

STUDIES IN THE REPRODUCTIVE BIOLOGY OF
Festuca contracta T. Kirk ON SOUTH GEORGIA:
II. THE REPRODUCTIVE PERFORMANCE

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ABSTRACT. Seed production and reproductive effort were investigated in exposed and sheltered *Festuca contracta* grassland populations on South Georgia. Seed production was reduced in the more severe habitat, both at the plant level and at the individual spikelet level. At the plant level, although vegetative-tiller numbers were not significantly affected by the harsher growing conditions, flowering-tiller numbers were markedly reduced. At the spikelet level, about 50 per cent of the florets did not develop seed under the exposed conditions. The proportional dry matter allocation into seed production (sexual reproductive effort) was significantly reduced in the exposed grassland plants. While sexual reproductive effort declined, dry matter investment into the root system increased. Vegetative-reproductive effort was apparently virtually unaffected by the harsher growing conditions.

The successful establishment of *F. contracta* seedlings in the field appeared to be quite scarce. Evidence suggests that the importance of sexual reproduction declines quite markedly with increasing habitat severity, whereas, apparently through a greater tolerance or vegetative-reproduction development to harsh growing conditions, asexual reproduction increases in importance under these conditions.

THE means by which a species achieves successful propagation reflects both the past and present environmental limitations of its habitat range. In polar and alpine regions the severity of the climate, and often the poor quality of the soils, impose major restrictions on plant growth and development. In order to qualify and quantify these effects, it is essential to gain an understanding of the reproductive performance of plant species growing in these environments both in terms of sexual and asexual reproduction. A considerable volume of work in this field has been accomplished on Arctic and alpine plants (Billings and Mooney, 1968; Bliss, 1971; Savile, 1972; Billings, 1974). In the Antarctic, owing to the more recent history of botanical research, relatively few studies on this subject have been made (Callaghan and Lewis, 1971a; Edwards, 1974; Tallowin and Smith, 1977; Tallowin, in press).

In the present study, the reproductive performance of *Festuca contracta* T. Kirk growing on South Georgia (lat. 53°30'–55°00'S., long. 35°30'–38°30'W.) has been assessed in terms of viable seed production, annual proportional dry matter allocation to seed, sexual reproductive development and vegetative development, and finally seed germination and subsequent seedling survival. These parameters were compared in contrasting sheltered lowland and exposed upland *Festuca contracta* populations, either growing *in situ* in previously undisturbed communities or under more controlled conditions in a series of pot experiments.

SEED PRODUCTION

Seed production was examined in two contrasting *F. contracta* grassland communities on South Georgia. Descriptions of these sites are provided in Table I. Although micro-meteorological data were recorded at both sites, they have not been completely processed and analysed, and cannot yet be presented. The most important climatic difference between the two communities was in the degree of exposure to wind. One community was situated on a windswept knoll exposed to the strong katabatic or föhn winds generated in the high Allardyce Range c. 10 km. away (Smith and Walton, 1975); the other community lay in a sheltered hollow protected from such winds.

Table II indicates how the seed productive potential (assuming all the florets produce viable seed) of the exposed grassland was significantly below that of the sheltered community. This was due largely to the lower cover abundance of *F. contracta* plants in the exposed community, but, as the results show, this factor was not entirely responsible for the reduced seed production. In the exposed grassland plants there was a marked decline in the number of flowering tillers relative to vegetative tillers. There was also a tendency for the overall floret number per panicle to decline under the exposed conditions. This was mainly due to a reduction

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TABLE I. DESCRIPTION OF *Festuca contracta* GRASSLAND STUDY SITES

	<i>Sheltered community</i>	<i>Exposed community</i>
Situation	Hollow on north-facing slope (30–40°) surrounded by tall tussock grass (<i>Poa flabellata</i>)	Level crest of stony knoll
Altitude	c. 25 m.	c. 80 m.
Insolation	High	High
Wind exposure	Low to moderate	High
Vegetation	Closed community of dense <i>Festuca contracta</i> with occasional <i>Acaena magellanica</i> , <i>Polytrichum alpinum</i> and <i>Tortula robusta</i> as chief associates	Open community of scattered <i>Festuca contracta</i> plants with <i>Acaena magellanica</i> and abundant <i>Chorisodontium aciphyllum</i> , <i>Polytrichum alpinum</i> , <i>Tortula robusta</i> and <i>Cladonia rangiferina</i>
Soil type	Deep, loamy tundra brown soil; pH 4.1	Shallow, stony mineral soil; pH 4.7

TABLE II. SEXUAL REPRODUCTIVE CAPACITY OF *Festuca contracta* IN TWO CONTRASTING GRASSLAND COMMUNITIES

	<i>Sheltered community</i>	<i>Exposed community</i>
Number of flowering tillers/m. ²	457 (±35)	179 (±43)
Number of vegetative tillers/m. ²	3,504 (±528)	3,866 (±545)
Ratio of flowering to vegetative tillers	1 : 7.7	1 : 21.6
Number of spikelets/m. ²	15,538	4,654
Number of spikelets/panicle	34 (±3)	26 (±4)
Number florets/spikelet	2.6 (±0.2)	2.6 (±0.4)
Number of florets/m. ²	c. 40,216	c. 12,100
Ground cover afforded by <i>Festuca contracta</i> (per cent)	c. 80	c. 45–55

Data are the means, with standard errors at 95 per cent confidence limits in brackets, derived from 50 25 cm. by 25 cm. quadrats.

in the number of spikelets per panicle, since the mean floret number per spikelet was not affected by the harsher growing conditions. The decline in spikelet number per panicle was correlated with a decline in panicle length.

