# PROLIFERATION OF SPIKELETS IN BRITISH GRASSES

## I. The Taxonomy of the Viviparous Races

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### 1. Introduction

The gramineous inflorescence may be resolved into units termed spikelets. Each spikelet consists of an axis bearing bracts or glumes. Except for the sterile glumes (two in most British grasses) which are inserted lowest upon the spikelet axis, the glumes bear florets in their axils. In this paper the terminology approximately follows that of Arber (1934). Glume will be used to denote any bract directly inserted upon the spikelet axis, but a glume subtending a floret is termed a lemma.

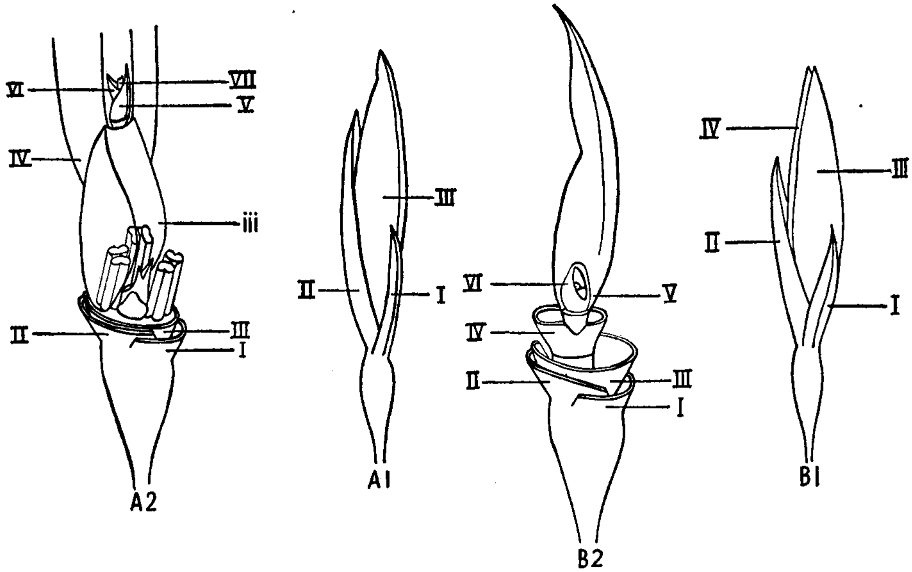

Fig. 1

A. *Festuca ovina* L. 1. Young spikelet (× 10); 2. Basal portion dissected to show floret development (× 25); I-VIII Glumes (I-III cut away); iii. Palea of lowest floret. B. *Festuca vivipara* Sm. 1. Young spikelet (× 10); 2. Dissected to show vegetative apex of the spikelet axis (× 25); I-VI Glumes (I-IV cut away).

Arber calls the continued growth of the spikelet axis, and the bearing of leaves distally upon it, 'vegetative proliferation.' The glumes are found in various stages of metamorphosis from their normal structure to foliage leaves. If the normal lemma has the upper portion of its midrib separated dorsally as an awn, then in proliferated spikelets transitions from awn to leaf-blade are found. The morphological significance has been discussed by Philipson (1934). The florets subtended by the glumes of the proliferated spikelets may be almost normal, male- or female-sterile, aborted or completely absent. Figure 1 shows young proliferated and flower-bearing spikelets of *Festuca*.

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The plants showing this proliferation may be divided into two classes. Firstly, those whose spikelets are usually proliferated; secondly, those in which proliferation is an ephemeral character.

In the first class the proliferated condition appears season after season, even when plants are transplanted from their natural habitats; their offspring, moreover, inherit the characteristic. In this group the cause is primarily genetic, and environmental factors are apparently secondary. The plants of this type form the ' viviparous races,' propagating themselves by plantlets formed from the deciduous leafy upper part of the proliferated spikelets.

## 2. TERMINOLOGY

Before discussing the viviparous races and, later, the problem of proliferation as a whole, it is necessary to review the terminology used in relation to this phenomenon.

The detached leafy buds are often described as bulbils, but *Poa bulbosa* L. var. *vivipara* Koel. is the only grass in which they are truly " bulbous." Bulbifery is not a satisfactory term, since it is applied to plants which bear bulbils in parts other than the inflorescence, e.g. *Dentaria bulbifera* L.

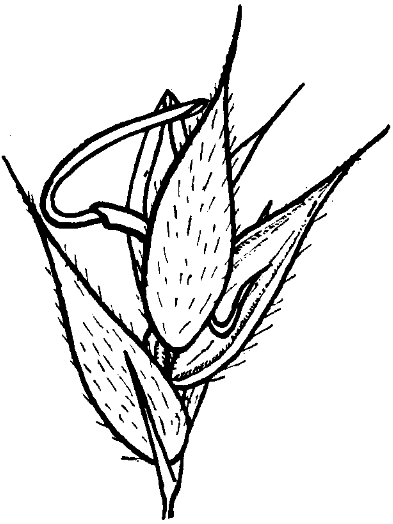

Fig. 2. *Festuca ovina* L. Carmarthen Fan, 14.ix.1950. Seed of an upper floret germinating in situ. Note the coleoptile (× c.7).

' Chloranthie ' is found in the French literature and in German ' auswachsende Ährchen,' 'Laubsprossen' and 'Vergrünung' are used. However, in literature in Dutch, English, French, and German may be found words derived from the Latin ' viviparus ' and ' prolifer.' Unfortunately there is confusion in their use.

The derivatives of ' viviparus ' were introduced by Linnaeus (1737). It is not clear from his description if this was because of a superficial likeness to an undetached seed germinating, or if he actually thought this to be the case. The term does indicate the ecologically significant fact that the propagules are dispersed in a ' living ' (i.e. not dormant) condition in most cases. Nannfeldt (1940) restricts the use of the term ' vivipary ' to those races in which the deciduous buds form the regular diaspores.

