STUDIES IN THE REPRODUCTIVE BIOLOGY OF
Festuca contracta T. Kirk ON SOUTH GEORGIA:
I. THE REPRODUCTIVE CYCLES

By J. R. B. Tallowin* *and* R. I. Lewis Smith

Abstract. The sexual reproductive cycle of *Festuca contracta* on South Georgia is divided between two growing seasons. Floral induction and initiation occur during the mid to late summer months of one season, and panicle development and seed production are not completed until towards the end of the following growing season. Each plant has a juvenile phase which persists for at least 2 years. The incidence of flowering is reduced in exposed upland habitats and appears to be correlated with a reduction in mean tiller and leaf size. All the flowers of *F. contracta* are apparently cleistogamous.

The vegetative reproductive cycle consists of two distinct phases during the growing season. In the spring there is negligible production of daughter tillers which, combined with a considerable mortality of vegetative tillers, results in an overall decline in the number of vegetative tillers in plants growing *in situ* in grassland communities. This phase is then followed by a period of rapid tiller production, starting around the time of anthesis in the sexual cycle, and continuing well into the autumn. The size of parent tillers and leaves appears to be important in the control of tiller production.

Comparatively few plant species have passed the rigorous environmental screening that enables them to survive in polar and alpine regions. This is particularly evident in the sub-Antarctic, where cold summers and geographical isolation from more temperate landmasses have resulted in an extremely depauperate vascular flora. To gain an insight into the evolutionary processes that have permitted the more abundant and widespread species to colonize this harsh environment, it is essential to understand the ways in which they achieve successful reproduction.

The present paper outlines the reproductive cycles, both sexual and vegetative, of *Festuca contracta* T. Kirk, a locally abundant fine-leaved fescue growing on the sub-Antarctic island of South Georgia (lat. 53°30′–55°00′S., long. 35°30′–38°30′W.). A description of the island has been provided by Smith and Walton (1975) and details of the vegetation have been given by Greene (1964).

THE REPRODUCTIVE CYCLES

On South Georgia the spring melt is complete in most lowland localities on the relatively sheltered north-east coast by the end of October. The first inflorescences of *Festuca contracta* growing in particularly favourable habitats in these areas emerge from their leaf sheaths by mid November. Examination of plants from both sheltered lowland and exposed upland localities at the time of spring melt, and at the onset of the winter season (late April–early May), revealed that floral initials were present in all the mature plants. From further studies during the growing season, it was found that floral initiation actually occurs in the mid to late summer months (late January–February).

At the same time as floral initiation is occurring, seed development is also in progress in panicles initiated in the preceding season. In fact, during a growing season three distinct reproductive cycles occur: two are sexual, involving the initiation of one cycle and the completion of another, and the third is a vegetative reproductive cycle which involves the production of daughter tillers.

THE SEXUAL REPRODUCTIVE CYCLE

Control of floral induction and initiation

Juvenility. This refers to the delay between seedling establishment and when a plant first becomes sensitive to floral inductive conditions. In order to determine the duration of the juvenile period in *F. contracta*, samples of plants grown from seedlings, both *in situ* in grassland and in pots containing *Festuca* grassland soil or vermiculite (exfoliated mica), were examined

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

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for the presence of floral primordia after either one or two growing seasons had elapsed. All of the pots containing seedlings were placed in a sheltered lowland site surrounded by robust flowering *F. contracta* plants. The plants growing in the vermiculite were watered occasionally with a modified Hoagland's solution (see Callaghan and Lewis, 1971). Each plant was carefully dissected but in none was there any evidence of floral initiation having taken place. Because it was not possible to extend this study beyond 2 years and also because it was impossible to age non-flowering plants in the field, it seems likely that the juvenile phase in *F. contracta* probably lasts longer than 2 years.

Once the juvenile phase is complete flowering occurs annually. Competence to flower, once gained, is apparently not easily lost. This was illustrated in an experiment (referred to as the "reciprocal transplant experiment") in which flowering plants were grown from individual vegetative tillers in approximately one and a half growing seasons. The vegetative tillers, each bearing an adventitious root, were separated from hitherto undisturbed mature flowering plants growing in sheltered lowland and exposed upland grassland communities. The tillers were matched, so that all consisted of three green leaves, then planted at three per pot in moist vermiculite and watered regularly with modified Hoagland's solution. The two populations were kept separate in the pots. After a 1 month establishment period in a cold frame, the plants were transferred to a sheltered field site (the I.B.P. primary site described by Smith (1971)) for the duration of the experiment. Although this experiment involved a dramatic reduction in plant size from a mature flowering plant to an isolated vegetative tiller, this treatment did not appear to inhibit flowering competence.

Table I indicates that the individual tillers from mature plants were relatively slow to become established and to produce daughter tillers. It was therefore surprising that, by the end of the first growing season, floral primordia had been initiated, whereas 15 month old plants (derived from seed) did not achieve floral initiation. The development of individual tillers and total above- and below-ground plant weights of these competent plants, and of the juvenile plants, is compared. The most striking difference between the two age groups of plants was that, although the overall plant size (as indicated by number of tillers and dry weight data) was significantly ($p = 0.05$) greater in the juvenile plants, the mean tiller weight was always significantly lower. It appears, therefore, that competence to flower and juvenility are controlled at the individual tiller rather than the whole-plant level.

