Vivipary, Proliferation, and Phyllody in Grasses

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Abstract

Some temperate grasses have the ability to produce in their inflorescence modified spikelet structures that act to reproduce the species vegetatively. These types may be either genetically fixed or an occasional expression of environmental change.

Vivipary sometimes refers to the development of separable vegetative shoots, as in the case of *Poa bulbosa,* wherein florets have been transformed into bulbils. At other times vivipary refers to the germination of an embryo *in situ* before the fall of the seed, as in *Melocalamus,* the fleshy seeded bamboo from Burma.

Vegetative proliferation refers to the conversion of the spikelet, above the glumes, into a leafy shoot. These leafy shoots are not usually an effective method of reproduction in the wild, but are somewhat easier to establish under controlled conditions.

Both vivipary and proliferation may produce conspicuously abnormal spikelets which the latin words *vivipara* and *prolifera* have been used to describe, usually without any further discrimination than to indicate their presence. Sometimes the enlarged lemmas are sufficiently similar to leaves to differentiate blade from sheath with a prominent collar and ligule, referred to as phyllody (the metamorphosis of spikelet bracts, glumes, lemmas or paleas, into leaves). An alternate spelling "filodia" was used by Martinez (1945) when reporting cases in *Cynosurus echinatus* and *Eragrostis virescens.* Glumes are much more stable than lemmas and paleas. The glumes usually remain unchanged but may occasionally become foliage leaves (Wycherley 1953). The lemma is usually present and altered (always enlarged and never reduced). Paleas are often reduced or absent. Stamens and pistils are also reduced or absent.

According to the literature there are many causes of vivipary, proliferation, and phyllody in grasses:

(1) hereditary genes
  (a) resulting in viviparous races
  (b) hybridization
  (c) polyploidy
(2) malformation (teratology)
  (a) caused by mechanical injury
  (b) caused by insects, nematodes, etc.
  (c) caused by fungi, etc.
(3) adverse environmental factors, any of which may lead to a hormonal imbalance which results in ephemeral proliferation; Wycherley (1954) supposes that in the viviparous races a considerably greater minimal concentration of the putative flowering hormone is required for flower induction, whereas in the seminiferous races this difference is not so great. In the viviparous races, the threshold for flower initiation is rarely exceeded so that perfect flowers appear only occasionally, while in the normally seminiferous races, the conditions arise only rarely where an amount of hormone is produced that is sufficient to initiate culms but insufficient to promote flowering.
  (a) excess water about the roots
  (b) excess shade
  (c) high humidity
  (d) submergence
  (e) abrupt changes in moisture, day length, or temperature
  (f) insufficient vernalization
(4) True vivipary

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Viviparous Races

Where the ranges of the viviparous races and related seminiferous forms overlap, the environment is not a primary cause of the manifestation of vivipary (Wycherley 1953). Wycherley considered the following British grasses exhibited a degree of constancy of vivipary (1) *Festuca vivipara,* (2) *Poa bulbosa* var. *vivipara,* (3) *Poa alpina* var. *vivipara,* (4) *Poa jemtlandica,* (5) *Deschampsia caespitosa* var. *pseudalpina* and (6) *Deschampsia alpina.* In addition to these British grasses genetic races have been recognized in (7) *Festuca rubra,* (8) *Phleum pratense, (9) Poa arctica,* (10) *Poa sinaica* and (11) *Poa tolmatchewii.*

Viviparous and seminiferous strains of *Poa alpina* were found by Muntzing (1940) to be morphologically similar and to have the same chromosome numbers ($2n = 26$ and 33 plus or minus 1); he suggested that in this case the character originated by mutation.

It is doubtful if studies of present day distribution (cf. Wycherley 1954) can indicate more than a north temperate or arctic-alpine origin for genetically controlled vivipary. Some pluvial or glacial period in the past must have intensified the conditions favorable to vivipary over a relatively long period of time and in this region species of *Poa, Deschampsia,* and *Festuca* would have made similar morphological responses to environment, a good example of epharmonic form. Flovik (1938) assumed that vivipary was relatively more common in the arctic flora than elsewhere owing to the combined action of hybridization, polyploidy, and extreme external conditions.

In *Poa bulbosa* and close relatives and in *Phleum pratense* there is an appearance of both bulbous bases of the culms and viviparous spikelets. There is a less direct association of the two characters in *Arrhenatherum* and *Melica.*

The genetically fixed taxonomic presence is overwhelmingly festucoid. Only in the case of *Festuca vivipara* has the presence of vivipary or proliferation been considered a characteristic indication of species formation and here the parameters of the species are not clear. However, unlike the genetic presence of variegated leaves which have been consistently described as forms, the tendencies to proliferation have been treated most frequently as varieties. According to Arber (1934) *Festuca ovina* in a normal sexual form is diploid, but in a type which has never been known to produce flowers is hexaploid. Forms in which proliferation was not altogether complete were intermediate as regards chromosomes (21, triploid, or 28 tetraploid).

