary and caryopsis, as in *tenuifolia*.

6. *Habitats of the forms.*

Sub-variety *grandiflora*: confined to soils more or less calcareous formed from the softer mesozoic rocks, fertile and, on the

whole, moderately humid. Its general habitat is therefore a more or less mesophytic one. In the coastal area of Glamorgan it is only found along the cliffs well beyond the reach of the sea, and usually well protected by higher strata of vegetation such as scrub or open canopy wood, or by the lie of the land, from the force of the prevailing winds. Inland it is found along roadsides, growing amongst the loose stones of less frequented roads, or on hedge-banks, especially upon the dust-heaps and sweepings, or even in the crevices of old limestone walls.

Sub-variety *tenuifolia*, confined to the sea-coast, is either the dominant, or a co-dominant plant in the following habitats:—

(i.) the salt-marsh, where it descends into the *Glycerietum* and is dominant above it, associated with typical halophytes.

(ii.) the pebble ridge, associated with xerophytes, e.g., *Poa bulbosa*, var. *vivipara*.

(iii.) the hard exposed rocks in scanty soil, calcareous and well-drained, associated with halophytes or more extreme xerophytes.

(iv.) the calcareous tufa of the cliff-face.

Fig. 2. Subvar. *grandiflora*. Transition from foliage leaf to prophyll. Nat. size.

In all these situations it occasionally comes under the influence of salt water, either by complete inundation or from spray.

Sub-variety *glaucescens*, so far as known, grows in the higher zones of the salt-marsh and of the littoral, generally out of reach of the salt water. Not in Glamorgan; the nearest point at which it has been found to Cardiff is the mouth of the Usk (Mon.) and stretching along the coast well into Gloucestershire.

III.—Comparative Morphology.

1. *The Branch-system.*

The subvariety *grandiflora* is loosely sub-cæspitose. Its lower branches are typically extravaginal, creeping for varying distances and then erect, bearing the characteristic prophyll and series of scale-leaves, 5–6 (occasionally 9) in number (Fig. 2). Under

normal conditions the branches reach a total length of about 8 cm. and their diameter varies from ·8 to 1 mm. If grown in the garden they are much longer, branch from the axils of the scale-leaves, and root at the nodes.

The subvariety *tenuifolia* is sub-cæspitose, that is its extravaginal branches are much shorter; and they are more slender (·7 mm. diam.). Even those first produced curve gently upwards from their base, rarely branch, and only occasionally root at the nodes. Only two or three such branches are produced, the rest are typically intravaginal (Fig. 3).

Fig. 3. Subvar. *tenuifolia*. Base of shoot. Nat. size.

The typical extravaginal branches are rarely found in the earlier stages of development of seedlings. In the majority of seedlings the first branch is intravaginal (Fig. 4 a); but in some the branch grows through the base of the subtending sheath, and then almost erect, having a more or less elongated prophyll followed by a scale-leaf, and then a normal leaf (Fig. 4 b). Occasionally the first branch has a shorter prophyll followed by two scale-leaves, then normal leaves (Fig. 4 c) and is therefore more typically extravaginal. The second and succeeding branches

of these seedlings are all intravaginal. From these observations it would appear that the intravaginal branch is the more primitive type, and that development has proceeded towards extravaginal branches accompanied by a change in the direction of growth, a reduction in the size of the prophyll, and a reduction in the succeeding leaves to scales by partial or complete loss of laminæ.

The third subvariety, *glaucescens*, in respect of the cæspitose habit approximates more to *tenuifolia*. Transference to garden soil affects both these forms by encouraging them to produce longer stolons, but even under these conditions they remain quite distinct from *grandiflora*.

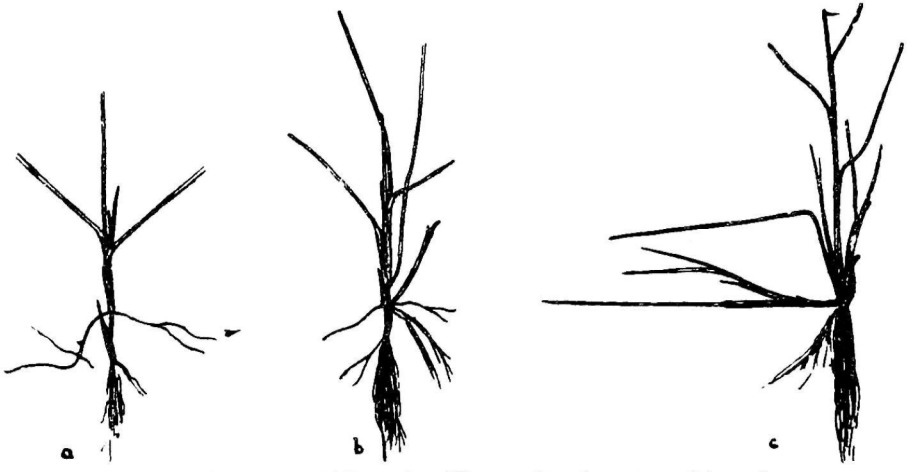

Fig. 4. Subvar. *tenuifolia*. Seedlings showing transition from true intravaginal to true extravaginal branch.

