

AN ASSESSMENT OF PRIMARY PRODUCTION IN A SUB-ANTARCTIC GRASSLAND ON SOUTH GEORGIA

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ABSTRACT. The standing crop of a *Festuca contracta* grassland on the sub-Antarctic island of South Georgia was examined by harvest methods. Two sampling procedures were used and their estimates for total standing crop compared. The non-random distribution of quadrats within the sampling area is shown to produce misleading data that can markedly affect estimates both of standing crop and dry-matter production in the community.

THERE is an increasing need for reliable quantitative data on the cycling of energy and nutrients in ecosystems, particularly carbon and nitrogen, to improve understanding not only of the functioning of the whole but also of performance in individual components. This is particularly true of polar ecosystems where annual production is thought to be low and where the paucity of vegetation has been variously interpreted as being due to limitations of either temperature or nutrients, particularly nitrogen, or an inadequate water supply (Wilson, 1957, 1966; Bliss, 1962; Billings and Mooney, 1968).

From Sørensen's (1941) account of the performance of vascular species in Greenland, it might be thought that individual plants are very active during the short growing season but, according to Wilson (1957), "rapid development does not necessarily involve fast growth in terms of dry weight increase". More recent work has indicated that rapid development is often achieved by a well-developed seasonal pattern of translocation and storage between above- and below-ground parts rather than the rapid accumulation of dry matter (Mooney and Billings, 1960; Billings and Mooney, 1968).

Most data relate to arctic and alpine regions, few being available from the polar communities of the Southern Hemisphere (Greene and Longton, 1970; Lewis and Greene, 1970). Jenkin and Ashton (1970) have given some preliminary figures for standing crop on Macquarie Island, Huntley (1972) for Marion Island and Callaghan (1973) comparative figures for the growth of *Phleum alpinum* on South Georgia and Disko Island, West Greenland. Data on growth rates of Antarctic bryophytes are also becoming available, Clarke and others (1971) having given values for species of *Pohlia*, *Philonotis* and *Tortula*, while Longton (1970, 1972) has given figures for species of *Polytrichum* and *Bryum*.

The purpose of this paper is to present an assessment of changes in dry-matter production on a ground-area basis during one growing season in a community of *Festuca contracta* (= *F. erecta*) grassland on the sub-Antarctic island of South Georgia. The work was carried out as part of the International Biological Programme Bipolar Botanical Project, 1967-71.

South Georgia lies in lat. 54°17'S., long. 36°30'W., just south of the Antarctic Convergence. It is a mountainous and heavily glacierized island with its highest point exceeding 2,800 m. A detailed account of the climate has been given by Pepper (1954) and Smith and Walton (1975), and it can be classed as cool oceanic, with no well-marked seasonal variation in the range of temperature. In sheltered areas at sea-level minimum temperatures rarely fall below -5° C in summer or below -15° C in winter, but for the year as a whole the greatest frequency occurs in the range +5° to +15° C. There is little seasonal variation in precipitation, although rain is more frequent than snow in summer. The average annual total precipitation is c. 1,400 mm. Gales are frequent with prevailing winds mainly from the west. The most sheltered areas of the island lie around Cumberland and Stromness Bays. Greene (1964) has described the limited phanerogamic flora of 24 native species, whilst Trendall (1953, 1959) and Skidmore (1972) have dealt with the geology and Clapperton (1971) with the geomorphology of parts of the north-east coast.

Site and field methods

MATERIALS AND METHODS

The site chosen for study was on the south shore of King Edward Cove, Cumberland East Bay (GR 130 120) on a 15° north-facing slope at c. 35 m. a.s.l. on well-drained stable ground.

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The site, which is the same as that referred to by Lewis and Greene (1970) and Smith (1971) as the "Primary Site", was sheltered to the west and south but was open to the north and east, thus experiencing moderate exposure to wind but receiving high insolation. Percentage frequency and percentage cover of the species comprising the grassland are given in Table I, while the results of chemical analyses of its soil are shown in Table II.