Although most spikelets have two or three florets, up to five have occasionally been found. However, these numbers do not include a very small rudimentary floret that terminated the apical meristem of the spikelet. Floret number alone does not provide a realistic indication of the seed-productive potential of a plant or community as not every floret on a spikelet (excluding the rudiment) developed into a seed. To obtain an estimate of the actual seed production on either a plant or individual panicle basis involved weighing individual florets at the time of seed fall in samples of panicles collected from the two communities. Fig. 1

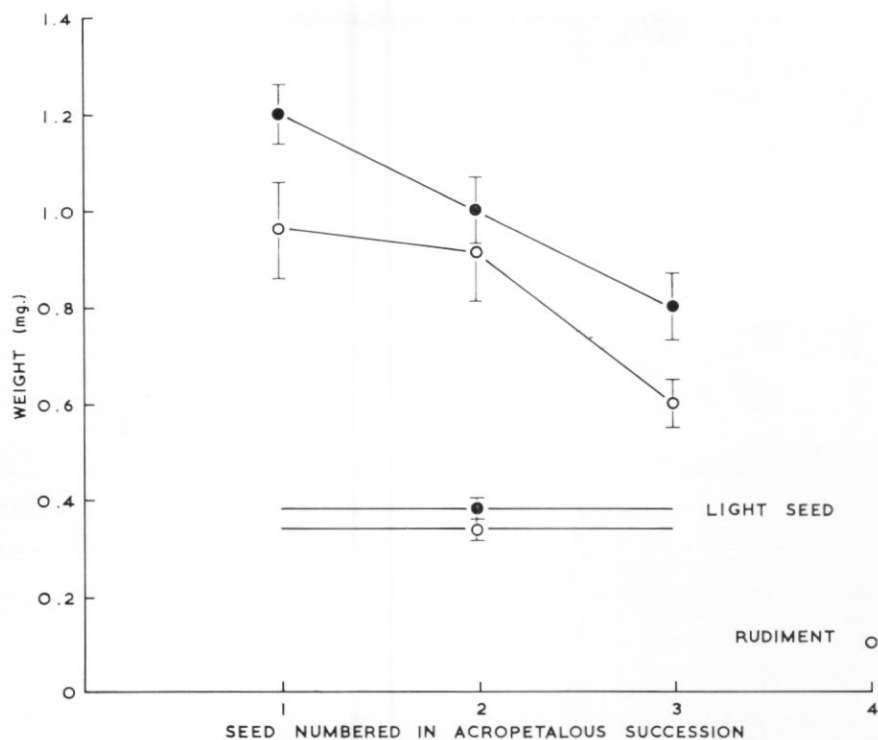


Fig. 1. The relationship between seed dry weight and position of seed within a spikelet for a *Festuca contracta* sample collected on 16 April 1971 from a sheltered population (●) and an exposed population (○). Vertical lines indicate the standard error ($p = 0.05$) of the mean (50 samples).

illustrates the analysis of floret weights in relation to the position within the spikelet, at the individual spikelet level. 50 complete spikelets (i.e. spikelets with the normal complement of florets present) were examined from both sheltered and exposed populations.

A significant decline in seed weight occurred in acropetalous succession in each spikelet, the lowermost seed being the heaviest (see Fig. 1). This seed was frequently up to 20 and 30 per cent heavier than the second and third ripe seeds, respectively. The analysis also indicated that there can be quite marked differences in seed weights not only within a spikelet but also between spikelets on the same panicle and on different panicles on the same plant. At the community level significant differences were also found; as Fig. 1 illustrates, seed weight in the exposed community was significantly ($p = 0.01$) lower than in the sheltered population plants.

The analysis of individual floret weights also revealed the presence of empty florets each of which weighed less than 0.5 mg. These florets consisted of a normal-sized lemma and palea; the mean lemma dimensions of both full seed and empty florets were *c.* 8.0 mm. long by *c.* 1.0 mm. wide, but the floral organs (ovary and anthers) of the latter were always completely atrophied. In a number of instances all the florets within a spikelet were empty, while in other spikelets only a single floret was empty. In the latter situation the empty floret was not restricted to any particular position within the spikelet. By weighing each floret in a random selection of 150 florets per site collected at the time of seed fall from each of the exposed and sheltered grassland communities, it was found that empty florets comprised about 20 per cent of the sample from the sheltered population and about 50 per cent of the exposed population sample. Further samples were weighed to check this result and in all cases there was a much higher percentage of empty florets in the exposed population seed sample. The cause of these empty florets is not known, although lack of fertilization of the ovary is probably the most

likely reason. However, they may also be caused by intense competition between individual florets or spikelets for available assimilate, resulting in the abortion of developing embryos.