' Vivipary ' is restricted by Pope (1949) to embryos developing continuously without any dormant period. He induced this in barley by supplying water directly to exposed germs. Such uninterrupted growth occurs in maize with defective endosperms (Eyster

1931). Germination of an undetached seed is included by Arber in 'true vivipary,' and she quotes *Spartina townsendii* H. & J. Groves as a British example. Germinating seeds may be distinguished from proliferated spikelets by the coleoptiles of the seedlings, see Figure 2.

The use of derivatives of 'prolifer' as recommended by Arber, has the support of antiquity. Tournefort (1700) used 'proliferum' in a synonym of *Poa bulbosa* var. *vivipara*. The viviparous forms of *P. alpina* L., *P. bulbosa* L. and *Festuca vivipara* (L.) Sm. are discussed by Scheuchzer (1719) under the general heading "... *Locustis foliaceis proliferis*" – proliferated leafy spikelets. However, 'proliferation' unless prefaced by 'vegetative' is not free from ambiguity. Among Arber's references to this phenomenon, a hybrid wheat of Biffen & Engledow (1926) is quoted. This wheat bore numerous florets on an elongated axis, but was innocent of vegetative development. Proliferation has been used to describe various pathological forms (e.g. in *Agrostis canina* L., Philipson, 1935) which do not bear leafy shoots.

Other sources of confusion are provided by vegetative shoots terminated by a group of many axillary buds separated by very short internodes. Especially when the buds grow out, the whole presents an appearance superficially resembling a proliferated culm, see Figure 3. The 'mop' habit of Arber falls into this category. The absence of glumes distinguishes these from proliferated culms, but the margin between extremely metamorphosed inflorescences and vegetative shoots is not sharp.

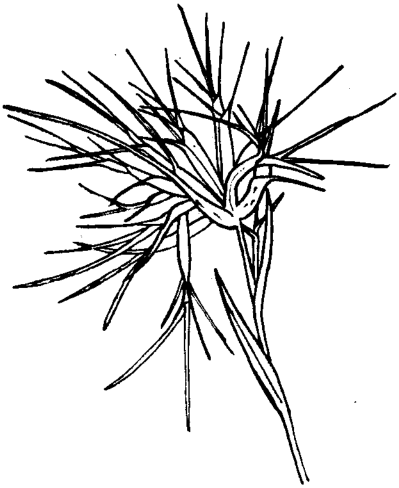

Fig. 3. *Puccinellia maritima* (Huds.) Parl. Blakeney, June 1950. A tuft of many shoots upon an elongated stolon, similar to 'mop' (Arber) (× c. $\frac{2}{5}$).

In this paper it seems natural to follow the general usage in the literature. 'Viviparus' derivatives will be used in ecological discussions, because they are strongly entrenched in the taxonomic literature and they emphasize the fact of growth at the time of dispersal. But, whenever morphological and physiological aspects are under review, the more accurate 'prolifer' words must be used.

## 3. The British races of viviparous grasses

The following are included in the British flora, but *Poa bulbosa* L. var. *vivipara* Koel. is almost certainly not native and the present author has never seen it growing wild.

| | |
|---|---|
| *Festuca vivipara* Sm. | A K L O |
| *Poa bulbosa* L. var. *vivipara* Koel. | K L W |
| *Poa alpina* L. var. *vivipara* L. | K L |
| *Poa* × *jemtlandica* (Almqu.) Richt. | L |
| *Deschampsia caespitosa* (L.) Beauv. var. *pseudalpina* (Syme) Druce | L |
| *Deschampsia alpina* (L.) Roem. & Schult. | K L O |

The initials after the plant names indicate Aberystwyth, Kew, London, Oxford and Wageningen. At these places transplanted specimens have retained their vivipary. The ranges of the viviparous races and related seminiferous forms overlap, confirming that environment is not a primary cause of the manifestation of vivipary in these races. The degree of constancy of vivipary will be discussed for each species or variety separately.

## 4. TAXONOMY OF FESTUCA VIVIPARA (L.) SM.

### 4.1. *Historical outline*

Figure 4 shows seminiferous and partially and fully viviparous spikelets.

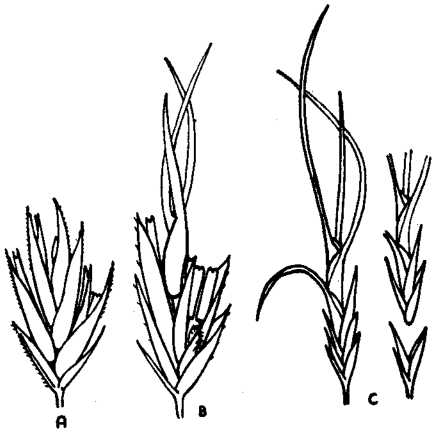

Fig. 4. *Festuca* spikelets.
A. *Festuca ovina* L., seminiferous (× c. 4). B. *Festuca vivipara semiviviparae* Turess. (× c. 4).
C. *Festuca vivipara viviparae* Turess., with a sketch to show dehiscence (× c. 2).

Ray (1690, 184) mentioned *Gramen montanum spica foliacea graminea* and recorded its growth amidst the summit detritus of the Welsh mountains. In 1703, p. 178, he was more certain his plant was Bauhin's *Gramen arvense panicula crispa*; since the latter was almost certainly *Poa bulbosa* var. *vivipara*, this identification was an error, but an error redeemed by an accurate description of the replacement of the flowers in the panicle by leaves.

Linnaeus (1737, 56) named this plant *Poa spiculis angustis, acutis vivipara.* The second comment is the ambiguous " *Loco feminum folia angusta, flore longiora protrudit, hinc instar qui in ipsa planta germinat, more animalium viviparum.*" Linnaeus (1745, 33) renamed this species *Festuca spiculis viviparis*, but in the *Species Plantarum* (1753, 73) he reduced it to a variety of *Festuca ovina.*

Specific rank was again conferred by Smith (1800, 114) as *Festuca vivipara* with the comment " *Videtur species a priore distincta.*" However, the property that so clearly marked the species was not its specialised mode of reproduction, but according to Smith (1824, 140) the shape and pubescence of the glumes. It was also noted that sometimes the spikelets are not fully viviparous, the lower florets being unmetamorphosed.