Tiller size. Flowering was reduced in plants growing *in situ* in exposed upland habitats, as indicated by the significantly ($p = 0.05$) higher ratio of vegetative tillers to flowering tillers, compared with sheltered lowland plants (Fig. 1). In exposed population plants in the reciprocal transplant experiment (see Table I) and in similar plants growing *in situ* in upland communities (see Fig. 2) the mean tiller weight was always lower than in sheltered lowland plants. There was also a significant ($p = 0.05$) difference between the length (from ligule to apex) and diameter (1 cm. above the ligule) of the lamina of mature plants growing in sheltered lowland and exposed upland populations. The mean length of 500 leaves was 18.0 ± 1.2 cm. and 14.8 ± 1.1 cm., respectively, and the mean diameter of 150 leaves was 0.74 ± 0.02 mm. and 0.67 ± 0.01 mm., respectively. The measurements were made on a random selection of leaves from many plants collected during January, February and March. Accurate measurement of leaf area in *F. contracta* is impracticable due to the setaceous nature of the leaf laminae; however, the differences in leaf length and width clearly indicate that the mean leaf area declines with increasing habitat severity. This was not compensated for by a significant increase in number of leaves per tiller. This suggests that there is a correlation between an overall decline in leaf size and consequently in leaf area per tiller and reduced flowering in plants growing in exposed upland situations. It appears that a tiller must attain a certain size or leaf area before it becomes competent to flower.

Environmental conditions. The result of the reciprocal transplant experiment, in which floral initiation occurred in tillers produced in late summer (February), indicates that floral competence is neither dependent upon winter vernalization of the shoot apex nor upon tiller age in mature plants.

Floral primordia were initiated only under long-day and warm temperature conditions in

TABLE I. VEGETATIVE AND SEXUAL DEVELOPMENT OF *Festuca contracta* TILLERS GROWN AT A SHELTERED GRASSLAND SITE

	Tillers derived from mature sheltered lowland population		Tillers derived from mature exposed upland population		Juvenile plants derived from seed from sheltered lowland population
	24 February 1971	27 April 1971	24 February 1971	27 April 1971	1 March 1973
	(70 days after planting)	(132 days after planting)	(70 days after planting)	(132 days after planting)	(447 days after planting)
Mean number of tillers	4 ± 1	12 ± 2	4 ± 1	11 ± 2	72 ± 13
Mean dry weight of individual tillers (excluding roots) (mg.)	$36 \cdot 1 \pm 5 \cdot 5$	$27 \cdot 9 \pm 5 \cdot 8$	$24 \cdot 4 \pm 5 \cdot 1$	$15 \cdot 2 \pm 3 \cdot 8$	$6 \cdot 5 \pm 1 \cdot 0$
Mean dry weight of entire plant (excluding roots) (mg.)	$165 \cdot 3 \pm 23 \cdot 3$	$363 \cdot 3 \pm 57 \cdot 7$	$111 \cdot 6 \pm 23 \cdot 8$	$167 \cdot 5 \pm 38 \cdot 2$	$476 \cdot 0 \pm 93 \cdot 0$
Mean root weight of entire plant (mg.)	$56 \cdot 0 \pm 8 \cdot 4$	$154 \cdot 8 \pm 21 \cdot 2$	$48 \cdot 8 \pm 9 \cdot 5$	$90 \cdot 9 \pm 17 \cdot 9$	$222 \cdot 0 \pm 31 \cdot 0$
Floral primordia	Absent	Present	Absent	Present	Absent

Data are the means (with standard error at 95 per cent confidence limits) of 30 plants in the tiller experiment and ten plants in the seedling experiment.
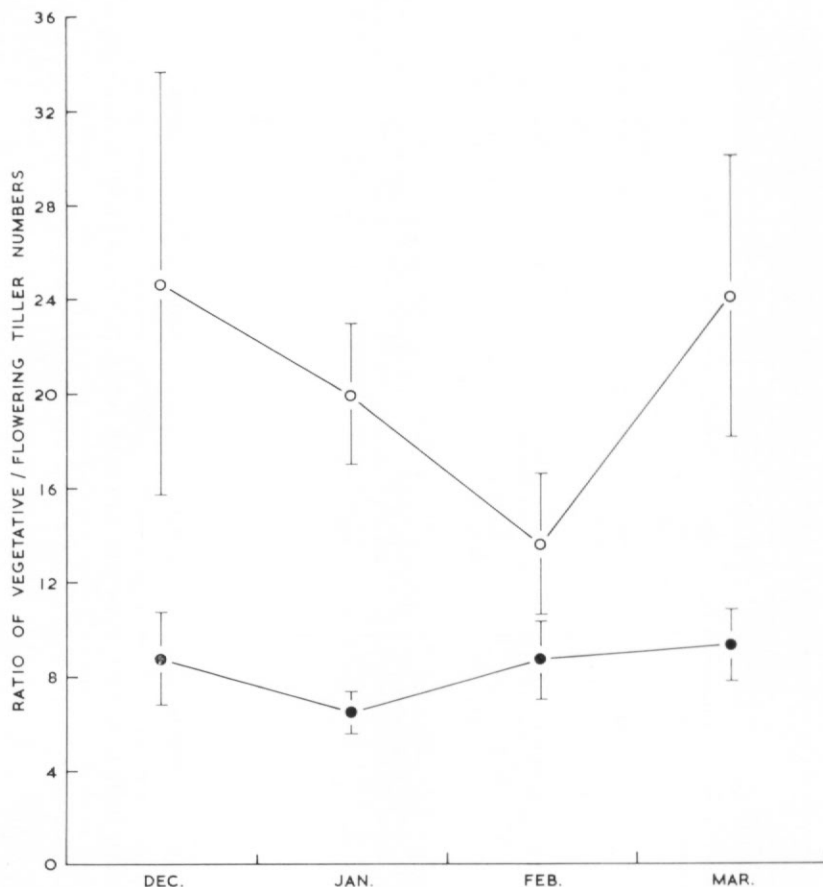
Fig. 1. Seasonal changes in the mean ratio of vegetative tillers to flowering tillers of *Festuca contracta* from an exposed upland population (○) and a sheltered lowland population (●). Vertical lines indicate the standard error ($p = 0.05$) of the mean (ten samples).

