PRELIMINARY GROWTH STUDIES ON *Festuca contracta* T. Kirk AND *Deschampsia antarctica* Desv. ON SOUTH GEORGIA

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Abstract. The results of some preliminary experiments investigating aspects of germination, growth, production and decomposition in *Festuca contracta* on South Georgia are reported. A parallel study of growth and production in *Deschampsia antarctica* was also undertaken.

Between 25 and 45 per cent of the *Festuca* seeds tested germinated after 50 days with the greater viability occurring in seeds which had not received cold pre-treatment. Growth of *Festuca* and *Deschampsia* seedlings in nutrient-treated vermiculite over a 15 month period resulted in *Deschampsia* attaining a mean total-plant dry weight of 55 times that of *Festuca*, due mainly to the exceedingly high production of tillers and leaves in the former species during the second summer. Changes in standing crop production in a *Festuca* grassland were followed through one growing season. Peak production occurred between late January and early February, and variations in rate of production appeared to be correlated with fluctuations in local climatic conditions. Standing dead and current year's green foliage of *Festuca* placed amongst the litter layer revealed an unexpectedly high annual rate of decomposition with up to 25 per cent dry-weight loss for standing dead material and 56 per cent for green leaves. The number of viable bacterial colonies isolated from *Festuca* litter and the underlying soil was considerably greater in the former.

Festuca contracta T. Kirk (= *F. erecta* D'Urv.) is an important component of the native vascular flora of South Georgia but, as with many of the phanerogams on that island, it is commonest and forms the most extensive closed stands in the Stromness Bay–Hound Bay area on the north-east coast (Greene, 1964). Elsewhere on South Georgia *F. contracta* is sparsely distributed among communities dominated by mosses (especially *Chorisodontium aciphyllum*, *Tortula robusta* and species of *Racomitrium*) and *Acaena magellanica* (= *A. decumbens*) where it occurs as short isolated tufts. It decreases considerably in abundance towards the northern and southern extremities and is rare on the south-west side of the island where the climate appears to be harsher, particularly during the growing season (November–March). A comparison between the weather at Bird Island, off the north-western extremity of South Georgia, and King Edward Point (Cumberland East Bay) revealed that the more northerly station had cooler summers but warmer winters than King Edward Point, as well as considerably less sunshine, particularly during the summer, greater cloud cover, more days of fog throughout the year and consequently a higher humidity. However, precipitation, converted to equivalent rainfall, was higher at King Edward Point (Richards and Tickell, 1968).

Within its principal area of distribution *Festuca* forms extensive grassland in lowland coastal areas. These stands range from closed dense swards of relatively tall grass, covering several hectares with low cover afforded by associated species, to more discontinuous grassland with high cover of bryophytes and lichens (e.g. *Chorisodontium aciphyllum*, *Polytrichum alpinum*, *Tortula robusta*, *Cladonia* spp.) and scattered phanerogams (e.g. *Acaena* spp., *Phleum alpinum*, *Rostkovia magellanica*). The more closed grassland develops on well-drained loamy to somewhat stony soil ranging from near sea-level to about 160 m. on level and sloping terrain, particularly where there is a northerly aspect, although scattered individual plants have been recorded to *c.* 575 m. Wherever the habitat becomes wetter *Festuca* decreases in abundance and the grassland rapidly intergrades with stands dominated by *Juncus scheuchzerioides*, *Rostkovia magellanica*, *Dicranoloma subimponens*, *Drepanocladus uncinatus*, *Tortula robusta* and other marsh bryophytes. At higher altitudes, where the environment is drier and more windswept, *Festuca contracta* develops a much shorter tufted growth form and the plants are almost always sparsely distributed.

Although *Festuca contracta* produces abundant viable seed, seedlings do not appear to be capable of rapid growth, tiller production or spread. Seedling establishment is most successful on the more organic substrata, particularly in moss banks formed by *Chorisodontium aciphyllum* and *Polytrichum alpestre* and also amongst *Festuca* plants themselves where a warmer, moister and more sheltered micro-climate exists. The intolerance of *Festuca* seedlings to highly mineral

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or permanently saturated soils probably accounts for the very sparse colonization of such habitats by the grass.

Deschampsia antarctica Desv. has a considerably wider ecological amplitude and distribution on South Georgia than *Festuca contracta*. *D. antarctica* is common in all areas of the island as isolated or coalesced tufts in most habitats, being present in most community types from sea-level to at least 560 m. It tends to develop a short, somewhat prostrate growth form in dry windswept situations, but it produces a taller more luxuriant tufted habit in sheltered wet habitats. However, in several localities *Deschampsia* forms extensive closed stands with only occasional bryophytes as associates (e.g. *Drepanocladus uncinatus*, *Calliergon sarmentosum*, species of *Brachythecium* and foliose hepatics). These swards develop on level, damp to permanently wet low-lying coastal areas, usually overlying decomposed peat formed by mosses or *Poa flabellata*, and often enriched by nitrogenous run-off from nearby seal or bird colonies.

In contrast to *Festuca contracta*, *Deschampsia antarctica* becomes a more important constituent of the vascular flora towards the northern and southern ends of the island. Its apparent ability to become established rapidly by seed and to tolerate prolonged snow cover, a wide range of edaphic conditions and exposure to wind must contribute towards the success of the species in the Antarctic botanical zone where it occurs as far as lat. 68°S. in Marguerite Bay (Greene and Holtom, 1971).

D. antarctica produces large quantities of viable seed which readily germinate on most moist substrata but unlike those of *Festuca* they have a greater rate of growth and tillering, and thus colonize available habitats much more rapidly.

During 1969–71 a programme was initiated (by C.S.) to investigate some aspects of the primary production of these native grasses, in order to determine their contribution to the biomass of two ecologically important grassland ecosystems on South Georgia.

Experiments

Growth of Festuca contracta and Deschampsia antarctica seedlings over a 15 month period

Method

Two-leaved seedlings of *Festuca contracta* and *Deschampsia antarctica* were collected from a sheltered low-altitude site and transplanted into vermiculite contained in 15 cm. diameter black polythene pots at a density of five plants per pot. These were then grown for about 2 months at a sheltered "nursery site" to allow the seedlings to become established. Throughout the duration of the entire experiment the pots were frequently supplied with a modified Hoagland's nutrient solution as described by Lewis and Greene (1970). After this establishment period, 30 pots of each species were matched in sets of three with regard to their aerial portions, and one set of ten pots (50 plants) of each species was harvested on 4 March 1970. Of the remaining two sets of pots of each species, one was transferred on that date to a moderately sheltered herbfield site on a north-facing *Festuca*-dominated slope at *c*. 40 m. altitude (= I.B.P. primary site, see Smith (1971)), and the other set to a fellfield site on a windswept knoll crest with sparse cryptogamic vegetation at *c*. 75 m. (= I.B.P. fellfield site, see Smith (1971)).

