

PSEUDO-VIVIPARY IN FUEGIAN AND FALKLAND ISLANDS GRASSES

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ABSTRACT. Pseudo-vivipary is present in natural populations of four grass species occurring at high latitudes in southern South America. In *Festuca subantarctica* Parodi and *Poa alopecurus* (Gaudich.) Kunth ssp. *fuegiana* (Hook. f.) Moore and Doggett, **comb. nov.** the axis of the spikelet undergoes metamorphosis into the leafy shoot of the propagule, while in *Poa robusta* Steudel and *Agrostis canina* L. var. *falklandica* (Hook. f.) Hack. this is derived by elongation of the lemma. In the first three species pseudo-vivipary is a constant feature of the reproductive system, but it appears to be rare in *Agrostis canina*. Completely or partly pseudo-viviparous plants are largely confined to the higher rainfall areas of south and west Fuego-Patagonia and at higher elevations there and in the Falkland Islands. *Poa fuegiana* (Hook. f.) Hack. ex Dusén and *P. pogonantha* Franchet are shown to represent pseudo-viviparous facies of the widespread austral species *Poa alopecurus*, whilst it is suggested that pseudo-viviparous populations referred to *Festuca subantarctica* are conspecific with the central and southern Chilean species *F. monticola* Phil. ex Hook. & Arceuthobium.

Vegetative proliferation of spikelets has been shown to be induced by abnormal environmental conditions in normally sexual inflorescences of *Agrostis flavidula* Steudel.

ASEXUAL reproduction by means of vegetative propagules which replace part or all of the inflorescence is known in several angiosperm genera, especially among species such as *Polygonum viviparum*, *Saxifraga foliolosa*, *Cardamine bulbifera*, *Saxifraga cernua*, *Allium carinatum* and *A. oleraceum*, which occur at higher latitudes and elevations in the Northern Hemisphere. Such pseudo-vivipary is particularly frequent among grasses belonging to the genera *Deschampsia*, *Poa* and *Festuca*, in which it has been shown to be correlated with their distribution in the recently glaciated areas of the Northern Hemisphere (Nannfeldt, 1940; Nygren, 1949; Wycherley, 1953a). Several workers (e.g. Jenkin, 1922; Philipson, 1934; Muntzing, 1940; Nygren, 1950; Wycherley, 1953b) have demonstrated the heritability of pseudo-vivipary in many species in which it is a constant feature of the reproductive system. However, Philipson (1935), Nygren (1949) and Wycherley (1953b) have shown that in such species as *Agrostis sylvatica* Huds., *A. canina* L., *A. pumila* L. and *Deschampsia caespitosa* (L.) P. Beauv. the condition can also be induced in normally sexual plants by exposure to short-day treatment or as a result of parasite attack, and it sometimes arises late in the flowering season to give asexual "late-season inflorescences".

In those species in which pseudo-vivipary is a constant feature of their reproduction the propagules have been shown to arise in two principal ways (Philipson, 1934; Wycherley, 1953b; Hubbard, 1968). Thus, in *Deschampsia caespitosa* the lemma may elongate to form the first leaf of the propagule, while in *Festuca ovina* L., *Poa alpina* L. and *P. bulbosa* L., for example, the axis of the spikelet is transformed into the leafy shoot. In some cases, such as *Deschampsia alpina* Roem. & Schult. and *Phleum pratense* L., both modes of propagule development have been found in a single plant.

Pseudo-vivipary has long been known in some grasses occurring at higher latitudes in the Southern Hemisphere, and the presence of proliferating spikelets in all or part of the inflorescence was noted in the original descriptions of the southern South American species *Poa fuegiana* (Hook. f.) Hack. ex Dusén, *P. pogonantha* Franchet and *Festuca subantarctica* Parodi. Whilst revising several groups of grasses in connection with our studies on the flora of Tierra del Fuego we have gathered together information from the literature and, particularly, from our own collections and field observations on the occurrence of pseudo-vivipary. This has been undertaken for three principal reasons. First, we wished to see whether the occurrence of pseudo-viviparous populations could be related to specific environmental parameters, as has been demonstrated in the Northern Hemisphere. Secondly, we wished to determine what floral modifications were involved in giving rise to the asexual proliferating spikelets, and whether these conformed to the patterns already known from North America and Eurasia. Thirdly, we were concerned to see to what extent the abnormal development of the diagnostically important features of the floret and spikelet as a result of pseudo-vivipary had given rise to taxonomic confusion.

