THE CHEMICAL COMPOSITION OF SOUTH GEORGIAN VEGETATION

By D. W. H. Walton *and* R. I. L. Smith

Abstract. Samples taken during 1970–71 of two pteridophytes, 14 phanerogams and five bryophytes were analysed for total sodium, potassium, calcium, magnesium, phosphorus and nitrogen. Plants from soils associated with seal and bird colonies had higher levels of phosphorus and nitrogen, while the burning of tussock grassland caused increases in these elements which lasted for more than a year. Seasonal trends were similar to those obtained for northern temperate species but absolute values were often considerably higher. Data are compared with those from Marion Island. Estimates are given of the total amounts of elements present in the aerial parts of *Festuca* and *Poa* grassland, *Acaena* dwarf-shrub communities and a bryophyte flush. The significance of the chemical component of standing dead and litter in terms of mineral cycling is discussed.

In any studies on the growth and primary production of natural communities, it is essential to gain some understanding of the cycling within the sytem of at least the important macro-nutrients in the principal plant species. Chemical analysis of soil samples is not an accurate guide to the element content of the plant material growing in a particular site. Some species can accumulate elements, which occur in very small concentrations in the soil, to levels which would be toxic to most plants (Sutcliffe, 1962), whilst the existence of ecotypes adapted to widely differing levels of essential soil nutrients has been amply demonstrated (Bradshaw and others, 1958). Indeed, Grundon (1972) has shown that native species may grow well on soils which produce deficiency symptoms in introduced species.

In the southern polar regions, some work on the chemical content of plants has been carried out with Allen and others (1967) and Holdgate and others (1967) giving data for mosses and *Deschampsia antarctica* from Signy Island, and Rastorfer (1972) providing element levels for four mosses from the Argentine Islands. Published data for sub-Antarctic vegetation are limited to those of Smith and Walton (1975) for 12 flowering plants, four mosses and one fern from South Georgia, and Smith (1976*a*, *b*) for Marion Island plant communities. In a wider context, there have been several recent studies on tundra vegetation (Haag, 1974; Chapin and others, 1975; various authors *in* Rosswall and Heal, 1975) and on temperate grasslands (Gerloff and others, 1964; Connor and others, 1970; Coupland, 1973; Harner and Harper, 1973), whilst Rodin and Bazilevich (1967) have attempted to provide comparable data for all vegetational types at world level.

As part of the International Biological Programme Bipolar Botanical Project (Callaghan and others, 1976) to investigate growth and productivity in ecosystems on South Georgia, most species of phanerogams (14 taxa), pteridophytes (two taxa) and bryophytes (five taxa) which are major components of the most widespread ecosystems were sampled throughout a summer. These data provide a basis for assessing nutrient turn-over within the principal ecosystems on the island. A general description of the climate, geology and biology of South Georgia will be found in Smith and Walton (1975).

Material and Methods

Most species were collected from single sites where each was a predominant representative of a community. However, *Callitriche antarctica*, *Deschampsia antarctica* and *Poa flabellata* were collected from several sites in order to determine the effect of animal manuring in seal wallows and bird colonies. *P. flabellata* was also sampled from an area of tussock grassland which was burnt in November 1969 as part of an investigation of growth and regeneration in this species. With the exception of a few samples of *P. flabellata*, all samples were collected in the area around King Edward Cove, Cumberland East Bay, South Georgia. Most species were sampled at approximately monthly intervals from mid-November 1970 to early April 1971 but a few were sampled only at the beginning and end of the growing season. Each monthly sample of a particular species was taken from within one site measuring a few square metres in area.

Within a few hours of collection the samples were cleaned of foreign material and the more prostrate species quickly washed in de-ionized water to remove soil particles. The larger species were divided into leaves, flowers and/or fruits and standing dead, but *Galium antarcticum*, *Callitriche antarctica*, *Ranunculus biternatus*, *Polystichum mohrioides* and the bryophytes were kept intact. The material was dried for several days at 55° C and stored for several months before analysis. For each harvest, material was thoroughly mixed and analyses carried out on one sub-sample. Total Na, K, Ca, Mg, P and N were determined, all results being expressed as percentages of sample dry weight. The methods of analysis used have been given by Allen and others (1974).

Results

Changes in chemical content throughout the growing season

Seasonal trends in most elements were fairly distinct in many species, although not always consistent within similar life forms, plant components or habitats for a particular element. In general, K, P and N decreased throughout the summer from relatively high peak values in November–December. Conversely, there was a tendency for Na, Ca and Mg to increase during the growing season.

Dwarf shrubs (Fig. 1)

Current year's leaves. Some of the most marked changes were recorded in the three taxa of *Acaena*. All had a mid-summer peak for Na, increasing about six-fold from the November value. Ca and Mg also increased but in the hybrid dropped to a seasonal minimum in January before increasing in the latter part of the summer. K, P and N declined, whilst in *Acaena tenera* levels rose from November minima to December maxima then declined. These general trends appear similar to those found in the leaves of many of the larger flowering plants of temperate latitudes.

A. magellanica and the hybrid are found on more organic soils than *A. tenera*. These have both higher nutrient status and moisture content than the mineral soils of the *A. tenera* habitats. This should facilitate more rapid uptake of nutrients early in the growing season following the spring melt and may account for the earlier (November) peaks in P and N.

Stem. There is generally little change in the element content of the creeping woody stem. Values are rather low with the exception of P and N in *A. tenera* and the hybrid.

Inflorescences. The seasonal changes in the flowers and scapes follow the same trend as in the leaves, although absolute values and monthly variation are considerably less. P is the only element which tends to occur at a higher concentration than in the leaves.