To determine changes in dry-matter production during the 1967-68 austral summer, an area 20 m. by 20 m. of a fairly homogeneous part of a *Festuca contracta*-*Acaena magellanica* (= *A. adscendens*) community was divided into two halves and 50 samples (each 25 cm. by

TABLE I. PERCENTAGE FREQUENCY AND PERCENTAGE COVER OF SPECIES IN SAMPLING AREA

Species	Upper half of site		Lower half of site	
	Percentage cover	Percentage frequency	Percentage cover	Percentage frequency
Phanerogams				
<i>Festuca contracta</i> T. Kirk	66.5	100	69.0	100
<i>Acaena magellanica</i> (Lam.) Vahl	26.0	86	34.3	100
<i>Phleum alpinum</i> L.	0.5	18	0.9	34
<i>Rostkovia magellanica</i> (Lam.) Hook. f.	0.1	4	0.2	4
Cryptogams				
<i>Polytrichum alpinum</i> Hedw.	18.2	92	5.1	52
<i>Tortula robusta</i> Hook. et Grev.	5.2	28	8.7	62
<i>Chorisodontium aciphyllum</i> (Hook. f. et Wils.) Broth.	0.7	26	0.0	0
<i>Bartramia patens</i> Brid.	0.0	0	0.1	4
<i>Barbilophozia hatcheri</i> (Evans) Loeske	7.0	94	6.3	98
<i>Cladonia</i> spp.	1.0	40	1.6	48
Substrata				
Bare soil	0.5	2	0.0	0

Data obtained in March 1968 from 50 25 cm. by 25 cm. random quadrats in each half of sample area.

TABLE II. CHEMICAL ANALYSES OF SOIL FROM THE *Festuca* GRASSLAND SITE

Horizon and depth	Percentage loss on ignition (at 550° C)	Extractable ions (mg./100 g.)					
		Na	K	Ca	Mg	P	Total N (per cent)
A (2-10 cm.)	34	6.0	10.3	14.8	6.9	1.6	1.5
B (10-20 cm.)	7	2.7	1.6	1.2	1.2	2.9	0.2

Data are means of four samples.

25 cm. by 35 cm. deep) were dug in one half on 6 December 1967 and the same number harvested from the other half on 27 March 1968. Immediately after collection the samples were deep frozen. Further sampling details have been given by Greene and others (1973). The "growing season", defined in terms of duration of snow-free ground, is considered to extend from about mid-October to late March (c. 170 days), the sample period of 112 days thus covering approximately three-quarters of the growing season.

Sample analysis

A total of 82 random samples was analysed from the 100 harvested. Of these, 68 were fully analysed for all plant material, half being from the first harvest and half from the second harvest. After removal from the deep-freeze they were thawed for 24 hr. before being divided as fully as possible into certain of the fractions listed in Table III, all these fractions being used only in the sub-sampling. After washing over sieves, each fraction was oven dried at 80° C to a constant weight.

Employing all the fractions for sorting listed in Table III, 14 further samples, representing seven per harvest, were analysed by a sub-sampling procedure similar to that outlined by Dahl and Gore (1969, appendix I). The above-ground material was clipped from each complete sample and treated as follows: after removal of the *Festuca contracta* shoots and large pieces of *Acaena magellanica*, the remaining material was thoroughly mixed to homogenize it and then repeatedly divided by a modification of the quartering method described by Gore (1969) to give 16 sub-samples. Eight of these were sorted carefully into all fractions, the remaining eight samples being grouped as a remainder. The previously extracted *Festuca contracta* material was treated in a similar fashion. The large *Acaena magellanica* shoots were all completely analysed into three categories. Detached litter on the soil surface was not sorted into fractions for individual species. The below-ground component was first washed out of the soil block and all the large *Acaena magellanica* rhizomes extracted. The remaining material was again analysed by the sub-sample method, using eight sub-samples for each field sample, into the fractions shown in Table III.