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RESULTS AND DISCUSSION

*Pseudo-vivipary in natural populations**Poa fuegiana*, *P. pogonantha* and *P. alopecurus*

The most commonly occurring pseudo-viviparous grass in Tierra del Fuego and southern West Patagonia has been referred to *Poa fuegiana* (Hook. f.) Hack. ex Dusén. It is a rather variable taxon in which some or, usually, all of the spikelets may proliferate. The axis of the spikelet undergoes metamorphosis to give the leafy shoot of the propagule (Fig. 1a), in addition to which it normally bears two or more florets at the base. In no case have these basal florets been found to contain seeds and they seem to be normally sterile. The lower floret most frequently contains an underdeveloped ovary; less commonly (16 per cent of examples studied) the florets bear elongated, slender anthers. The ovaries or anthers are rudimentary or absent in the upper florets. The palea is reduced or, in the uppermost floret, rudimentary. The uppermost lemma is elongated to enclose the modified spikelet axis, which is very compact and bears leaves which may have a small ligule, do not subtend florets and are not spaced along the rachilla.

These plants show very close affinities with the widespread, austral, dioecious species *Poa alopecurus* (Gaudich.) Kunth. A detailed comparison of a wide range of characters has revealed differences between the two taxa in only three characters. Thus, in *P. fuegiana* the glumes, the lemma (of the basal floret) and the panicle tend to be slightly larger than in *P. alopecurus* (Fig. 2). Similar differences in these characters are shown between pseudo-viviparous and sexual plants undoubtedly belonging to the same species (see e.g. *Poa robusta*, p. 107). In consequence there seems to be no reason to maintain *P. fuegiana* and *P. alopecurus* as distinct species. From Fig. 3 it can be seen that the pseudo-viviparous populations have a generally more southerly and westerly distribution than the sexual populations, being largely restricted to the areas of higher rainfall. Because of the modally distinct morphological differences, resulting from the different patterns of reproduction, and the generally different

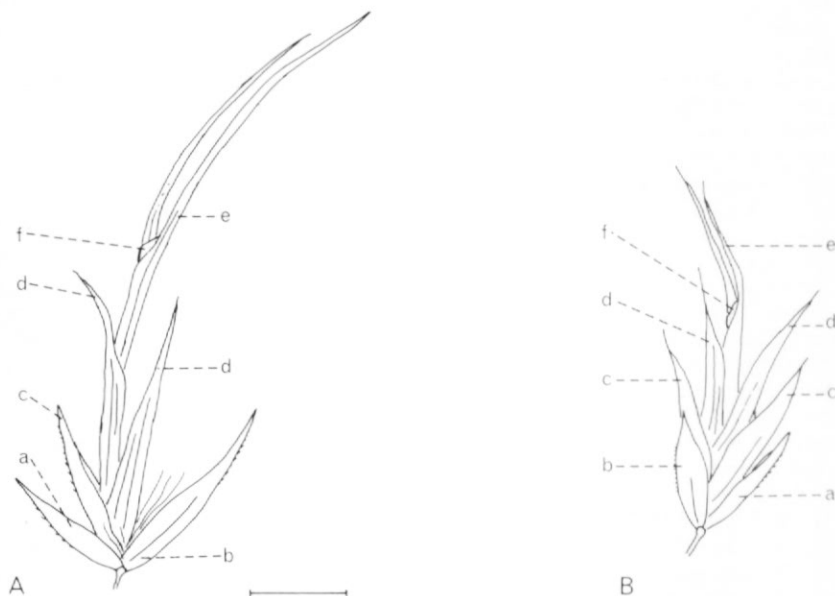


Fig. 1. Pseudo-viviparous spikelets of (A) *Poa alopecurus* ssp. *fuegiana* and (B) *Festuca subantarctica*. a, lower glume; b, upper glume; c, floret; d, elongated lemma; e, propagule lamina (metamorphosed spikelet axis); f, ligule. Scale = 5 mm.