Hybridization

On the basis of chromosome morphology and numbers as well as the morphology of the glumes, Flovik (1938) suggested that *Festuca 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 visualized 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 Jenkin 1922) backcrosses with *F. ovina* yielding the seminiferous plant (2n = 21). Jenkin and Thomas (1949) report weak seminiferous hybrids (2n = 42) of *F. ovina* and *F. rubra.* Nanfeldt (1937) criticizes Flovik's hybridization schemes, because the general form and growth habit of *F. vivipara* is not intermediate between the supposed parents.

Poa X *jemtlandica,* in which non-viviparous specimens are not known, is considered to be a hybrid between *P. alpina* and *P. flexuosa. Poa herjedalica* is considered a hybrid between *P. alpina* and *P. pratensis.* Nygren (1949) suggested that the hybridization of forms with different life rhythms might be the origin of vivipary.

Flovik (1938) found *Festuca ovina* from Spitzbergen (2n=49) to have arisen through a cross between *F. rubra* var. *arenaria* (2n=42) and *F. ovina* var. *brevifolia* (2n=28). *F. ovina* var. *vivipara* (2n = 28) from arctic Norway is regarded as having arisen from a cross between *F. rubra* var. *arenaria* (2n = 42) and *F. ovina* (2n = 14). A chromosomal basis for proliferation is also indicated by certain experiments in which spikes with proliferated spikelets occurred as a result of crossing wheats with 28 chromosomes with others having 42 (Biffen and Engledow 1926, according to Arber 1934).

Polyploidy

Turreson (1930, 1931) found that the normal, sexually reproducing *Festuca ovina* in Scandinavia was diploid (2n = 14), whereas the viviparous forms were triploids and tetraploids and in one case hexaploid (2n = 21, 28 or 42). As vivipary was found to be most pronounced in the high polyploid forms Turreson suggested a relationship between polyploidy and vivipary. Flovik (1938) found viviparous *Deschampsia alpina, Festuca ovina* var. *vivipara* and *Poa alpigena* var. *vivipara* to be of allopolyploid origin.

Malformation

It is characteristic of the majority of those proliferating types which are not genetically controlled viviparous races, that they normally produce flower-bearing culms, but occasionally the spikelets in whole or in part of an inflorescence are proliferated. While these proliferations may produce new adult plants they do not inherit any tendency to proliferate under normal conditions.

Mechanical Injury

Sometimes this type of injury is self inflicted, for example if the sheathing leaves are too tight for the rapidly developing inflorescence to free itself. The resulting vegetative anomalies have been described as "contortions" (Martinez C. 1947).

Pathology

Aberrations due to pathological events are numerous and usually are not related to vivipary, proliferation, or phyllody but they may cause changes which mimic them. Some are caused by rusts and smuts. Martinez C. (1945) reported abnormal spikelets in *Bromus unioloides* and *Festuca hieronymi* due to "algun insecto". Similar spikelets are common in *Bromus marginatus* in Wyoming. Molliard (1894) reported abnormal spikelets in *Bromus secalinus* caused by *Phytoptus dubius,* a mite. Martinez C. (1947) reported abnormal spikelets in *Panicum dumissum* parasitized by the pupa of diptera (a fly). Philipson (1937) found the outstanding effects of the nematode *(Anguillina agrostis)* in *Agrostis tenuis* are the unequal elongation of the glumes and the elongation of the lemma. These are only a few examples from a vast literature.

Environment

Viviparous races survive in areas and habitats where moist conditions prevail. Proliferation commonly occurs in autumn when the natural day length is decreasing and especially after a wet summer. According to Wycherley (1954) "humidity for these viviparous races is necessary for the establishment of plantlets, but not for the induction of the phenomenon." In *Deschampsia caespitosa* var. *rhenana* a submerged plant produced only proliferations while neighboring plants which had not been swamped bore flowers and fruit (Arber 1934).

Abrupt changes in environment have been thought to produce vivipary. In *Cynosurus cristatus* after long days had made some progress toward inflorescence initiation short days were applied and resulted in proliferation. In greenhouse to field transplants Wycherley (1954) indicated that insufficient vernalization may be a cause of proliferation.

True Vivipary

An embryo may germinate before the fall of the seed only if there is no dormancy. Pope (1940) induced this type of vivipary in barley by watering. According to Eyster (1931) such uninterrupted growth occurs in corn with defective endosperms. In corn Manglesdorf (1930) found that the tendency to premature germination, starting as early as the milk stage, was inheritable. Arber (1934) cites an example in *Spartina townsendii.* Wycherley (1953) illustrates an example in *Festuca ovina.*

While *Poa sinaica* is closely related to *Poa bulbosa* and produces basal bulbils, the var. *vivipara* of Tackholm from Mt. Sinai is based on "germinating in the panicle" which would indicate the condition of true vivipary.

Annotated Species List

Agropyron cristatum (L.) Gaertn. Reported by Piper (1921).

Agropyron repens. Beauv.

Reported by Wycherley (1954) as "ephemeral" proliferation and not a "viviparous race."

Agrostis alba L. var. *prolifera* Aschers. and Graebn. Syn. Mitteleurop. Fl. 2:174. 1899.
Reported by Duval-Jouve, 1871.