Attached dead leaves and petioles. Although this achlorophyllous material was apprently dead, there appeared to be a significant accumulation of Na, Mg and to a lesser extent K, Ca, P and N throughout the summer. The highest values were around mid-season. The spring samples comprised only petioles of the previous season's leaves, the laminae of which had completely decomposed. From mid-summer onwards, this category contained an increasing amount of senescent current year's leaves.

Rushes and grasses (Figs. 2–5)

Current year's leaves. In the majority of species the levels of most elements declined throughout the growing season. Na frequently reached a February minimum then increased slightly at the

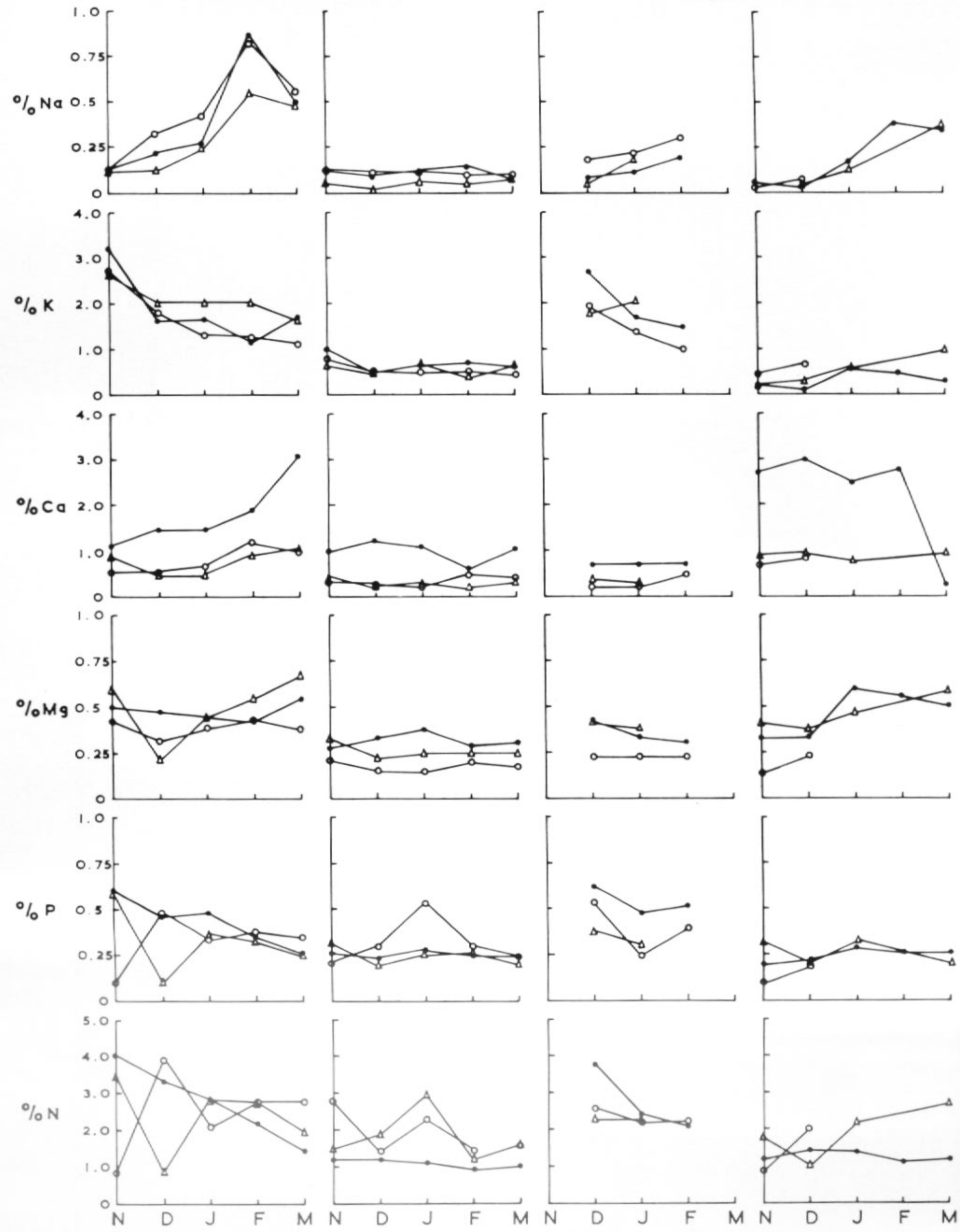

Fig. 1. Seasonal changes in the element content of *Acaena magellanica* (Lam.) Vahl (solid circles), *A. tenera* Alboff (open circles) and *Acaena magellanica* × *tenera* (solid triangles). a. Living leaves; b. Stems; c. Inflorescences; d. Attached dead leaves and petioles.