2. *The Vegetative Shoot.*

All branches develop a shoot which remains purely vegetative during the first season's growth. The extent of development depends upon whether it is laid down early or late in the season. The usual number of leaves on a shoot is four or five. They are produced according to a regular alternation but become twisted out of position by a torsion of the axis. From the axils of these "radical" leaves branches arise; extravaginal from the older ones, intravaginal from the younger. Each shoot thus becomes the centre of a rapidly increasing branch system. The intravaginal branches form a compact turf; the extravaginal ones spread out in all directions. All become new centres of growth, thus tending to a raising of the general level of the turf. When, as frequently happens, the turf becomes covered with loose soil, débris or alluvium, not only do the new growths extend upwards but the

short internodes of the vegetative axes elongate, often quite considerably, and take on the appearance of stolons. The same may also occur with the intravaginal branches. The result is, in the case of a shortly creeping form like *tenuifolia*, a false appearance of creeping at length; hence the necessity of selecting typical specimens for determination (see p. 265)

The sheath of the radical leaf is entire at first but later splits from above and below, ultimately separating into irregular fibrous strands which persist for some time after withering. The sheath surface serves to distinguish the three subvarieties; that of *grandiflora* is pubescent, especially in the upper exposed portion of the older sheaths; that of *tenuifolia* is hispidulous, having minute, retrorse, sharply-pointed hairs; that of *glaucescens* is perfectly glabrous. The sheaths of all develop a reddish-purple colour before withering.

The ligule is a slight ridge or cushion across the base of the lamina, and ends laterally on each side in a slight lobe at the edge of the sheath. The edges of the lamina also thicken somewhat as they pass into the sheath forming a second (upper) lobe which is often rather more pronounced in *tenuifolia* than in the other two forms. But the differences between the three subvarieties in this respect are too minute to be of real value for determination.

The lamina of subvar. *grandiflora* is rather more rigid than are those of the other two forms. It stands erect at first and in a straight line with the sheath. Fully developed it attains a length of 25—33 cm., and the broadest diameter of the elliptical transverse section is 1·0 mm. It is complicate with acute apex, polished and dark-green below, the "mat" upper surface raised into five longitudinally-running ridges. That of subvar. *tenuifolia* attains a total length of 20—25 cm., and is slender (·8 mm. diam.) and flexible. The lower surface is dark glaucous green, having the appearance of a "bloom"; the upper surface is just as in *grandiflora*. The leaves form densely matted masses when their growth is not interfered with. Subvar. *glaucescens* has laminæ also with a "bloom," like those of *tenuifolia* except that their colour is a lighter more yellowish green. These colour differences are a ready means of distinguishing the three forms.

3. *The Haulm.*

The stronger vegetative shoots continue their development in the second season to produce a haulm terminated by the inflorescence.