Agrostis alba L. var. *vivipara* Sweet, Hort. Brit. 443. 1826, nom. nud.

Agrostis canina L. var. *vivipara* Peterm. Fl. Lips. 83. 1838. Described from Germany.

Agrostis palustris Huds.
Diseased states caused by infection with *Anguillina agrostis,* (a nematode) have, according to Philipson (1937) been described as *A. polymorpha* var. *vivipara* Trin. Unifl. 200. 1824. and *A. stolonifera* var. vivipara Reichb. Agrost. Germ. 1:13. 1834. Other synonyms include *A. sylvatica* Huds., *A. polymorpha* var. *sylvatica* (Huds.) Gray and *Vilfa alba* var. *sylvatica* (Huds.) Gray

Agrostis stolonifera L.
Reported by Jan. & Wacht. Nederl. Kruidk. Archief 50:113. 1940. as *A. vulgaris* var. *stolonifera* m. *vivipara* and as *A. stolonifera* var. *major* f. *prolifera.*

Agrostis tenuis Sibth.
Agrostis vulgaris var. *vivipara* Reichb. I. Agrost. Germ. 1:12. 1834. Characterized by Philipson, 1937, as a diseased state of *A. tenuis* Sibth.
Philipson (1937) further characterizes the following names as describing *A. tenuis* infected with *Tilletia decipiens:*
Agrostis pumila L. Mant. Pl. 1:31. 1767.
A. polymorpha Huds. var. *pumila* (L.) Huds. Fl. Angl. ed 2. 31. 1778.
A. vulgaris With. var. *pumila* (L.) Pers. Syn. Pl. 1:75. 1805.
A. laxa Gray var. *pumila* Gray, Nat. Arr. Brit. Pl. 2:148, 1821
A. tenuis var. *pumila* (L.) Druce, List. Brit. Pl. 79. 1908.
A. capillaris Huds. var. *pumila* (L.) Druce, Fl. Oxfordsh. Ed. 2. 474. 1927.
Other synonymy of *A. tenuis* Sibth included:
A. vulgaris var. *vivipara* Spenner, Fl. Friburg 1:93. 1825, from Germany.
A. vulgaris var. *vivipara* Opiz, Sezn. Rostl. Ceske 12. 1852, from Czechoslovakia.
A. vulgaris var. *vivipara* Parl. Fl. Ital. 1:183. 1848. from Italy.
A. vulgaris var. *vivipara* St. Lager, in Cariot, Etude des fleurs ed. 8. 2:902. 1889, from France.

Alopecurus pratensis L.
Reported by Wycherley (1954) as "ephemeral " proliferation and not a viviparous race."

Arrhenatherum avenaceum Beauv.
Mentioned by Arber (1934) cf. page 385 and reported by Wycherley, 1954, as "ephemeral " proliferation and not a "viviparous race."

Avena sativa L.
Reported by Duval-Jouve, 1871, and Nielsen (1941).

Briza subaristata Lam.
An example of "filodia" is reported by Martinez C. (1944).

Bromus inermis Leyss f. *proliferus* Louis-Marie, Rev. d'Oka 14:144. 1940. Also reported by Nielsen (1941).

Bromus macranthus Desv.
An example of "filodia" is reported by Martinez C. (1944).

Bromus purgans L.
Reported by Nielsen (1941).

Bromus unioloides (Willd.) HBK)
Martinez (1945) reports malformation due to "algus insecto."

Coix lachryma-jobi L.
Normally producing a spathe below the inflorescence, but in some cultivars this leaf-like structure is completely reformed above the maturing female.

Cynosurus cristatus L.
var. *viviparus* Koel., Descr. Gram. 373. 1802.
var. *viviparus* S.F. Gray, Nat. Arr. Brit. Pl. 2:126. 1821.
var. *viviparus* Gus. Fl. Sic. Prodr. 1:88. 1927.
var. *viviparus* Lojac. Fl. Sicul. 3:333. 1909.
Reported by Wycherley (1954) as "ephemeral " and not a "viviprous race" and more frequent in autumn. Wycherley (1952) applied "short-day treatment" which resulted in a strong proliferation of the fertile spikelets also. Arber (1934) reports "In *Cynosurus cristatus* L. I have seen *** the sterile spikelets, which constantly accompany those that are fertile, may be prolonged so as to bear numerous leaves; in the spikelet drawn there were twenty-six. This sample from the Dog's-tail-grass, since it affects spikelets which are sterile even in the normal spike, indicates that spikelet-proliferation falls into place as a further stage in that sterilization process which we have already noticed in the normal reproductive shoot in the Gramineae. A special vegetative development in the inflorescence, which I have called the 'bouquet' abnormality, can also be illustrated from the Dog's-tail-grass; in this form, lateral axes, which are more or less naked, terminate in tufts of spikelets."

Cynosurus echinatus L.
Martinez C. (1945) reported "numerous casos de filodia de glumelas" in this annual. Penzig (1922) "anota casos de filodia para esta especie (sub *viviparidad).*

Cynosurus elegans Desv. var. *viviparus* Lojac, Fl. Sicul. 3:334. 1909. Described from Sicily.