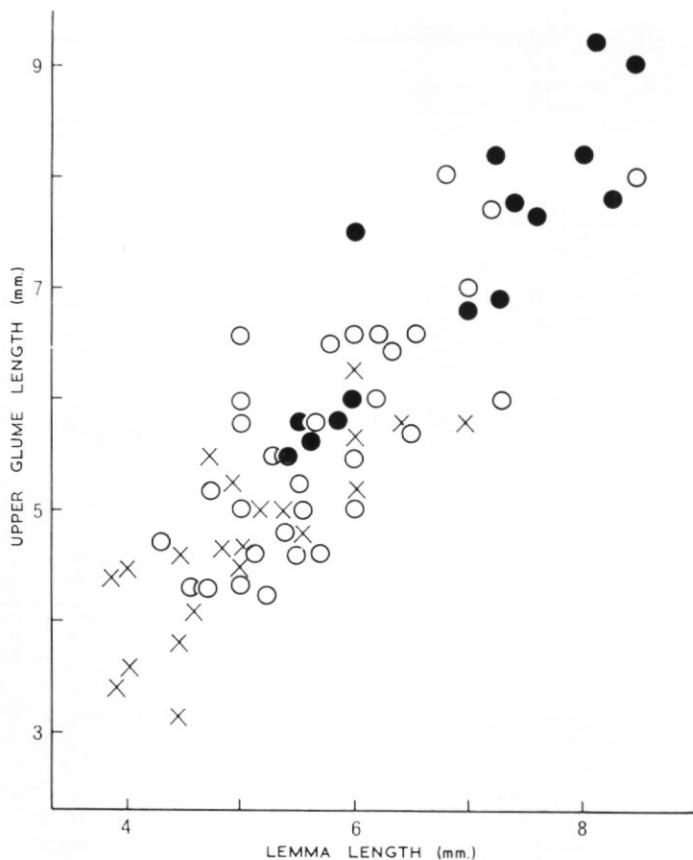


Fig. 2. Length of lemma and upper glume in *Poa alopecurus* ssp. *alopecurus* (○ female; × male) and ssp. *fuegiana* (● pseudo-viviparous).

geographical distributions, it seems appropriate to recognize the pseudo-viviparous populations as a subspecies within *P. alopecurus*. The necessary formal combination is as follows:

***Poa alopecurus* (Gaudich.) Kunth ssp. *fuegiana* (Hook. f.) D. M. Moore and M. Doggett, comb. nov.**

Festuca fuegiana Hook. f., *Fl. Antarct.*, 1, Pt. 2, 380, t. 141 (1847).

F. pogonantha Franchet, *Mission scient. Cap Horn*, 5, 387, t. 10 (1889).

Poa fuegiana (Hook. f.) Hack. ex Dusén, *Wiss. Ergebn. schwed. Exped. Magellänsland*, 3, Lief. 5, 225 (1900).

P. pogonantha (Franchet) Parodi, *Revta argent. Agron.*, 20, No. 4, 180 (1953).

Poa pogonantha (Franchet) Parodi was described, under *Festuca*, from a collection made by Savatier at Puerto Edén, Isla Wellington, prov. Magallanes, Chile, and has subsequently been reported from two collections in the mountains behind Ushuaia along the Canal de Beagle (Alboff, 1896). It is recorded as being usually female, rarely pseudo-viviparous, and is said to be more slender than *Poa fuegiana*, with a laxer panicle and always with two fertile florets in the spikelet. None of these characters provides any clear separation from the *Poa alopecurus*-*P. fuegiana* complex and *P. pogonantha* evidently comprises partially pseudo-viviparous plants which are the expected reproductive intermediates between *P. alopecurus* ssp. *alopecurus* and ssp. *fuegiana*. In view of the very sporadic occurrence of such plants, it