These empty florets are obviously of considerable importance in any estimation of the sexual reproductive performance of *F. contracta* on South Georgia. An estimate of the actual seed production on an area basis (by adjusting the data for number of florets/m². in Table II, using the empty floret percentages noted above) indicated that c. 32,450 seeds/m² were produced by the sheltered grassland, compared with only c. 6,050 seeds/m² in the exposed grassland. When considering the greater percentage of empty florets in the exposed population panicles, it is obvious that the sexual reproductive performance, in terms of viable seed production, is reduced even at the individual spikelet level. This is not indicated in an assessment of floret production alone.

When determining the proportional weight contribution of the seed to either the panicle or whole culm, it was impracticable to separate the empty florets from the full seed in every analysis. Therefore, the combined seed + empty floret weights were used in preparing Table III.

TABLE III. MEAN DRY WEIGHT OF SEED, PANICLE AND WHOLE REPRODUCTIVE SHOOT IN SHELTERED AND EXPOSED POPULATIONS OF *Festuca contracta*

	<i>Sheltered community</i>	<i>Exposed community</i>
Reproductive shoot weight (mg.)	250 (± 10)	122 (± 15)
Panicle weight (mg.)	101 (± 5)	63 (± 8)
Seed weight (mg.)	0.82 (± 0.06)	0.59 (± 0.15)
Seed weight/panicle (mg.)	c. 72	c. 40
Seed weight as a percentage of panicle weight	c. 71	c. 63
Seed weight as a percentage of reproductive shoot weight	c. 29	c. 33

All data are the mean of 50 samples. Standard errors at 95 per cent confidence limits are given in brackets. The weight differences between the two populations are significant at the 95 per cent confidence level.

Although there was a significant reduction in the actual culm, panicle and mean seed weight in the exposed population plants, the proportional dry matter allocation into the seed with respect to dry matter investment into the whole culm was the same between the two populations, with the ripe seed + floret weight representing c. 30 per cent of the total culm weight. This similarity was mainly due to the reduced dry weight allocation into the non-panicle components of the culm, mainly through a reduction in culm height in exposed population plants (Tallowin and Smith, 1977). The evidence suggests that under stress conditions secondary sexual development (such as culm elongation) is affected to a relatively greater extent than seed development, and in this way seed production can be maintained under the stress conditions.

Besides the decline in seed weight with increasing habitat severity, it also appears that exposure affects the type and/or proportions of the stored food reserves in the seed. Seed samples, consisting of between 500 and 1,000 seeds, collected from each of the exposed and sheltered grassland populations, were dried at 70° C for 24 hr. and then extracted for 24 hr. in a Soxhlet apparatus using chloroform as the solvent. The solvent was then evaporated under vacuum and the lipid extract weighed. Two seed samples were analysed for each population. The sheltered population seed had a mean of 64.6 mg./g. dry weight of lipid compared with a mean of 55.0 mg./g. dry weight in the exposed population seed, the difference being significant at the 95 per cent confidence level. No data are available for seed carbohydrate levels.

SEED REPRODUCTIVE EFFORT

Ogden (1974) defined the sexual reproductive effort of a plant as "the proportion of the total annual net assimilate allocated to the seeds", or

$$\text{Sexual reproductive effort} = \frac{\text{Total seed weight per plant}}{\text{Total net annual gain in dry weight by the whole plant}}$$

This definition was used in calculating the sexual reproductive effort of *F. contracta* plants growing on South Georgia.

The data used for the calculation of sexual reproductive effort in *F. contracta* were obtained from a reciprocal transplant experiment. Single vegetative tillers, each bearing an adventitious root, were separated from hitherto undisturbed mature flowering plants growing in exposed upland and sheltered lowland grassland communities. The tillers were matched so that they all consisted of three green leaves, all the dead leaves being removed. The tillers were planted, three per 15 cm. diameter pot, in moist vermiculite (exfoliated mica), the two populations being grown in separate groups of pots. The vermiculite was watered regularly with a modified Hoagland's solution (see Callaghan and Lewis, 1971*b*) throughout the duration of the experiment (1½ years). After a 1 month establishment period in a cold frame at a sheltered "nursery" site, half of the plants from each population were transferred to a sheltered study site and the other half to an exposed site. These field sites were the I.B.P. primary and cryptogamic sites, respectively, described by Smith (1971). Harvests, consisting of 30 plants (i.e. ten randomly selected pots) per population per site, were taken at the end of the establishment period (January), after 1 month at the field sites (February), at the beginning of winter (April), at the onset of the spring melt (October), during the second summer (beginning of February) and at the end of the second summer (April). The plants were separated into shoot (above the level of the first adventitious root) and root, the latter being washed clean of all vermiculite. The shoot was separated into dead leaves, vegetative tillers and flowering tillers (which were further divided into panicle and non-panicle fraction of the culm). Each plant part was dried at 80° C to constant weight.