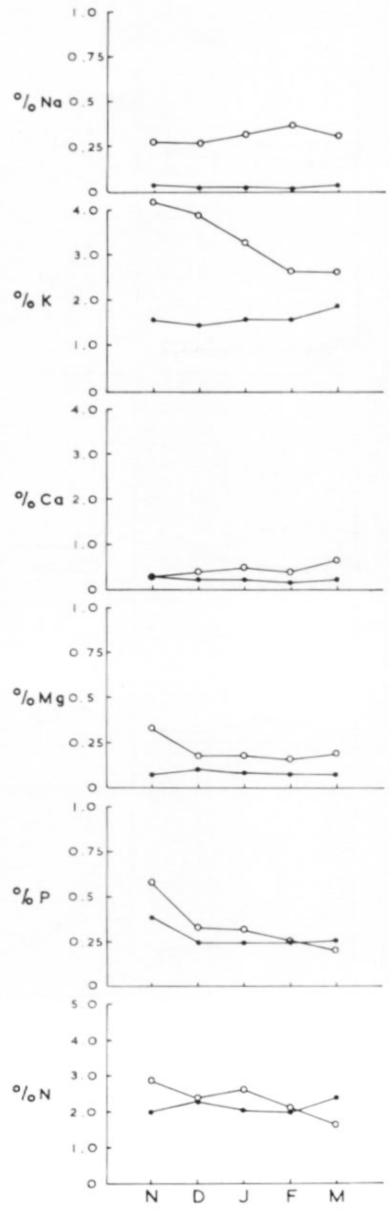

Fig. 2. Seasonal changes in the element content of living leaves of *Rostkovia magellanica* (Lam.) Hook. f. (solid circles) and *Juncus scheuchzeriodes* Gaudich. (open circles).

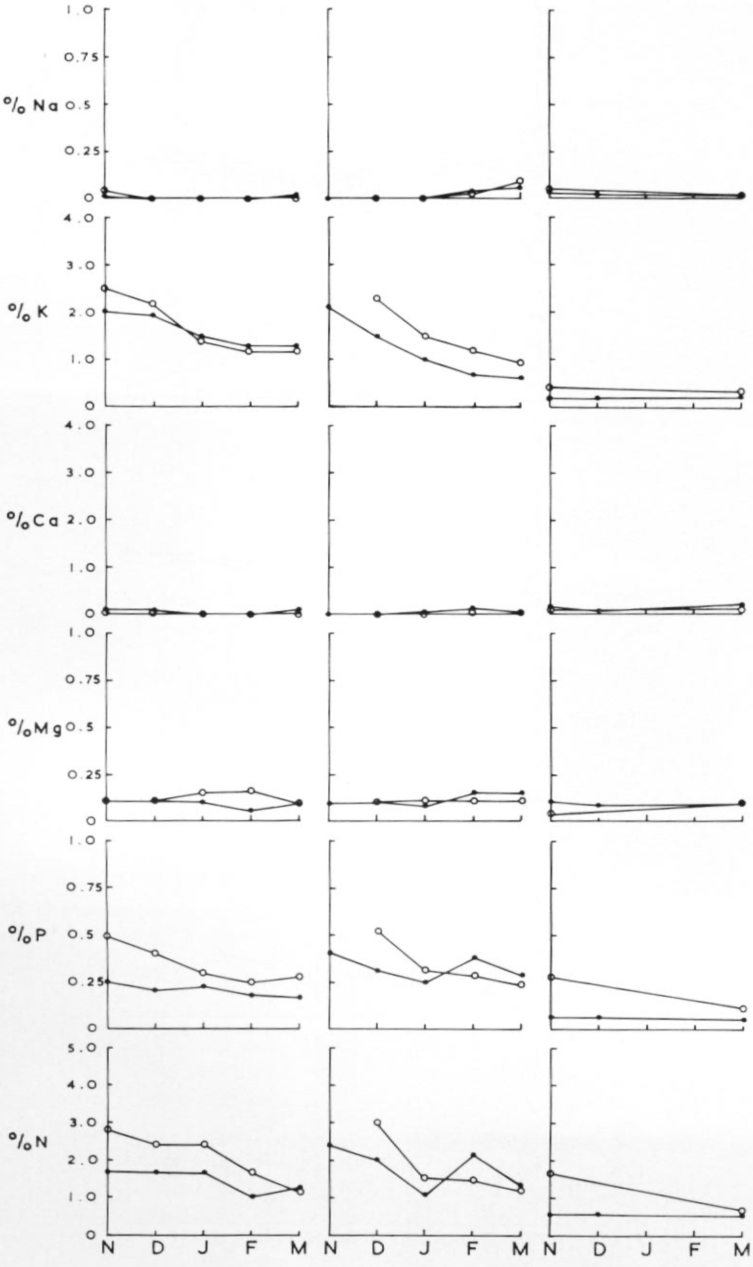

Fig. 3. Seasonal changes in the element content of *Festuca contracta* T. Kirk (solid circles) and *Phleum alpinum* L. (open circles). a. Living leaves; b. Inflorescences; c. Standing dead leaves.