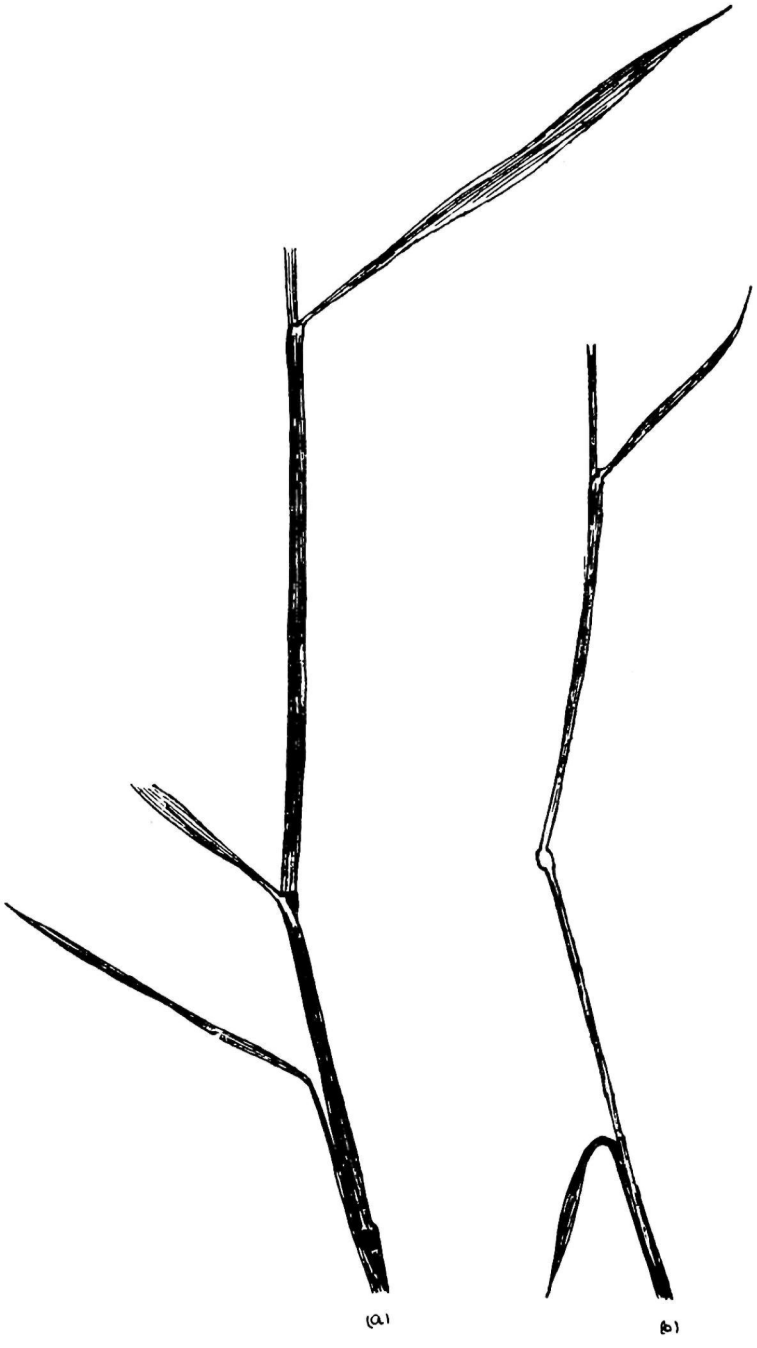

Fig. 5. Haulms of (a) *grandiflora* and (b) *tenuifolia*.

The latter makes its appearance about the end of May and has attained its maximum height about the middle of June. That of *grandiflora* is the largest of the three. Two well developed samples of (1) *grandiflora* and (2) *tenuifolia*, collected on June 14th, 1914 and compared showed :—

	grandiflora.	*tenuifolia.*
Height	76 cm.	52 cm.
Diameter	1·8 mm.—1·0 mm.	1·0 mm.—0·8 mm.
	Upper $\frac{3}{5}$rds. naked	Upper $\frac{1}{3}$ naked.

The number of cauline leaves is generally three for *grandiflora*, two to three for *tenuifolia*, and only two for *glaucescens*. The cauline leaf sheaths of *grandiflora* are as long as or slightly longer than the internode; they may be slightly pubescent above, or perfectly glabrous (Fig. 5 a). In *tenuifolia* the sheaths are usually, shorter than the internodes (Fig. 5 b), and quite smooth. In all, the sheath is split from top to base and the edges overlapping considerably. The lateral lobes of the ligule are broad and rounded in *grandiflora*, but raised into a definite pointed auricle in *tenuifolia*. The lamina is flat, somewhat involute when dry. The highest lamina on the haulm of *grandiflora* has nine longitudinal ridges along its upper surface; that of *tenuifolia* has only five to seven and is shorter; that of *glaucescens* is very poorly developed.

4. *The Panicle.*

The panicle of subvar. *grandiflora* is well developed and loose, attaining a total length of about 18 cm. (Fig. 6 a), That of subvar. *tenuifolia* is only about half this size (6—9 cm. long) and is of quite different shape, especially at anthesis (Fig. 6 b). That of subvar. *glaucescens* is smaller and less well developed in every respect.

In subvar. *grandiflora* the lower rhachillæ are widely separated and long-stalked. The following numbers were obtained from specimens of *grandiflora* and *tenuifolia*:—

Lengths of internodes (from below).

grandiflora, 5·5 cm., 3·0, 2·0, and the rest 1·0.

tenuifolia, 1·8 cm., 1·3, 1·0, 0·8, and the rest 0.6.

Number of spikelets on branches of panicle (from below)

grandiflora, 8 and 5, 6 and 3, the rest 2 each to terminal 1.

tenuifolia, 4 and 2, 2 and 1, „ „ 1 „ „ „ 1.

The flanks of the internodes of axis and rhachillæ in subvar. *tenuifolia* are lined with small, upwardly directed barbs which makes the axis somewhat prickly to the touch; in subvar. *grandiflora* they are practically smooth.