Hackel (1882, 88) put all viviparous plants into a subvariety thus : *F. ovina* subsp. *eu-ovina* var. *supina* subvar. *vivipara.* In 1925 Howarth revised the sheep's fescues in Britain and found viviparous specimens of *F. capillata* Lam. (i.e. *F. tenuifolia* Sibth.), *F. ovina* L. *sensu stricto*, *F. supina* Schur and *F. longifolia* Thuill. (he raised Hackel's subspecies to species). He suggested that perhaps only specimens of *F. supina* were constant in their vivipary.

Virtually the only vegetative character that divides *F. supina* from *F. ovina* is that the radical sheaths are entire over their lower third in the former, but completely split in *F. ovina.* Better subepidermal sclerenchyma development was found by Howarth in *F. supina.* Extensive cultivation of seminiferous and viviparous specimens convinced Turesson (1926-7) that it was impossible to group all constant viviparous forms under one head and the distinction between *F. supina* and *F. ovina* had no value. Subsequent works have not revived *F. supina* as an important taxon.

Tutin (1952, 1426) gives specific rank to four segregates of *F. ovina* agg., namely : *F. ovina* L. (of which two subspecies, subsp. *ovina* and subsp. *tenuifolia* (Sibth.) Tutin are admitted), *F. vivipara* (L.) Sm., *F. trachyphylla* (Hack.) Krajina [non Hack.] (i.e. *F. longifolia* Thuill.) and *F. glauca* Lam. This is satisfactory except for the statement that viviparous plants resemble vegetatively *F. ovina* subsp. *tenuifolia*, which is the *F. capillata* of Howarth.

The characters of the segregates are tabulated in Table 1. Fully viviparous fescues must be determined by vegetative characters. Robustness of the laminae and length of inflorescence parts increases from subsp. *tenuifolia* via subsp. *ovina* to *F. trachyphylla.*

TABLE 1

Characters to distinguish *Festuca ovina* subsp. *tenuifolia*, *F. ovina* subsp. *ovina* and *F. trachyphylla*

| | | *tenuifolia* | *ovina* | *trachyphylla* |
|---|---|---|---|---|
| Width of the leaf-blade in millimetres | | 0·3–0·5 | 0·3–0·7 | 0·6–1·1 |
| Length of leaf proportional to culm height | | Long, ½ culm or more | Short· | |
| Auricles | | Markedly lobed | Rounded | |
| Length of spikelet | mm | 3–6 | 4–8 | 6–10 |
| Length of lemma | mm | 2·5–4 | 3–5 | 4–5·5 |
| Points of lemmae | | Mucronate | Awned<br>Awn - 1 mm | Awned<br>Awn - 3 mm |

Sometimes hairy leaf-sheaths and scabrid rhachides are given as additional *F. trachyphylla* characters, but they are neither constant for *F. trachyphylla* nor always absent in the *F. ovina* subspecies. Leaf length and auricle characters for *F. trachyphylla* are not given, but the present author finds that they approach the subsp. *ovina.*

### 4.2. *Observations*

Thirty-eight specimens of *F. vivipara* (both partly and fully viviparous) were collected in different parts of the British Isles. Twenty-nine have survived transfer to London, twenty-two have since produced culms. In addition twenty-seven other living specimens, of which twenty-four survived, were assembled; some were gifts from other collections. Seminiferous fescues have also been grown.

Vivipary was retained by both fully and partially viviparous plants, the latter bearing both florets and bulbils as in nature. Thus vivipary and partial vivipary are constant.

Under the rather dry pot-cultivation in London the leaf-blades are shorter and thicker. Perhaps owing to this thickening, the lobing of the auricles, which is a *tenuifolia* character, appears to be less. However, cultivated plants did not acquire the glaucescence commoner in *F. trachyphylla* than in *F. ovina* subspp. Fully viviparous plants must be assigned to a category by leaf characters, and there is an overall tendency for cultivated plants to gain an appearance further to the right in the relationship :–

*F. ovina* subsp. *tenuifolia* → *F. ovina* subsp. *ovina* → *F. trachyphylla*

This is most marked in life, but dried leaves reflect the same bias. Where it was possible to examine inflorescence characters, they were found to be more conservative.

In Table 2 the thirty-eight specimens are classified, using all available characters.

TABLE 2

Classification of fescues

| | *tenuif.* | *tenuif.-ovina* | *ovina* | *trachy.* | *rubra*-like |
|---|---|---|---|---|---|
| Completely viviparous | 7 | 12 | 10 | 1 | |
| Partially viviparous | 3 | | 4 | | 1 |

The groupings are: *Festuca ovina* L. subsp. *tenuifolia*, plants of mixed or intermediate characters subspp. *tenuifolia–ovina*, *F. ovina* subsp. *ovina*, *F. trachyphylla* and lastly a plant with many characters closer to *F. rubra* agg. than *F. ovina* agg.

Howarth (1948) states that vivipary is known in all varieties of *F. tenuifolia* Sibth. and *F. ovina* L. and in the var. *genuina* of *F. longifolia* Thuill.

Leaf-length/culm-height ratios are probably liable to environmental variation and pot-culture throws doubt on leaf characters. Clearly, then, it is impossible to confine the constantly viviparous fescues to one form approaching that of one of the lower seminiferous taxa.

In order to include all British viviparous fescues, Smith's description should be amended to admit plants with glaucous leaves or with lower glumes metamorphosed. The viviparous fescues are a group of asexually reproducing forms restricted in range by their mode of propagation. It is useful ecologically and systematically to include all under one specific name. It is not departing from general usage to adopt *F. vivipara* Sm. for this purpose.