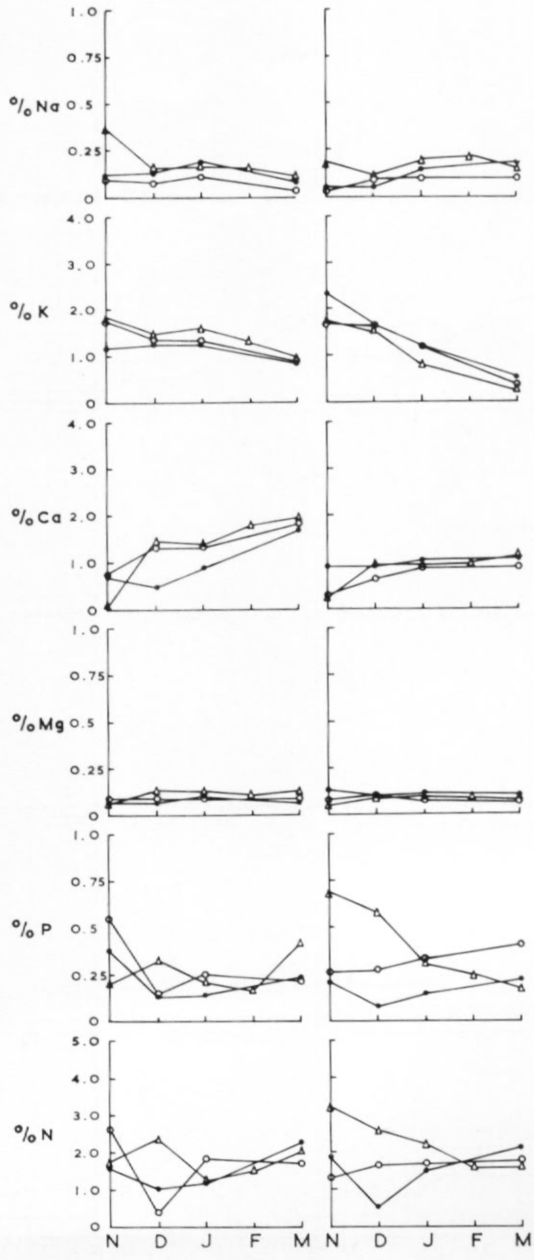

Fig. 4. Seasonal changes in the element content of *Poa flabellata* (Lam.) Hook. f. (unburnt site, solid circles; burnt site, open circles; wallows site, solid triangles). a. Living leaves; b. Flowers.

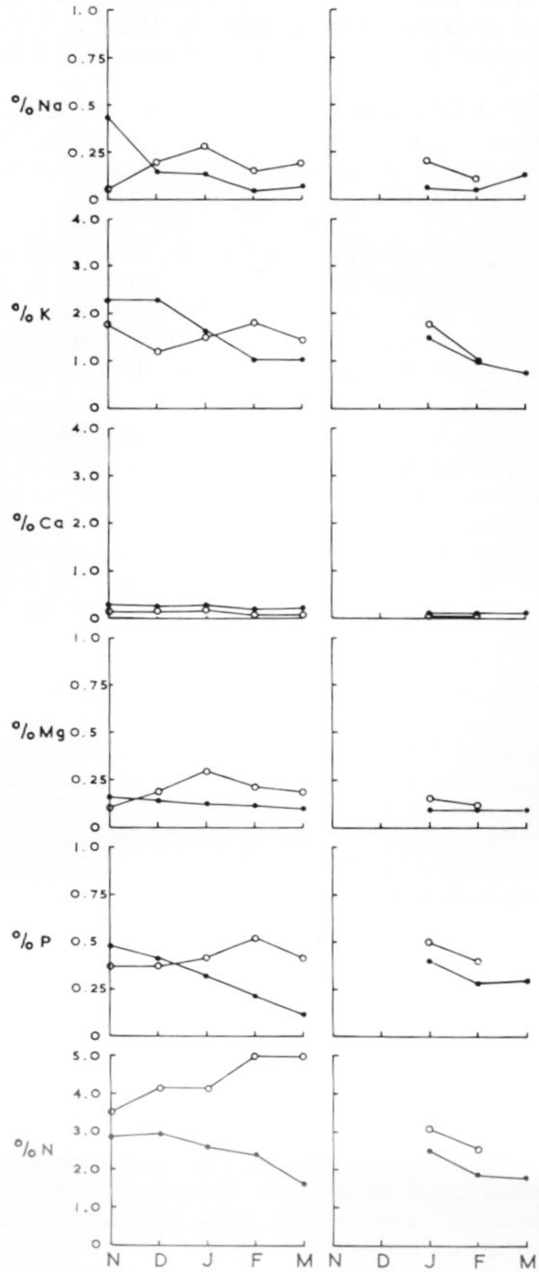

Fig. 5. Seasonal changes in the element content of *Deschampsia antarctica* Desv. (unenriched site, solid circles; wallows site, open circles). a. Living leaves; b. Flowers.

end of the summer. In *Juncus scheuchzerioides*, the only rush of eutrophic flushes which was sampled, the maximum value was attained in February. Both *Poa flabellata* and *Juncus* attained their maximum Ca levels at the end of the summer. K, Mg, P and N decreased or remained relatively unchanged except in *Poa* which showed autumn maxima for P and N.

Inflorescences. Only the grass flowers were analysed. There was a marked increase in Na in all four species throughout the summer. Ca and Mg remained almost constant. K, P and N decreased but in *Poa* and *Festuca* minimum values were reached in December and January, respectively.

Standing dead leaves and culms. Unlike the dwarf shrubs, there appeared to be little change in element content of attached dead material during the summer. In general, levels declined slightly with only minor exceptions. In *Festuca* and *Poa* the standing dead was at least 1 year old. A large proportion of the live green foliage in *Festuca*, *Poa*, *Juncus* and *Rostkovia* over-winters and leaf die-back occurs slowly throughout the following summer.

Forbs (Figs. 6–8).

In the small non-graminaceous herbs, each sample comprised all current year's growth, i.e. shoots, leaves and inflorescences. There was a tendency for all elements to decrease throughout the summer from spring peaks. In *Ranunculus biternatus* and *Galium antarcticum*, early season values for Na dropped sharply to a December minimum before rising for the rest of the summer, whilst *Callitriche antarctica* had a December peak. K and Ca also reached maximum values in December–January for *Callitriche* and *Galium*, whilst Mg had a December minimum in *Galium*. P and N declined steadily.