Each axis of the panicle is terminated by a spikelet. The spikelet is shortly stalked and bears two basal sterile glumes, of which the lower shorter one is narrow, somewhat keeled, one-nerved, and the higher larger one broader and three-nerved. Both are mucronate. Above these in regular alternation are borne from five to seven or eight fertile glumes, the last one terminating the spikelet axis. Each is five-nerved; in *grandiflora*, aristate, the awns up to 3 mm. long; in *tenuifolia* the lower ones are mucronate, the upper aristate with awns up to 2·5 mm. long. The upper edges of the glumes of *grandiflora* are more broadly scarious, and more abruptly narrowing into the awn than in *tenuifolia*. In both

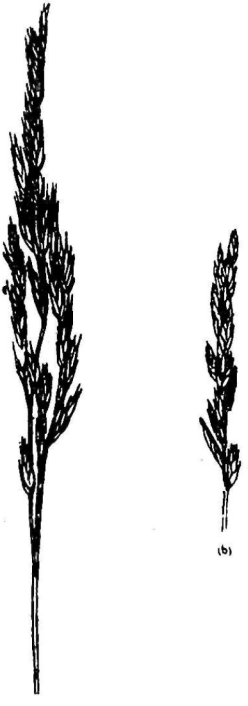

Fig. 6. Panicles of (a) *grandiflora* and (b) *tenuifolia*. ×½.

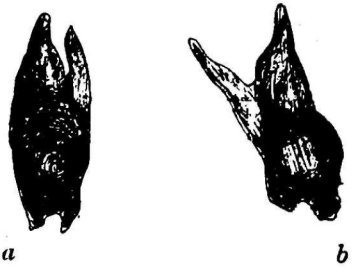

Fig. 7. Lodicules of (a) *grandiflora* and (b) *tenuifolia*. ×18.

the awns and margins the glumes are covered with minute upwardly directed prickles. The spikelets are green at first, but may become slightly tinged with violet in *tenuifolia*, more so in *glaucescens* where they are covered with minute hairs and a "bloom."

The apex of the superior palea is rather pilose in *grandiflora*, more hispid in *tenuifolia* and *glaucescens*. The lodicule forks above unequally; in *grandiflora* one prong is thicker than the other and each has a blunt apex (Fig. 7 a), in *tenuifolia* and *glaucescens* the

arms are more nearly equal and have acute apices (Fig. 7 b). The lower portion is much more swollen in *grandiflora* than in either of the other two forms. The result is that the flowers of *grandiflora* open widely, whilst those of the other two open just sufficiently to allow the projection of stamens, between the two points of the paleæ, and later the stigmas, between the two overlapping edges of the paleæ. At this stage the larvæ of *Thrips* attack the flowers of *grandiflora* and the young ovules shrivel.[1] On the other hand the flowers of *tenuifolia*, even though growing side by side, are immune. Possibly *Thrips* has easy access to the ovules of *grandiflora* through the well separated glumes, whilst the closed glumes of *tenuifolia* make access difficult or impossible. Massee (10) has "frequently seen the ear (of barley) well out of the leaf sheath, and many or all of the grains presenting a shrivelled appearance . . . due to the work of *Thrips ceralium* Halid."

The anthers dehisce about the second week in June. The almost sessile feathery stigmas are receptive about a week later. In subvar. *tenuifolia* the ovary after fertilisation elongates considerably and when full grown is about three mm. long. It has a deep median posterior furrow. It is ready for dispersal about the end of August.

IV.—Comparative Anatomy and Histology.

1. *The Rhizome* (*Stolon*).

Extravaginal branches of *grandiflora* and *tenuifolia* were sectioned across their basal internodes (Fig. 8). In *grandiflora* the epidermis is slightly cuticularised, but in *tenuifolia* the walls are thickened, with a well developed cuticle. The cells of the hypodermis in the latter are also somewhat thick-walled. In *grandiflora* there are only three to four layers of cortex, and when mature the cells below the hypoderm break down in places, forming large cavities; in *tenuifolia* there are about six layers of cortical cells which persist. The mechanical tissue is in the form of a tube which is more centrally placed in *tenuifolia* than in *grandiflora*. The radial and inner walls of the external fibres are much more thickened than the outer walls; those placed between and within the vascular bundles are uniformly thickened (Fig. 8 c). In *grandiflora* there are about twenty-five vascular bundles; in *tenuifolia* only about ten. They vary in size individually, but on the whole those of *grandiflora* are larger. They are of the usual grass type (Fig. 8 a and 8 b).

[1] Whether *grandiflora* would set good seed if protected from *Thrips* remains to be determined.

Sections taken across the younger internodes of *grandiflora* show the cortex to be entire and composed of large parenchymatous cells loosely placed. Stomata occur occasionally in the epidermis of both forms.

In older rhizomes the scale-leaves wither and split into shreds. In *grandiflora* the tissues outside the fibrous zone practically disappear, but in *tenuifolia* they tend to persist, though shrivelled.