Statistical analysis of data

The mean for each fraction at both harvests was calculated for all 68 fully analysed samples, cumulative fractions, e.g. total vascular above-ground living material, having been treated similarly. The significance of the difference between the harvest means of each fraction has been determined (Table IV), together with their standard errors, all means and standard errors for the original quadrat data (625 cm.²) being converted to a square metre basis.

The total net change in dry weight per square metre over the period between harvests for each fraction has been calculated as the difference between the means for two harvests. The rate of change in g./m.²/day can be determined by dividing the total change by 112, i.e. the number of days between harvests.

For the seven samples per harvest treated by the sub-sampling technique, the data were analysed in the following way: first, the total dry weight of each sample was found and apportioned in the same ratio as the various fractions within each sub-sample, thus yielding eight replicates for the weight of all fractions within that component. All 112 values for an individual component (i.e. two harvests, seven quadrats and eight replicates) were then processed using a single classification analysis of variance to give estimates of the variance due to harvests (S_h^2), to quadrats within harvest and (S_q^2) to replicates within quadrats (S_r^2). The analyses of variance for *Festuca contracta* living photosynthetic fraction are shown in Table V.

Using the separate variances, it is possible to calculate the variance of the harvest mean for any number of replicates per quadrat and number of quadrats per harvest from:

$$\text{Variance of harvest mean} = \frac{1}{xyz} [S_h^2 + zS_q^2 + yzS_r^2],$$

where x = number of harvests (in this case 2),

y = number of quadrats per harvest (i.e. 7),

and z = number of replicates per quadrat (i.e. 8).

The variance of harvest means for the important fractions, when based on two, eight and 32 quadrats each of one, two, four or eight replicates, i.e. the sub-samples, are shown in Table VI.

TABLE III. FRACTIONS USED IN SAMPLING PROCEDURES

<i>Fractions used in whole-sample analysis</i>	<i>Fractions used in sub-sample analysis</i>
<i>Festuca</i> living shoots	{ <i>Festuca</i> living photosynthetic <i>Festuca</i> living non-photosynthetic <i>Festuca</i> living reproductive
<i>Festuca</i> living roots	<i>Festuca</i> living roots
<i>Festuca</i> dead roots	<i>Festuca</i> dead roots
<i>Acaena</i> living shoots	{ <i>Acaena</i> living photosynthetic <i>Acaena</i> living non-photosynthetic
<i>Acaena</i> living roots/rhizomes	<i>Acaena</i> living roots/rhizomes
<i>Acaena</i> dead roots/rhizomes	<i>Acaena</i> dead roots/rhizomes
<i>Phleum</i> living shoots	{ <i>Phleum</i> living photosynthetic <i>Phleum</i> living non-photosynthetic
<i>Phleum</i> living roots	<i>Phleum</i> living roots
<i>Phleum</i> dead roots	<i>Phleum</i> dead roots
<i>Rostkovia</i> living shoots	
<i>Rostkovia</i> living roots	
<i>Polytrichum</i> living	<i>Polytrichum</i> living
<i>Polytrichum</i> litter	<i>Polytrichum</i> litter
Other bryophytes	{ <i>Tortula</i> living <i>Chorisodontium</i> living <i>Barbilophozia</i> living Other bryophytes
Lichens	Lichens
Unspecified roots living and dead	Unspecified roots living and dead
Detached vascular litter and standing dead	{ Detached vascular litter <i>Phleum</i> standing dead <i>Festuca</i> standing dead <i>Acaena</i> standing dead