Serial analyses were restricted to *Polystichum mohrioides* fronds. There was a marked increase in Na early in the summer in the over-wintering green fronds, although those of the current year showed only a slight increase. Ca and Mg increased for both frond categories, whilst K, P and N decreased. Element levels in attached dead fronds showed a similar pattern in the early part of the summer with Ca being the only element to occur at a higher level than in live fronds. Mid-summer levels in *Lycopodium magellanicum* were generally lower than in *Polystichum* with Na and P having higher values in the underground rhizome than in the shoot. Analyses of *Blechum penna-marina* on Marion Island (Smith, 1976*a*) showed Ca and Mg levels are higher in the litter than in the living fronds.

Bryophytes (Figs. 9 and 10)

The mineral* and nitrogen contents of the five bryophytes were relatively low in comparison with those of the vascular species. Na increased throughout the season with January peaks for two of the flush species, *Pohlia wahlenbergii* and *Marchantia berteroana*. In all species, except *Polytrichum alpestre*, Ca, Mg, P, K and N had a declining seasonal trend.

Bryophytes have no control either over passive uptake or loss of nutrients by leaching. *Tortula robusta*, *Pohlia* and *Marchantia* grow in continually flushed habitats and their chemical composition seems likely to reflect the fluctuations occurring in their respective substrata. Thus it is surprising that *T. robusta*, a dominant moss of eutrophic bogs characterized by high extractable Ca concentrations (Smith and Walton, 1975), contained such a consistently low level of Ca. The comparatively dry acid peat of *P. alpestre* and *Chorisodontium aciphyllum* habitats contains fairly high concentrations of most elements which, on Signy Island at least, attain maximum levels during winter (Northover and Allen, 1967). The declining amounts of nutrients present during summer may explain the slight decreases recorded in *Chorisodontium*. In the endohydric *Polytrichum* the increased levels of several elements may suggest some degree of

*In the current biological context the words "element" and "mineral" are used interchangeably.

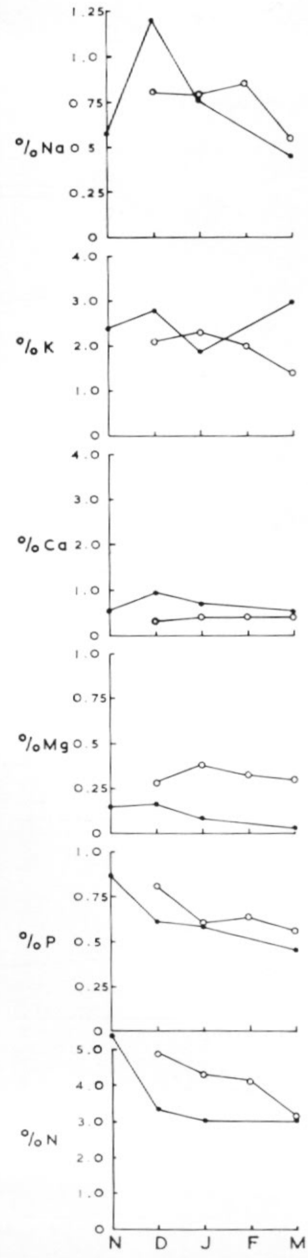

Fig. 6. Seasonal changes in the element content of whole plants of *Callitriche antarctica* Engelm. ex Hegel (unenriched site, solid circles; wallows site, open circles).

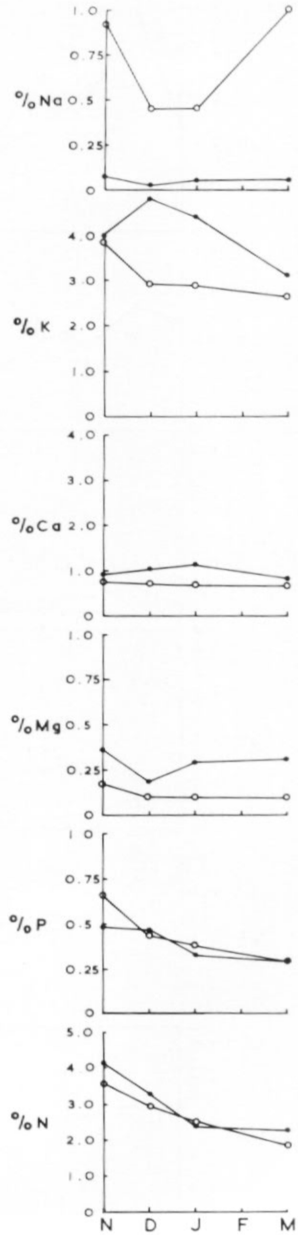

Fig. 7. Seasonal changes in the element content of whole plants of *Galium antarcticum* Hook. f. (solid circles) and living leaves of *Ranunculus biternatus* Sm. (open circles).

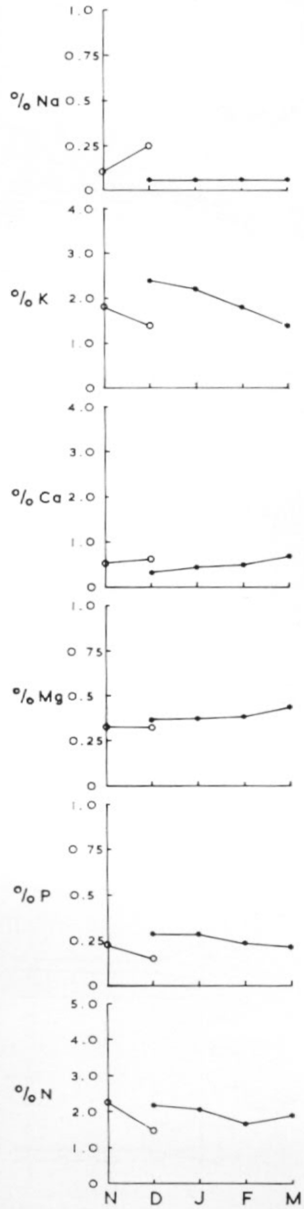

Fig. 8. Seasonal changes in the element content of overwintering (open circles) and new (solid circles) fronds of *Polystichum mohrioides* (Bory) C. Presl.