the field. Further work, using controlled environment conditions, is necessary to elucidate the floral inductive requirements of this grass.

Control of floral development

Winter dormancy and factors limiting floral development. All floral development ceased during the winter months (from late April until October). At the onset of winter the partially developed inflorescences were still completely enclosed within the leaf sheaths of the parent tiller. At this time the inflorescence initials are usually only *c*. 10 mm. in length and the spikelet primordia are clearly distinguishable. Occasionally, inflorescence initials reach quite an advanced state of development by the beginning of winter; one, found in late April, was 52 mm. in length with the individual spikelets quite distinct.

Floral development is controlled by both day length and temperature. Evidence for this was provided by the results of a series of controlled environment experiments. Mature *F. contracta* plants were dug up in the late autumn (mid April) and shipped to England, being stored with occasional watering for 6 weeks at 4° C in the dark. They were planted in 20 cm. diameter plastic pots containing moistened loamless compost to supplement the natural soil adhering to the roots. The compost contained nutrients bound in the soil matrix so that during the
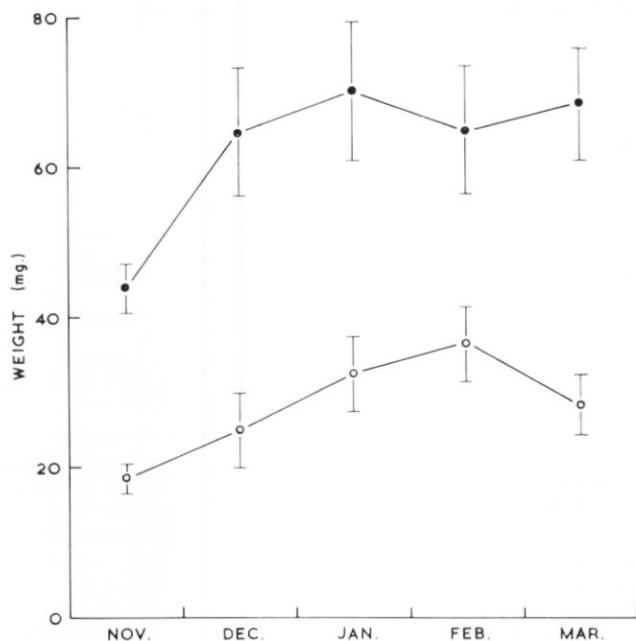
Fig. 2. Seasonal changes in mean dry weight of individual vegetative tillers of *Festuca contracta* from exposed upland (○) and sheltered lowland (●) plants. Vertical lines indicate the standard error ($p = 0.05$) of the mean (ten samples).

course of the study no further addition of nutrients was required. One group of five plants was transferred to a cold frame exposed to the vagaries of the English summer climate. A second group of five plants was transferred to a controlled environment cabinet providing long days (17 hr.) at 10° C and short nights (7 hr.) at 2° C; but after a period of 1 month, during which no floral development occurred, the night temperature was raised to 10° C. A third group of five plants was transferred to a similar cabinet providing a regime of short days (8 hr.) at 10° C and long nights (16 hr.) at 2° C, but again when no floral development had occurred after 1 month the night temperature was raised to 10° C.

It was not possible to study the effects of higher day temperatures on floral development as the temperature control on the growth cabinets became unreliable above 10° C and required major alterations to the cabinets. Both cabinets were illuminated by mercury vapour and tungsten lamps providing a radiation level at canopy height of c. 1.4 J cm.$^{-2}$ min.$^{-1}$, which corresponded to c. 50 per cent of the mean summer-day radiation at the study area on South Georgia.

Inflorescence development was resumed almost immediately in the plants growing in the cold frame. However, as Table II illustrates, there was no development in the cabinets until the night temperature was raised in the long-day regime. No inflorescence development could be induced under the short-day regime until the day length had been increased to 12 hr.

Since night temperatures as high as 10° C very rarely occur on South Georgia, even within the vegetation (personal communication from D. W. H. Walton), it is therefore probable that the temperature that triggered the resumption of floral development was, in fact, less than 10° C. It is possible that temperature behaves in a cumulative manner in controlling inflorescence development; instead of an actual temperature threshold, there may be a requirement for a minimum number of degree hours above 0° C per day over a period of several consecutive days to induce development. This theory would then account for the anomaly of the high night temperature inducing inflorescence development in the growth cabinets.