Dactylis glomerata L.
f.m. *vivipara* Lange, Bot. Tidsskr. 188. 1877-1879, nom. nud., from Denmark.
var. *vivipara* Parl. Fl. Ital. 1:459. 1848, from Italy.
Martinez C. (1947), reported both "filodia y proliferation."
Arber (1934) reported the 'bouquet' effect. Wycherley (1954) reported an example as "ephemeral" and not a "viviparous race."

Deschampsia alpina (L.) R. & S.
According to Lawrence (1945) "another close relative of *D. caespitosa* is *D. alpina* (L.) R. & S., which differs in being viviparous and in occupying an ecologic zone to the north of *caespitosa.* *** is a hexaploid *** The high polyploidy and variation in chromonumber observed in *alpina* is characteristic of species that propagate asexually." *D. alpina* is of allopolyploid origin according to Flovik (1938).

D. caespitosa (L.) Beauv.
This species is characterized as non-viviparous by Lawrence (1945) but Nygren (1949) caused proliferation of spikelets in normal seminiferous *Deschampsia caespitosa* (L.) Beauv by shortday treatment. Both var. *pseudalpina* (Syme) Druce described in 1888 and var. *rhenana Gren.* described in 1872 have been used in reference to viviparous forms. Also reported by Duval-Jouve (1871).

Deschampsia caespitosa var. *vivipara* S.F. Gray, Nat. Arr. Brit. Pl. 2: 137. 1821 described from Great Britain.

Deschampsia caespitsa var. *vivipara* Opiz, Sezn. Rostl. Ceske 37. 1852. nomen; Cheval. Fl. Envir. Paris ed. 2:806, 1861, described from France.

Deschampsia flexuosa (L.) Trin.
Stahlin (1929) found viviparous and non-viviparous plants to have the same chromosome number, 2n = 28.

Eleusine indica (L.) Gaertn.
Martinez Crovetto (1945) reports "filodia."

Eragrostis brizoides (L.f.) Nees
Bews (1918) illustrates (Fig. 23) *E. brizoides* showing vivipary which he says was common in several kinds of grasses during the wet season of 1917 in Africa.

Eragrostis capensis (Thumb.) Trin.

Eragrostis prolifera (Sw.) Steud.
A North American grass common on subtropical sandy beaches, the branches often fascicled, or developing extensive stolons with tufts of branches, suggesting the name "prolifera," the spikelets, however, apparently do not proliferate.

Eragrostis virescens Presl.
Martinez C. (1945) found an example of "filodia de las glumelas."

Festuca alpina Suter. var. *prolifera* Schur. Enum. Fl. Transsilv. 785. 1866. Described in Rumania.

Festuca arundinacea L. f. m. *vivipara* Junge, Jahrb. Hamburg Wissenschaft Anstalt 22: Beih. 3, 66. 1905.
Described from Austria.

Festuca durisuscula var. *vivipara* Opiz, Lotus 3:182. 1853, nomen. Described from Austria.

Festuca fuegiana Hook. f. forma *vivipara* Hack. Engl. Bot. Jahrb. 6:247. 1885.

Festuca hieronymi Hack.
Martinez C. (1945) reports a malformation due to "algun insecto."

Festuca obtusa Spreng.
Reported by Nielsen, 1941.

Festuca purpurascens Banks et Sol.
Martinez C. (1945) reports an example of "filodia."

Festuca ovina L.
See discussions under *Festuca vivipara* and *Festuca rubra.*

Festuca rubra L.

Flovik (1938) says viviparous *Festuca ovina* (2 n = 49) from Spitsbergen arose through a cross between *Festuca rubra* var. *arenaria* (2 n = 42) and *F. ovina* var. *brevifolia* (2 n = 28) *Festuca ovina* var. *vivipara* (2 n = 28) from arctic Norway is a cross between *F. rubra* var. *arenaria* (2 n = 42) and *F. ovina* (2 n = 14).

Names used for viviparous *F. rubra* include:

Festuca rubra prolifera Piper, Contrib. U.S Nat. Herb. 10:21. 1906.

F. rubra var. *prolifera* Piper, in Robinson, Rhodora 10:65. 1908.

F. prolifera (Piper) Fernald, Rhodora 35:133. 1933.

F. rubra var. *subvillosa* f. *vivipara* Eames, Rhodora 11:89. 1909.

F. rubra var. vivipara S.F. Gray, Nat. Arr. Brit. Pl. 2:122. 1821.

F. rubra var. *vivipara* Bluff & Nees, Consp. Fl. Germ. ed. 2. 1:179. 1836, nomen.

Wycherley (1954) reports an example of "ephemeral" proliferation and not a "viviparous race."

Festuca vivipara (L.) Sm. Fl. Brit. 1:114. 1800.

Festuca vivipara was first described by Ray (1690) in Synopsis Methodica Brittanicarum. London) as "spica foliacea."