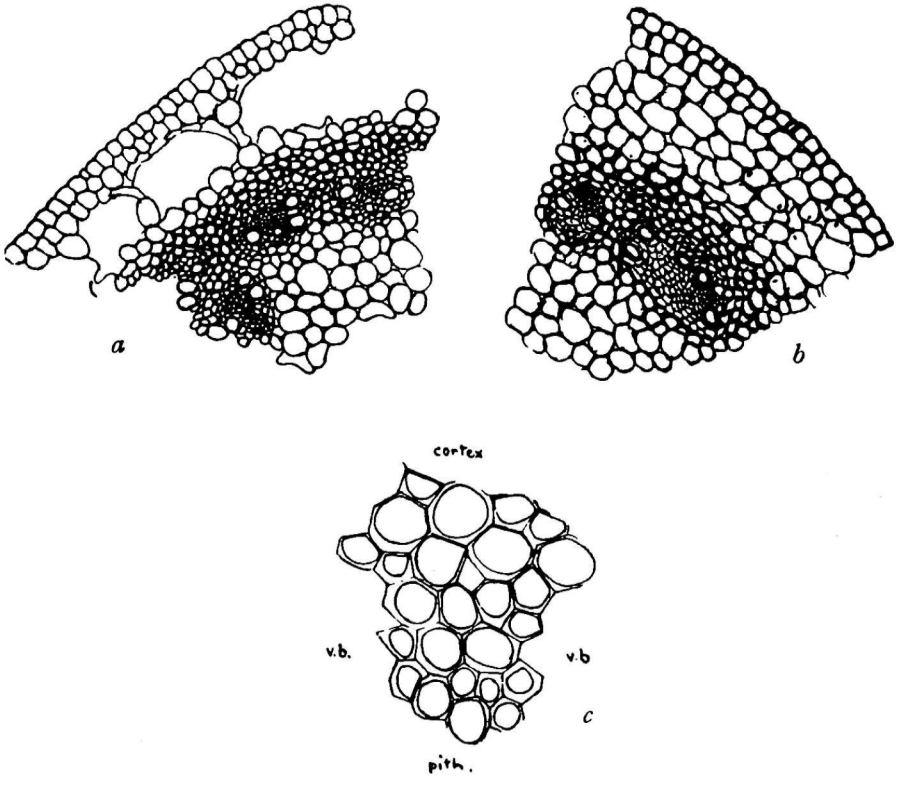

Fig. 8. *a*, Transverse section of internode of *grandiflora*. *b*, Ditto of *tenuifolia*. ×75. *c*, Fibres of pericycle in trans. sect. ×360.

2. *The Shoot.*

As the rhizome axis continues into that of the shoot, and successive leaf-sheaths are given off, there is a gradual diminution in its diameter. The vascular bundles from the sheaths pass into the axis. The midrib maintains its identity through two internodes, but the lateral bundles form lateral plates on which the steles of the nodal roots are inserted. The rest of the ground tissue is parenchymatous; the cells are rich in protoplasmic contents and starch. The tissues maintain their extensibility, the internodes remaining capable of elongation.

3. *The Adventitious Root.*

In *grandiflora* two or three adventitious roots arise simultaneously with the axillary branch and below it; in *tenuifolia* there is usually only one root, which is almost exactly below the midrib of the subtending leaf. This may be supplemented by others, according to the nature of the soil. As the young root grows out through the cortex the cells of the latter form a sheath of two to three layers which grows out with it, acting like the coleorhiza to the radicle The first roots are all tetrarch, their finer branches diarch.

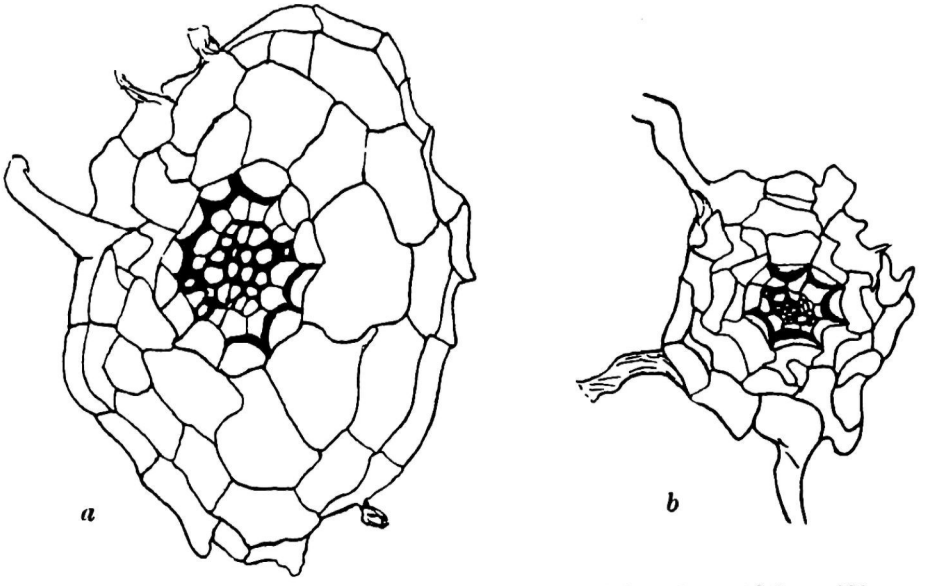

Fig. 9. Transverse section of fine root of (a) *grandiflora*, (b) *tenuifolia*. × 330.

