VEGETATIVE PROLIFERATION IN *Festuca contracta* T. Kirk ON SOUTH GEORGIA

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ABSTRACT. Vegetative proliferation in a native grass is reported for the first time in the vegetation of the sub-Antarctic islands. This phenomenon occurs in *Festuca contracta* growing on South Georgia and it appears to be produced in response to changing light and high temperature conditions. The stimulus necessary for the complete differentiation of the floral primordia into a sexually reproductive panicle apparently declines as the summer advances and day length decreases. It is suggested that excessively high temperatures increase the tendency of developing inflorescences to become vegetatively proliferated, although the most important factor is decreasing day length. Although this phenomenon has been found in the field, its scarcity indicates that propagules do not perform an important reproductive function. In contrast to the normal vegetative means of reproduction by tillering, vegetative proliferations are in no way essential for the survival of the species on South Georgia.

VEGETATIVE proliferation in perennial grasses is an aberration from normal seed formation within the spikelet to the development of a leafy shoot in their place. This has been recorded in many grasses throughout the world, not only as an ephemeral character in a considerable number of normally seed-setting species but also as an inherent character in some species.

Vegetative proliferation in grasses is often associated with high latitudes, high altitudes or a high moisture regime. In Britain, the occurrence of this phenomenon in a number of native grasses is considered to be an indication of a glacial relic element in the flora (Wycherley, 1953). However, vegetative proliferations are by no means restricted to grasses of the polar and alpine or the high rainfall regions. Nielsen (1941) has recorded it in *Festuca obtusa* Spreng. and *Bromus inermis* Leyss. growing under relatively xeric conditions in Arkansas, U.S.A. Similarly, *Poa bulbosa* L., a species in which the inflorescence is normally proliferated, is a plant of dry disturbed habitats (Wycherley, 1953). They also occur in grasses growing in the tropics, and Jain and Pal (1969) have recorded the phenomenon in ten genera occurring in India.

Records of vegetative proliferation within the Gramineae of the cool-temperate regions of the Southern Hemisphere are not so widely reported as those in the Northern Hemisphere. This is probably largely due to the more limited botanical work that has been carried out in these regions. However, there are a number of records in species from Tierra del Fuego and southern South America (personal communication from D. M. Moore). According to A. F. Mark (personal communication), vegetative proliferations have not been recorded in New Zealand grasses.

This paper discusses the only known occurrence of vegetative proliferation from the sub-Antarctic, in *Festuca contracta* T. Kirk growing on South Georgia (lat. 53°58′–54°53′S., long. 35°46′–38°17′W.). This fine-leaved, short tussock-forming fescue occurs throughout much of the cool-temperate and sub-polar regions of the Southern Hemisphere, between lat. 45° and 55°S. (Moore, 1968).

MORPHOLOGY

The morphology of a typical vegetatively proliferated spikelet in *Festuca contracta* is illustrated diagrammatically in Fig. 1a. The general appearance of a normal spikelet is shown in Fig. 1b and that of a proliferated spikelet is given in Figs. 1c and 2.

Festuca contracta normally produces entirely sexual panicles under field conditions on South Georgia. However, occasionally partially or completely proliferated panicles have been found in the autumn. In the partially proliferated panicles, leafy shoots may develop in only one or two of the lowest spikelets but, as the vegetative character of the panicle becomes more advanced, an increasing number of spikelets becomes proliferated and the abnormality of the inflorescence becomes increasingly marked.

The first two glumes of a spikelet may become elongated by up to 1·5 times their normal

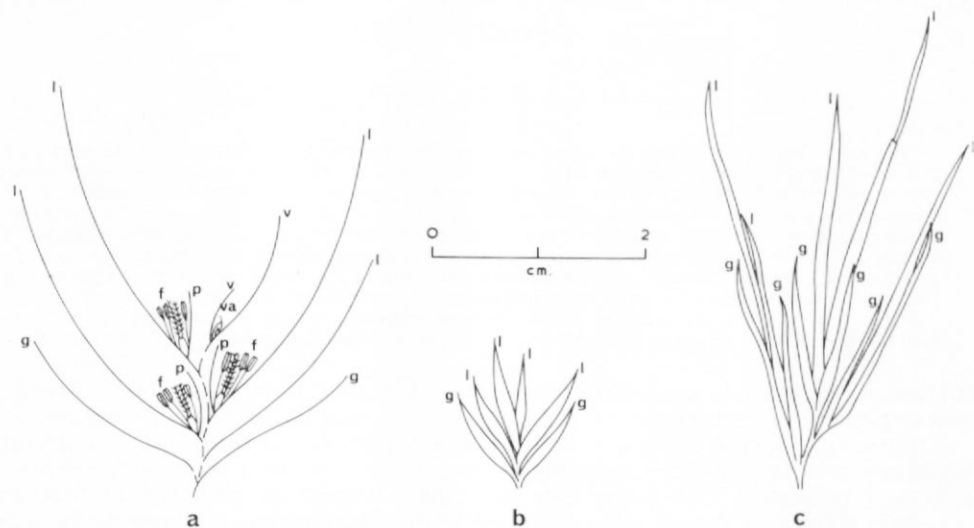* Present address: The Grassland Research Institute, Hurley, Maidenhead, Berkshire SL6 5LR.