According to Wycherley (1953) in Great Britain "the viviparous fescues are a group of asexually reproducing forms restricted in range by their method of propagation. It is useful ecologically and systematically to include all under one specific name." Turreson (1926, 1930, and 1931) found seminiferous amphimicts, viviparous apomicts, and intermediates he called ampho- apomicts. Howarth (1948) found vivipary in all known varieties of *F. tenuifolia* and *F. ovina* as well as in *F. longifolia* var. *genuina*. As Wycherley (1953) says, "the origin of *F. vivipara* is unknown, but its variation is certain." Flovik (1938) suggested that the different forms of *Festuca vivipara* are products of crossing between *F. rubra* and *F. Ovina* and therefore of allopolyploid origin.

The very complicated synonymy of these viviparous races including the following names:

F. ovina var. *vivipara* L. Sp. Pl. 73. 1753; ed. 2. 1:108. 1762.

F. ovina var. *vivipara* Huds. Fl. Angl. 36. 1762.

F. vivipara Hornem, Fl. Dan. 12 (fasc. 35); pl. 2043. 1832.

F. ovina var. *vivipara* (Smith) Reichenb. Icon. Fl. Germ. Helv. 1:25. 1834.

F. ovina var. *vivipara* Hartm. Handb. Skand. Fl. ed. 4. 37. 1834.

F. ovina var. *vivipara* (Smith) Bab. Man. Brit. Bot. 372. 1843.

F. ovina var. *vivipara* (Hornem) Blytt, Norgess Fl. 143. 1861.

F. supina var. *vivipara* (L.) Richt. Pl. Eur. 1:93. 1890.

F. ovina subsp. *eu-ovina* var. *supina* subvar. *vivipara* Hack.

F. vivipara (L.) Sm. var. *hirsuta* (Lge.) Schd. in Devold & Schol. Fl. Pl. and Ferns of Southeast Greenland 140. 1933.

Festuca tenuifolia Sibth (including *F. capillata* Lam.)

Festuca trachyphylla (Hack.) Kruj. (including *F. longifolia* Thuill.)

F. longifolia var. *trachyphylla* (Hack.) Howarth

F. ovina var. *duriuscula* subvar. *trachyphylla* Hack.

F. tenuifolia Sibth. var. *vivipara* (Smith) Ducomm. Taschenb.

Hierochloe alpina R. & S. var. *vivipara* Scheutz ex Fedtsch. Bull Jard. Bot. Pierre le Grand 14 (Suppl. 2): 47. 1915, nomen.

Described from Russia.

Ichnanthus pallens (Sw.) Munro

Described by Fournier as "*Panicum schlechtendalii monstrosum*" in Mex. Pl. 2: 31. 1886. Martinez (1945) reports the same occurrence, a multiplication of glumes and lemmas to give the appearance of species of *Eragrostis*, rather than the typical species of *Ichnanthus* with a single fertile floret.

Koeleria cristata (L.) Pers. var. *vivipara* Opiz, Seznam 56. 1852. nomen; Holuby, Oesteer. Bot. Zeitschr. 22:79. 1872.

Koeleria glauca var. *typica* f. *vivipara* Domin, Bibl. Bot. 65:56. 1907.

Koeleria gracilis f. *vivipara* Domin, Bibl. Bot. 65:181. pl. 2.f.7. 1907.

Koeleria phleoides (Vill.) Pers.

According to Martinez C. (1947) a case of "filodia."

Koeleria pyramidata (Lam. Domin, f. *vivipara* Domin. Bibl. Bot. 65:145. 1907.

Lolium multiflorum Lam.

According to Martinez (1947) "contorsion en el raquis y proliferacion y filodia en las espiguillas con diferentes grados de intensidad."

Lolium perenne L.f. *vivipara* Junge, Jahrb. Hamb. Wiss. Aust. 22 (Beih. 3): 68. 1905, without description, cf. *f. viviparum* Koch, Syn. ed. 2:956. 1844.

Also treated as a variety as follows:

var. *viviparum* Hein, Graeserfl. 136. 1877, from Europe.

var. *viviparum* Mutel, Fl. Franc. 4:139. 1837, from France.

var. *viviparum* S.F. Gray, Nat. Arr. Brit. Pl. 2:93. 1821, from Gt. Britain.

Wycherley, 1954, reports "ephemeral" proliferation, not a viviparous race; cf. Jenkin, 1922.

Melica papilionaceae L.

Martinez C. (1945) reports "proliferation" and "tendenacia a la filodia."

Molinia coerulea var. *vivipara* Boenn. Prodr. Fl. Monas 28. 1824.

Also treated as a variety as follows:

var. *vivipara* Blytt, Norges Flora 140. 1861.

var. *vivipara* Merino, Fl. Descr. Illustr. Galicia 3:319. 1909.

Panicum antidotale Retz.

The synonymy of this species includes *Panicum proliferum* Lam. Tabl. Encycl. 4:747. 1798.

Panicum demissum Trin.

Martinez (1947) reports injury by dipterous flies.

Panicum virgatum L.

Reported by Nielsen (1941).

Panicum viviparum Schumach. Beskr. Guin. Pl. 82. 1827. from Guinea, Africa.

Panicum viviparum Nees ex Steud. Syn. Pl. Glum. 1:97. 1854. also from Guinea, Africa.