TABLE II.   DEVELOPMENT OF INFLORESCENCES INDUCED UNDER VARIOUS
CONTROLLED PHOTOPERIOD AND TEMPERATURE REGIMES

Temperature (°C)		Photoperiod (hr.)	Inflorescence development
Day	Night		
10	2	17	Absent
10	10	17	Present
10	2	8	Absent
10	10	8	Absent
10	10	12	Present

Day length and temperature probably become limiting at approximately the same time the autumn (about mid April); however, in the spring it is probable that temperature remains limiting after the critical day length has been exceeded (during September). In winter the short day lengths and relatively low temperatures probably inhibit any development during periods of thaw when plants might become snow-free for short periods.

Floral development in summer. After surviving the winter the inflorescence initials may develop in one of three ways: (i) they may abort while still in the unemerged stage; (ii) they may develop normally and eventually produce seed; (iii) the inflorescences may become vegetatively proliferated.

i. *Abortion.* The premature death of the inflorescence usually occurs before the culm begins to elongate in the early part of the summer (November–December). Abortion appeared to be more common in plants growing in exposed situations than in plants in sheltered lowland habitats. Survival of plants growing under stress conditions, such as exposed upland habitats, depends upon a reproductive strategy in which the emphasis, with regard to utilization of photosynthate, is towards vegetative reproduction and maintenance rather than sexual reproduction. It is possible that the early season "thinning" of potential inflorescences is part of an adaptive strategy by which the sexual reproductive sink for assimilates is reduced at an early stage in the sexual reproductive cycle.

It appears that abortion may be controlled by intrinsic factors such as stress in the form of low reserves of assimilate. Light and temperature are presumably not responsible, otherwise the resumption of floral development would not have occurred. Water is unlikely to be limiting at the time of melt and for some time afterwards. Nutrients such as inorganic and organic nitrogen, phosphorus and potassium, are at their highest levels in *Festuca* grasslands immediately after melt (Smith and Walton, 1975). However, available nitrogen is relatively low at all times in the grassland ecosystem and competition between flowering tillers for this element may be a cause of some abortions; however, it is certainly not the main cause as aborted inflorescences were found in grassland plots that had been treated with nitrogen-rich fertilizer.

ii. *Normal panicle development.* Having survived the spring "thinning", the majority of inflorescences proceed to develop into flowering panicles. The first indication of the resumption of floral development in the spring is a noticeable swelling of the stem bases of flowering tillers. Initially, inflorescence development involves a phase of elongation and differentiation. In both the sheltered and exposed study populations, the majority of the inflorescences had attained their maximum length by mid December (see Fig. 3a and b). During the early part of this phase of elongation (up to early December) there is little dry weight gain by the inflorescences and the glumes of each spikelet become fully
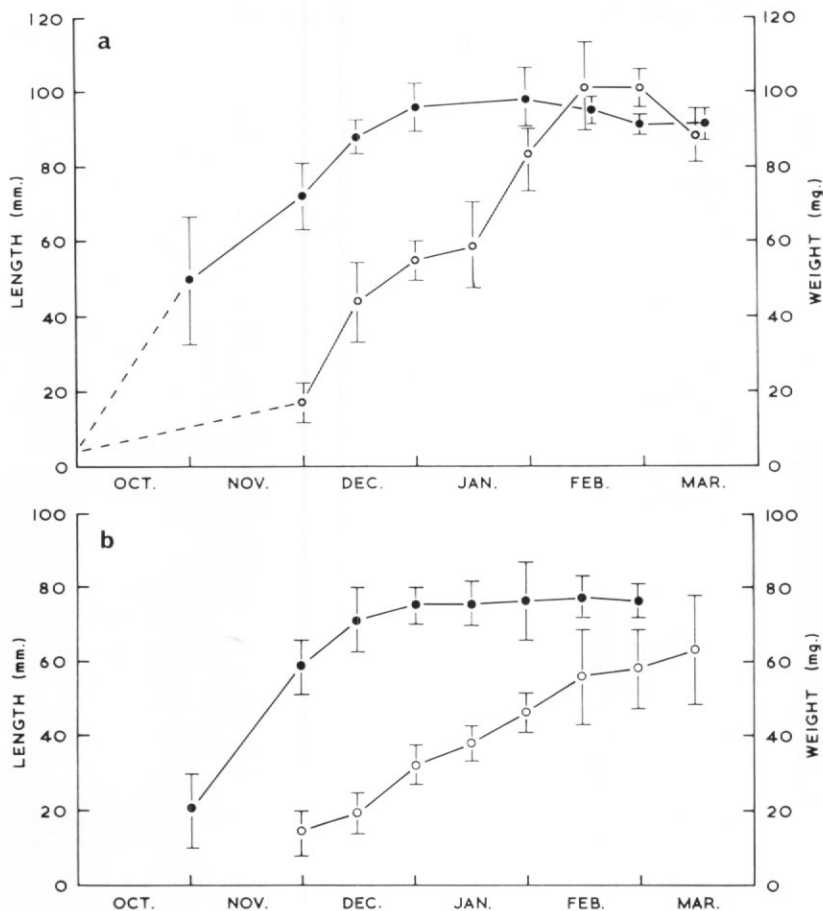
Fig. 3. Seasonal changes in mean length (●) and dry weight (○) of *Festuca contracta* panicles. a. Sheltered lowland population plants. b. Exposed upland population plants. - - - - Assumed pattern of elongation. Vertical lines indicate the standard error ($p = 0.05$) of the mean (five samples).

differentiated and attain their maximum length. The lemmas and reproductive organs (ovary and anthers) develop much later, and in most reproductive tillers the complete differentiation of the spikelet is not achieved until early January when anthesis occurs in the majority of florets. When anthesis commences there is a temporary cessation in dry weight gain by the panicle (see Fig. 3a and b). This indicates the interphase between the completion of floral development and the beginning of seed development.