After 6 weeks at these field sites, five pots of each species (25 plants) were harvested on 17 April 1970 at each site. The remaining five pots per species per site were left *in situ* until the end of the following summer when the final harvest was taken on 31 March 1971. During this period the plants had been covered by snow from mid-April until mid-October. The vermiculite was also frozen continuously during this period as well as periodically before the onset of winter and after the disappearance of the snow cover until late November. During the winter the shallow-rooted *Festuca contracta* seedlings at the fellfield site were subjected to frost heaving which destroyed all the plants, although the *Deschampsia antarctica* seedlings were not affected.

At each harvest the entire plants were carefully removed from the vermiculite which was subsequently washed free from the roots. The plants were then divided into roots, shoots and leaves, the latter being considered as the blade beyond the leaf sheath and below which was included as part of the stem. *Festuca contracta* has a rigid rolled leaf and consequently the leaf area could not be determined using an air-flow planimeter. The approximate area was

estimated by measuring the length and diameter of a section of each leaf and treating the lamina as a cylinder. The area of the very narrow but more flattened leaves of *Deschampsia antarctica* was similarly determined by measuring the length and breadth of each leaf and treating the lamina as a rectangle. The areas thus determined for each species are suitable only for intra-specific comparisons.

The individual fractions of each plant were dried at *c*. 80° C and the dry weights determined. From the dry-weight data the mean relative growth rate (RGR) for each partition of the plants was calculated, while the net assimilation rate (NAR) and leaf-area ratio (LAR) were obtained for the leaf fractions. The formulae employed for these calculations have been described by Callaghan and Lewis (1971). Due to the long winter period, when no growth occurred and some of the leaves died or were broken off by the weight of snow, the calculations of relative growth rate for the third harvest were determined from the time when the pots became free of snow, i.e. mid-October.

Results

The values obtained for the mean dry-weight measurements, relative growth rates, net assimilation rates, leaf-area ratios and other growth parameters for *Festuca contracta* and *Deschampsia antarctica* seedlings at two field sites are given in Tables I and II.

Growth during first summer

Although the initial dry weights of the corresponding fractions of each species were almost identical, by the first harvest following a 2 month establishment period at the nursery site, *Deschampsia* had already almost doubled the dry weight of each fraction and number of leaves that had been produced by *Festuca*. The fact that there was little difference in their respective leaf areas was largely due to the greater length of the *Festuca* leaves. Relative growth rates for *Deschampsia* were correspondingly higher. This magnitude of difference between the various fractions of each species was maintained throughout the first season at each site. Between harvests 1 and 2, dry-weight investment in each species proceeded at a parallel rate so that after the 6 weeks at the field sites production of each fraction in both species doubled. However, the difference in the relative growth rates at the second harvest between respective fractions of the two species at either site was small and not significant.

No tillers were produced by either species during the first summer. At the more exposed fellfield site, dry-weight production and all growth parameters, with the exception of LAR, were depressed for each fraction of both species. An analysis of variance revealed that the differences in RGR of the entire plant per pot for each species between sites at the second harvest were not significant.

By the end of the first season, *Deschampsia* had established a net assimilation rate approximately 50 per cent greater than that of *Festuca*, although values for both species were comparatively low, particularly at the fellfield site. However, the leaf-area ratios at the second harvest were considerably higher in *Festuca* at both sites than in *Deschampsia*, which had a substantially smaller increase in leaf area in relation to total dry weight compared with that of *Festuca*. This was the only growth measurement at the fellfield site which exceeded the corresponding parameter at the herbfield site during the duration of the experiment.

Growth during second summer

After winter, *Deschampsia* appeared to recover very quickly from the prolonged snow cover during which time the rooting medium had been continually frozen, and growth and tillering proceeded rapidly throughout the following summer, particularly at the herbfield site. Because of their relatively shallow rooting system, the *Festuca* plants were damaged by frost heaving more than the *Deschampsia* plants and consequently none of the former survived the winter at the fellfield site, while those at the herbfield site remained fairly healthy but further growth and development was rather slow. Between the second and third harvests the mean total-plant dry weight of *Festuca* at the herbfield site increased by *c*. 7 times while that of *Deschampsia* at the same site increased by *c*. 170 times and *c*. 32 times at the fellfield site. By the end of the

TABLE I. MEAN GROWTH DATA FOR *Festuca contracta* AND *Deschampsia antarctica* SEEDLINGS GROWN IN NUTRIENT-TREATED VERMICULITE AT TWO SITES FOR 15 MONTHS

Date of harvest and site	*Festuca contracta*								*Deschampsia antarctica*							
	Dry weight/plant (mg.)				*Above: below ground dry wt. ratio*	*Total leaf area/ plant* (cm.²)	*Number of leaves/ plant*	*Number of tillers/ plant**	*Dry weight/plant* (mg.)				*Above: below ground dry wt. ratio*	*Total leaf area/ plant* (cm.²)	*Number of leaves/ plant*	*Number of tillers/ plant**
	Roots	*Shoots*	*Leaves*	*Total plant*					*Roots*	*Shoots*	*Leaves*	*Total plant*				
Seedlings planted: 8 January 1970 (mean of 50 plants)																
Nursery site	0·10	0·08	0·24	0·42	3·20	—	2·0	0	0·11	0·07	0·26	0·40	0·30	—	2·0	0
1st harvest: 4 March 1970 (mean of 50 plants)																
Nursery site	1·45	1·00	1·70	4·15	1·86	0·56	3·6	0	2·45	2·30	2·40	7·15	1·92	0·65	6·9	0
2nd harvest: 17 April 1970 (mean of 25 plants)																
Herbfield site	3·20	2·20	3·20	8·60	1·69	0·96	6·5	0	5·30	5·90	5·40	16·60	2·13	1·30	14·8	0
Fellfield site	2·50	2·30	2·80	7·60	2·04	0·84	6·1	0	4·10	4·90	4·50	13·50	2·29	1·11	12·0	0
3rd harvest: 31 March 1971 (mean of 25 plants)																
Herbfield site	11·90	17·20	21·50	50·60	3·25	c. 8·00	51·0	20·4	663·00	1,328·30	819·70	2,811·00	3·24	c. 100·00	408·7	136·9
Fellfield site	No plants survived								143·3	158·1	128·2	429·6	2·00	c. 20·00	168·8	54·2

* Excluding parent plant.