Transverse sections show the root of both subvarieties to have much the same general structure. The piliferous layer of *grandiflora* (Fig. 9 a) has few root hairs, a cortex of two layers of parenchyma, an endodermis with "horseshoe" thickening broken by two sets of passage cells, a pericycle of one layer of regular cells alternating with those of the endodermis, and a diarch xylem plate. In *tenuifolia* (Fig. 9 b) the root is similar, but has less than half the diameter; the root hairs are quite as stout and relatively more numerous. In later formed roots of both forms, when the root-hairs have ceased to function, the piliferous layer collapses, the exodermis becomes suberised and the endodermis uniformly thickened; the xylem is tetrarch to polyarch. The whole of the cortex may later wither, but it persists around the endodermis and in *tenuifolia* the cell-walls of the pericycle become thickened so that it forms a second protective layer within the endodermis.

4. *The "Radical" Leaf.*

The outer epidermis of both sheath and lamina is composed of elongated cells, from twelve to fifteen times as long as broad, alternating with short cells. The short cells of the outer epidermis of the sheath may grow out as hairs (Fig. 10), or may develop into stomata, which are found especially in the cell rows close to the vascular bundles. The short cell divides longitudinally but unequally, and the larger of the two again divides longitudinally. Thus a central cell is cut off from two lateral ones. The latter

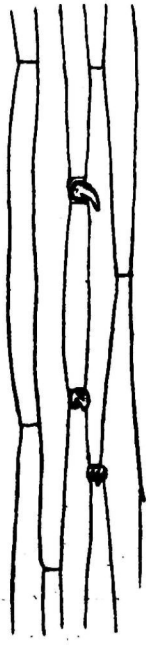

Fig. 10. Subvar. *tenuifolia.* Surface of sheath. ×120.

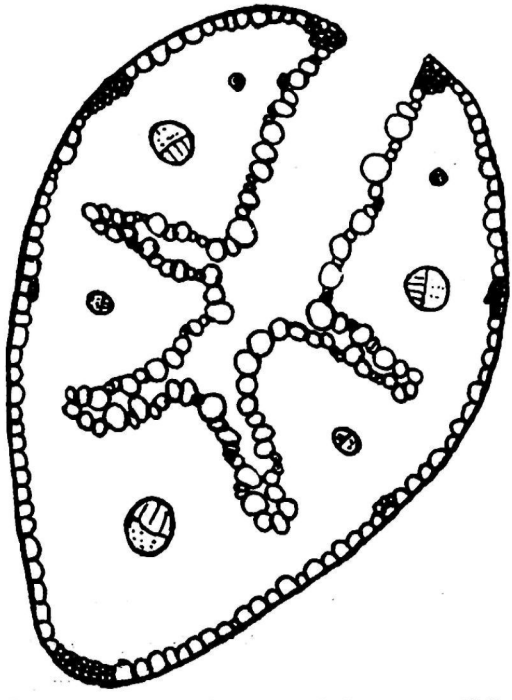

Fig. 11. Subvar. *tenuifolia.* Trans. sect. of lamina. ×120.

become the subsidiary cells, and the central cell now divides longitudinally into two cells, each of which becomes a guard cell. The structure and mechanism of the guard cells has been fully described by Haberlandt (6, p. 451). The main differences between the sheath of the two forms are that in *grandiflora* there are about nine vascular bundles and a loose mesophyll; in *tenuifolia* only five to seven bundles, a compact mesophyll, and more thickened epi- and hypo-dermis. The outer sheaths decay and split, the vascular bundles being preserved intact by the protective endodermis and thus the lamina is enabled to continue its function for some time, after the sheath has split.

At the top of the sheath there is a slight overfolding of the tissue; then the upper fold becomes free from the lower and the edges pass round into the ligule and lamina.

The sheath is cylindrical for the greatest part of its length, but just previous to splitting a slight fold appears in it on the side opposite that from which the lamina passes off. The upper limb of this fold becomes free from the lower by the disappearance of the connecting plate of tissue and the sheath is now split, the free edges passing into the ligule and lamina.

The ligule is merely a slight ridge or cushion of thin walled parenchyma. The cells of the outer surface grow out as short papillæ or trichomes.