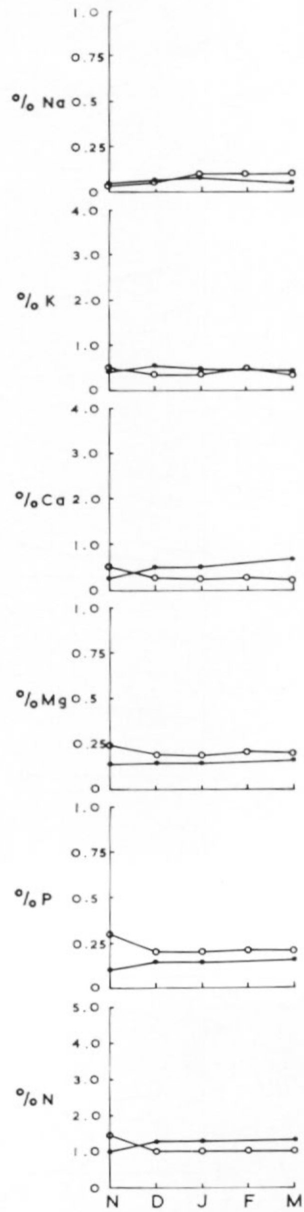

Fig. 9. Seasonal changes in the element content of *Polytrichum alpestre* Hoppe (solid circles) and *Chorisodontium aciphyllum* (Hook. f. et Wils.) Broth. (open circles).

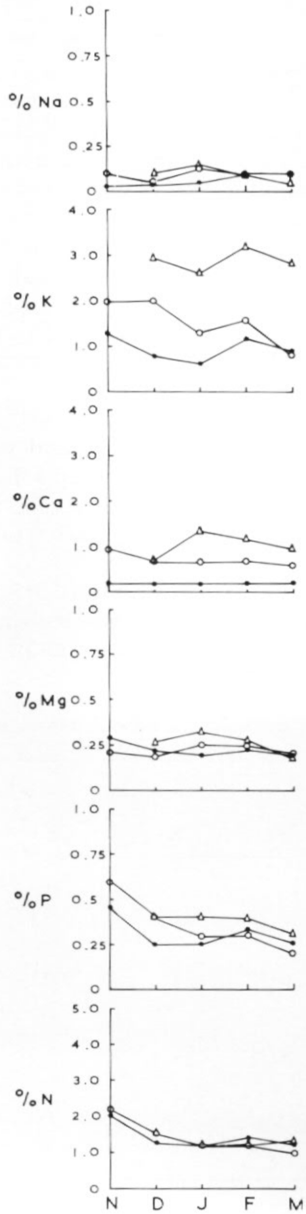

Fig. 10. Seasonal changes in the element content of *Tortula robusta* Hook. et Grev. (solid circles). *Pohlia wahlenbergii* (Web. et Mohr) Andrews (open circles) and *Marchantia berteroana* (open triangles).

accumulation, although bryophytes generally have no mechanisms for selective ion uptake and no specialized storage tissue.

Influence of enrichment of the habitat on plant chemical content

The large numbers of birds and seals found on most vegetated areas of South Georgia must provide considerable mineral input to the terrestrial ecosystems. Three herbaceous species, *Callitriche antarctica*, *Deschampsia antarctica* and *Poa flabellata*, were sampled from areas of elephant seal wallows and from stands well away from the influence of these animals. *P. flabellata* was also sampled from two stands on the Nuñez Peninsula, one of which was the nesting site of dove prions (*Pachytila desolata*) which burrowed into the base of the tussock stools, and the other several hundred metres away from this where there appeared to be no direct bird influence. Plant productivity appears to be considerably enhanced by the high nutrient content of bird and seal excrement, the foliage of tussock grass being much darker green in colour and the plants having much less standing dead. This colour difference can serve as an accurate means of locating the breeding sites of albatrosses and burrowing petrels around the coast of South Georgia.

A third series of *P. flabellata* samples was taken from two adjacent stands on a steep south-facing scree slope above King Edward Point. One stand was burnt on 22 November 1969 before much new growth had occurred. Almost all dead foliage was removed in this way and after a few weeks new shoots appeared in abundance. The control site lay to the windward of the burnt site and was not affected by any ash blown from the latter.

Seals. With the exception of Ca in *Deschampsia* and *Callitriche*, plants growing in the wallows had higher levels of all elements than those in non-biotically disturbed stands (Figs. 4–6; Table I). The seasonal trends followed those for non-wallow plants, although there were mid-

TABLE I. ELEMENT LEVELS IN CURRENT YEAR'S FOLIAGE OF *Poa flabellata* IN BIOTICALLY ENRICHED HABITATS

Habitat	*Element* (per cent dry weight)					
	Na	K	Ca	Mg	P	N
Tussock with dove prion (*Pachyptila desolata*) nest burrows in pedestal, Nuñez Peninsula	0·48	1·4	0·11	0·15	0·40	3·1
Tussock *c*. 100 m. from nearest dove prion nests, Nuñez Peninsula	0·38	1·1	0·11	0·11	0·28	1·6
Tussock at margin of elephant seal (*Mirounga leonina*) mud wallow, King Edward Point	0·14	1·4	0·15	0·10	0·34	2·6
Tussock on steep well-drained hillside (uninfluenced by birds or seals)	0·13	1·2	0·05	0·06	0·14	1·0

All samples collected in late December 1970.

season peaks for most elements in *Deschampsia* and *Callitriche*. Levels in the inflorescences of *Deschampsia* and *Poa* were correspondingly higher than in non-wallow plants except for Ca in *Deschampsia* and K in *Poa*. The concentrations of P and N are generally high in wallow muds (unpublished data of R. I. L. Smith). Data for species growing in wallows on Marion Island (Smith, 1976*c*) support all these observations.