### 4.3. *Subdivision of* F. vivipara *(L.) Sm.*

Turesson (1926-7, 1930 & 1931) named the seminiferous forms amphimicts, the viviparous forms which had at any time borne flowers amphi-apomicts, and one group of fully viviparous plants, on which he had never found flowers, apomicts. He distinguished between the usually partially and fully viviparous plants by the names *semiviviparae* and *viviparae*. The former are amphi-apomicts, and because of occasional serotinous flower-bearing culms most of the *viviparae* are also amphi-apomicts.

The *viviparae* were divided by Turesson into 18 types constant in cultivation. Wilmott (in Campbell, 1945) applied this classification to specimens gathered in the field and added a further type. However, many characters such as culm rigidity, shape and laxity of the panicle, size of the bulbils and root development are likely to depend on the time and place of collection. This in no way detracts from the value and importance of Turesson's original work, but renders inadvisable the use of the key for wild specimens.

The groups *semiviviparae* and *viviparae* are useful to denote partially and fully viviparous plants. The two are easily determined, appear to be constant and have differing potentialities. Both may be included in *F. vivipara.*

### 4.4. *Cytology and Origin*

All Turesson's seminiferous plants of *F. ovina* had a chromosome number of $2n = 14$, but the *viviparae* had numbers of $2n = 21$, 28 and 42. Stählin (1929) and Church (1936) give $2n = 14$ for "*F. capillata* Lam." (= subsp. *tenuifolia*). They find or quote for various seminiferous segregates of *F. ovina* agg. the following numbers: $2n = 14$, 28, 42, 56 and 70. Thus polyploidy is not peculiar to the viviparous forms.

Flovik (1938) investigated Spitzbergen plants and found: *F. ovina* var. *brevifolia* $2n = 28$, *F. rubra* var. *arenaria* $2n = 42 \pm 1f$ and *F. vivipara* $2n = 49$. Tromsö and Narvik plants gave: *F. ovina* $2n = 14$, *F. vivipara semiviviparae* $2n = 21$, *F. vivipara viviparae* $2n = 28$ and *F. rubra* var. *arenaria* $2n = 42$. On the basis of chromosome morphology and numbers and the morphology of the glumes he suggested that *F. vivipara* on Spitzbergen was the hybrid ($2n = 49$) of an unreduced *F. ovina* var. *brevifolia* gamete ($n = 28$) and a reduced *F. rubra* var. *arenaria* ($n = 21$) gamete. In Norway he visualised the reduced gametes of *F. ovina* ($n = 7$) and *F. rubra* ($n = 21$) giving rise to a fully viviparous fescue ($2n = 28$), which by means of an occasional flower (see also Jenkin, 1922) backcrosses with *F. ovina* yielding the semiviviparous plant ($2n = 21$).

Jenkin & Thomas (1949) report sickly seminiferous hybrids ($2n = 42$) of *F. ovina* and *F. rubra.* Nannfeldt criticises Flovik's hybridisation schemes, because the general form and growth habit of *F. vivipara* is not intermediate between the supposed parents.

Seed was obtained by Jenkin (1922) from late-arising inflorescences of viviparous fescues, pollination being possibly by nearby seminiferous *Festucae.* Four plants were raised from seed, two being virtually normal seminiferous plants. The other pair showed strong signs of the parental vivipary. One would appear to have been a fairly normal *semiviviparae* form; the second was somewhat monstrous.

The occurrence of flower-bearing by *viviparae* and the existence of the *semiviviparae* permit of genetic exchange between the viviparous forms and their seminiferous relatives. Thus, even if vivipary originated among the fescues but once, there is no reason to expect uniformity to have remained. The origin of *F. vivipara* is unknown, but its variation is certain.

## 5. POA BULBOSA VAR. VIVIPARA KOEL.

Caspar Bauhin (1620, 6) described *Gramen arvense panicula crispa* and illustrated it by a woodcut. Tournefort (1700, **1**, 523) quoted this, but renamed it as *Gramen paniculatum, proliferum.* Scheuchzer (1719, 45) cited both the former authors and Jean Bauhin, and included the plant in his group of proliferated grasses. It is difficult to tell if Bauhin meant only the viviparous form, although the already mentioned error by Ray indicated that he believed this plant to be viviparous. Bauhin's plant was certainly of *Poa bulbosa* agg. and a seminiferous form was separately described by Scheuchzer (1719, 40) under Lobel's name *Gramen xerampelinum.*

The specific name *Poa bulbosa* was due to Linnaeus (1753, **1**, 70) and all the above names are quoted. Halperin (1933) has reviewed the subsequent literature, stating that all except one of Linnaeus' specimens were viviparous. Halperin concluded that the correct name is *Poa bulbosa* var. *vivipara* Koel. (Koeler, 1802, 189).

Figure 5 illustrates spikelets of both forms.

Since the early authors agree that Bauhin's plant was viviparous, the first reference to the phenomenon may be due to him, although the present author has yet to discover a clear description of it in his works.

Parkinson (1640, 1157) included *Gramen arvense panicula crispa* (joined with a grass which was probably *Apera spica-venti* (L.) Beauv.), but the description concluded thus : " I have thought good to adde the figure of that Grasse that Lugdunnensis calleth *Bulbosum Dalechampij*, because Bauhinus saith it is this, but not well expressed, but surely I doubt it is another sort." This cannot therefore be counted the first record of *P. bulbosa*, viviparous or otherwise, in Britain.

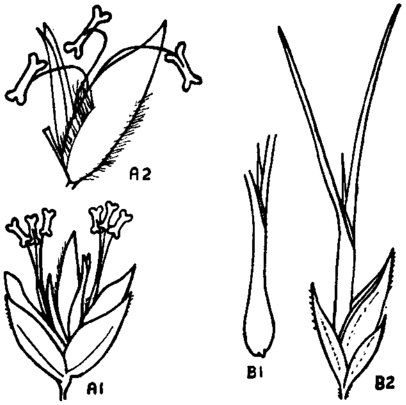

Fig. 5. A. *Poa bulbosa* seminiferous; 1. Spikelet (× 4·5); 2. floret (× 7). B. *Poa bulbosa* var. *vivipara* 1. Spikelet (× 3·5); 2. base of bulbil.