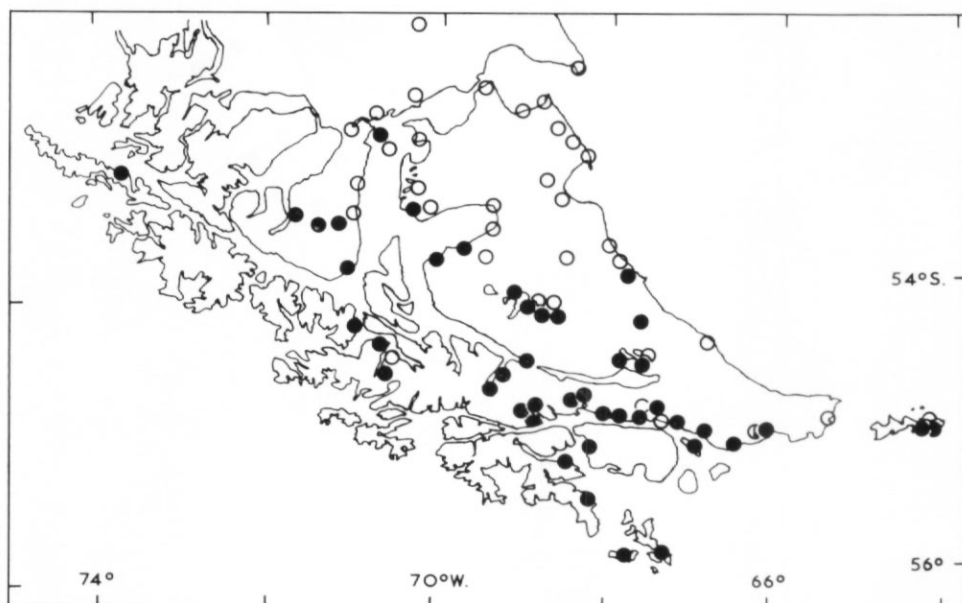


Fig. 3. Distribution in Tierra del Fuego and adjacent Patagonia of *Poa alopecurus* ssp. *alopecurus* (○ sexual) and ssp. *fuegiana* (● pseudo-viviparous). Only ssp. *alopecurus* occurs in the Falkland Islands.

is not clear whether this partial apomixis represents a constant feature of their reproduction or whether it is induced by local environmental conditions. Taxonomically, however, it seems best to include them in *P. alopecurus* ssp. *fuegiana*, with which *P. pogonantha* is consequently synonymous as indicated above.

Although *P. alopecurus* occurs widely at higher elevations (up to 705 m.) in the Falkland Islands (Moore, 1968), pseudo-vivipary is unknown there and the material is referable to ssp. *alopecurus*.

It is interesting to note that in collections of *Poa alopecurus* ssp. *alopecurus* from Tierra del Fuego female plants (58 per cent) are somewhat more frequent than males (42 per cent). In consequence, it is interesting that plants attributed to *Poa pogonantha* were noted as pre-eminently female, while those referred to *Poa fuegiana* are five times more likely to have traces of ovaries than anthers. This would appear to indicate that female plants have a greater likelihood of the inception of pseudo-vivipary but there is too little information on this phenomenon in dioecious species to say whether this is of wider application.

Festuca subantarctica Parodi

This species is restricted to the southern and western parts of the Fuegian archipelago (Fig. 4). The degree of pseudo-vivipary is rather variable, with some plants having inflorescences in which most of the spikelets are proliferating while others can bear both pseudo-viviparous and sexual inflorescences. As in *Poa alopecurus* ssp. *fuegiana*, it is the axis of the spikelet which undergoes metamorphosis to give the leafy shoot of the propagule (Fig. 1b). Up to 3(–5) florets may be present below the proliferating region; in all cases they showed an elongated lemma and a very membranous, frequently much-reduced, palea. All of the florets appear to be sterile, having the ovary and anthers vestigial or absent, although they show the least extreme reduction in the lowest floret.