Fig. 1. a. Diagrammatic representation of a vegetatively proliferated spikelet of *Festuca contracta* showing the vegetative apex (va) and normal leaves (v) compared with the modified reproductive structures of the florets. g, glume; l, lemma; f, floral organ (ovary, stigma and anthers); p, palea.
b. Drawing of a normal spikelet compared with a vegetatively proliferated spikelet (c).

Fig. 2. Proliferated spikelet of *Festuca contracta* from South Georgia. The leaf-like structures are elongated glumes (light colour) and lemmas (dark colour) with the latter beginning to differentiate into lamina and sheath.

length, reaching 8–10 mm. Above these lower glumes there may be one or more sterile lemmas (i.e. lemmas not subtending the floral structures of ovary, stigma, anthers and palea) which, when present, usually become more than twice the length of a normal glume. Slight differentiation into leaf lamina and sheath is often apparent as the proliferation matures. The fertile lemmas (i.e. those subtending the floral structures) become very elongated and often distinctly differentiated into lamina and sheath. The palea eventually atrophies with little if any elongation having taken place. The ovary, stigma and anthers are all frequently present, although sometimes either the gynoecium or androecium or both can be absent. These organs, when present, also eventually atrophy completely. The vegetative apex of the spikelet axis appears to produce normal leaves. In these proliferations the lower lemmas usually tightly enclose the younger ones above, giving the appearance of a single compact tiller with the vegetative apex being completely enclosed and protected by the bases of the lemmas.

VEGETATIVE PROLIFERATION INDUCED UNDER FIELD AND EXPERIMENTAL CONDITIONS

Vegetative proliferation in *F. contracta* was first noticed in an experiment carried out in 1971–72 to investigate dry-matter production in exposed and sheltered populations of the grass. Single vegetative tillers were collected from each population in December 1970 and planted in vermiculite contained in polythene pots and watered regularly with a modified Hoagland's nutrient solution (Callaghan and Lewis, 1971). The plants were grown for a period of 16 months until mature (i.e. when inflorescences were produced), half at a sheltered site 25 m. a.s.l. and the other half at an exposed site 80 m. a.s.l. During the autumn of the second season 30 per cent of the exposed population plants grown at both sites and 15 and 20 per cent of the sheltered population plants grown at the exposed and sheltered sites, respectively, produced vegetatively proliferated panicles. An intensive search for such a phenomenon in the field during one growing season revealed that they occur infrequently and apparently only in the autumn.

Vegetative proliferations were produced by *F. contracta* plants brought back to England and grown in open unheated frames at Birmingham. During the early to mid-summer months (May–July), all the inflorescences that developed were completely sexual. However, as the summer advanced, vegetative proliferations began to appear on the later emerging panicles. *F. contracta* plants from the same sample were grown in controlled environment cabinets (Tallowin, in press) providing a regime of long days (17 hr.) and short nights (7 hr.) with a uniform day and night temperature of 10° C. The total light intensity in the cabinet was *c.* 0·3 cal. cm.$^{-2}$ min.$^{-1}$, supplied by a 400 W MBFRU mercury vapour lamp and a 150 W tungsten lamp. This light intensity is about 50 per cent of the summer noon-day illumination on a sunny day on South Georgia. No proliferations were produced by the plants grown in the cabinets.

STIMULI INDUCING VEGETATIVE PROLIFERATION

It appears that during the course of panicle development in *F. contracta* two distinct stimuli are involved, one inducing inflorescence initiation and the other promoting the differentiation of the floret. The results obtained from the long-day treatment indicated that all floral primordia initiated during the autumn of one season are capable of developing into completely sexual panicles in the next season. Vegetative proliferations were only formed when the day length was declining and when the temperatures were relatively high. On South Georgia the summer temperature conditions usually persist into April and often the highest temperatures of the season occur briefly in March, as shown in Table I. Table II illustrates the variation in other climatic parameters through the year.

In *Poa bulbosa*, a grass in which vegetative proliferation of the inflorescence commonly develops, Youngner (1960) suggested that floret differentiation is controlled by a stimulus produced under long-day and high-temperature conditions. He also suggested that this stimulus behaved quantitatively, the changes in the intensity of the stimulus following a parallel course to the changes in photoperiod and/or temperature during the summer months. Complete sexuality of the floret would only be promoted by the high-intensity stimulus produced under long days and relatively warm temperature conditions.