The lamina is complicate (Fig. 11). Along the upper surface are five longitudinal ridges, clothed with minute hairs, which give a dull green appearance to the surface. The shape of transverse sections varies slightly in passing from ligule to tip. From Hackel's description it would appear that he used herbarium material in which the softer tissues had shrunk, the resulting shape depending upon the position and amount of resistant tissues. The vascular bundles, five to seven in number, pursue a straight course from base to apex. At intervals branches pass out into the mesophyll. Each branch consists of a row of short, stout, spirally-thickened tracheides, connected at one end with the reticulate narrower elements of the main bundle, and ending either in contact with mesophyll cells or with an intercellular space. Each branch strand is surrounded by cells containing large nuclei and granular protoplasm. These branch strands are more numerous in *grandiflora*. The sub-epidermal strands of sclerenchyma are larger in *grandiflora* than in *tenuifolia*: hence the somewhat greater rigidity of the lamina of the former.

The lower (outer) epidermis in surface view consists of alternating long and short cells. The former are from six to fourteen times as long as broad and their long anticlinal walls are corrugated. The surface walls are furnished with the so-called marginal pits, which occupy the troughs of the undulations of the anticlinal walls on one side only, and extend obliquely upwards and outwards from the cell-cavity towards the surface (Fig. 12). The short cells in the neighbourhood of the ligule project beyond the general surface as hairs. The outer walls are strongly thickened, and the thickening extends to about midway along the anticlinal walls.

The upper (inner) epidermis also consists of long and short cells. The former are thin-walled, narrow at either end, but swelling out in the middle where their diameter is greatest. They are arranged in longitudinal rows and the cells of each row alternate with those of adjacent rows. As a result the short cells are sunk in depressions or troughs between the broad, protruding portions of the long cells. The long cells are more or less circular in transverse section and in the middle portion of their length from $\frac{1}{3}$ to $\frac{1}{2}$ of their surface is free and exposed. The short cells may produce short hairs or stomata. The latter are thus to some extent

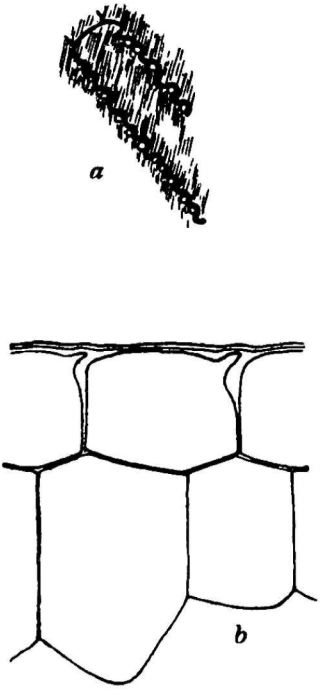

Fig. 12. Subvar. *tenuifolia*. Lower epidermis of lamina showing marginal pits. *a*, Surface view. ×300. *b*, Trans. sect. ×860.

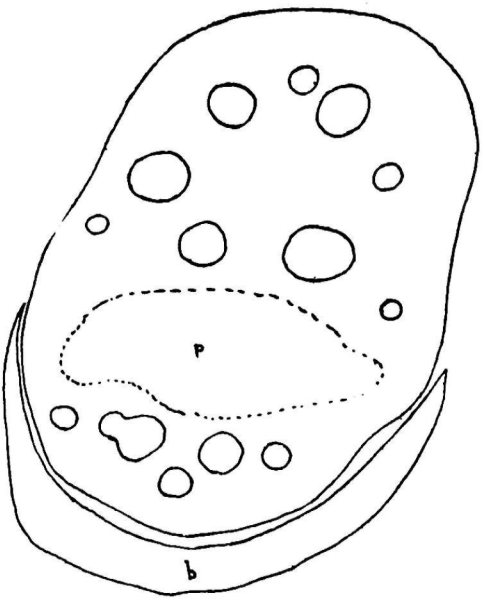

Fig. 13. Subvar. *tenuifolia*. Trans. sect. of node of panicle. *b*, bract. *p*, parenchyma. ×85.

protected even when the leaf is open. The ratio of the number of stomata on equal areas of surface of *grandiflora* and *tenuifolia* is 12 : 11. The epidermal cells situated along the bottoms of the longitudinal furrows are not clearly differentiated from the rest of the epidermis either in size or in the thickness of their walls. They cannot therefore be said to form specialised structures, though the lamina, in folding, hinges on these cells.

Seen in transverse section the cells of the mesophyll radiate outwards from the vascular bundles, but in longitudinal section the palisade cells can be distinguished as being regular and compact, each cell directed slightly obliquely upwards from the bundle towards the outer epidermis of the lamina.

5. *The Cauline Leaf.*

The lamina of the cauline leaf has a comparatively short life, but is nevertheless a specialised structure as regards drought resistance. When open it is more or less flat and stands out practically at right-angles to the axis. A transverse section of the highest lamina on the axis of *grandiflora* showed nine longitudinal ridges along the upper surface, and in the furrows there are specialised "motor" cells, larger than the rest, which are scarcely raised above the general level of the surface. The hairs on the surface are more numerous and longer than those of the radical leaves. Groups of sclerenchyma occur below both upper and lower surfaces, in some cases in contact with the vascular bundles. Stomata are numerous on the upper epidermis. In *tenuifolia* the cauline lamina has only five to seven ridges, and is poorer in sclerenchyma.