TABLE II. MEAN RELATIVE GROWTH RATES, NET ASSIMILATION RATES AND LEAF-AREA RATIOS FOR *Festuca contracta* AND *Deschampsia antarctica* SEEDLINGS

	Festuca contracta				*Deschampsia antarctica*			
	Roots	*Shoots*	*Leaves*	*Total plant*	*Roots*	*Shoots*	*Leaves*	*Total plant*
RGR (g./g./week)								
Between planting and harvest 1 : nursery site	0·33	0·32	0·245	0·29	0·39	0·44	0·28	0·35
Between harvests 1 and 2:								
herbfield site	0·13	0·13	0·10	0·12	0·12	0·15	0·13	0·13
fellfield site	0·09	0·13	0·08	0·10	0·08	0·12	0·10	0·10
Between harvests 2 and 3:								
herbfield site	0·06	0·09	0·08	0·08	0·21	0·24	0·22	0·22
fellfield site	—	—	—	—	0·16	0·15	0·15	0·15
NAR (g./dm.²/week)								
Between harvests 1 and 2:								
herbfield site				0·10				0·16
fellfield site				0·08				0·12
Between harvests 2 and 3:								
herbfield site				0·06				0·54
fellfield site				—				0·28
LAR (dm.²/g.)								
Between harvests 1 and 2:								
herbfield site				1·23				0·85
fellfield site				1·23				0·87
Between harvests 2 and 3:								
herbfield site				1·35				0·57
fellfield site				—				0·64

The time between planting and harvest 1 was 7·9 weeks and between harvest 1 and harvest 2 was 6·3 weeks. The time between harvests 2 and 3 is taken as 23 weeks commencing in mid-October when the pots became uncovered by winter snow.

second summer at the herbfield site the mean total dry weight of *Deschampsia* was about 55 times greater than that of *Festuca*. Most of this increase was due to shoot production resulting from the very large number of tillers per plant. At the end of the first summer there was little difference between the mean dry weight of the various fractions of either species at corresponding sites, but by the end of the following year there was considerably greater dry-weight production of shoots than of roots or leaves in *Deschampsia* at the herbfield site, although in *Festuca* there was little difference in dry-weight partitioning. However, in *Deschampsia* at the fellfield site there was again little difference between fractions but the values were very much less than those at the more favourable site. In the case of *Festuca* the leaves contributed a slightly greater dry weight than the shoots, probably due to their much greater length than those produced by *Deschampsia*.

Although there was a considerable difference in dry-weight production between the two species throughout the experimental period, particularly at the end of the second summer, the mean above : below ground dry-weight ratio in both species remained similar at each site at respective harvests. This suggests that the rate of dry-weight partitioning in the two grasses follows a similar pattern when grown in the same environmental conditions.

Despite the high rate of production of tillers and leaves in both species during the second summer, the mean number of leaves per tiller decreased appreciably in *Festuca* from 6, for the entire plant (= single tiller) at the end of the first season, to 2·5 by the end of the second season, and in *Deschampsia* from 15 to 3 at the herbfield site, and from 12 to 3 in the same species at the fellfield site. While the mean dry weight of the aerial parts (shoots + leaves) per tiller (= entire plant) doubled during the first summer in both species, by the end of the following summer the high production of tillers reduced the mean dry weight of this combined fraction per tiller to half that existing at the end of the previous summer in *Festuca* at the

herbfield site and in *Deschampsia* at the fellfield site. However, this ratio increased by about half in *Deschampsia* grown at the herbfield site, the bulk of this weight increase being in the shoots of the large number of tillers. There was no evidence of the development of inflorescences in either species. Although leaf-area measurements at the end of the second summer were only approximate, specific leaf area (leaf area/leaf) in *Deschampsia* at the herbfield site more than doubled due to the production of relatively broad long leaves. At the fellfield site, *Deschampsia* leaves were fairly tightly rolled. The specific leaf area for these plants and for *Festuca* at the herbfield site increased only marginally.

By the end of the second season the relative growth rates of the three fractions of *Festuca* at the herbfield site had decreased since the previous harvest, notably that of the root. In contrast, the relative growth rates of each fraction in *Deschampsia* increased considerably at the herbfield site, particularly the root fraction. However, RGR's calculated over such a long time are not very meaningful since they represent a mean for the season, incorporating both periods of rapid growth early in the season and negative growth later in the summer. During the second year the mean dry weight of *Festuca* roots per tiller decreased five-fold compared with the corresponding value at the end of the first season, whereas the value for *Deschampsia* was similar in each season at both sites. Since the ratio of total-plant dry weight to leaf area of *Deschampsia* greatly exceeded that of *Festuca* in the second season, the respective net assimilation rates for the two species at the herbfield site differed significantly. *Deschampsia* attained a relatively high value at both sites. Although the leaf-area ratios decreased slightly in the second summer, those of *Deschampsia* were again lower than *Festuca* because of the lower leaf-area : total dry-weight ratio.

The rapid growth and development of *Deschampsia antarctica* in a nutrient-treated medium suggests that this species is much more successful than *Festuca contracta* in the relatively severe conditions prevailing on South Georgia. Under natural conditions *D. antarctica* may be considered a pioneer species as it is one of the few vascular species which commonly colonizes barren mineral soils of fellfield areas, moraines and fluvio-glacial detritus, and is one of the very few species which occurs on nunataks and at high altitudes (i.e. above 500 m.) on the island. *F. contracta* is a frequent but sparse associate in fellfield communities but its ecological amplitude is considerably narrower than that of *Deschampsia*. The tolerance of *D. antarctica* to adverse situations may help to explain its success as one of the two vascular species which occurs in the maritime Antarctic as far as lat. 68°S. on the west coast of the Antarctic Peninsula (Greene and Holtom, 1971).

Seasonal changes in standing crop production in Festuca contracta grassland

Method

Although *Festuca contracta* produces locally extensive closed swards, at least 75 per cent of the cover is afforded by standing dead foliage and detached litter. In such stands, because of the dense growth of the coalesced *Festuca* tufts interwoven with dead foliage, few associated species are present and provide little cover. The site selected for study was a stand of closed *Festuca contracta* situated at *c.* 40 m. a.s.l. on a moderately sheltered, gently sloping north-facing hillside *c.* 100 m. east of the herbfield site described in the previous experiment. The distribution of the associated species was very uniform, although *Polytrichum alpinum* and *Tortula robusta* tended to be somewhat contagious. The principal phanerogamic associate was *Acaena magellanica*, while scattered leaves of *Rostkovia magellanica* occurred throughout the stand. Several species of foliose hepatic were frequent amongst the mosses and over the *Festuca* litter but lichens were almost entirely absent.