Plants from Bahía Orange, Peninsula Hardy, Isla Hoste, Chile (Godley 990 (CHR, K)), possessed both pseudo-viviparous and sexual inflorescences. The characters of the non-proliferating panicles, as well as the vegetative organs, agreed well with those given by Parodi (1953) for the central and southern Chilean species *Festuca monticola* Phil. Although we have

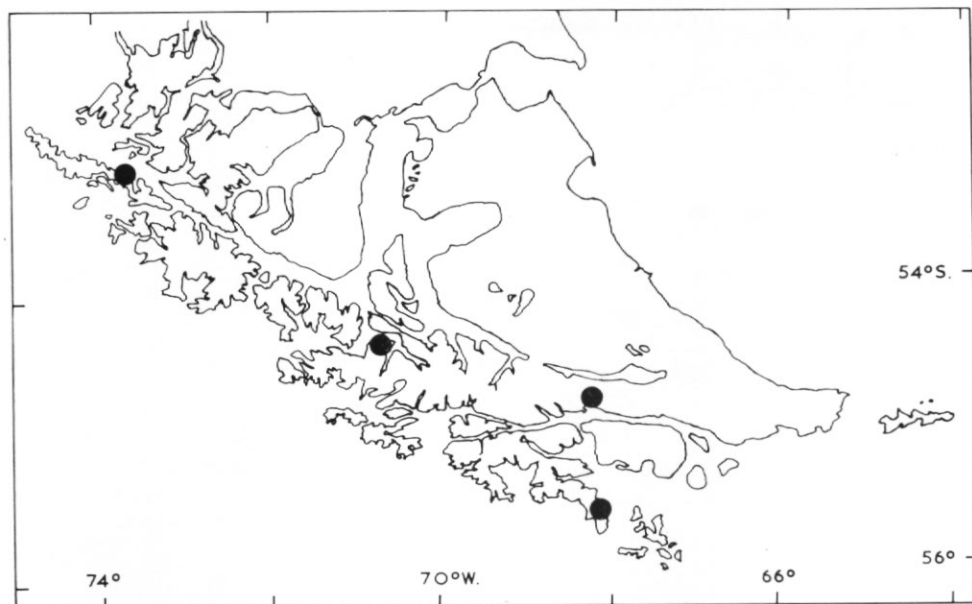


Fig. 4. Distribution of *Festuca subantarctica*.

not been able to examine type material of this species, we are of the opinion that *F. monticola* and *F. subantarctica* will prove to be conspecific, the latter epithet referring to the partially or completely pseudo-viviparous populations occurring in the higher rainfall areas of Fuegia and southern West Patagonia and the former to the sexually reproducing populations farther north.

Poa robusta Steudel

There is no previous report of apomixis in this hermaphrodite species and all material examined from the Falkland Islands and north of the Straits of Magellan to its limit at about lat. 52° S. in West Patagonia has been found to be sexual. In Tierra del Fuego, however, we have found several pseudo-viviparous specimens, usually in association with sexual material, in the southern and western parts of the species' range (Fig. 5).

In proliferating material it is the lemma which undergoes transformation to give the propagule (Fig. 6). The spikelet in this species is 2- to 3-flowered and all florets are modified. The lemma of the lowest floret is greatly enlarged and encloses a slightly elongated palea, as well as the ovary and anthers. It also encloses the bases of the other lemmas, which are not spatially separated on the rhachis. The upper lemmas are elongated, narrower and leaf-like, sometimes possessing developing ligules. From the base of the spikelet upwards each successive lemma subtends a progressively reduced palea and sex organs which are eventually absent. In addition to the much longer lemmas and reduced ovary and anthers, apomictic *P. robusta* is distinguished from sexual material by the slightly longer glumes (Fig. 7).

Agrostis canine L. var. *falklandica* (Hook. f.) Hack.

This species, which is variable and widespread in the temperate regions of North America and Eurasia, also occurs in southern Andean Patagonia, Tierra del Fuego and the Falkland Islands. In the Northern Hemisphere pseudo-vivipary has been recorded only infrequently in the species as a response to abnormal environmental conditions (Philipson, 1935). As a general rule, the Southern Hemisphere populations also produce only sexual inflorescences. However, plants with proliferating spikelets have been found in the Falkland Islands, where