Birds. Element levels were generally considerably higher in samples from the bird colony than in those from the wallows (Table I). Even in the bird "control" stand, the concentrations were comparatively high and this must be the result of aerial deposition of bird excreta when vast numbers of dove prions flock around their nesting sites at dawn and dusk. Analyses by Smith (1976*b*) of *Poa cookii* grassland with extensive petrel burrows on Marion Island also showed enhancement of N and P levels in both soils and plants. Smith suggested that lower Ca and Mg levels in these soils may be due to neutralization of nitrate ions by these elements, the soluble salts being subsequently leached out.

Burning. The immediate effect of burning the tussock grassland was to increase the nutrient content considerably (Fig. 3). The increased uptake of elements from the plant ash continued until the following November, a year after burning, after which leaching resulted in a steady decrease until the end of the second summer. Ca showed a different trend to the other elements, increasing on both sites throughout the sampling period. Although this suggests a slow release of the element from the ash at the burnt site, the similar trend at the unburnt site indicates that this is not the complete explanation.

Mineral content of standing crops

Using the chemical data together with biomass values for five communities, estimates can be made of the total amounts of nutrients bound within vegetation (Table II). Of the dominant species in the South Georgian flora, *Acaena magellanica*, with its deciduous leaves which have high levels of all elements, must be one of the most important in terms of nutrient re-cycling. Leaf decomposition is rapid, with a dry weight loss on South Georgia from fresh leaf material in litter bags in closed stands of over 90 per cent in only 14 weeks. Smith (1976*a*) reported similar rates on Marion Island. In the more open *Festuca contracta* grasslands with a high cover abundance of *Acaena magellanica*, the nutrient turn-over must be higher than in the closed grasslands where the dwarf shrub is sparse. Decomposition of standing dead *Festuca* leaves, which comprise *c*. 70 per cent of *Festuca–Acaena* communities (Walton and others, 1975), and up to *c*. 85 per cent of dense *Festuca* grassland (Smith and Stephenson, 1975) is comparatively slow, although once material becomes detached and incorporated into the litter component decomposition appears to proceed more rapidly. *Poa flabellata* has a high proportion of over-wintering green leaves and, since the rate of decomposition is similar to that of *Festuca* material (Smith and Stephenson, 1975), the return of nutrients to the substratum is likely to be relatively slow.

Moss turves formed in flushes by loose but extensive stands of *Pohlia wahlenbergii* and/or *Philonotis acicularis* present another example of rapid nutrient turn-over. The previous year's growth of these mosses dies back entirely during winter leaving a matrix of mildly acid decomposing litter. The large standing crop of shoots contains high levels of nutrients which are returned to the substrate in winter and are lost by leaching at the spring melt.

Discussion

An intensive programme of analyses to obtain a statistically realistic assessment of inter-plant, inter-stand or seasonal variation in chemical composition is excessively costly. Ball and Williams (1968) investigated the chemical properties of grassland soils in Snowdonia and concluded that spatial variation in these was so great that any seasonal trends were masked. Whilst it is probable that similar variation occurs within the vegetation of a particular stand on South Georgia, it was hoped that by harvesting a large number of plants, bulking the material before ashing and using aliquots of the ash for determination, an acceptable mean value for each element would be obtained. No true assessment of variance is possible by this method.

TABLE II. ESTIMATED TOTAL ELEMENT CONTENT (g./m.²) OF ALL ABOVE-GROUND COMPONENTS OF GRASSLAND, DWARF-SHRUB AND BRYOPHYTE-FLUSH COMMUNITIES

Plant community		Na		K		Ca		Mg		P		N		*Total ash*	
*Festuca contracta** grassland	Live	0·4	0·3	5·9	3·5	1·6	1·0	1·0	0·6	1·3	0·6	8·4	5·0	18·6	11·0
(1st column January, 2nd	Dead	0·2	0·2	2·2	2·1	1·8	1·9	1·1	1·1	0·6	0·6	6·6	6·5	12·5	12·4
column March)	Total	0·6	0·5	8·1	5·6	3·4	2·9	2·1	1·7	1·9	1·2	15·0	11·5	31·1	23·4
Festuca contracta—Acaena	Live		0·8		6·5		4·9		1·4		1·2		7·5		21·3
magellanica† heath (March)	Dead		0·3		3·5		3·1		1·8		0·9		10·6		20·2
	Total		1·1		9·9		8·1		3·3		2·1		18·0		41·5
Acaena magellanica‡ sward	Live	2·0	1·5	12·7	10·0	14·5	11·5	4·9	3·5	4·2	3·1	21·8	13·8	60·1	43·4
(1st column January, 2nd	Dead	0·9	0·8	3·2	1·6	11·5	2·2	2·9	1·5	1·5	0·9	6·7	4·0	26·7	11·0
column March)	Total	2·9	2·3	15·9	11·6	26·0	13·7	7·8	5·0	5·7	4·0	28·5	17·8	86·8	54·4
Poa flabellata§ grassland	Live	13·5		120·0		10·5		9·0		16·0–25·5		90·0–195·0		259·0–373·5	
(January–February)	Dead	8·5		14·0		9·5		4·5		20·0		150·0		206·5	
	Total	22·0		134·0		20·0		13·5		36·0–45·5		240·0–345·0		465·5–580·0	
Pohlia wahlenbergii+ *Philonotis acicularis*‖ flush (March)	Live		1·0		16·9		8·3		2·6		3·2		13·7		45·7

Element: Na, K, Ca, Mg, P, N.