Syme (1872, 112) knew that continental *P. bulbosa* was sometimes viviparous, but stated that only the seminiferous form was British. All references previous to Riddelsdell (1907) apparently refer to seminiferous *P. bulbosa*. Riddelsdell's plant was viviparous, found on a pebbly shore near Barry, Glamorganshire, S. Wales. At that time Barry was already a well-developed port.

With material of French and Dutch origin both the seminiferous and viviparous forms have been found constant in London. Schuster (1910) found vivipary in *Poa bulbosa* to be constant, although in culture occasional temporary ' reversions ' to flowering occurred.

Åkerberg (1942) gives the chromosome number of *Poa bulbosa* (seminiferous) as $2n = 28$ and 45. Tutin (1952) mentions for the viviparous plant $2n = 35$.

### 6. POA ALPINA VAR. VIVIPARA L. AND P. × JEMTLANDICA (ALMQU.) RICHT.

The species *Poa alpina* was first designated by Linnaeus (1753, **1**, 67) quoting in his description his own earlier work (1745, 28) and Scheuchzer (1719), who recorded a seminiferous plant (p. 40, no. 4) and a proliferated plant (p. 45, nos. 2 and 3a). Linnaeus makes the second of these his β variety and inserts the adjective '*vivipara*' into Scheuchzer's name.

In addition to mentioning that *P. alpina* in Britain is usually viviparous, Syme (1872, 114) drew attention to a plant he considered to be *P. stricta* Lind., a subspecies of *P. laxa* Hänke (*eu-laxa* not being viviparous). Druce (1903) named this plant *P. alpina* L. var. *acutifolia* Druce. However, Nannfeldt (1937) has traced the history in detail. The plant was given the name *P. alpina* subsp. *jemtlandica* by Almquist (1883) ; Richter (1890) raised it to a species, *P. jemtlandica*. It is considered to be a hybrid between *P. alpina* and *P. flexuosa* Sm., and non-viviparous specimens are not known.

*P.* × *jemtlandica* bears florets low in the spikelets, but the sex organs are always sterile in contrast to *P. alpina*. Seminiferous forms and male fertile florets in the viviparous inflorescences are known in *P. alpina*. Table 3 gives the main characters to distinguish the two viviparous forms. Figure 6 shows seminiferous *P. alpina* and viviparous *P.* × *jemtlandica* spikelets.

TABLE 3

| | *Poa* × *jemtlandica* | *Poa alpina* var. *vivipara* |
|---|---|---|
| Leaf sheath | Persistent | Very persistent in nature |
| Cauline sheath | Smooth waxy green | Green with yellow ribs |
| Ligules | Usually all long and pointed | Upper long and pointed; lower often blunt |
| Leaf blades | Green, flat, tapering to a point gradually | (Often glaucous), green; usually folded, narrowing abruptly to a hooded tip |
| Uppermost knot | Covered | Exposed |

The authorities are not agreed upon any clear glume features that may be used to distinguish the species.

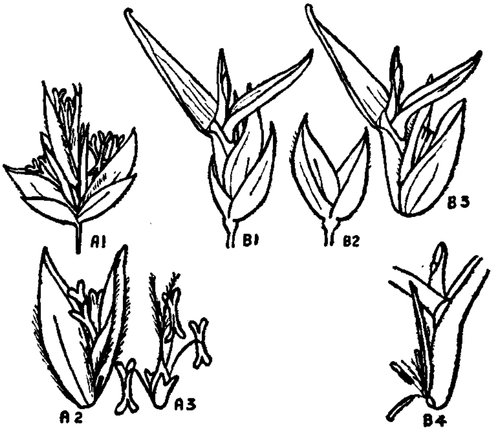

Fig. 6. A. *Poa alpina* seminiferous: 1. Spikelet (× 3); 2. floret (× 4·5); 3. floral organs (× 4·5). B. *Poa* × *jemtlandica*; 1. Spikelet (× 3); 2. lower glumes; 3. bulbil and lowest floret; 4. as 3, but lemma removed to show the aborted nature of the sex organs.

In London, seminiferous *P. alpina* was constant. Few viviparous plants of these *Poae* were collected in this investigation, because of their rarity. Three of *P. alpina* and two of *P.* × *jemtlandica* were taken; they survived only one year, but produced viviparous culms. Bulbils of *P. alpina* var. *vivipara* bore flowers at the end of the summer in which they were borne and struck, but produced viviparous inflorescences next spring. Exo (1916) reported an exactly similar experience with this variety. Schuster found this variety constant in vivipary, except for occasional ' throw-backs ' as in *P. bulbosa*, especially on poor soil.

Seminiferous *P. alpina* is recorded with chromosome numbers of $2n = 19\text{-}46$, 49, 51-54, 57, 64, 65, 67, 72 and 74 (see Nannfeldt's review (1940)). Apomixis has been demonstrated by Åkerberg (1942), Engelbert (1940) and Müntzing (1933, 1940).

*P. alpina* var. *vivipara* has $2n = 26$, $33 \pm 1$ (Müntzing, 1940), 35 (Tutin, 1952) and $42 \pm 4$ff, 44 (Flovik, 1938). *P.* × *jemtlandica* has $2n = 37$, (39) (Nygren, quoted by Á. & D. Löve, 1948).

## 7. THE VIVIPAROUS DESCHAMPSIAE

### 7.1. *Historical outline*

Linnaeus (1753, **1**, 64-5) named *Aira cespitosa* and *A. alpina*. The characters given for the former were flat leaves, a spreading panicle and short straight awn, but in *A. alpina* the leaves were described as subulate, the panicle as thick and the glumes as silvery with a very short awn. These were synonymous with species 63 and 69 in the *Flora Suecica* (1745, 23 and 26). The further details were given that sp. 63 (*A. cespitosa*) has a β variety found in wet places in Lappland and whose long thin panicle is often viviparous. Thus the first mention of vivipary in this genus was for a variety of *A. cespitosa*.