TABLE IV. DIFFERENCES IN DRY WEIGHT BETWEEN HARVESTS OF EACH FRACTION ANALYSED

Fraction	Mean dry weight (g./m. ²)		Standard error of means	Net change in dry weight (g./m. ²)	Significance of difference
	Harvest I 6.12.1967	Harvest II 27.3.1968			
<i>Festuca</i> living shoots	100.6	205.1	15.5	104.5	***
<i>Festuca</i> living roots	32.6	100.8	11.3	68.2	***
<i>Festuca</i> dead roots	69.0	43.2	8.1	-25.8	*
<i>Acaena</i> living shoots	49.0	217.3	26.1	168.3	***
<i>Acaena</i> living roots	426.2	623.7	64.3	197.4	*
<i>Rostkovia</i> living shoots	0.8	0	0.3	-0.80	NS
<i>Rostkovia</i> living roots	1.3	0	0.9	-1.3	NS
<i>Phleum</i> living shoots	2.7	1.6	1.3	-1.2	NS
<i>Phleum</i> living roots	3.0	1.1	1.4	-1.9	NS
<i>Phleum</i> dead roots	0.1	0	0.05	-0.1	NS
Detached vascular litter and standing dead	1,264.5	1,597.6	109.4	333.1	*
Unspecified roots living and dead	833.8	913.3	51.5	79.5	NS
<i>Polytrichum</i> living	697.1	92.2	129.0	-605.0	**
<i>Polytrichum</i> litter	140.3	56.6	44.5	84.2	NS
<i>Tortula</i> living	22.6	58.2	15.4	35.7	NS
Other bryophytes living	147.0	15.0	25.0	-132.0	***
Lichens	12.5	4.6	3.0	-7.8	NS
Total living vascular above ground	153.1	424.0	29.8	270.9	***
Total living and dead vascular below ground	1,297.0	1,638.9	86.7	341.9	*
Total living vascular (plus non-quantifiable dead roots)	1,450.1	2,062.9	96.6	612.8	***
Above and below ground vascular litter and standing dead	1,333.6	1,640.8	115.7	307.3	*
Living cryptogams	879.2	170.1	144.2	-709.1	***
Total standing crop	3,803.1	3,929.9		126.8	

All values means of 34 samples.

* Significant at 5 per cent level.

** Significant at 1 per cent level.

*** Significant at 0.1 per cent level.

NS Not significant.

TABLE V. ANALYSIS OF VARIANCE FOR *Festuca* LIVING PHOTOSYNTHETIC FRACTION OF *Festuca* COMPONENTS IN SUB-SAMPLES

Source	Sum of squares	Degrees of freedom	Variance
Between harvests	26.36	1	26.36
Between quadrats within harvests	972.91	12	81.76
Between replicates within quadrats	661.76	98	6.75
TOTAL	1,660.66	111	

$$\text{Variance due to harvests } [S_h^2] = \frac{26.36 - 81.76}{7 \times 8} = -0.99$$

(in which case the best estimate of variance due to harvests is taken to be zero as variance cannot be negative).

$$\text{Variance due to quadrats } [S_q^2] = \frac{81.76 - 6.75}{8} = 9.38.$$

$$\text{Variance due to replicates } [S_r^2] = \frac{6.75}{1} = 6.75.$$

By combining the data for various components, it has been possible to calculate the total dry weight of the more important fractions on a quadrat basis and thus dry matter per metre square at each harvest.

In this way, it has been possible to obtain information supplementary to that given by the completely analysed quadrats, for example the apportioning of the above-ground living *Festuca contracta* fraction between its photosynthetic and non-photosynthetic parts.

RESULTS

The data for the 34 completely analysed samples from harvest II have already been published by Greene and others (1973) and they are included in Table IV, together with the data from the 34 first-harvest samples. Of the 17 fractions used for sorting, the changes between the first and second harvests were not significant for nine of them, but they were highly significant for four. Eight of the fractions with small changes contributed less than 4 per cent to the total standing crop at harvest II. The ninth fraction, unspecified roots, showed a change of less than 10 per cent of the first-harvest standing crop so it would not be expected to be significant.

Of the three fractions with changes significant at the 1 per cent level, the most important was litter and standing dead. *Acaena magellanica* living root, another fraction significant at the 1 per cent level, gave the second highest production rate. The considerable amount of dry matter contributed at both harvests by rhizome and root material of the *Acaena* was in marked contrast to the amount of the *Festuca* plants. The change in *Polytrichum alpinum* living material was found to be significant at the 1 per cent level, but it was a negative change, there being an apparent decline in dry matter between the first and second harvests of over 600 g./m.². Since Longton (1970) has shown that production in pure *Polytrichum* communities on South Georgia is normally between 450 and 500 g./m.² in a growing season, the present figure is clearly anomalous.