Table IV illustrates the results of this growth-study experiment in terms of the percentage

TABLE IV. NET ANNUAL DRY MATTER ALLOCATION INTO THE PANICLE AND SEED AS A PERCENTAGE OF THE TOTAL NET CHANGE IN WHOLE-PLANT DRY WEIGHT, IN TWO *Festuca contracta* POPULATIONS GROWN IN A RECIPROCAL TRANSPLANT EXPERIMENT AT TWO CONTRASTING FIELD SITES

Source of tillers and experimental site	Percentage dry matter allocation		
	(October 1971–February 1972) Panicle	(April 1971–April 1972) Panicle Seed	
Sheltered population grown at sheltered site	11.7	7.3	5.2
Exposed population grown at sheltered site	8.9	3.9	2.5
Sheltered population grown at exposed site	10.6	3.5	2.3
Exposed population grown at exposed site	No data available	4.4	2.7

dry matter allocation into the panicle and seed (sexual reproductive effort) in the two populations at the two sites. Clearly, the sheltered population plants grown at the sheltered site have a considerably greater sexual reproductive effort. Under the exposed growing conditions, the reduced dry matter allocation into sexual reproductive development was balanced by an increased allocation to the root system (see Fig. 2). Allocation into the vegetative shoot remained unaffected as did the allocation to the dead-leaf fraction (although material could have been lost through wind abrasion especially at the exposed site).

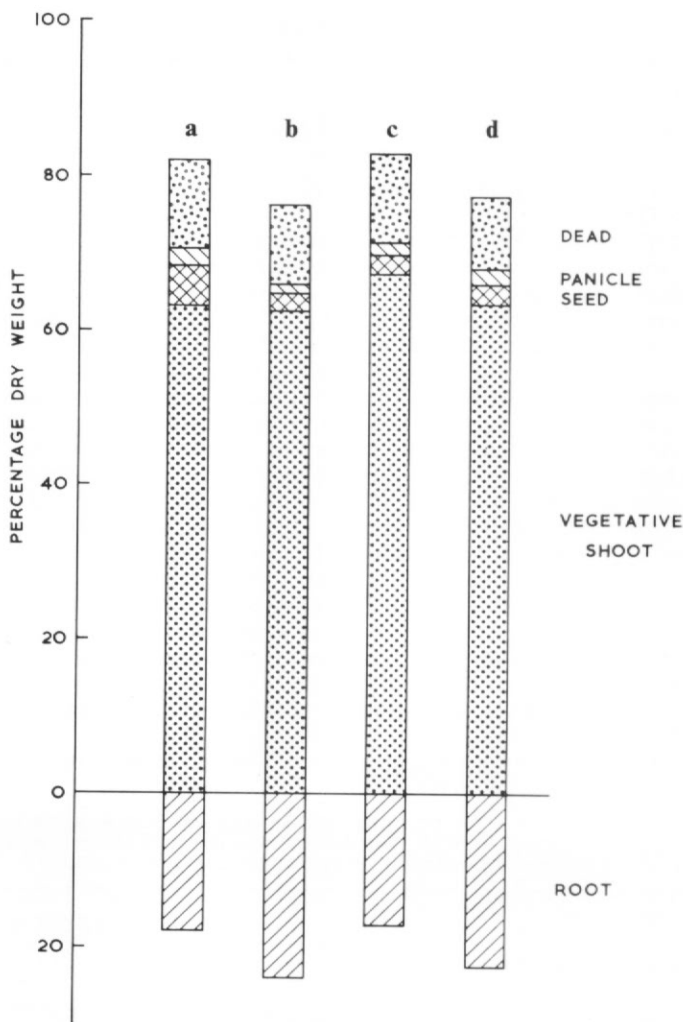


Fig. 2. The proportional dry matter allocation to the root, vegetative shoot, dead leaf lamina, panicle and seed fractions during a growing season. Sheltered population plants grown at a sheltered site (a) and an exposed site (b); exposed population plants grown at a sheltered site (c) and an exposed site (d). The length of each segment represents the percentage of the total dry weight gain by the plants during the season.

The reduced sexual reproductive effort in the exposed population plants growing at the sheltered site was largely due to the lower numbers of flowering tillers per plant compared with the sheltered population. This reduction was apparently caused by the production of relatively few competent tillers by each plant during the first growing season of the experiment. Individual tiller size appears to be important in determining floral competence in *F. contracta* (Tallowin and Smith, 1977); in the exposed population plants the mean tiller weight was significantly lower than in the sheltered population throughout the course of the experiment. This difference also occurred in *in situ* populations, where both flowering- and mean vegetative-tiller weights were found to decline with increasing habitat exposure. In the reciprocal transplant experiment, the exposed population plants at the sheltered site had an increased dry matter allocation to the vegetative-shoot fraction, when compared with the sheltered

plants at this site. This, as illustrated in Fig. 2, compensated for the reduced sexual reproductive effort in the exposed population plants.

The relatively high early season dry matter allocation to the panicle (see Table IV) was caused by differences in the timing of the sexual and vegetative reproductive developmental phases (Tallowin and Smith, 1977). This was revealed by data obtained from a series of small harvests taken at fortnightly intervals through a growing season in a closed (c. 80 per cent ground cover) sheltered grassland community (Fig. 3). Each harvest consisted of five randomly selected 25 cm.² quadrats, in which all the aerial shoots were clipped to ground level and separated into vegetative and flowering tillers and dead leaf laminae. These fractions were then dried at 80° C to constant weight. Each point in Fig. 3 represents the mean of the two harvests, taken 2 weeks apart, for a particular month. During the early part of the growing season (November–January) emphasis was on dry matter allocation into the flowering shoot, whereas during the latter part of the season (January–March) dry matter allocation into the vegetative shoot became increasingly important.