The sampling plot, measuring 6 m. by 1·5 m., was subdivided with string into a grid of 10 cm. by 10 cm. squares. Harvesting occurred at 3 week intervals, commencing in late November 1969 and continuing until late March 1970. Samples were taken only from alternate horizontal and vertical rows in the grid, thus preventing any two adjacent samples being taken during the same or between different harvests. In this way any "edge effect" was eliminated. At each harvest 20 of the 10 cm. by 10 cm. squares, selected from a table of random numbers, were clipped to ground level and subsequently sorted into various above-ground fractions, namely the sub-division of each species into photosynthetic, non-photosynthetic and standing

dead material. The detached and partly decomposed litter fraction was not sampled. The culm of the grass was included in the non-photosynthetic fraction, while the green panicle was included in the photosynthetic fraction. Towards the end of summer, after seed formation, the entire inflorescence became dry and woody and was then treated as standing dead material. Each fraction was dried at *c*. 80° C before its dry weight was determined.

Results

The mean dry-weight data for the living photosynthetic, living non-photosynthetic and standing dead fractions of each species at each harvest are given in Table III, while the relative growth rates for the living aerial fractions are given in Table IV. Total sunshine, mean air temperature and mean wind-speed data for each of the growing periods of the experiment are given in Table V.

Although the sampling site was representative of well-developed closed *Festuca contracta* grassland, it is evident from the results that the major living constituents of the community were bryophytes despite their visually low percentage cover. All species of moss and liverwort were grouped together as a single fraction, although it comprised mainly *Tortula robusta* and *Polytrichum alpinum*. It is also clear that the bulk of the vegetation is dead *Festuca*, which represents the accumulation of leaf production over several years. This fraction does not include detached *Festuca* litter which, in its decomposing state, is considered as being no longer part of the plant community but rather a component of the soil with which it is partially incorporated. The other constituents of the stand, *Acaena magellanica* and *Rostkovia magellanica*, contributed only a small proportion of the total living phytomass.

Changes in the dry-weight production of living (i.e. photosynthetic + non-photosynthetic) and standing dead *Festuca* and total vascular species, and of living bryophytes are illustrated in Fig. 1. Net production for each of the growing periods between harvests appeared to be fairly closely correlated with fluctuations in amount of solar radiation, recorded as mean daily hours of sunshine, and with mean daily air temperature.

Changes in living phytomass

The production of new *Festuca*, *Acaena* and bryophyte growth was well under way by the time of the first harvest but a proportion of the previous season's grass leaves were still chlorophyllous. Dry-weight production of living *Festuca* and *Acaena* increased steadily until late January to early February by which time most leaf growth, elongation of culms and expansion of the spikes had taken place in the grass. During the period 27 November–18 December, growth conditions were very favourable with relatively high mean air temperature and total sunshine resulting in a substantial increase in dry weight and RGR of both living fractions. During the following 3 weeks mean data for both these climatic parameters decreased considerably and the rate of dry-weight production and the RGR of the photosynthetic and non-photosynthetic material were almost halved. Between 9 and 28 January there was an increase in total solar radiation and a slight rise in mean air temperature, which was reflected in an increased rate of living dry-weight production, particularly in the non-photosynthetic fraction of *Festuca*. This increase in the grass resulted from the elongation of the culms which consequently produced a relatively high RGR. Although leaf production was largely completed by mid-January, the continued increase in dry weight of photosynthetic tissue was due to the development of the immature spikes, which at that stage were green and therefore considered as part of the photosynthetic fraction.

From early February onwards the grass leaves gradually died back from the apices and, following the production of mature seed about mid-February, the inflorescences rapidly lost their moisture, became woody and also died. During this period there was also a progressive decrease in the dry weight of *Acaena*. Between 28 January and 18 February the total number of hours of sunshine decreased by one-third and the mean air temperature also dropped marginally. This coincided with the commencement of dry-weight loss in the photosynthetic fractions of the grass and shrub producing a negative RGR. The non-photosynthetic fraction of *Festuca*, on the other hand, being composed of culms and leaf sheaths, continued to increase in dry weight although with a reduced RGR. Between 18 February and 13 March there was

Table III. Mean dry weight per harvest and mean daily production between consecutive harvests for aerial fractions of all components of *Festuca contracta* grassland

Species and fraction	*Harvest 1* *27 Nov. 1969* (g./m.²)	*Harvest 2* *18 Dec. 1969* (g./m.²)	(g./m.²/day)	*Harvest 3* *9 Jan. 1970* (g./m.²)	(g./m.²/day)	*Harvest 4* *28 Jan. 1970* (g./m.²)	(g./m.²/day)	*Harvest 5* *18 Feb. 1970* (g./m.²)	(g./m.²/day)	*Harvest 6* *13 Mar. 1970* (g./m.²)	(g./m.²/day)	*Harvest 7* *31 Mar. 1970* (g./m.²)	(g./m.²/day)
Festuca contracta													
Living photosynthetic	50·2	78·0	1·32	93·3	0·70	128·1	1·83	115·6	−0·60	105·0	−0·46	71·5	−1·86
Living non-photosynthetic	23·0	38·8	0·75	51·5	0·58	86·4	1·84	98·0	0·55	90·1	−0·34	81·2	−0·49
Standing dead	639·5	652·0	0·60	660·0	0·36	665·0	0·26	671·5	0·31	709·0	1·63	751·0	2·33
Acaena magellanica													
Living photosynthetic	7·1	13·2	0·29	19·2	0·27	26·9	0·41	25·0	−0·09	9·3	−0·68	4·3	−0·24
Living non-photosynthetic	27·3	19·5	−0·37	27·6	0·37	27·7	0·05	26·1	−0·08	18·1	−0·35	20·6	0·14
Standing dead	2·1	3·6	0·07	3·8	0·01	5·4	0·08	5·2	−0·01	9·2	0·17	8·0	−0·07
Rostkovia magellanica													
Living photosynthetic	0·6	3·1	0·12	4·4	0·06	2·6	−0·09	3·5	0·04	2·0	−0·07	2·1	0·01
Living non-photosynthetic	0·3	1·5	0·06	1·9	0·02	1·1	−0·04	1·8	0·03	0·9	−0·04	1·8	0·05
Standing dead	3·6	4·1	0·02	6·0	0·09	3·0	−0·16	5·0	0·10	3·0	−0·09	4·0	0·06
Bryophytes													
Living photosynthetic green	115·6	156·0	1·92	149·3	−0·30	139·1	−0·54	121·4	−0·84	104·1	−0·75	100·4	−0·21
Living non-photosynthetic brown	116·0	131·0	0·71	156·8	1·17	136·4	−1·06	120·4	−0·76	90·5	−1·30	95·3	0·27
Total above-ground phytomass													
Living photosynthetic	173·4	250·3	3·66	266·1	0·72	296·6	1·61	265·5	−1·48	220·4	−1·96	178·2	−2·34
Living non-photosynthetic	166·6	190·7	1·15	237·8	2·14	251·5	0·72	246·3	−0·25	199·5	−2·04	198·8	−0·04
Standing dead	645·2	659·7	0·69	669·7	0·45	673·4	0·20	681·7	0·40	721·2	1·72	763·0	−2·32

"Standing dead" does not include the [illegible]ched and partly decomposed litter fraction.