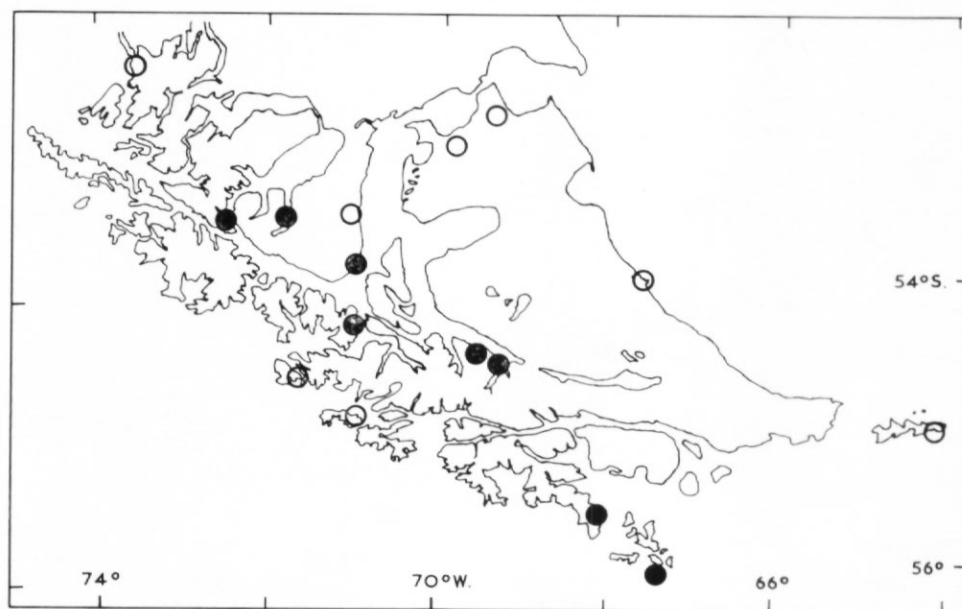


Fig. 5. Distribution in Tierra del Fuego and adjacent Patagonia of *Poa robusta* (○ sexual plants only; ● viviparous and sexual plants present). Only sexual plants occur in the Falkland Islands.

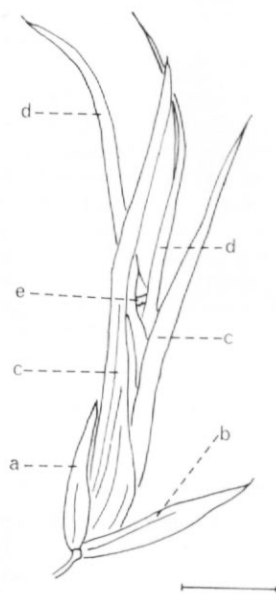


Fig. 6. Pseudo-viviparous spikelet of *Poa robusta*.
a, lower glume; b, upper glume; c, elongated lemma; d, propagule lamina (metamorphosed lemma); e, ligule. Scale = 5 mm.

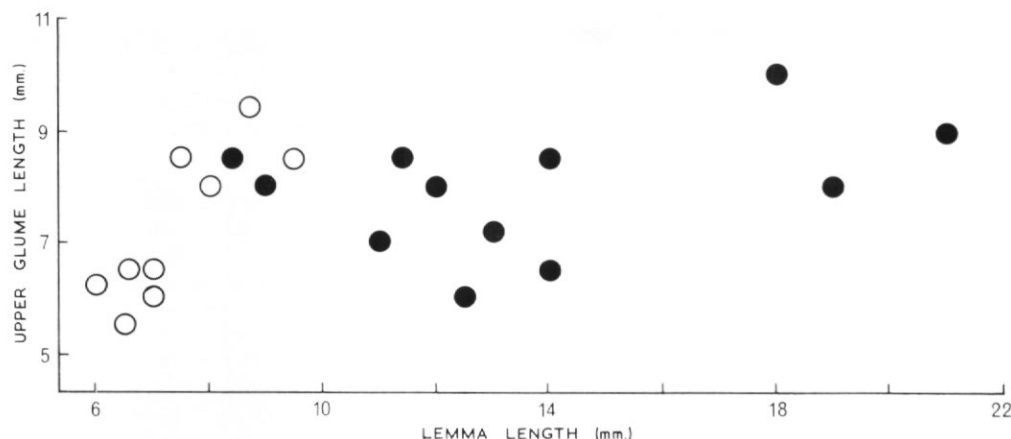


Fig. 7. Length of lemma and upper glume in sexual (○) and pseudo-viviparous (●) plants of *Poa robusta*.