Examination of the mean weights of *Polytrichum alpinum* at each harvest suggested that the moss was not equally represented in the two parts of the site (Table I), and from the data in Table VII, the non-random distribution of the *Polytrichum* within the site is clearly seen. It is interesting to observe that *Chorisodontium aciphyllum* also showed a departure from random distribution as this species was the major component of the "other bryophytes" fraction in Table IV which also showed a negative growth rate. The distribution of *Acaena magellanica* also appears to have been slightly skewed, but all other species were apparently represented equally in both halves of the area.

If the *Polytrichum* fractions are excluded from the calculation of the rate of production for the total standing crop of the community, production rates would rise from +1.13 to

TABLE VI. VARIANCE OF HARVEST MEANS FOR QUADRATS ANALYSED BY SUB-SAMPLE METHOD

Fraction	Mean dry weight (g./625 cm. ²)		2 quadrats				8 quadrats				32 quadrats			
	Harvest I	Harvest II	Number of replicates/quadrat				Number of replicates/quadrat				Number of replicates/quadrat			
			1	2	4	8	1	2	4	8	1	2	4	8
1 <i>Festuca</i> , living photosynthetic	4.15	5.12	4.04	3.19	2.77	2.55	1.01	0.80	0.69	0.64	0.25	0.20	0.18	0.16
1 <i>Festuca</i> , living non-photosynthetic	1.86	3.06	1.54	1.11	0.89	0.79	0.53	0.42	0.36	0.34	0.27	0.25	0.23	0.23
1 <i>Festuca</i> standing dead	38.81	48.43	116.39	112.62	110.73	109.78	29.10	28.16	27.68	27.45	7.28	7.04	6.92	6.86
1 <i>Festuca</i> living roots	1.11	2.48	1.33	1.00	0.84	0.76	0.60	0.52	0.48	0.46	0.42	0.40	0.39	0.39
1 <i>Festuca</i> dead roots	2.13	2.17	4.03	2.61	1.89	1.54	1.01	0.66	0.48	0.39	0.26	0.17	0.12	0.10
1 <i>Polytrichum</i> , living	1.92	0.76	2.51	2.28	2.16	2.10	0.63	0.57	0.54	0.53	0.16	0.15	0.14	0.14
1 <i>Barbilophozia</i> living	0.12	0.11	0.0038	0.0028	0.0023	0.0020	0.0010	0.0007	0.0006	0.0005	0.0003	0.0002	0.0002	0.0002
2 <i>Polytrichum</i> , living	28.45	12.40	192.28	183.45	179.04	176.83	62.20	59.99	58.88	58.33	29.67	29.12	28.85	28.71
2 <i>Tortula</i> living	0.15	1.70	1.62	1.53	1.48	1.45	0.61	0.59	0.57	0.57	0.36	0.35	0.35	0.35
2 <i>Barbilophozia</i> living	1.75	0.74	0.83	0.69	0.61	0.57	0.31	0.27	0.25	0.24	0.18	0.17	0.16	0.16
2 <i>Festuca</i> standing dead	13.46	5.86	29.64	28.74	28.29	28.06	14.17	13.94	13.83	13.77	10.30	10.24	10.21	10.20
3 Unspecified roots living and dead	60.16	99.26	601.5	588.5	582.0	578.5	378.0	375.0	373.5	372.5	322.5	321.5	321.0	321.0
3 <i>Polytrichum</i> living	3.06	6.09	13.50	11.78	10.84	10.40	3.38	2.93	2.71	2.60	0.85	0.74	0.68	0.65
3 Detached litter	23.15	11.73	127.3	110.65	102.3	98.15	36.65	32.45	30.40	29.35	13.95	12.90	12.40	12.15