Panicum viviparum Nees, Linnaea 8:57. 1883, in obs.

Paspalum proliferum Arech. Anal. Mus. Nax. Montevideo 1:63. 1894. Described from Uruguay.

Phalaris vivipara Pacluc. Fl. Marchig. 19. 1891, in syn of *P. brachystachys* Link.

Phleum boehmeri (L.) Wiebel var. *vivipara* Schur, Oestr. Bot.

Zeitschr. 9":5/ 1859. refers to a var. of *Phleum phleoides* (L.) Karst.

Phleum pratense L. f. *monstrosae*

Phleum pratense L. f. *proliferium* Waisb. Magyar Bot. Lapok 4:66. 1905.

Arber (1934) found timothy "near Cambridge, where these leafy 'spikes' are developed season after season; I have found them here in eight different years. The best time to look for them is between September and December. They illustrate the conservation of the outer empty glumes, which retain their normal character with sharing in the proliferation," (see page 385). Evans (1927) illustrated three types of proliferation (1) "proliferating florets, each having one bract enlarged to resemble a leaf. Either the pistil or stamens, or both are usually present." (2) Proliferous shoots, capable of developing directly into plants. In a proliferation of this type there are several leaflife parts, but no pistil or stamens." and (3) "spikelets with elongated rachilla."

Phleum pratense var. *vivipara* Schur, Oestr. Bot. Zeitschr. 9:15. 1859. from Rumania.

Phleum pratense var. *viviparum* S.F. Gray, Nat. Arr. Brit. Pl. 2:139. 1821, from Britton.

Phleum pratense f. *viviparum* (S.F. Gray) Louis-Marie, Rev. d'Oka. 14:144. f. 10, no. 3. 1940.

According to Wycherley (1945) vivipary in *Phleum pratense* is "ephemeral" and not leading to a "viviparous race." Martinez C. (1945) describes a "torsion de la inflorescencia." Vivipary in *Phleum* is reported by Tourney (1891) and Nielsen (1941).

Poa

The sections suggested for *Poa* have not always been totally natural. For example *Poa annua* clearly does not belong in the # Annuae but in the # Pratenses with *Poa pratensis*. Nevertheless there appears to be a certain amount of natural grouping into sections of the viviparous species of *Poa*. These species have been treated variously in either # Pratenses (# Stoloniferae), # Palustres, or # alpinae.

P. alpigena (Fries) Lindm.

var. *colpodea* Th. Fries) Scholand. Vasc. pl. Svalb 89. 1934.

var. *vivipara* (Malmgr.) Scholand. Skriftom Svalbard og Ishavet 62: 88 f. 42. 1934.

Poa stricta subsp. *colpodea* Th. Fries in Ofvers. Vet. Ak. 26:138. 1869.

Poa alpigena f. *vivipara* Malmgr. Ofvers. Vet. Ak. Forhandl.

Poa alpigena var. *vivipara* Hulten, Acta Univ. Lund. n. ser. 38: 198. 1942, from Norway.

Poa arctica var. *vivipara* (Malmgr.) Schol. ex Flovk, Hereditas 24: 24:516. 1938.

Poa alpigena var. *vivipara* is of allopolyploid origin according to Flovik (1938).

Poa alpina L.
Poa bulbosa L. var. *alpina* Ascherson, Fl. Brand. 1:845. 1864.
Poa alpina var. *vivipara* L. Sp. Pl. 67. 1753, from Switzerland.
Poa vivipara (L.) Willd. Enum. Pl. Hort. Berol. 105. 1809.
Poa alpina var. *vivipara* (L.) S.F. Gray, Nat. Arriv. Brit. Pl. 2:105. 1821, based on "*Poa vivipara* L." which was never described.
Poa alpina f. *vivipara* L. Sp. Pl. ed. W, In. p. 386, cf. Arber, 1934, page 385; cf. also Goebel, 1905.
Poa alpina var. *vivipara* Bluff. Nees, Comp. Fl. Germ. ed. 2. 1:159. 1836.
Poa alpina var. *vivipara* Parnell, Grasses Brit. 212. pl. 94. 1845.
Poa alpina vivipara (Willd.) Scribn. & Merr. Contr. U.S. Nat. Herb. 13:68. 1910.
In East Greeland this plant is common on solifluction soils (Bocher et al. 1968) and common along the entire Scandinavian mountain range (Nygren 1950).
This plant was described in preLinnaean literature by Schuechzer (1719). Stahlin (1929) found viviparous and non-viviparous plants to have the same chromosome number, 2 n - 42, but Nygren (1949) found varying numbers for both, between 31 and 57. For details on this species refer to Zollikofer (1930).

Poa annua L. var. *vivipara* S.F. Gray, Nat. Arr. Brit. Pl. 2:106. 1821.

Poa annua L. var. *vivipara* Mutel, Fl. France 4:72. 1837

Poa arctica R.B.
P. arctica var. *stricta* (Lind.) Nannfeldt is viviparous according to Nygren (1950).
P. arctica var. *vivipara* Hooker, Fl. Bor. Amer. 2:246. 1840. cf. Hooker in Parry, Jour. Third. Voy. 206. 1826, nomen.
Poa arctica is very polymorphous in Scandinavia with chromosome numbers from 39 to 92.