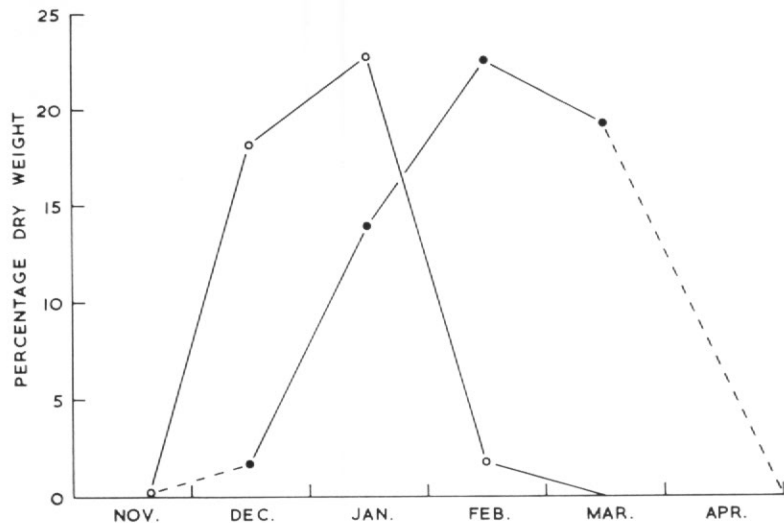


Fig. 3. Seasonal changes in the dry weight of the vegetative shoot (●) and flowering shoot (○) as a percentage of the overall shoot dry weight gain during a growing season in a sheltered grassland.

SEED DORMANCY AND GERMINATION

Seed samples were collected during the late autumn (mid April) from sheltered lowland (c. 15–30 m. a.s.l.) and exposed upland (c. 80–100 m. a.s.l.) grassland populations. Only seed ripe to fall, i.e. those easily shaken from the panicle, were kept for a series of germination trials. From collection to the time of testing, the seed were stored dry at c. 15° C. For all the germination trials the seed were placed on moistened soil in covered petri dishes, under daylight illumination of between 10 and 14 hr. duration and at a temperature of between 15° and 20° C. Four widely differing soil types were used during the trials:

- i. A loamy soil (pH 3.9) from a sheltered lowland *Festuca* grassland.
- ii. An acid peat (pH 3.1–3.6) from a *Poa flabellata* community influenced by elephant seals.
- iii. A sandy fluvio-glacial soil (pH 4.8) from an extensive, relatively exposed *Festuca* grassland.
- iv. A mineral soil (pH 4.6) from an exposed upland *Festuca* grassland.

As Fig. 4 illustrates, germination was very poor immediately following seed collection but improved dramatically with time, indicating the presence of a post seed-fall ripening requirement. This germination control prevents seed germination in the late autumn, when seedlings

would be particularly at risk from frost, cryoturbation and desiccation. The ripening requirement was quite variable within the seed sample, as shown by the continued increase in germination percentage up to trial III. This could reflect differences in the state of maturity at the time of seed fall, or possibly differences in the actual ripening requirement of the seed embryo. It is also possible that at trial III some viable seed still remained ungerminated.

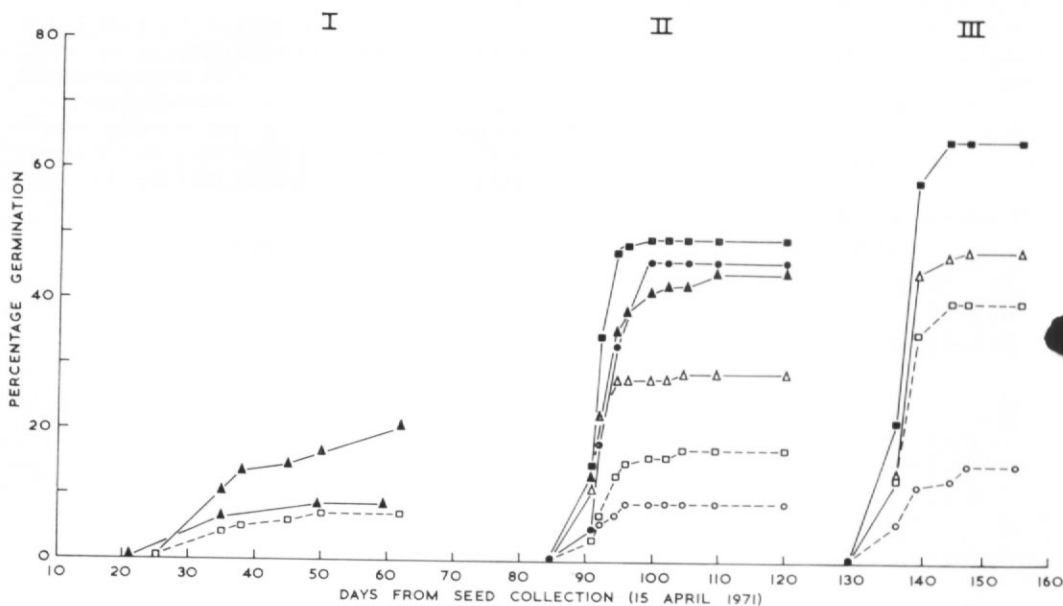


Fig. 4. Increase in the mean percentage seed germination with time, for sheltered population seed grown on a *Festuca* grassland loam (▲), a *Poa flabellata* peat (●), a *Festuca* grassland fluvioglacial sandy soil (■) and an upland *Festuca* grassland mineral soil (△), and for exposed population seed on the fluvioglacial soil (□) and the mineral soil (○). The seed were sown 21, 25, 84 and 130 days, respectively, after collection.