TABLE I. MEAN AND EXTREME MONTHLY TEMPERATURES FOR KING EDWARD POINT, SOUTH GEORGIA, 1970–73

	Highest maximum (°C)	Mean maximum (°C)	Mean (°C)	Mean minimum (°C)	Lowest minimum (°C)
January	13·2	7·6	4·5	2·0	−1·3
February	15·2	7·6	4·7	2·1	−1·0
March	16·1	7·7	4·8	2·3	−2·2
April	12·9	5·1	2·6	0·3	−4·3
May	10·6	2·6	0·3	−1·7	−6·7
June	10·6	1·1	−1·2	−3·2	−8·9
July	8·8	0·6	−1·7	−3·7	−9·3
August	8·4	1·9	−0·8	−2·9	−8·4
September	11·6	3·5	0·8	−1·6	−7·2
October	12·1	5·1	1·8	−0·5	−5·3
November	14·0	6·3	3·2	0·5	−3·9
December	16·0	7·8	4·5	1·9	−1·2

TABLE II. MEAN MONTHLY DATA FOR WIND SPEED, PRECIPITATION, CLOUDINESS AND SUNSHINE AT KING EDWARD POINT, SOUTH GEORGIA, 1970–73

	Mean wind speed (m. sec. $^{-1}$)	Maximum wind speed (m. sec. $^{-1}$)	Total precipitation (as equivalent rainfall) (mm.)	Mean daily cloud (oktas)	Mean daily sunshine* (hr.)
January	4·1	33·0	102·2	6·2	5·01
February	4·4	29·0	179·5	6·1	4·26
March	4·8	32·0	143·3	5·8	3·87
April	3·8	31·0	202·9	5·8	—
May	3·8	28·5	314·5	5·8	—
June	3·6	34·5	139·6	5·3	—
July	3·2	35·0	196·4	4·9	—
August	4·2	35·5	197·1	5·2	—
September	3·8	30·0	127·6	5·3	—
October	3·6	27·5	100·3	5·6	4·77
November	4·1	27·5	65·7	5·6	4·79
December	4·0	32·0	99·3	6·2	5·13

*Sunshine data for April–September do not relate to the experimental sites *c.* 0·5 km. away, as the meteorological station is in the shade of a mountain for part of each day.

According to Latting (1972), sexual reproduction in arctic-alpine grasses is apparently favoured by low temperatures and long day lengths. Vegetative proliferation, however, is associated with short day lengths with the intensity of proliferation increasing if the plants are subjected to excessively high temperatures under either short or long days.

Vegetative proliferation in *F. contracta*, when grown under late summer conditions in England, could have been promoted by declining day length combined with temperatures which were abnormally high (i.e. over 40° C at grass level) for this cool-temperate species. Grass-level temperatures of 35–40° C have also been recorded during the summer on South Georgia. The relatively common occurrence of vegetative proliferation in the pot experiment carried out on South Georgia could again be accounted for by relatively high temperatures combined with declining day length. Although the pots, which were of black polythene, were buried, the upper perimeter was exposed, forming a black body around the plants and the resulting heat exchange with the vermiculite caused the pot temperatures to be higher than in the surrounding soil (personal communication from D. W. H. Walton). The greater percentage of vegetative proliferation in the exposed population plants seems to indicate an increased sensitivity to abnormally high temperatures.

In discussing the stimuli involved in floral initiation, differentiation and development, it is assumed that the basic control is regulated by changing environmental conditions affecting the

rate of production of different hormones and the hormone balance within the plant. It was observed that vegetative proliferations did not form in all late emerging panicles; in some instances, plants bore emerging vegetatively proliferated and unproliferated panicles concurrently. This situation may be explained by hormonal gradients existing within the plant, so that some late differentiating floral primordia receive sufficient hormonal stimulus for complete sexual development while others do not. This observation also indicates a high degree of individuality between each flowering tiller, a feature known to exist in floral induction (Gardner and Loomis, 1953). Floret differentiation in the majority in the *F. contracta* inflorescences occurs in the early part of the summer, when both the temperature conditions and day length are increasing. Relatively few panicles remain unemerged by the end of January, when declining day length possibly promotes only a weak stimulus and thus reduced panicle sexuality. This factor probably accounts for the scarcity of vegetative proliferations in the field.

POSSIBLE SIGNIFICANCE OF VEGETATIVE PROLIFERATION

It seems unlikely that vegetative proliferation performs an important reproductive role in *F. contracta*. All experimentally produced proliferated panicles died without any of the propagules becoming detached or producing roots and only dead vegetatively proliferated panicles were found in the early summer months in the field. If the propagules became free of the parent plant, they would, like seedlings, be exposed to the hazard of desiccation during the process of becoming established. Successful seedling establishment is particularly rare and slow in polar and alpine regions (Billings and Mooney, 1968). It is likely that the establishment of vegetative propagules would be no different, especially as their greater size and low numbers would give them less chance than seeds of falling on to moist sheltered substrates.

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