Poa bulbosa L.
Poa bulbosa var. *vivipara* Koel. Descr. Gram. in Gallia et Germania 189. 1802.
Paneion bulbosum var. *viviparum* (Koch.) Lunell, Amer. Midl. Nat. 4:222. 1915.
Poa bulbosa var. *vivipara* Koch. Fl. Syn. Germ. et. Helv. 802. 1837.
Poa prolifera Schmidt in Mayer, Samml. Phys. Aufs. 1:188. 1791.
Poa crispa Thuill. La Flore des environs de Paris. ed. II., 45. 1799.
Poa bulbosa spp. *adulterina* Aschers. & Graebn. Syn. Mitteleur. Fl. 2:392. 1900.

P. bulbosa
var. *badensis* (Haenke) Aschers. Fl. Brand. 1:845. 1864. based on *Poa badensis* Haenke, Baden, Austria.
subsp. *badensis* var. *gelida* (Schur) Achtaroff, Isv. Bulg. Bot. Drush. (Bull. Soc. Bot. Bulgaria) 8:128. 1959.
var. *calciola* Schur, Snum. Pl. Transsilv. 772. 1866. (from Rumania).
spp. *concinna* Gaudin) Douin in Bonn. Fl. Compl. 12:29. 1927-1932. based on *Poa concinna* Gaudin (Switzerland) also Hayek, Repert. Sp. Nov. Fedde Beih. 50: 260. 1932.
ssp. *eubulbosa* var. *concinna* (Gaud.) Hayek, Fl. Balk. 3:260. 1932.
var. *concinna* (Gaudin) Beck, Fl. Nieder-Osterr. 1:82. 1890.
spp. *concinna* var. *thessala* (Boiss. et Orph.) Achtaroff, Izv. Bulg. Bot. Druzh. (Bull. Soc. Bot. Bulgarie) 8: 129. 1939. Based on P. *thesala* Boiss. et.Orph. in Boiss, Diagn. 2. IV., p. 135., *P. pumila* Host var. *thessala* (Boiss. et. Orph.) Fl. Or., p. 605.
ssp. *debilis* Velen. Fl. Bulg. Suppl. 1:300. 1898. (Bulgaria)
var. *erubescens* Schur, Enum. Pl. Transsilv. 772. 1886. (Rumania)
ssp. *eu-bulbosa* Hayek, Fl. Balk 3:359. 1932.
var. *typica* Flori, Nuov. Fl. Anal. Ital. 1:128. 1923.
ssp. *eubulbosa* var. *brizaeformis* Trab. in Batt. & Traub. Fl Alg. 207. 1895.
P. psammophila Schur. Enum. Transs. p. 773. 1866.
P. bulbosa var. *psammophila* (Schur) Asch. & Graebn. Syn. Mitteleur. Fl. 2:393. 1900. (Rumania)

Poa badensis Haenke spp. *psammophila* (Schur) Nyar, Bulet. Grad. Bot. Cluj 11:40. 1951.

Poa bulbosa
var. glabriflora Roshev. in Fedtsch. Fl. Turkm. 1:143. 1932, in Russian.
ssp. *leucoglossa* Velen. Fl. Bulg. Supply. 1:300. 1898. (Bulgaria)
var. *normalis* Trautv. Acta Hort. Petrop. 7:524. 1881. (Russia)
var. *nuda* Somm. & Lev. Acta Hort. Petrop. 16:452. 1900. (Russia)
var. *praecox* (Borb.) Richt. Fl. Eur. 1:85. 1890.
Based on *Poa praecox* Borb. Oesterr. Bot. Zeitschur. 28:135. 1878.
var. *prolifera* K. Gmel. Fl. Badens. 1:194. 1805 (Germany)
var. *prolifera* Schur, Enum. Pl. Transsilv. 772. 1866 (Czechoslovakia)
ssp. *pseudoconcinna* (Schur) Domina, Acta Bot. Bohem. 11:31. 1936.
Based on *P. pseudo-concinna* Schur. Enum. Transsilv. 773. 1866.
var. *pseudoconcinna* (Schur) Beck, Wiss. Mitt. Bosn. Herzog 9:444. 1904.

Poa bulbosa Rasse II. *pseudoconcinna* (Schur.) Aschers. & Graebn. Sym. Fl. 2:392. 1900, based on *P. pseudoconcinna* seu. *P. protuberata* Schur
Poa bulbosa ssp. *timoleontis* (Heldr.) Bornm. Beih. Bot. Centralbl. Abt. II. 26:437. 1910. Based on *P. timoleontis* Heldr. (Greece)
var. *umbrosa* Schur, Enum. Pl. Transsilv. 772. 1866 (Rumania)
var. *verticillata* Coss. & Germ. Fl. Env. Paris 2:642. 1845. (France)
var. *vivipara* Koel. Descr. Gram. 189. 1802. (Europe)
(same combination made many other times but all of later date)
In pre-Linnaean literature *Poa bulbosa* var. *vivipara* was described by Bauhin (1620), by Tournefort (1700) and by Scheuchzer (1719). Akerberg (1942) gives the chromosome numbers of *Poa bulbosa* (seminiferous) as 2n = 28 and 45. Tutin (1952) mentions for the viviparous plant 2 n = 35. When normal lemmas are pubescent their proliferated counterparts may be glabrous.