The prolonged dormancy of some seed could account for the protracted period over which germination occurs in the field. However, much of the variability observed in the field was due to differences in the micro-climate of the habitats into which the seed fell. Fig. 5 shows the changes in seedling numbers during a growing season as a percentage of the total number of seedlings found during the season in a sheltered grassland. One to two-leaf seedlings were counted at fortnightly intervals in five randomly selected 25 cm.² quadrats. Peak germination occurred between December and February. The changes in seedling appearance followed a parallel course to the mean monthly temperature curve, which suggests that the temperature requirement for germination is fairly variable within the seed population.

Seed viability in *F. contracta* is variable both within and between populations. The maximum germination (65–70 per cent) found during the trials was in seed samples collected in the 1970–71 growing season from a sheltered population; this compared with only 40 per cent for the exposed population seed (see Fig. 4). Samples of seed also collected in mid April from the same sheltered grassland population in the following year (1971–72) had a maximum germination percentage of less than 20 per cent, while the corresponding figure for the exposed population was 37 per cent, only slightly lower than that of the preceding season. Identical storage and germination conditions were used in both years. The reason for the decline in seed viability in the sheltered population is not known. If it was in response to differences in the climate of the seasons, both populations may be expected to have been affected to the same degree; however, this was clearly not the case. The lowest seed viability occurred in a high-altitude (c. 250 m. a.s.l.) population growing on an exposed windswept col. Here the mean

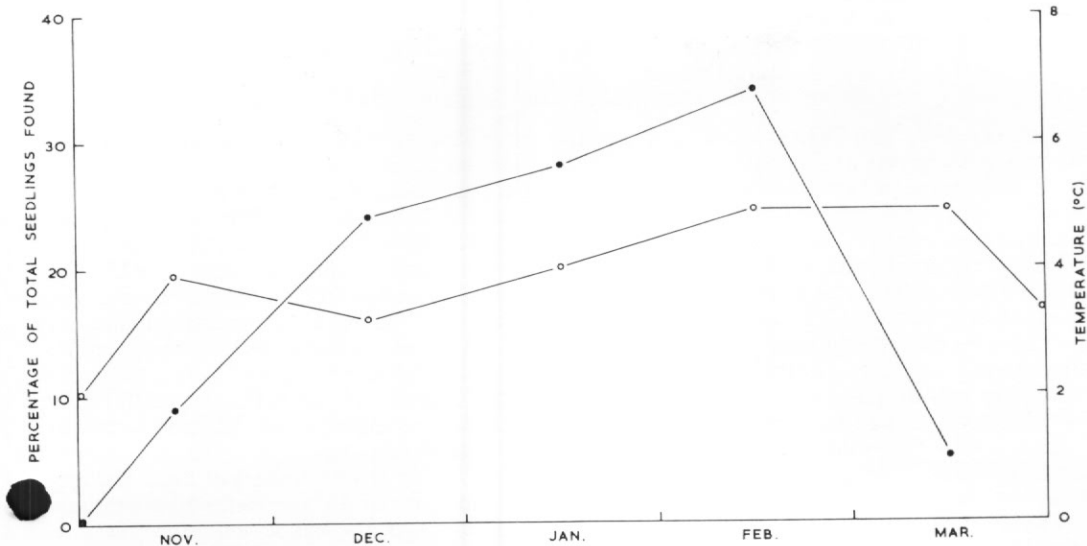


Fig. 5. Seasonal changes in mean numbers of seedlings as a percentage of the total numbers of seedlings found during 1971-72 in a sheltered grassland (●) in relation to mean monthly air temperature (○).

maximum percentage germination was less than 15 per cent. It is probable that the general tendency for lower seed viability in exposed populations was due to the greater proportion of "empty" florets produced by these plants.

The reduced germination on the mineral soil (Fig. 4) was correlated with an increased fungal attack on the seed placed on this soil (Fig. 6). A large percentage of the seed became covered by fungal hyphae, which then persisted in most cases until the trial was terminated. Fungal attack was much less severe and less persistent on the other soil types (Fig. 6). This suggests, assuming it is a naturally occurring soil fungus, that it may kill many of the seed on the