The panicle of *F. contracta* is erect and spike-like when it emerges and it remains so until well after seed fall when it is eventually broken by wind. The florets were never observed to open and only occasionally were the anthers found exserted; these were always in sheltered situations and usually in only one or two florets in the panicle. This phenomenon occurred in occasional sheltered panicles in less than 1 per cent of the plants in an exposed upland population compared with 13 per cent of the plants in a sheltered lowland population. It therefore appears that the great majority of the flowers of *F. contracta* are cleistogamous.

The culm internodes, especially the one immediately below the panicle, begin to elongate rapidly during December and continue to do so until seed fall commences in late March (Fig. 4). There is also a marked reduction in the length of both panicle and
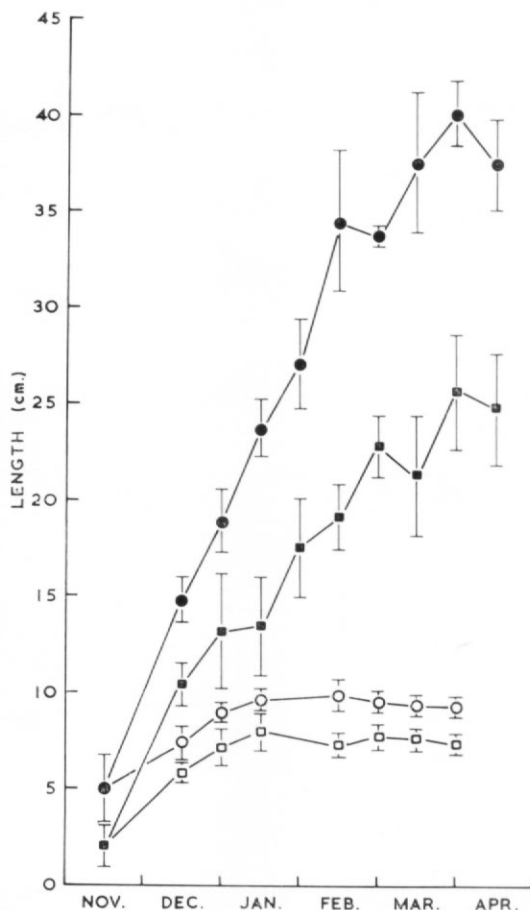
Fig. 4. Seasonal changes in mean panicle elongation (open symbols) and culm elongation (closed symbols) in sheltered (circles) and exposed (squares) populations of *Festuca contracta*. Vertical lines indicate the standard error ($p = 0.05$) of the mean (ten samples).

culm in exposed population plants compared with plants growing in sheltered lowland situations.

Seed fall began in early March in the sheltered grassland site and towards mid March in the exposed grassland site. In both populations the bulk of the seed appeared to be shed at the beginning of winter (late April–early May). There are periods during early winter when snow cover is very variable and the panicles of *F. contracta* frequently project above the snow surface. Movement of the panicle and culm by wind causes the formation of a "chimney" in the snow and during strong winds the violent buffeting against the sides of the "chimney" dislodges the seed from the panicle. When the snow surface is ice-glazed, the seed is blown and scattered evenly over a wide area.

iii. *Vegetative proliferation.* Occasionally, some late-developing panicles become either partially or completely vegetatively proliferated (Tallowin, 1977). No proliferations were found to survive for more than 1 or 2 months in the field or in experimental plants on South Georgia and, although the phenomenon was quite common in plants returned to and grown in England, again none survived or became rooted. It therefore seems unlikely that vegetative proliferation performs an important reproductive role in *F. contracta*.

VEGETATIVE REPRODUCTIVE CYCLE

Pattern of tillering through a growing season

Fig. 5 illustrates the changes in number of tillers per unit area in a closed sheltered *Festuca* grassland community through a growing season. During the early part of the season (November–December), when panicle differentiation and development is occurring, there is a marked decline in vegetative tiller numbers. Since the number of tillers at the time of the spring melt is high, this decline indicates a heavy spring mortality amongst the tillers that overwintered. However, it was not possible to determine whether this loss predominated in a particular tiller age class. Associated with this decline there was a significant increase in the mean dry weight of vegetative tillers. The latter was apparently partly due to an overall increase in shoot height (Fig. 6) and leaf-lamina height (Fig. 7) due to basal meristematic activity. The increase in the
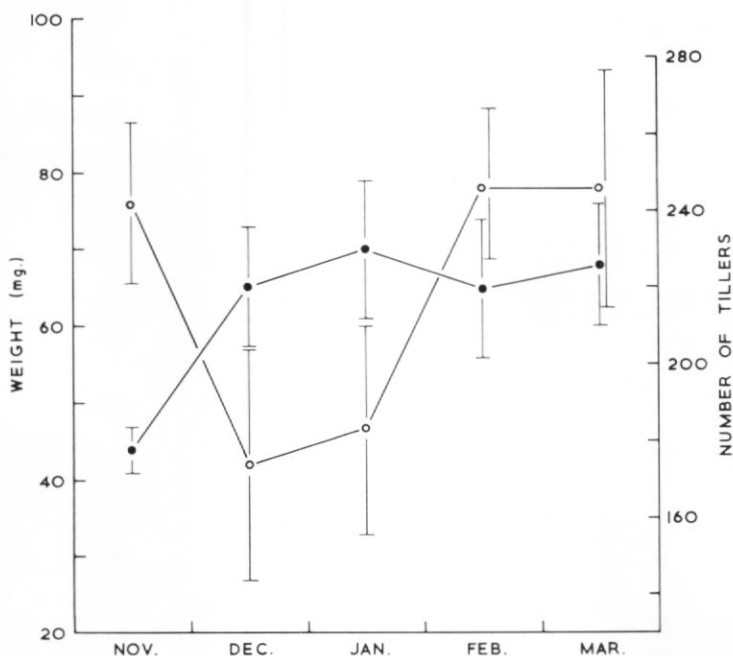