TABLE IV. RELATIVE GROWTH RATES FOR PRINCIPAL AERIAL FRACTIONS OF SOME COMPONENTS OF *Festuca contracta* GRASSLAND

Species and fraction	*Relative growth rate* (g./g./week)					
	Harvest 1–2	*Harvest 2–3*	*Harvest 3–4*	*Harvest 4–5*	*Harvest 5–6*	*Harvest 6–7*
Festuca contracta						
Photosynthetic	0·147	0·057	0·116	−0·034	−0·029	−0·149
Non-photosynthetic	0·174	0·090	0·192	0·042	−0·010	−0·041
Total living	0·155	0·069	0·145	0·000	−0·020	−0·096
Acaena magellanica						
Photosynthetic	0·207	0·119	0·124	−0·025	−0·301	−0·305
Bryophytes						
Photosynthetic green	0·100	−0·014	−0·027	−0·045	−0·047	−0·014
Total photosynthetic (all species)	0·122	0·019	0·040	−0·037	−0·057	−0·083

TABLE V. CLIMATIC DATA RECORDED AT KING EDWARD POINT FOR GROWING PERIODS

Climatic parameter	*Between harvests 1 and 2 27 Nov.– 18 Dec. 1969*	*Between harvests 2 and 3 18 Dec. 1969– 9 Jan. 1970*	*Between harvests 3 and 4 9– 28 Jan. 1970*	*Between harvests 4 and 5 28 Jan.– 18 Feb. 1970*	*Between harvests 5 and 6 18 Feb.– 13 Mar. 1970*	*Between harvests 6 and 7 13– 31 Mar. 1970*
Mean daily air temperature (°C)	5·6	4·3	4·45	4·1	4·9	1·5
Total number of days ≤0° C	4	4	1	4	6	14
Total sunshine (hr.)	165·1	109·1	126·4	85·8	112·9	41·1
Mean daily sunshine (hr.)	7·5	4·7	6·3	3·9	4·7	2·2
Mean daily wind speed (m./sec.)	6·6	4·4	4·7	4·5	4·9	4·1

another improvement in weather conditions with increased radiation and higher temperatures. However, by this time in the season all new growth had virtually ceased and both living fractions showed negative RGR's as die-back of leaves and inflorescences progressed. During the second half of March both the total duration of sunshine and mean air temperature had decreased very considerably, while air frost was recorded on 78 per cent of the days. There was a marked decrease in dry weight of both living fractions producing substantial negative growth rates, particularly for the photosynthetic material. By now, up to two-thirds of the distal portions of most living grass leaves were dead.

It should be noted that a small proportion of the lower part of many *Festuca* leaves, together with their sheaths, remain green and apparently alive throughout the winter, gradually dying completely during the early summer of the following year.

Although much bryophyte growth had occurred before sampling commenced in late November, total production of green and brown material continued until early January. From then onwards there was a steady decline in dry weight presumably due to decomposition of the lower portion of the moss shoots. The high rate of production early in the season coincided with the period when the mean daily sunshine and air temperature was highest and

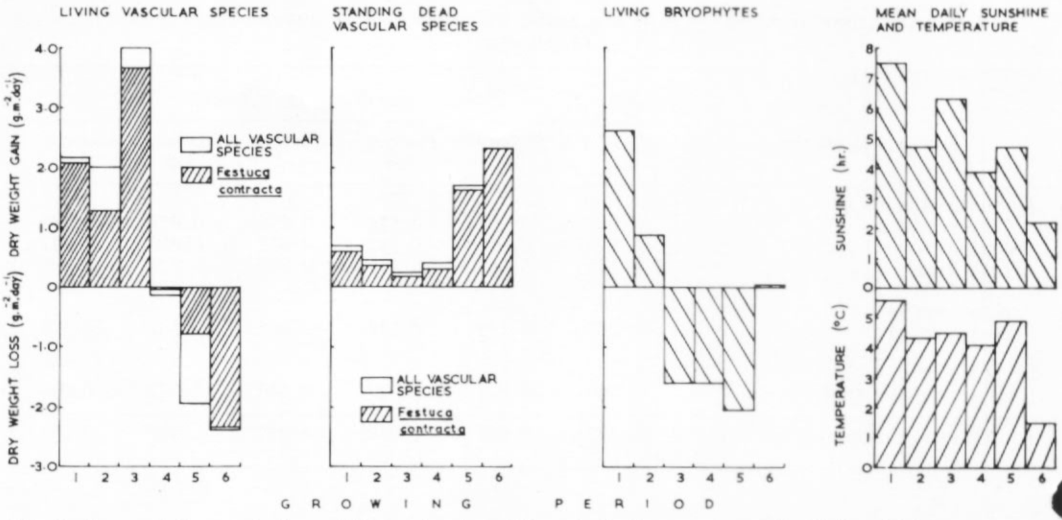

Fig. 1. Seasonal changes in dry-weight production of the principal components of a sheltered *Festuca contracta* grassland related to mean daily sunshine and air temperature. Growing periods: 1. 27 November–18 December 1970; 2. 18 December 1970–9 January 1971; 3. 9–28 January 1971; 4. 28 January–18 February 1971; 5. 18 February–13 March 1971; 6. 13–31 March 1971.

when the loamy grassland soil attained its greatest moisture content following the spring melt.

Changes in dead phytomass

At the beginning of the season the dry weight of standing dead *Festuca* contributed 85 per cent of the total vascular component. This was reduced to 70 per cent by late January but increased to 80 per cent by the end of the summer.