they were collected at an altitude of 275 m. on the summit of Sharp Peak, Roy Cove, on the north coast of West Falkland (Moore 849 (LTR)). These plants, in which the lemmas were greatly elongated, were present in low frequency in the same populations as the more abundant sexual plants. In such pseudo-viviparous individuals, the whole inflorescence showed proliferation and the florets possessed abnormal ovaries and no anthers. In view of the extremely localized and sporadic occurrence of these plants, despite the examination of a wide range of material from southern South America, it seems likely that such apomixis represents a non-heritable response to environmental conditions. It is nevertheless interesting that these "late-season inflorescences" might play a part in the natural reproduction of this species in the Falkland Islands as they do in several grasses in north temperate regions.

Pseudo-vivipary in cultivated material

The above four species constitute the only examples known to us of naturally occurring pseudo-vivipary among the grasses of southernmost South America and the Falkland Islands. However, we have occasionally noted proliferation in the inflorescences of cultivated material of species for which we have no evidence of its occurrence in natural habitats.

Agrostis flavidula Steudel

This species occurs in the drier northern areas of Tierra del Fuego and southern Patagonia, where it always appears to reproduce sexually. Material was grown in the experimental garden at Reading from seed collected in Tierra del Fuego and throughout most of the flowering period the cultivated plants produced fertile, sexual florets. However, at the end of the season some proliferating spikelets arose at the base of the panicle which still retained ripe seed in some of the florets. The propagules developed by proliferation of the spikelet axis. It seems clear that this is an example of the production of "late-season inflorescences" in response to the environmental stress under cultivation during the latter part of a rather dry Northern Hemisphere summer. As noted earlier, such environmentally induced pseudo-vivipary is known from several Northern Hemisphere members of the genus. We have noted that occasional cultivated plants of sexual species of Fuegian *Poa* develop pseudo-viviparous spikelets as a result of nematode infestations but these will not be considered here.

Occurrence and Distribution of Pseudo-vivipary at Higher Southern Latitudes

It is clear from the data presented that in the pseudo-viviparous grasses of Tierra del Fuego and the Falkland Islands the apomictic propagules arise by one or other of the two methods known from Northern Hemisphere studies—either by proliferation of the spikelet axis or

by transformation of the lemma. In *Poa alopecurus* ssp. *fuegiana*, *P. robusta* and *Festuca subantarctica* pseudo-vivipary is a permanent feature of the reproduction of a substantial number of populations. Such populations have been shown to occupy the southern and western parts of the species' distribution in areas having the highest rainfall. This, again, is in agreement with data on the distribution of pseudo-viviparous grasses in the Northern Hemisphere.

The local occurrence of pseudo-vivipary in *Agrostis canina* var. *falklandica* at higher elevations in the Falkland Islands would also conform to the above pattern. However, in view of its uncommon appearance in otherwise sexual populations, such proliferation seems likely to be environmentally induced and there is no evidence that it constitutes an important or constant feature of the reproduction of southern South American populations of this species.

Undoubtedly environmentally induced pseudo-vivipary, observed in cultivated plants of *Agrostis flavidula*, parallels similar observations from the Northern Hemisphere. There is no evidence that such reproduction plays any part in the natural populations of this species. The only other example of pseudo-vivipary known to us in southern cool-temperate species has been found in cultivated material of *Festuca contracta* T. Kirk originating from South Georgia (personal communication from J. R. B. Tallowin), which had an elongated rhachilla similar to that found in *Dactylis glomerata* L. by Philipson (1934), and it seems likely that this also has arisen in response to local environmental stress.

Finally, it is interesting to note that in the Northern Hemisphere pseudo-vivipary plays an important role in the reproduction of high-latitude populations of *Deschampsia*. Several species of the genus are known at high latitudes in southern South America, and indeed, one species (*D. antarctica* Desv.) is one of the two flowering plants present in Antarctica. Nevertheless, we have not found any evidence for either permanent or transient pseudo-vivipary in austral members of this genus.

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