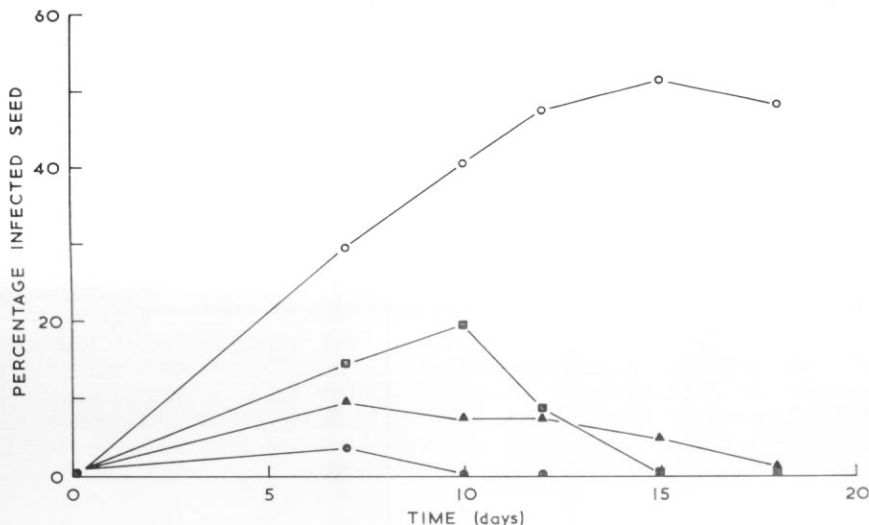


Fig. 6. Percentage of the sheltered population seed samples infected with fungal hyphae on a *Festuca* grassland loam soil (▲), a *Poa flabellata* peat (●), a *Festuca* grassland fluvio-glacial sandy soil (■) and an upland *Festuca* grassland mineral soil (○).

mineral soil, whereas on the more organic acid soil types the fungal vigour was reduced, possibly by soil antibiotic activity which is apparently lacking in the mineral soils.

SEEDLING ESTABLISHMENT AND SUBSEQUENT SURVIVAL

Between 1971 and 1973, *F. contracta* seedling establishment was studied in several habitats, namely a sheltered lowland (0–c. 50 m. a.s.l.) grassland community and an exposed upland (c. 50–100 m. a.s.l.) community, and an area of loam soil cleared of vegetation in the former grassland and an exposed barren mineral soil adjacent to upland *Festuca* stands. In each habitat all seedlings and immature plants were removed from two marked quadrats (1 m.²) which were established in 1971. These quadrats were re-examined in the autumn of 1973, when the numbers of live immature plants, consisting of more than one tiller, were recorded. None, other than apparently transient one-leaf seedlings, was found on the bare mineral soil and only two had become established in the quadrats on the loam soil. In the grassland communities, only two immature plants had become established in the sheltered lowland area where senescing mature plants had caused an opening in the canopy; in the exposed grassland five immature plants had become established, all of which were in either moss cushions or turves.

Frost heaving, followed by desiccation, was probably responsible for the majority of seedling losses on bare soil; this was indicated by the relatively large numbers of dead seedlings lying on the soil surface. Competition for light and nutrients within the sheltered community probably accounted for the scarcity of immature plants. It appears that seedlings are recruited into the population only where a gap in the ground cover has been created, providing a situation free from intense competition for light. The scarcity of immature plants in the more open upland communities is probably largely due to the low production of viable seed by the mature plants growing in these areas. The high winds, prevalent especially in the upland areas of South Georgia, may also be an important contributory factor to the low seedling survival. The whipping and buffeting action tends to raise the weakly rooted young plants from the soil and exposes them to desiccation.

On South Georgia *F. contracta* is a secondary colonizer with successful establishment being largely confined to mesic bryophyte communities. Isolated plants in exposed upland areas tend to be confined to sheltered rock crevices or amongst stable scree and in the lee of large boulders. The growth habit (tufted and erect) makes the species particularly vulnerable to wind damage and, not surprisingly, plant stature declines markedly with increasing altitude and exposure.

F. contracta is also absent from wetter areas, apparently due to its intolerance to the anaerobic conditions which prevail in bog habitats. Evidence for this was provided by an experiment in which 60 vegetative tillers were planted in individual pots containing a *Festuca* grassland loam soil. 30 pots were placed in a *Rostkovia*–*Juncus* bog, with the soil surface in the pots level with the surface of the bryophyte understorey in the bog; the pots became waterlogged immediately. The remaining 30 pots were placed in an adjacent stand of *Festuca* grassland, again with the soil in the pots level with that of the grassland soil. A further 60 tillers were planted individually in pots in the highly organic bog soil; half the pots were placed in the *Festuca* grassland and half in the bog.

All the tillers planted in both soil types in the bog area had died within 4–6 weeks. The tillers planted in the bog soil and placed in the *Festuca* grassland all flourished and actually grew far better than the tillers planted in the grassland soil at this site. None of the bog soils examined *in situ* was particularly acid, although those dominated by *Rostkovia magellanica* and *Polytrichum alpestre* are usually 1.2–2.5 pH units lower than those dominated by *Juncus scheuchzerioides* and *Tortula robusta* (Smith and Walton, 1975). In some cases the soil pH increased slightly along line transects from the drier *Festuca* grassland areas (pH 4.0) into the bog areas (pH 4.5). Unfortunately, it was not possible to determine the oxygen requirements and limiting conditions for the root system of *F. contracta*.

DISCUSSION

The limitations of the sub-Antarctic environment on plant growth and development have produced similarities in the reproductive behaviour and performance of *F. contracta* that are

common to many species found in other cold regions of the world. The evolution of autumnal floral initiation and the development of cleistogamous flowers are adaptations necessary for ensuring the completion of the sexual reproductive cycle, fertilization of the ovary and subsequent seed development in these environments. Even so, polar environments are not conducive to successful sexual reproduction; this is perhaps indicated most clearly by the scarcity and slowness of seedling establishment (Billings and Mooney, 1968; Billings, 1974). Not surprisingly, the relative importance of asexual reproduction increases under conditions of increasing environmental stress, while sexual reproduction declines in importance (Bliss, 1971).