Until mid to late February, the mean dry weight of the standing dead fraction had remained fairly constant, although there was considerable variation between samples within each harvest. The small but steady increase in standing dead was probably attributable to the progressive death of the partially live overwintering *Festuca* leaves. However, after mid-February the mature grass spikes were largely dead and included in the standing dead fraction. The culms retained their moisture and chlorophyll until about mid-March when they too became dry and woody, and formed a component of the standing dead fraction. The relatively large increase in dead *Acaena* towards the end of the season was attributable to leaf death. By the onset of winter all leaf laminae of this deciduous shrub had died.

Between late January and mid-February the loss in weight of living material was more or less balanced by the increase in weight of standing dead. However, between late February and early March the increase in standing dead was twice the loss in dry weight of the living fractions. Besides sampling error, it is possible that this apparent anomaly resulted from continued growth of the non-photosynthetic culms after harvest 5 followed by their rapid death prior to harvest 6. It is also possible that this increase in dry weight was due to the lignification of the culms, deposition of minerals in cell walls or formation of additional crystals within cells.

End of season standing crop and nutrient content

Greene and others (1973) have presented standing crop data for a late March harvest in a *Festuca contracta* stand (I.B.P. primary site) *c.* 100 m. from the present study area. Although both sites contained approximately the same standing crop of *Festuca*, other graminoids and cryptogams, the contribution afforded by living *Acaena magellanica* was *c.* 9 times greater at the former site. Table VI compares late March cover and dry-weight data for both sites and

TABLE VI. PERCENTAGE COVER AND DRY WEIGHT OF ABOVE-GROUND STANDING CROP OF COMPONENT SPECIES IN TWO *Festuca* GRASSLAND SITES SAMPLED IN LATE MARCH

	Data derived from Table III		*Data derived from Greene and others (1973)*	
Species	*Percentage cover*	*Dry weight* (g./m.^{2})	*Percentage cover*	*Dry weight* (g./m.^{2})
Living				
Festuca contracta	85	153	68	205
Acaena magellanica	4	25	30	217
Phleum alpinum	1	4 (with *Rostkovia*)	1	2 (with *Rostkovia*)
Rostkovia magellanica	1		1	
Chorisodontium aciphyllum	2	196 (bryophytes combined)	1	165 (bryophytes combined)
Polytrichum alpinum	14		12	
Tortula robusta	3		5	
Barbilophozia sp.	10		7	
Cladonia spp.	<1	0	2	5
Total living standing crop		378		594
Total dead standing crop		763 (excludes litter)		1,654 (includes litter)

emphasizes how the total standing crop can vary considerably within a relatively small area of dense closed *Festuca* grassland as a result of variation in dwarf-shrub cover. It also illustrates the difficulty of obtaining valid production and standing crop data for an ecosystem in which there is commonly considerable heterogeneity in species abundance both between and within stands.

Greene and others (1973) emphasized the importance of *Festuca* litter and standing dead as a source of nutrients in this grassland ecosystem. The ratio of standing dead *Festuca* to total dead *Festuca* (standing dead + detached litter), as determined from two other independent studies of nearby *Festuca* stands, was *c.* 1 : 1·5 in late December and *c.* 1 : 3 in late March (personal communication from D. W. H. Walton and J. R. B. Tallowin). From the data in Table III it is estimated that there is *c.* 250 g./m.^{2} of detached *Festuca* litter in addition to the 751 g./m.^{2} of standing dead *Festuca*. By applying data from a chemical analysis of the individual species of the community to the standing crop data in Table VI the relative amounts of several nutrients contained in living and dead components of the ecosystem have been determined for the end of the growing season (Table VII). The *Festuca* standing dead + litter fraction frequently contains between 40 and 60 per cent of the total nutrient content of the above-ground vegetation. Leaching of these nutrients from the litter layer, particularly during the spring melt, may be an important stimulus to growth early in the season. The comparatively high Na, Ca and Mg content of living *Acaena magellanica* can increase the community total considerably in stands where the shrub is abundant, while bryophytes also contribute a relatively large amount of most elements due to their high standing crop.

Seed viability in Festuca contracta and Deschampsia antarctica

Method

Seeds of *Festuca contracta* and *Deschampsia antarctica* were collected at the end of the 1970 summer (April) from plants growing on a sheltered moss bank on the south side of King Edward Cove at *c.* 2 m. a.s.l. and from an exposed fellfield site to the east of Gull Lake at

TABLE VII. NUTRIENT CONTENT (g./m.²) OF LIVING AND DEAD ABOVE-GROUND COMPONENTS OF *Festuca contracta* GRASSLAND ECOSYSTEM IN LATE MARCH

Component		Na	K	Ca	Mg	P	N
Total living vascular plants	a.	0·12	2·16	0·82	0·28	0·33	2·41
	b.	0·80	3·56	5·67	1·29	0·90	5·51
Total living bryophytes	a.	0·14	1·37	0·20	0·35	0·31	2·55
	b.	0·12	1·16	0·17	0·30	0·26	2·15
Total standing dead+detached litter (*c.* 98 per cent *Festuca contracta*)	a.	0·20	2·10	1·90	1·10	0·60	6·50
	b.	0·32	3·36	3·04	1·76	0·96	10·30
Total live+dead vegetation	a.	0·46	5·63	2·92	1·73	1·24	11·46
	b.	1·24	8·08	8·88	3·35	2·12	17·96

Chemical analysis of plant material provided by The Chemical Service, Institute of Terrestrial Ecology, Merlewood Research Station, Grange-over-Sands, Lancashire.
a. Nutrient values based on authors' production data (see Table VI).
b. Nutrient values based on production data derived from Greene and others (1973) (see Table VI).

c. 100 m. a.s.l. The mean dimensions of 100 *Festuca* seeds from the sheltered site were 9·70 mm. (including awn) by 0·93 mm., while those from the exposed site were 8·84 mm. by 0·79 mm. No measurements were made on *Deschampsia* seed, although data have been provided by Holtom and Greene (1967).

Germination tests were carried out over a period of 50 days commencing in early August 1970, using sets of 100 seeds of both species derived from a large number of spikes from each site, one set of each having been treated at −10° C for 2 weeks and the other set stored at room temperature. The seeds were placed on filter paper moistened by distilled water in closed petri dishes and kept near a window in a laboratory at a fairly constant temperature of *c.* 20° C. The seeds were supplied with artificial light from a 100 W bulb approximately 2 m. from the dishes for 15 hr. per day, although daylight was available for much of that period also.