The character given by most subsequent authors as the mark of *A. alpina* is the dorsal insertion of the awn above the middle of the lemma, i.e. not basal as in *A. cespitosa*. Linnaeus however, did not discuss the point of insertion; it can only be inferred from the statements that the awn is short in *A. cespitosa* and very short in *A. alpina*. No mention of vivipary in *A. alpina* was made.

A note by Davies was quoted by Smith (1800, 85) that a viviparous variety of *A. caespitosa* (note changed spelling) is found in alpine places. Smith (1811) received from Don viviparous plants from Clova and a seminiferous plant from near Dundee, which were named *A. laevigata*. The main characters are that roughness is confined to the lamina edges, the base of the floret is bearded, but the rhachilla is very short and smooth (in *A. cespitosa* the rhachilla is long and hairy). *A. laevigata* bears culms a month earlier than *A. cespitosa*, is usually viviparous and never attains more than a foot in height.

P. de Beauvois (1812) split the genus *Aira* and designated the group including *A. cespitosa* and *A. alpina* as *Deschampsia*. The following viviparous forms are given by Roemer & Schultes (1817, 685 et seq.) : *D. cespitosa* Beauv. γ var. *alpina*, *D. alpina* (L.) Roem. & Schult. and *D. laevigata* (Sm.) Sm. In 1824 (p. 105) Smith states that *A. laevigata* is within *A. alpina* L., which is now *D. alpina*.

Roemer & Schultes defined the insertion of the awn on the lowest lemma in *D. alpina* as somewhat below the open bifidity. Further details given were : the awn scarcely projects beyond the glumes, the upper lemmas bear terminal awns, the back and edges of the glumes are smooth. These features contrast with the sub-basal awn insertion and scabrid glume keels in *D. cespitosa*. The leaves of *D. alpina* are said to be short, always rolled, yellow-green and subulate.

Discussing the *Deschampsia* section of *Aira*, Syme (1872, 63-6) gave a variety γ *pseudalpina* (Syme's spelling was *Pseud-alpina*) of *A. cespitosa*, which is distinguished from the main form by smoother panicle branches and larger spikelets which are nearly always viviparous. He then described *A. alpina* L., stating that the panicle branches are smooth, the keels of the glumes are sometimes rough towards the apex but otherwise smooth and the awn is from about the middle of the lemma. He observed that all his specimens of *A. alpina* were viviparous and this species had often been confused with *A. cespitosa* var. *pseudalpina*. He considered the presence or absence of roughness on the lower portion of the glume keels the key to distinguishing the viviparous forms, and the point of insertion of the awn the main point for distinction of *D. alpina* from *D. cespitosa*.

Later it will be seen that difficulties arise because the state of the awn in viviparous forms other than *D. alpina* has never been defined, and the lower portion of the glume keels is quite smooth in all viviparous plants met with in this study.

Druce (1888) mentions *D. cespitosa* Beauv. var. *pseudalpina* (Syme). This is the earliest reference found by the present author, in which *pseudalpina* is given as a variety of *D. cespitosa,* and not of *A. cespitosa.* Thus, strictly, *D. cespitosa* (L.) Beauv. var. *pseudalpina* (Syme) Druce is correct.

Seminiferous specimens of *D. alpina* are rare, although Linnaeus never mentioned vivipary in *A. alpina.* Don sent a flower-bearing plant to Smith (1811). Parnell (1842) describes and illustrates only seminiferous forms. Nygren (1949) received a sexual seed-bearing plant. The present author found a plant most of whose spikelets bore florets only. Another plant in culture (see below) produced a completely flower-bearing culm, although strongly viviparous when gathered in Harris.

### 7.2. *Morphological observations*

During the course of this study no viviparous specimens have been seen with a basally inserted awn. The awn is sometimes inserted about the middle of the third glume (i.e. the lowest lemma); this is the typical *D. alpina* arrangement. Often the third glume is so metamorphosed that the awn appears as a terminal bristle or is absent. This, being the only other widespread form, is presumably the *D. cespitosa* var. *pseudalpina* condition.

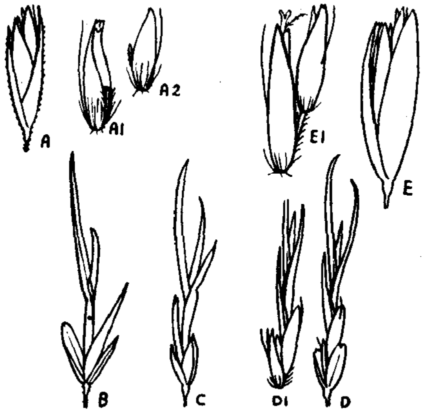

Fig. 7. *Deschampsia* spikelets.

A. *Deschampsia caespitosa* seminiferous (× 5·5) : 1. lower floret ; 2. upper florets. B. *Deschampsia cespitosa* var. *pseudalpina* ; C. *Deschampsia* ' intermediate ' viviparous type. D. *Deschampsia alpina* viviparous ; 1. lower glumes removed to display the poorly developed floret (B, C and D are all × 1·4). E. *Deschampsia alpina* seminiferous (× 7) ; 1. lower glumes removed.

There is an intermediate group, in which the awn is a hair lying between the twin ear-like terminal lobes of the third glume. In these intermediate forms there is a very short subterminal awn which is not clearly separated from the glume ; it neither appears ' to arise ' nor ' to be inserted.' Argument for inclusion with either of the main forms may be advanced, perhaps more strongly for *D. alpina.* In Figure 7 these types are illustrated.