6. *Rhachillæ.*

The lowest rhachilla is subtended by a small bract, whose base encircles the axis, but whose upper part is free and crescent-shaped in section (Fig. 13). It is composed of parenchymatous cells whose somewhat thickened walls are pierced by numerous pits. These cells are continued into the cortex of the axis at the node. At the higher nodes there is no obvious bract, but the cortical cells are developed in the same way.

The morphology of the paired rhachillæ is evident from a study of serial transverse and of longitudinal sections through the node. The bract is a simple structure; it is present as a slight ridge of tissue around the stem just below the insertion of the paired rhachillæ, highest on the side from which these are given off, lowest on the opposite side. It does not suggest any fusion, so that there is every reason to believe that it subtends a single primary branch, which is the larger of the pair of rhachillæ. From this is given off almost immediately a weaker secondary branch, the smaller member of the pair. There is no trace of a bracteole.

This view is supported by tracing the various vascular bundles from the axis below the node into the rhachillæ. The vascular

Fig. 14. Subvar. *tennifolia*, dwarfed seedling. $\times \frac{3}{4}$.

system of the axis divides into two distinct groups of bundles ; the larger group remains in the axis whilst the smaller group belongs to the primary branch. This latter, slightly higher up, resolves itself into six distinct bundles which appear as two groups of three, one group of which consists of larger bundles and passes up the primary branch axis, the other group of smaller bundles belonging to the secondary branch. Thus the vascular system of the secondary branch joins up with that of the primary forming a single group which takes its place in the main axis.

V.—Temporary Modifications

The effect of certain types of habitat is seen in modifications of external form and internal structure which are of a temporary nature, and there is a reversion to normal when the plant is transferred to normal conditions.

Specimens of *tenuifolia* collected from scanty soil on exposed rocks have proved difficult to identify until transferred to the garden and their subsequent growth observed. They show a peculiar stunted growth, a kind of nanism, induced by the extreme xerophytic conditions under which they grow (Fig. 14). The leaves are shorter and more fleshy ; the laminæ stand out from the axis and gently curve upwards. The base of the shoot is stouter and the plant more densely cæspitose. The panicle is reduced to a few small spikelets. These modifications are the result of a very exposed situation, extreme dryness of habitat, and probably also halophytic influence. Similar modifications, though not quite so marked, are seen in the plants which grow on the scantier soil of the pebble-ridges, where great extremes of moisture and temperature on and near the surface must be encountered.

VI. Summary.

The three forms studied, which have been referred to the subvarieties *grandiflora*, *tenuifolia* and *glaucescens* respectively, are quite stable, distinct in both vegetative and floral characters, and in choice of habitat.

The first form corresponds with *Festuca rubra*, var. 1 *genuina*, subvar *β. grandiflora* (Hack). Its general habitat is a more or less mesophytic one and its morphological and anatomical characters are practically those of a mesophyte, though with certain xerophytic tendencies. It possesses fairly long, creeping rhizomes and is loosely sub-cæspitose ; well fitted for producing a rich carpet of vegetation. It has a well developed root-system and its dark green leaves are perfectly glabrous. Its panicle is loose and well-developed, and the spikelets are large.

The second form also belongs to the variety *genuina* (Hack) and is entitled to rank as a new subvariety; it is given the subvarietal name *tenuifolia*. It is capable of growing under the most extreme xerophytic conditions and is generally associated with halophytic conditions. Its morphological and anatomical structure support the view that it is certainly a xerophyte, and under the influence of salt water it shows certain halophytic tendencies. It is fairly densely cæspitose; its rhizomes are short and more or less curved and ascending from the base. The leaves are slender and dark glaucous green, having a "bloom." The panicle is more compact than in *grandiflora*; the internodes rough; the spikelets fewer, but the individual glumes large and as numerous as in *grandiflora*, with shorter awns. This new form is of special interest because it appears to be peculiar to certain habitats.

The third form also comes under Hackel's variety *genuina* and probably corresponds to subvar. *glaucescens* Hack. Its main points of difference are the yellowish-green colour of its leaves, the perfectly glabrous sheaths, and the size of the panicle, with fewer spikelets, and fewer glumes with longer awns than in the other two subvarieties. It is distinctly violaceous and hispidulous with a "bloom."

I am indebted to Professor Trow for drawing my attention to these grasses and placing his garden material at my disposal: to Mr. G. Claridge Druce for kindly examing specimens and confirming my determinations; and to Mr. R. S. Adamson for helpful criticism of the manuscript.

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