Results

No germination was recorded in *Deschampsia*, although the seeds were mature and swollen. Holtom and Greene (1967) found that the optimum germination conditions for *D. antarctica* required cool pre-treatment (5° C) for 15 days followed by a fluctuating temperature of 16 hr. at 5° C and 8 hr. at 18–20° C per day. J. A. Edwards (personal communication) has confirmed that cold pre-treatment followed by a 5–20° C fluctuating temperature is essential for reasonable germination success.

Germination success of the *Festuca contracta* seeds is presented in Fig. 2. Despite a fairly high incidence of fungal infection, between 25 and 45 per cent germination success was recorded for all treatments. Germination commenced several days earlier in the vernalized seed with 7 and 12 per cent success after 10 days in seed from the sheltered and exposed sites, respectively, although no germination had yet occurred in the untreated seed. However, after 15 days these values had risen to 15 and 19 per cent, respectively, while the corresponding non-vernalized sheltered and exposed seed had already attained 17 and 20 per cent germination. The rapid rate of germination continued in the latter seed until about 25–30 days, after which time there was little further increase. Although the vernalized seed commenced germination earlier, the rate of increase was slower but levelled off at about the same time as that of the untreated seed. After 41 days, 44 per cent of the non-vernalized seed from the sheltered site had germinated compared with 38 per cent for the corresponding seed from the exposed site, 31 per cent for the vernalized exposed site seed and 26 per cent for the vernalized sheltered site seed. No further increases had occurred by 50 days.

Seed of *Festuca contracta*, as with all South Georgian vascular species, must be subjected during winter to a prolonged period of low temperatures fluctuating between about 5° and −15° C. However, seed which is shed before the onset of winter may not experience such a

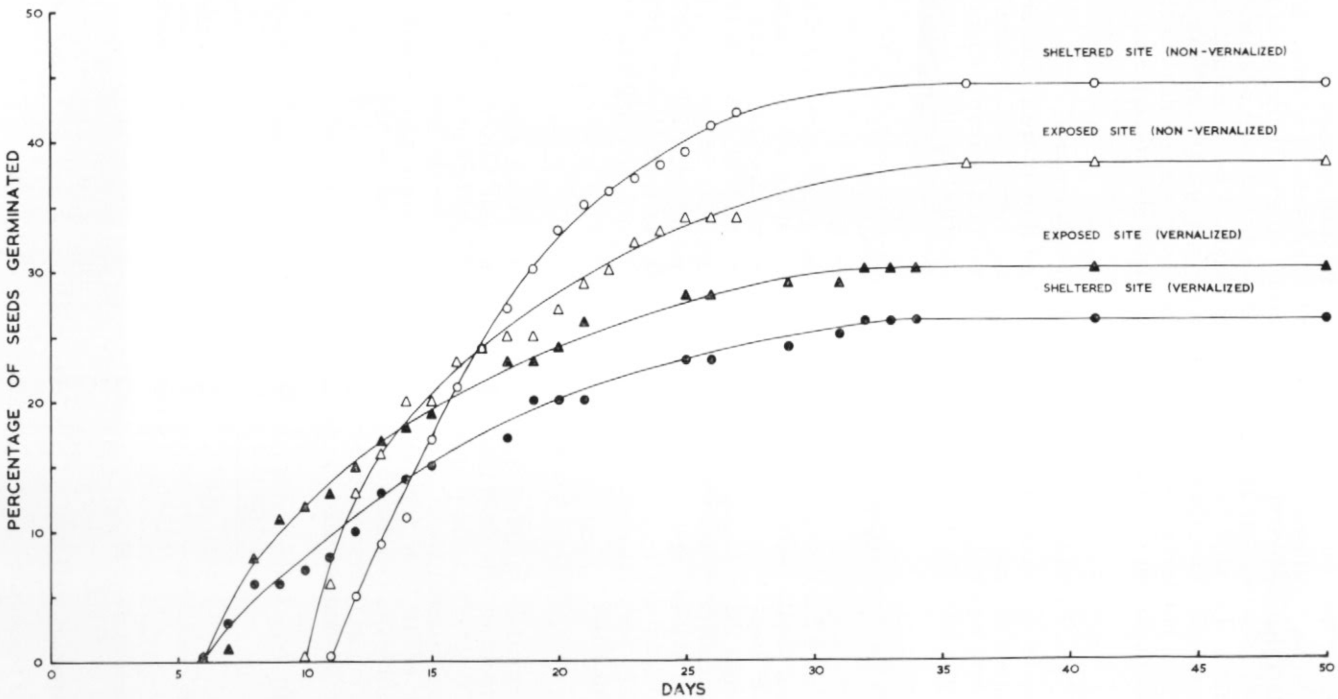

Fig. 2. Rate of germination of untreated and cold-treated *Festuca contracta* seeds from low-altitude sheltered and high-altitude exposed populations.

range of temperature due to insulation by snow. Certainly, the sheltered site plants from which seeds were collected for the above tests were covered by deep snow for over 6 months, while those at the fellfield site were only periodically covered by shallow snow and often exposed to high winds and low temperatures. Natural seedling establishment is frequent but seldom abundant and the fact that non-vernalized seed demonstrated a higher degree of viability than cold-treated seed may suggest that *Festuca contracta* is not very well adapted to the South Georgian environment. The slightly higher viability obtained by vernalized seed from the exposed site may be an indication of a higher degree of adaptation to the more severe conditions to which plants in such habitats must be subjected. However, the germination tests described above were carried out on too small a scale for much reliability to be placed on these conclusions.

Decomposition in Festuca contracta grassland

In order to obtain an indication of the rate of decomposition of living and dead foliage in *Festuca contracta* grassland ecosystems, a small-scale experiment was designed to examine dry-weight loss of plant material *in situ* over a 14½ month period, and an attempt was made to assess the quantity and biomass of bacteria, one of the principal agents of decomposition, in soil and litter.

Decomposition using litter bags

Method

One-year-old standing dead leaves and young current year green leaves of *Festuca contracta*, excised above the leaf sheath, were oven dried at *c.* 60° C and 2 g. of each fraction placed in fine mesh nylon litter bags. Five of each of these bags were placed in each of three *Festuca* grassland sites amongst the litter and left *in situ* from January 1970 to March 1971. The sites selected were: on a moderately sheltered north-facing slope at *c.* 35 m. a.s.l. (I.B.P. primary site), a fairly exposed west-facing gentle slope at *c.* 75 m. a.s.l. (near I.B.P. fellfield site), and a moderately exposed steep north-facing slope at *c.* 170 m. a.s.l. on Brown Mountain. After 14½ months, the bags were retrieved, the material re-weighed and any loss in dry weight attributed to decomposition.