Fig. 5. Seasonal changes in mean vegetative tiller number (○) and dry weight of vegetative tillers (●)/25 cm.² in a sheltered lowland *Festuca contracta* grassland. Vertical lines indicate the standard error ($p = 0.05$) of the mean (ten samples).

mean vegetative-tiller weight was also probably partly due to a low production of daughter tillers during the early part of the growing season. Such depressed tillering rate during the early summer months is a phenological pattern found in many perennial grasses (Langer, 1958; Langer and others, 1964; Laude and others, 1967, 1968).

During December, tiller numbers began to increase again and a distinct tillering phase occurred from mid January until late February (Fig. 5). This was correlated with a slight decline in the mean vegetative-tiller weight as the large numbers of young low-weight tillers entered the population. Vegetative-tiller production ceased from late February onwards and live tiller numbers remained stable through the winter. In the reciprocal transplant experiment, the numbers of tillers in the autumn and in the following spring were virtually identical in both sheltered and exposed populations grown at sheltered and exposed sites, respectively (see Fig. 8). The mean tiller weight declined during the late autumn and early winter months (April and May) due to leaf die-back. This accounted for the low mean tiller weight in spring. Senescence of the leaf tip during winter mainly affects the taller shoots and the leaves towards
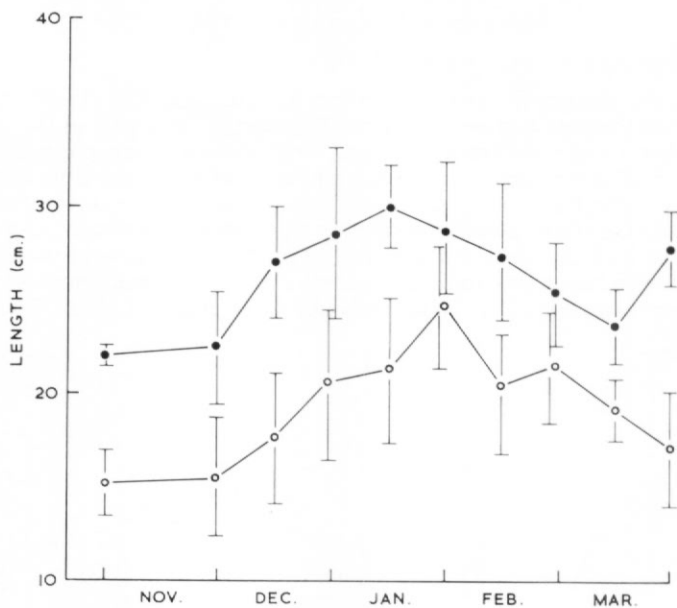
Fig. 6. Seasonal changes in mean maximum shoot length in exposed upland (○) and sheltered lowland (●) *Festuca contracta* grassland populations. Vertical lines indicate the standard error ($p = 0.05$) of the mean (five samples).
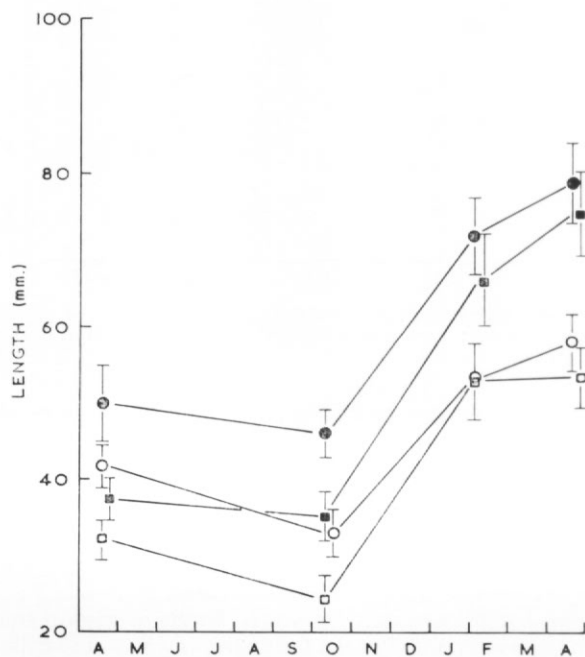