1 Material from *Festuca* component.

2 Material from remaining above-ground component.

3 Material from remaining below-ground component.

TABLE VII. PROBABILITY TEST TO ASSESS THE RANDOMNESS OF SPECIES DISTRIBUTION IN THE TWO HARVEST AREAS

Species	<i>t</i> value	Significance
<i>Festuca contracta</i>	0.60	NS
<i>Acaena magellanica</i>	2.04	*
<i>Phleum alpinum</i>	0.36	NS
<i>Polytrichum alpinum</i>	4.03	***
<i>Rostkovia magellanica</i>	1.02	NS
<i>Tortula robusta</i>	1.41	NS
<i>Bartramia patens</i>	1.26	NS
<i>Chorisodontium aciphyllum</i>	2.48	*
<i>Barbilophozia</i> sp.	0.58	NS
<i>Cladonia</i> spp.	1.21	NS
Bare soil	1.01	NS

* Significant at 5 per cent level.

*** Significant at 0.1 per cent level.

NS Not significant.

+7.29 g./m.²/day for the whole community, whilst the vascular component alone increases at the rate of +5.47 g./m.²/day. The increase of the vascular litter and standing dead at 2.74 g./m.²/day was a most significant part of the ecosystem. The grassland normally appeared to consist to a very large extent of standing dead *Festuca contracta* leaves and inflorescences, an impression confirmed by the data in Table IV which showed that over 40 per cent of the total standing crop of the community was classed as litter and standing dead, comprising c. 70–80 per cent of the *Festuca* above-ground component.

The analysis in Table VI of the variance of harvest means illustrates the usefulness of the sub-sampling method when large numbers of samples need to be analysed. For most categories, an increase in replicates/quadrat from four to eight for the analysis of eight quadrats did not show any significant decrease in variance. In all cases, increasing the number of quadrats rather than the number of replicates/quadrat gave a reduction in variance, e.g. for *Festuca contracta* standing dead the variance for four replicates at the two-quadrat level was 110.73, whilst for a similar number of sorted samples, i.e. one replicate at the eight-quadrat level, the variance fell to 29.10. It is possible to decrease the variance even more by taking more than 32 samples and using more than eight replicates per sample, but in any experiment there is a point after which the reduction in variance produced by increased sampling is no longer justifiable. Unfortunately, the optimum sampling number for some fractions may be sub-optimal for others. For instance, in the eight-quadrat sample, an increase in replication for the *Festuca* dead roots produced a decrease in variance of c. 40 per cent but for unspecified roots the change was less than 2 per cent. In general, it appears that for categories with large variances the only satisfactory method of reduction is to increase the sample number and not the replicate number, though for those categories with fairly small variances substantial reductions can be made by increasing the replicate number alone.

DISCUSSION

Festuca contracta grassland on South Georgia is a characteristic and important community type on well-drained areas of the central north-east side of the island. The species composition of particular stands can vary considerably, with the more exposed stands containing a very high cryptogamic content, whilst the more sheltered areas are composed largely of phanero-

gams. Various *Festuca contracta* associations were described by Greene (1964), who suggested that the dense, closed grassland formation is probably the climax vegetation over much of the north-east coast of South Georgia. A detailed analysis of the standing crop of a typical *Festuca contracta*-dominated area is therefore of importance in any attempt to understand the energetics of stable plant associations on the island.

The data given here have shown that a very considerable proportion of the total standing crop of the community examined was attributable to *Festuca contracta* standing dead and litter, both at the beginning and at the end of the growing season. This fraction comprised c. 41 per cent of the total standing crop and 71 per cent of the above-ground material at the end of season harvest. Much of the standing dead material was apparently several years old before it fell to the ground and became detached litter. The decomposition results of Smith and Stephenson (1975) have shown that, after a leaf has died and become dry standing dead material, decomposition is slow. It was thought that low numbers of bacteria or arthropods may have been responsible for this but available data suggest that this may not be so.