The specimens in the herbaria of Linnaeus and Smith (Linn. Soc. Lond.) and of Syme (B.M.) were consulted. There are no specimens labelled *A. alpina* by Linnaeus but in his collection are two viviparous plants, apparently *D. alpina* with slight intermediate tendencies, labelled ' Lapp ' and joined to *A. cespitosa.*

The plants in Smith's collection appear to be a seminiferous *D. alpina* labelled *A. alpina*; viviparous ' intermediate ' plants marked ' *A. laevigata,*' which he later considered *A. alpina*; and finally a viviparous plant of var. *pseudalpina* placed under *A. cespitosa.* (To avoid damage the specimens could not be very closely examined.)

Syme had two viviparous plants of ' intermediate ' type from North Wales under *A. cespitosa*, which in the absence of others are presumably his var. *pseudalpina*. There are forty-seven Scottish viviparous specimens, all labelled *A. alpina*, but including in the present author's opinion the var. *pseudalpina*, intermediate plants and *D. alpina* Evidently Syme used glume-keel smoothness as a key character. But this course includes in *A. alpina*, as interpreted by Syme, many plants hard to bring into *D. alpina*, and in fact all viviparous *Deschampsiae* in this present study.

In order to escape from this impasse of conflicting and overlapping definitions and the lack of any other names free from ambiguity, awn-insertion is used here as the criterion and an ' intermediate ' category maintained.

All the seminiferous plants with basally inserted awns (*D. cespitosa*) have been found to have markedly scabrid leaves, panicle branches and glumes.

Since var. *pseudalpina* is a segregate of *D. cespitosa*, a gradation of certain characters from seminiferous *D. cespitosa* through the var. *pseudalpina*, the ' intermediate,' to the typical *D. alpina* might be expected.

Forty-six viviparous *Deschampsia* specimens have been classified by the condition of their third glume's awns at the time of collection. Other features were not consistently distributed, so this one major criterion was selected. Even so, the spikelets in a panicle are not all the same, and in deciding the category the whole was considered. It is partly for this reason that the ' intermediates ' have not been lumped with *D. alpina*, and also because the specimens placed by Syme in *A. cespitosa* are intermediate.

In Table 4 the numbers of the plants with different characters are given, and in the first column the condition in seminiferous *D. cespitosa*.

The leaves and panicle branches are rougher in proportionately more var. *pseudalpina* than *D. alpina* plants, but smooth forms occur in both, although the trend is in agreement with the postulated gradation.

The midribs of lower glumes of all viviparous plants are innocent of roughness in their lower portions, hence this character from Roemer & Schultes, and Syme, does not separate these plants. Hairiness about the floret base is typical of seminiferous *D. cespitosa*, but only var. *pseudalpina* plants were naked.

Living portions of the plants discussed above were also collected; sixteen bore culms in London the next year. In April the *Deschampsiae* were making poor growth and were brought into a glass cabinet, where they obtained additional warmth and illumination. This speeded shooting and was responsible probably for the greater degree of floret-bearing in these conditions than in nature. Except the *D. alpina* plant which became fully flower-bearing, none of the inflorescences were completely free of proliferation. Established bulbils also bore viviparous culms. Here vivipary is a hereditary character modified by environment. The inflorescences obtained in culture are classified by awn type in the lower part of Table 4. It will be seen that there has been a shift towards *D. alpina* features.

It is suggested that this tendency towards *D. alpina* is associated with the bearing of more floral organs in the forced plants. These plants were further studied and it was noted, especially in the ' intermediate ' group, that, where fully-floret-bearing and viviparous spikelets occurred in the same panicle, the floret lemmas were of a *D. alpina* character, but the proliferated spikelets usually bore third glumes of an ' intermediate ' or *pseudalpina* type. As flower-bearing increases, so the awn becomes more clearly distinguished, longer, and inserted lower. Thus decreasing proliferation is accompanied by an approach to *D. alpina*, and if the trend could be continued, to the typical seminiferous *D. cespitosa* form.

Conversely, increasing vivipary causes a transition from the seminiferous *D. caespitosa*

TABLE 4

Characters of viviparous *Deschampsiae*

| | | *D.c.* | *Dcp.* | *D.i.* | *D.a.* |
|---|---|---|---|---|---|
| Forty-six as originally collected :— | | | | | |
| Third glume awn-insertion | Sub-basal | × | | | |
| | Subterminal/central dorsally | | | | 17 |
| | Slightly subterminal | | | 9 | |
| | Terminal (or awn absent) | | 20 | | |
| Leaves | Rough | × | 1 | 1 | |
| | Slightly rough | | 12 | 3 | 8 |
| | Smooth | | 7 | 5 | 9 |
| Panicle branches | Rough | × | | | |
| | Slightly rough | | 9 | 4 | 3 |
| | Smooth | | 11 | 5 | 14 |
| Lower portion of glume keels | Rough | × | | | |
| | Smooth | | 20 | 9 | 17 |
| Hairs at floret (or third glume) base | Many and long | × | 10 | 6 | 13 |
| | Few and short | | 5 | 3 | 4 |
| | Absent | | 5 | | |
| Sixteen plants which bore culms in culture :— | | | | | |
| Classified by their original awn-insertion :— | | | 8 | 3 | 5 |
| Awn-insertion after cultivation in London | *Dcp.* | | 4 | | |
| | *D.i.* | | 2 | 2 | 1 |
| | *D.a.* | | 2 | 1 | 4 |
| Classified by their final awn-insertion | | | 4 | 5 | 7 |

Typical condition of seminiferous plants indicated by '×'

Abbreviations : *D.c.* – *Deschampsia cespitosa* seminiferous type; *Dcp.* – *Deschampsia cespitosa* var. *pseudalpina*; *D.i.* – *Deschampsia* intermediate viviparous type; *D.a.* – *Deschampsia alpina*.