Fig. 7. Seasonal changes in mean length of leaf laminae of *Festuca contracta* from sheltered population plants grown at a sheltered site (●) and an exposed site (○), and from exposed population plants grown at a sheltered site (■) and an exposed site (□). Vertical lines indicate the standard error ($p = 0.05$) of the mean (30 samples).
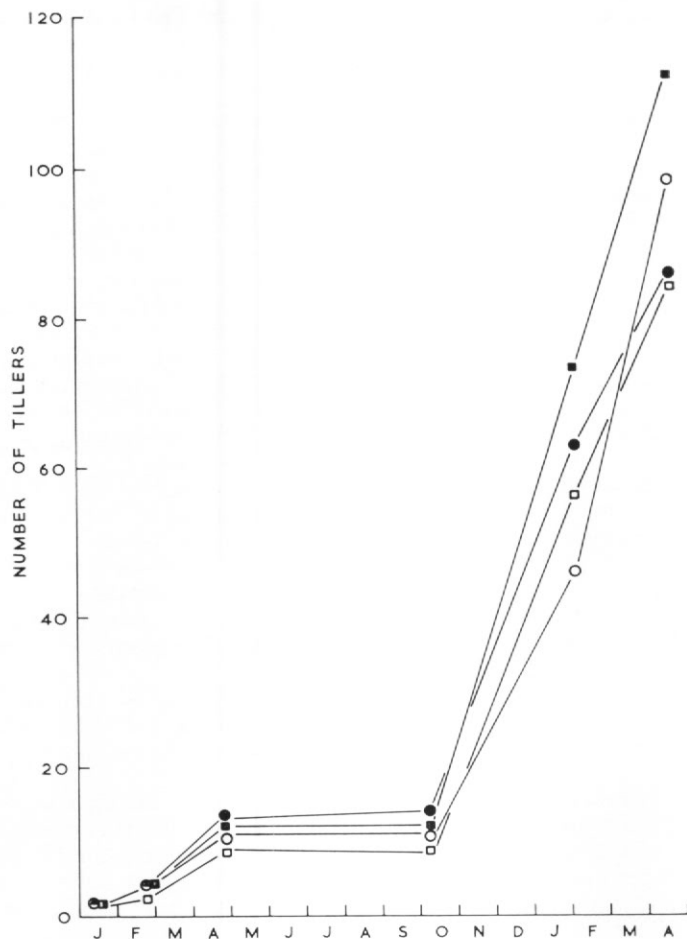
Fig. 8. Seasonal changes in mean number of vegetative tillers per plant in *Festuca contracta* from a sheltered lowland population grown at a sheltered site (●) and an exposed site (○), and from an exposed upland population grown at a sheltered site (■) and an exposed site (□).

e outside of the tussock, but a considerable proportion of the shoot remains green throughout the winter. Chlorophyll levels in leaf laminae collected around mid-winter (July) were only *c.* 25–30 per cent below mid-summer (January) levels, i.e. 3·0–3·5 and 4·0–4·5 mg./g. dry weight, respectively.

Control of tillering

Daughter tillers are produced intravaginally, usually in the axis of the fourth or fifth emerged green leaf (numbered from the youngest). However, daughter tillers have been found in the axil of the third leaf and it appears that in sheltered grassland plants a minimum of two fully emerged leaves is required before tiller development commences. In exposed populations the minimum number appears to be increased to three fully emerged leaves.

It was suggested above that leaf area per tiller may be important in the control of floral induction and subsequent initiation. It also appears likely that leaf area, either of the axillant leaf or of the whole tiller, may be important in the control of tillering; this was indicated by the differences in the minimum number of emerged leaves that were required by exposed and

sheltered population plants before tiller development began. The higher minimum number of emerged leaves required for tiller initiation in the exposed plants was probably largely due to the reduced leaf dimensions of these plants compared with the leaves of plants from sheltered lowland habitats.

Although adverse growth conditions significantly reduced both overall plant stature and leaf size, the effect on vegetative-tiller production was not so marked with the number in sheltered and exposed grassland communities being remarkably similar. The growing season mean (of 50 samples) for the sheltered grassland was $3,504 \pm 528$ vegetative tillers/m.^{2} compared with $3,866 \pm 545$/m.^{2} for the exposed grassland. This similarity is highly significant when the more open nature of the exposed grassland is considered, for in this community individual *F. contracta* plants afforded *c.* 40–55 per cent of the total ground cover, whereas in the sheltered community the grass contributed between 70 and 90 per cent of the ground cover.

In the reciprocal transplant experiment, vegetative-tiller production was not significantly affected by the exposed growing conditions (Fig. 8). This result, therefore, complements the field observations (as described above) and suggests that adverse growth conditions reduce the sexual but not the vegetative reproductive capacity of *F. contracta*. The reduced flowering may in fact enhance the vegetative tillering capacity; the significantly ($p = 0.05$) greater production of vegetative tillers by the exposed population plants grown at the sheltered site, compared with the sheltered population plants at this site (see Fig. 8), was correlated with a significant reduction in the number of flowering tillers produced by the exposed plants. At the sheltered site, flowering tillers developed in only 50 per cent of the exposed population plants producing a total of 33 panicles, whereas 80 per cent of the sheltered population plants flowered at this site, producing a total of 70 panicles. At the exposed site, again only 50 per cent of the exposed population plants flowered, producing 24 panicles, but flowering was reduced in the sheltered population with only 60 per cent of the plants developing flowers and only 24 panicles were produced.

The results indicate that there are fundamental differences between the environmental controls of floral induction and initiation, and vegetative-tiller induction and initiation. The latter, being more tolerant of stress situations, allows at least some clonal spread in upland and exposed areas.

In all of the *F. contracta* populations examined on South Georgia there was a strong emphasis on vegetative reproduction. In either sheltered lowland or exposed upland populations the majority of the live tillers was always vegetative. For example, vegetative tillers represented over 85 per cent of the total live tiller population in a sheltered grassland community at any time during the year, while in an exposed community they constituted *c.* 95 per cent of the tiller population throughout the year.