Poa cusickii Vasey
Herbarium specimen seen; probably insect damage.

Poa herjedalica H. Smith, Veg. Utvecklingshist. Centralsvensk. (Norrland-sktHandbibl. 9): 150. 1920. From Sweden.
According to Nygren (1950) "the hybrid between *Poa alpina* and *Poa pratensis alpigena*, named *Poa herjedalica* by Smith in 1920, plays a rather great role in the plant communities of the northern Scandinavian mountain range. ********* three different complexes of viviparous *Poa* forms occur in the Scandinavian mountains. For the first, the complex of viviparous *Poa alpina,* for the second that of the viviparous *Poa pratensis alpigena,* and for the third that of *Poa herjedalica* which bridges the two other complexes, by which all three complexes form a long series with transitional forms."

Poa iridifolia Hauman, Anal. Mus. Nac. Hist. Nat. Buenos Aires 29:407. pl. 1. 1917.
A case of "filodia" reported by Martinez C. (1945)

Poa jemtlandica (Almq.) Richt. Pl. Eur. 1:84. 1890.
P. alpina subsp. *jemtlandica* Almq. Bot. Centralb. 14:320. 1883.
According to Nygren (1950) "up to now a single hybrid combination is known for *Poa laxa flexuosa,* viz. the hybrid *Poa alpina vivipara* which occurs in Scandinavia as well as in Scotland, but which has not hitherto been found on Iceland. For many reasons this hybrid is assumed to have originated only once, and therefore it must be supposed to be very old (cf. Smith, 1920, Nannfeldt, 1937). *P. jemtlandica* is morphologically uniform all over its entire distribution area and has the chromosome number 2 n = 37 in Scandinavia, which means that a reduced female gamete with 21 chromosomes from *flexuosa* should have fused with a male gamete with 16 chromosomes from viviparous *alpina."*

Poa laxa Haenke var. *flexuosa* (Smith) Hartm. Handb. Skand. Fl. 57. 1820.
Said to be one of the parents of the hybrid *P. jemtlandica*

Poa laxa Haenke var. *vivipara* S.F. Gray, Nat. Arr. Brit. Pl. 2:106. 1821.

Poa laxa Henke var. *vivipara* Anderss. Fl. Scand. Gram. 45. 1852.

Poa pratensis L.
var. *alpigena* Blytt. Norgas Fl. 130. 1861.
According to Nygren (1950) viviparous races occur.
var. *colpodea* (Th.Fr.) Schol. based on *Poa colpodea* T. Fries. Ofv. Svensk. Vet. Akad. Förh. 26: 138. 1869. A viviparous plant with 2 n - 35 or 35 plus 4, occurs in Greenland (Bocher et al. 1968.)
var. *prolifera* Ostenf. Meddel. Grland 64:197. 1923. nomen. cf. Ostenf. op. cit. 68:9. 1926.
var. *vivipara* Huds. Fl. Angl. ed. 2. 39. 1778, from Wales.

Poa sinaica Steud.
P. sinaica var. *vivipara* V. Tackh. in V. & G. Tackholm, Flora of Egypt, Egypt. Univ. Faculty Sci. Bull. no. 17: 172. 1941.
"spikelets violet-flushed (in type green) germinating in the panicle (in type not)."

Poa sublanata Reverd.
A variety *vivipara* Tzvel. was described in 1964.

Poa tolmatchewii Roshev.
The variety *stricta* (Lindeb.) Tzvel. includes as snynonyms *P. arctica* ssp. *stricta* (Lindeb.) Nannf., *P. artica* var. *stricta* (Lindeb.) Hyl., *P.*

stricta Lindeb. and *P. artica* var. *vivipara* auct.

Poa trivialis L.

According to Wycherley (1954) who quotes Jenkin (1922), prolifery observed "in greenhouse or experimental conditions" and therefore "ephemeral" and not leading to a "viviparous race ."

Scleropogon brevifolius Phil.

Herbarium specimen seen, probably a case of insect damage.

Sorghum

Arber (1934) reports Laude, H.H. and F.C. Gates (1929): "one of the extremest instances of proliferation, which have been described, is a sterile head of *Sorghum*, in which the lower spikelet of each pair bore, in succession to the outer glumes, a series of as many as 28 to 41 scale-leaves closely inserted on the spikelet axis."

Zea mays L.

According to Eyster (1931) "vivipary, the continuous development of the sporophyte in maise, is determined by genetic factors and is strongly influenced in its expression by environmental factors." He says further that "vivipary is regarded as a primitive plant character which, by the interaction of genetic factors and unfavorable growth conditions, may be inhibited," leading to the advanced character dormancy which enables survival through unfavorable growth conditions.

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