In closed swards, the erect dead leaves remain attached to the parent tiller for some years with the lamina becoming tightly inrolled and the entire leaf remaining very dry. Anatomical examination has shown that stomata are apparently restricted to the ventral surface of the leaf, the dorsal surface being covered by a thick cuticle. The standing dead material therefore presents an almost impermeable surface whilst in an upright position, and decay appears to be very slow until such time as the leaf becomes detached litter when it becomes part of a continuously moist and frequently warm environment. Chemical analysis of both standing dead and living *Festuca contracta* leaves has shown that, although the levels of nitrogen, potassium and phosphorus are considerably less in dead than living material, the total amounts of these nutrients bound in the slowly decaying fraction can comprise nearly 50 per cent of the total present in the aerial parts of this ecosystem according to data collected by R. I. L. Smith and D. W. H. Walton.

O. W. Heal (personal communication) has suggested that there are three sources of variation in rates of decay, and these are attributable to differences between species, between seasons and the depth of litter burial, the within-site variation often being much higher than that between sites of a similar soil type. On South Georgia, similar experiments to those with *Festuca contracta* have been carried out using *Acaena magellanica* leaves and have resulted in a much higher decay rate (Walton, 1973). From the limited results of the decomposition experiments carried out to date on the island, inter-site variation appears to be less important than species variation, but no experiments have yet been undertaken to determine variation in decomposition rates at increasing soil depths.

The two methods of analysis used, i.e. whole-sample analysis and sub-sample analysis, have allowed independent estimates for both harvests of the biomass of various fractions on a g./m.² basis and the differences in the results are striking. Table VIII shows the mean weights

TABLE VIII. A COMPARISON OF THE WEIGHT OF VARIOUS FRACTIONS AT HARVEST II
ESTIMATED BY TWO SAMPLING METHODS

	Sub-sample analysis (g./m. ²)	Whole-sample analysis (g./m. ²)
<i>Festuca</i> living photosynthetic	81.92	205.12
<i>Festuca</i> living non-photosynthetic	48.96	
<i>Festuca</i> standing dead and litter	1,062.72	1,597.60
Roots unspecified	1,588.16	913.28
<i>Festuca</i> living roots	39.68	100.80
<i>Festuca</i> dead roots	34.72	43.20

of various fractions at the second harvest calculated from data obtained by the two methods. There appears to be some trend towards a lower estimation of standing crop by the sub-sample method, with the unspecified roots showing a reverse trend. As this trend was consistent for both harvests, the estimates of daily production rates from the sub-sample data were also considerably lower than the estimates made from the whole-sample data. It is important to note, however, that the number of field samples used per harvest for the sub-sample technique was considerably fewer than the optimum number predicted from the variance analysis.

There appear to be two important implications to be drawn from the above results. First, as each method provided a unique form of standing-crop estimate, the importance of describing the technique used in a particular investigation, both accurately and in detail, is clearly underlined since fairly small changes in the methods of analysis can apparently produce important differences in the final calculations for standing crop. Secondly, comparisons between data obtained by different workers in different areas must be attempted with considerable caution, especially if the estimates for community standing crop are only based on a single method of determination. The importance of independent assessments of standing crop and production by various techniques has also been recognized by other workers (Van Dyne and others, 1970).

The figures for end-of-season standing crop in the *Festuca contracta* community can be compared with figures for a herb-grass community on the Taimyr Peninsula, U.S.S.R. (Schamurin and others, 1972) and an *Agropyron* community in southern Saskatchewan (Milner, 1970), both of which have high litter and standing dead components. The Canadian site had a standing crop approaching that of the *Festuca* community, whilst at the Russian site it was apparently only about 25 per cent of the level of the South Georgian grassland. Since Dennis and Johnson (1970) have shown that environmental limitation on standing crop is generally restricted to the above-ground portion, the comparison between the *Festuca* grassland and other grassy sites suggests that conditions on South Georgia may be considerably less severe than those experienced at other tundra sites. Indeed, from an examination of the standing-crop figures for a large number of tundra sites given by Wielgolaski (1972), it appears that the South Georgian figures are more comparable with those to be expected from alpine rather than arctic sites. The relatively long growing season and the oceanic nature of the climate of the island further support the contention that, on present knowledge, at least in the north-eastern coastal areas some South Georgian phanerogamic sites and communities might be considered as being more similar to "low-altitude" alpine rather than sub-arctic polar sites.

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