DISCUSSION

A reproductive cycle involving the autumnal induction and initiation of floral primordia in one season, and the subsequent development of these inflorescences to produce seed in the following season, is a common feature of cold-region plants (Sørensen, 1941; Billings and Mooney, 1968; Billings, 1974). In the Antarctic and sub-Antarctic, however, there are very few records of this type of reproductive cycle. Edwards (1974) has discussed autumnal initiation in *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv., and Smith and Walton (1975) have reported it in *Poa flabellata* (Lam.) Hook. f.

The adaptive significance of autumnal initiation is that it allows floral development to begin as soon as the plant is released from the winter snow cover, thus ensuring maximum utilization of the available growing season. However, it also means that flowering in any one season is dependent upon the environmental conditions prevailing during the preceding season (Billings and Mooney, 1968). Autumnal initiation in *F. contracta* determines only the number of panicles per plant and not the final seed production per panicle which is controlled during floret differentiation in the second season.

Competence to flower in *F. contracta* plants is not achieved before the third growing season. The factors that control the duration of this juvenile period are not fully understood, although both tiller size and total leaf area per tiller appear to be important. Other factors, such as the

status of the carbohydrate reserve, are also considered as possible controls; Allsopp (1965) found that high carbohydrate levels shortened the juvenile period in some species. However, in the present growth study, competence to flower was maintained in many of the individual tillers despite the reduction in their carbohydrate reserves which is assumed to have taken place when they were isolated from the parent plant and during their re-establishment. It therefore appears that carbohydrate reserves were not important in controlling floral competence, at least under the experimental conditions. The results of the reciprocal transplant experiment also indicate that individual tiller age in mature plants was not a factor directly involved in flowering control. The long juvenile period in *F. contracta* could have considerable survival value in that it prevents flowering during the critical establishment period when the young plant requires all its assimilate for vegetative growth.

Once a *F. contracta* plant has become competent to reproduce sexually, flowering occurs annually. The floral inductive requirements have not been fully elucidated but it appears that both long days and warm temperatures are involved. A combined day length–temperature control of flowering has been reported in the New Zealand snow-tussock grasses, *Chionochloa* spp., in which flowering is more prolific in years following particularly mild growing seasons (Mark, 1968). No such irregular flowering pattern has been observed in *F. contracta* and it may be that, in comparison with the snow-tussock species, different or more rigid controls over the flowering cycle have evolved. This subject certainly requires further investigation, in particular with controlled environment studies.

The apparent lack of any over-riding intrinsic flowering controls in *F. contracta*, such as a minimum tiller age or a vernalization requirement, allows for the maximum use of the limited growing season time available for floral induction and initiation.

The winter dormancy of the floral embryo in *F. contracta* is under a combined day length–temperature control and is therefore entirely opportunistic, allowing the prompt resumption of growth and development in the spring. This feature is particularly marked in Arctic tundra plants where there is a remarkably rapid response to the rise in temperature in the spring (Sørensen, 1941). However, for this response to be really effective, the plant requires the immediate availability of photosynthetic tissue at the time of melt when water and nutrients are suddenly abundant. It is therefore not surprising that the evergreen or winter green habit is relatively common in cold-region plants. In *F. contracta* the majority of green tillers present at the onset of winter remain alive and green throughout the winter. The vulnerability of overwintering green shoots to wind and snow abrasion is offset by the persistence of large numbers of standing dead leaves which act as a protecting sheath around the living leaves. Grasses have the added advantage of possessing a basal meristem which permits continued growth of the leaves in spring even when the apical parts are killed during the winter. It is these adaptations and characteristics that may be largely responsible for the success of grasses in cold regions (Savile, 1972).

A proportion of the overwintering floral primordia was found aborted in the spring. The cause of this abortion is not known and it has not been widely discussed with regard to other cold-region plants. In the Southern Hemisphere, Mark (1970) found it to be common in several of the tufted alpine *Celmisia* species of New Zealand but, as there was no clearly defined pattern to the losses in these species, it seemed unlikely that low winter temperatures were entirely responsible. It is possible that competition between developing inflorescences for available assimilates could be a cause of these abortions. It may also be that in *F. contracta* abortion of floral primordia could account for the reduced flowering in plants growing under stress conditions.

Although the first panicles emerge relatively soon after snow melt (October–November), there is little synchrony either within or between different plants and communities. Some panicles may remain unemerged until February or even March. However, these late-emerging panicles fail to produce viable seed, as it cannot develop and mature before the onset of winter. The majority of panicles are completely sexual. The only aberration from normal panicle/seed development is the occasional production of vegetatively proliferated panicles in the autumn (Tallowin, 1977).

Environmental conditions have imposed important restrictions on gene flow within *F. contracta* on South Georgia. This is illustrated by the fact that the species is probably entirely

cleistogamous on South Georgia; there is also a marked emphasis towards vegetative reproduction in all habitats.

The vegetative reproductive cycle consists of two distinct phases during the growing season; in spring and early summer (November–December) there was virtually no daughter tiller production, the tillering phase being confined to late summer (January–February). Either axillant leaf area or the total leaf area per tiller appeared to be important in the control of daughter-tiller initiation and development. Although the number of flowering tillers declined with increasing habitat severity, vegetative-tiller numbers remained unaffected. This reproductive behaviour is shared with Arctic and alpine plants in which sexual reproduction becomes less important than asexual reproduction under environmental stress (Bliss, 1971).

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