Results

The very high proportion of standing dead material in *Festuca contracta* stands suggests a low rate of decomposition. However, the results given in Table VIII indicate decomposition rates ranging from 20 per cent at the more exposed site to 25 per cent at the relatively sheltered site for standing dead material and *c.* 56 per cent at each site for the less fibrous green leaves. Although the mesh of the litter bags was fine, it is not known what proportion of these percentage dry-weight losses was due to fall-out of material from the bags.

These values were higher than expected considering the coarseness of the grass, but it is important to note that the material used was attached standing foliage which was then detached

TABLE VIII. PERCENTAGE DRY-WEIGHT LOSS OVER 14½ MONTHS OF *Festuca contracta* MATERIAL AT THREE GRASSLAND SITES

Festuca contracta grassland site	*Mean percentage dry-weight loss with standard error*	
	Standing dead leaves	*Green current year's leaves*
Low-altitude, moderately sheltered site (35 m.)	25·3±2·4	56·8±1·6
Medium-altitude exposed site (75 m.)	19·9±1·2	55·8±4·7
High-altitude, fairly exposed site (150 m.)	22·2±0·9	56·9±1·9

All data are mean of five samples.

and placed amongst the moist and frequently warm actively decomposing litter. Under natural conditions it takes several years before most current year's standing material becomes incorporated into the litter so that the values for decomposition presented here are unnaturally high. However, beetles commonly graze the basal portion of living leaves which become detached and incorporated into the litter layer (personal communication from J. R. B. Tallowin). Once material reaches the litter layer in this grassland ecosystem, decomposition proceeds fairly rapidly, particularly with fresh chlorophyllous tissue in which much of the dry-weight loss is due to leaching of minerals.

No data are available for fungal and invertebrate decomposers, although some preliminary comparative numbers for certain invertebrate groups which are herbivores or detritus feeders have been obtained at different times throughout one summer. However, the data are too incomplete to detect seasonal trends in numbers. Invertebrates were extracted over a period of 6 days from community cores using a simplified Tüllgren funnel method. Numbers of invertebrates are given in Table IX for the moist sheltered and the drier more exposed *Festuca* *contracta* sites. Although the data were obtained from single 15 cm. diameter samples, they indicate considerable differences between the two sites. At most sampling times the numbers of invertebrates were greatest at the sheltered site but with relatively high Collembola and mite populations throughout the summer. Although large numbers of beetles were sometimes present at the sheltered site, it is unlikely that they had any influence on the decomposition results obtained from the litter-bag experiment, as they would have been too large to penetrate the nylon mesh.

TABLE IX. NUMBERS OF SOME HERBIVOROUS AND DETRITUS-FEEDING INVERTEBRATES IN SHELTERED AND EXPOSED *Festuca contracta* GRASSLAND

Site and sampling data	*Numbers/m.²*				
	Acarina	*Collembola*	*Coleoptera*		*Enchytraeid oligochaetes*
			Adults	*Larvae*	
17 November 1970					
Sheltered site	28,675	15,835	55	395	115
Exposed site	25,450	14,990	0	55	735
11 January 1971					
Sheltered site	12,105	17,985	285	115	2,770
Exposed site	3,960	6,900	0	170	285
8 February 1971					
Sheltered site	22,400	27,150	285	115	3,110
Exposed site	16,970	22,905	0	0	735
8 March 1971					
Sheltered site	26,585	28,280	455	620	170
Exposed site	19,795	9,615	0	0	170

Bacterial numbers and biomass

Method

The dilution-plate count technique described by Clark (1965) was used to estimate total numbers of bacteria in *Festuca contracta* grassland. Samples of *Festuca* litter and of soil from *c*. 5 cm. in the A horizon of the loamy brown soil beneath the grass were taken from a sheltered and an exposed stand of *F. contracta* (I.B.P. primary site and near the I.B.P. fellfield site). 10 g. fresh weight of each sample were shaken for 10 min. in 95 ml. sterilized water. 10 ml. aliquots of the suspension were diluted by a factor of 10^2, 10^3, 10^4 and 10^5 with sterilized water. Four 1 ml. replicates of each dilution were pipetted on to petri dishes into which 12 ml. of egg-albumen agar at 42° C was poured; the dishes were then incubated in semi-darkness at 28° C. Since the bacteria were briefly subjected to a high temperature, any psychrophiles

present may have been killed. After 14 days the numbers of bacterial colonies per plate were counted.

Litter and soil samples were analysed at three times during the 1970–71 season, namely in spring (November), summer (January) and in autumn (March).

Results

Since the mean number of bacteria in the higher dilutions (10^{-3}–10^{-5}), when multiplied by the dilution factor, provided comparatively similar results, a sample mean was calculated and converted to total number of bacteria per gram fresh weight and dry weight (determined on separate sub-samples) (Table X). From the former data, the fresh-weight biomass of bacteria

TABLE X. TOTAL NUMBER AND BIOMASS OF BACTERIA IN LITTER AND SOIL FROM *Festuca contracta* GRASSLAND

Site, soil type and sampling data	*Mean total number of bacteria* ($\times 10^3$/g. fresh weight)	*Mean total number of bacteria* ($\times 10^3$/g. dry weight)	*Estimated fresh weight of bacteria* (μg./g. fresh weight)
November			
Litter: sheltered site	15·82	79·12	0·0237
exposed site	0·95	3·80	0·0014
Soil: sheltered site	4·41	5·88	0·0066
exposed site	0·79	0·99	0·0012
January			
Litter: sheltered site	133·10	665·50	0·1997
exposed site	14·10	58·44	0·0212
Soil: sheltered site	14·22	18·96	0·0213
exposed site	10·20	12·75	0·0153
March			
Litter: sheltered site	418·00	2090·00	0·6270
Soil: sheltered site	24·30	32·40	0·0365

All data are the mean of three dilutions each with four replicates.

per gram fresh-weight sample has been estimated on the basis that the fresh weight of an average bacterium is $1 \cdot 5 \times 10^{-12}$ g. (Alexander, 1961).

Bacterial activity in the litter was considerably greater than in the loamy soil and in each microbial biomass increased throughout the season. Although no data were obtained for the exposed site at the end of the summer, the numbers of bacteria in both litter and soil in the earlier samples were much lower than in the corresponding samples taken from the sheltered site. For comparison, late-season samples from a nearby *Poa flabellata* stand provided $1 \cdot 50 \times 10^6$ bacteria/g. dry litter (0·45 μg./g. fresh weight) and $0 \cdot 07 \times 10^6$ bacteria/g. for the dry, comparatively organic soil (0·06 μg./g. fresh weight).

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