In *F. contracta* the sexual reproductive performance, represented by the seed production, either on a plant or area basis, declined significantly with increasing habitat severity, principally exposure to high winds. Not only were fewer flowering tillers initiated per plant (Tallowin and Smith, 1977) but also the fecundity of the panicle was reduced under the exposed growing conditions. Reduced floret and seed production resulting from severe habitat conditions has also been found in another South Georgian grass, *Phleum alpinum* (Callaghan and Lewis, 1971a). The reduced seed production in *F. contracta* at the panicle/spikelet level was caused mainly by a high percentage of empty florets in the exposed population. The cause of these is not known but certainly the phenomenon deserves further research.

Mean seed weight in *F. contracta* also declined with increasing habitat severity. A similar "stress" effect on seed weight has been reported by Baker (1972), who found a correlation between mean seed weight and altitude in the Californian mountains. He suggested that this could represent a strategy in which reduction in available photosynthate is reflected in smaller seeds. Certainly this, together with a study of stress effects on stored food reserves in the seed, would be worth examining in *F. contracta*. In the present study, the lower lipid levels in the exposed population seed indicated that significant changes in stored reserves do occur. The heavier sheltered population seed, with their greater food reserves, might be expected to have a competitive advantage over the lighter seed when germinating in communities dominated by plants with tall growth forms, where shading during seedling establishment is likely to occur. This situation exists in lowland areas but not in the open exposed upland communities where plant stature is usually significantly reduced. Therefore, it is possible that the lighter seed, presumably with lower food reserves, do not confer an overall reduction in survival chances in exposed upland habitats, as there is likely to be little competition for light even in the initial stages of seedling establishment. The lighter seed also have a greater dispersibility, although perhaps this is largely offset by the reduced production of viable seed in these communities.

A study of dry matter partitioning within mature *F. contracta* plants revealed that the annual seed reproductive effort was between 2.3 and 5.2 per cent of the net annual gain in whole plant dry weight. The sexual reproductive effort was significantly reduced under exposed growing conditions. This result is interesting because Lambert (1968), working on *Dactylis glomerata*, found similar levels of sexual reproductive effort, but in this grass the reproductive effort was reduced by aerial competition (for light) but not by edaphic factors (such as low nitrogen levels), except when both light and nitrogen were limiting together. In *D. glomerata*, when the plants were competing neither for light nor nitrogen, the seed reproductive effort was 4.9 per cent. However, it was 4.7 per cent when the plants were competing for light, 6.4 per cent when they were competing for nitrogen and 4.3 per cent when they were competing for both. In the reciprocal transplant experiment on *F. contracta* there was little aerial competition between plants and, as the soil medium was watered regularly with a nutrient solution, it is probable that there was little or no competition for nutrients. This suggests that in this species the reduction in sexual reproductive effort was caused by micro-climatic factors.

The results of this experiment also indicated that there was strong genetic control over sexual reproductive effort in the exposed population plants. However, it is possible that there are ecotypic differences between the population, resulting from isolation through inbreeding and the more vegetative reproductive strategy of plants growing in such rigorous environments.

Under the exposed growing conditions there was a significant reduction in the dry matter investment into the shoot region (vegetative+flowering) and a corresponding increase in the investment into the root system. The reduced allocation to the shoot mainly reflected the effect on sexual reproductive effort, as the dry matter investment into the vegetative shoot remained similar between the plants growing at the sheltered and exposed sites, with the

exception of the greater investment into the vegetative shoot in the exposed population plants growing at the sheltered site. The latter was apparently caused by the reduced flowering in the exposed population plants, which diminished the overall seasonal competition for assimilate between vegetative and sexual reproductive development. A greater tolerance by vegetative reproduction to stress conditions compared with sexual reproduction has also been found in *Phleum alpinum* on South Georgia (Callaghan and Lewis, 1971a); in this species, although seed production was generally negatively correlated with habitat severity, vegetative reproduction proved to be very similar in exposed and sheltered habitats.

The viability of *F. contracta* seed was variable between different populations. There was a general tendency for it to decline with increasing exposure and/or altitude. This was probably largely due to the greater percentage of empty florets produced by plants growing under stress conditions. A post seed-fall ripening requirement is necessary before germination can occur. This type of seed dormancy is not common in cold-region plants and Amen (1966) reported it in only two (*Cerastium beringianum* and *Saxifraga rhomboidea*) of the 60 alpine species he examined. The adaptive significance of this after-ripening requirement in *F. contracta* is that it inhibits seed germination during the late autumn when intense frost action is prevalent. The frequent freezing and thawing of the soil forces the roots of the seedlings to the surface where they are exposed to desiccation which ultimately results in their death. Once the ripening requirement is satisfied, germination is apparently opportunistic. However, it appears that considerable variation exists between seeds both in their ripening and their germination requirements. This was indicated by the appearance of seedlings in the field throughout much of the summer (December–February).

Successful seedling establishment is largely confined to situations where the ground is stable and not susceptible to frost heaving, such as within moss cushions and turves, and degenerating *Festuca* and *Phleum* tussocks. In common with most Arctic and alpine species of the Northern Hemisphere (Billings and Mooney, 1968; Billings, 1974), successful seedling establishment in *F. contracta* is apparently both rare and slow.

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