Waviness of panicle branches, leaf rolling, blade/sheath lengths ratio and leaf/culm height ratio were tried, but abandoned as they vary within seminiferous *D. cespitosa* as well as amongst the viviparous forms.

through *D. alpina* to the extreme var. *pseudalpina* type, in which the third glume has lost all lemma-like qualities and resembles a foliage leaf. Morphologically the var. *pseudalpina* is farther from normal *D. cespitosa* than *D. alpina*.

Ecological discussion is deferred, but, briefly stated, seminiferous *D. caespitosa* in all its forms is the most widely distributed ecologically and geographically. In Britain, var. *pseudalpina* has the greatest range among the viviparous *Deschampsiae* and *D. alpina* the least. 'Intermediate' forms are found mainly within the range of *D. alpina*, but also beyond, as in North Wales. Some botanists report *D. alpina* in N. Wales; they may either have found this species in the strictest sense, have been unaware that all viviparous specimens are not within *D. alpina*, or have taken a broader view on the 'intermediate' types, which is reasonable.

## 7.3. *Cytological Observations*

Seminiferous *D. cespitosa* has chromosome numbers of: 2n = 26 (Lawrence, 1945), 2n = 28 (Avdulow, 1931; Nielson & Humphrey, 1937; and Hagerup, 1939). Seminiferous *D. alpina* 2n = 26 (Nygren, 1949). Slightly or partly viviparous *D. alpina* 2n = 39 (Flovik), strongly or fully viviparous *D. alpina* 2n = 41, 49, 52 and 56 (Flovik, 1938; Hagerup, 1939; and Nygren, 1949). Nygren traced a series of increasing vivipary with polyploidy.

In the present work, various root squash techniques were unsuccessfully attempted. Therefore root-tips were sectioned and the chromosomes in metaphase plates counted by means of a camera lucida (total magnification × 1,000). Chromosomes were about 5 $\mu$ long. In sectioned material there is no certainty that plates are complete or that long chromosomes have not been cut into parts. In practice the best plates were counted and the modal number taken. The numbers in Table 5 are given as approximate and not as a critical study. But they are adequate to demonstrate that cytology is a poor key to the classification of the viviparous *Deschampsiae*.

TABLE 5
Approximate Diploid Chromosome Numbers of *Deschampsiae*

| Location | var. *pseudalpina* | " *intermediate* " | *D. alpina* |
|---|---|---|---|
| West Mayo | 44, 44, 47, 47, 49 | 34, 37 | 34 |
| North Wales | 37 | | |
| Lake District | 32 | | |
| Grampians | (31–32), 41 | | 38 |
| Western Isles | 36 | 39 | 36 |

The numbers are erratic. The morphological characters are also somewhat randomly arranged if awn-type is used as a key. This suggests that there is considerable variation due to occasional sexual reproduction. In *D. alpina* especially, good stamens are common and not infrequently well-formed pistils are found.

## 7.4. *The employment of the names* Deschampsia alpina *(L.) Roem. & Schult. and* Deschampsia cespitosa *var.* pseudalpina *(Syme) Druce*

All facets of the subject, historical, morphological and cytological, show how weak is the distinction between the two forms. All forms cannot be brought within *D. alpina* (L.) R. & S., unless absence of an awn due to metamorphosis is counted as insertion above the middle of the third glume. This is supported by the transition series and that, in this series, *D. alpina* stands closer to seminiferous *D. caespitosa* than the var. *pseudalpina*, which is allegedly a segregate of the latter.

The different ranges argue for their retention and fuller knowledge may be lost by failing to distinguish them, especially as these observations are confined to the British Isles.

Two forms are recognized: *Deschampsia alpina* (L.) Roem. & Schult. in which the awn is inserted about the middle or upper part of the dorsal rib of the third glume (lemma of the lowest floret), and *D. cespitosa* var. *pseudalpina* (Syme) Druce in which proliferous metamorphosis prevents the distinction of a separated awn. There are intermediate forms between them, and spikelets of the same panicle may not all fall into one category.

The literature yields no well defined name free from ambiguity which covers either all the viviparous *Deschampsiae,* or all those other than *D. alpina.*

## 8. SUMMARY

8.1. The continued growth of the spikelet axis and the bearing of foliage leaves distally upon it is termed the vegetative proliferation of spikelets. If these leafy shoots form deciduous plantlets, which are the regular diaspores of the plant, the phenomenon is called vivipary by many authors.

The history and confusion of these terms is traced. Proliferation is an older and more accurate usage and should be employed in morphological and physiological discussions. Vivipary is useful in its restricted sense to describe regular propagation in this manner, as it has ecological meaning.

8.2. Five races of viviparous grasses are native in Britain; these have an arctic-alpine range about the North Atlantic.

*Festuca vivipara* (L.) Sm.
*Poa alpina* L. var. *vivipara* L.
*Poa* × *jemtlandica* (Almqu.) Richt.
*Deschampsia cespitosa* (L.) Beauv. var. *pseudalpina* (Syme) Druce.
*Deschampsia alpina* (L.) Roem. & Schult.
*Poa bulbosa* L. var. *vivipara* Koel., a plant of dry disturbed places, is an alien in the British flora.

8.3. The names of the *Poae* are accepted without discussion.

8.4. *Festuca vivipara* is clearly of the *F. ovina* agg. The vegetative variation within *F. vivipara* is almost as wide as in *F. ovina* agg., thus *F. vivipara* cannot be placed as a subspecies or variety of a segregate of *F. ovina.*

*F. vivipara* includes both fully and partially viviparous forms, which may be distinguished by Turesson's names *viviparae* and *semiviviparae* respectively.

8.5. *Deschampsia cespitosa* var. *pseudalpina* and *D. alpina* are recognized. Although only the latter is at all well defined, and transition forms exist between the two. Neither vivipary nor the characters that distinguish the forms are completely constant. The forms are not separate cytologically.

An argument is advanced that the more proliferated var. *pseudalpina* is further from seminiferous *D. cespitosa* than *D. alpina.* They are left separate, partly in view of their differences in ecological range and partly because of the lack of a suitable well known name.

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