Chemical data applied to standing-crop data provided by: *Smith and Stephenson (1975), †Walton and others (1974), ‡Walton (1973), §Smith and Walton (1975), ‖Clarke and others (1971).

The seasonal trends noted in several of the elements are similar to those obtained in Northern Hemisphere temperate species (Allen and others, 1974, p. 73). In general, for a particular species, the more mobile elements (Na, K, P and N) tended to follow one seasonal pattern, whilst the less mobile elements (Ca and Mg) followed another. Nitrogen values are generally higher than those for comparable species and habitats in the Northern Hemisphere and the high Na levels reflect the strong maritime influence. In fact, comparison of the present data with those from other tundra and temperate regions, irrespective of their "oceanicity", suggests that the element content of plants from the King Edward Cove area of South Georgia tends to be considerably higher than for related species in Alaska (Chapin and others, 1975), Siberia (Vassiljevskaja and others, 1975), Antarctic Peninsula (Rastorfer, 1972), South Orkney Islands (Allen and others, 1967; Holdgate and others, 1967), Marion Island (Smith, 1976*a*), New Zealand (Connor and others, 1970), Eire (Moore and others, 1975) and the United Kingdom (Allen and others, 1974, appendix A).

Although considerable differences in concentration were recorded from different species, the levels of an element in a particular life form tended to be of the same magnitude. For some elements, levels were highest in species of different life forms but growing in wet habitats where there is a small but continuous flow of nutrients through the substratum. The percentage Na content was highest in forbs growing in flushed habitats (*Callitriche* 1·20; *Ranunculus* 1·05) and in dwarf shrubs (*Acaena magellanica* 0·88; *A. tenera* 0·82). K was highest in forbs of mineral soils (*Galium* 4·8; *Colobanthus quitensis* 4·3) and in species of flushed habitats (*Juncus scheuchzerioides* 4·30; *Ranunculus* 3·80). Low percentages of both Na and K were recorded in graminoids and forbs on acid or dry soils. Calcium attained greatest concentrations in the dwarf shrubs (*Acaena magellanica* 3·10; *A. tenera* 1·40), whilst Mg was also highest in these plants (*Acaena magellanica* 0·55; *Acaena* hybrid 0·68). All other species had very low Ca levels. Phosphorus was highest in dwarf shrubs (*Acaena magellanica* 0·78; *A. tenera* 0·79) and in species of eutrophic bogs (*Callitriche* 0·86; *Ranunculus* 0·67; *Juncus* 0·56). Nitrogen reached maximum concentrations in the dwarf shrubs (*Acaena magellanica* 5·50; *A. tenera* 4·65), whilst *Deschampsia* from the wallows site and *Callitriche* from a stream margin also reached high values. Most other species contained between 1·0 and 3·0 per cent of N throughout the summer. With the exception of P and N, bryophytes from wet habitats (*Pohlia* and *Marchantia*) had higher mineral levels than those from drier situations (*Polytrichum* and *Chorisodontium*).

Comparison of these data with those obtained by Smith (1976*a*, *b*, *c*) for Marion Island plants shows many points of general agreement. He found high Ca and N levels in *Acaena magellanica*, K was the most prominent ash element in all species and N content was at most only twice that of K. The mineral contents given by him were not as high in many cases as in the South Georgian material where sampling through the season allowed determination of maximum values. He did carry out multiple determinations on each species and his standard errors show clearly the variability of the material.

Whilst Harner and Harper (1973) found grassland production in Utah was directly correlated with soil water content, they noted that the mineral content of the plants did not seem dependent on soil chemistry to any marked extent. The effect of manuring on South Georgian soils certainly raises plant mineral content for some elements and enhances vegetative production, but in general there appears to be little direct correlation between mineral levels in the plants and their associated soils (unpublished data of R. I. L. Smith). Northover and Allen (1967) established seasonal trends for Na, P and N in Signy Island soils and it will be interesting to see if such patterns can be found on South Georgia. They are most likely to be found near concentrations of animals and may show similar seasonal trends to those in plants.

The increased mineral and nitrogen content of foliage after the burning of the tussock grassland persisted for up to 16 months; similar results were obtained by Wein and Bliss (1973) in a burned *Eriophorum* community in the Arctic. In tundra regions, although the low soil temperatures often inhibit bacterial activity so that nutrient re-cycling can be very slow

(Haag, 1974), microbial activity in the relatively warm South Georgian soils may be of considerable importance. Freeze–thaw cycles appear to result in the physical release of nutrients (Cheng and others, 1971) and this process, together with the large amount of available soil water, may account for the increased element concentrations in the spring leaves at the burnt site. In the absence of intense leaching, the influence of added nutrients to an ecosystem is likely to persist longer than 16 months, since a fertilizer trials experiment on *Festuca contracta* grassland was still showing enhanced production 2 years after application (personal communication from J. R. B. Tallowin).

The retention of significant quantities of elements in the standing dead and litter fractions of the grasslands and the low decay rates characteristic of this type of community ensure that nutrient re-cycling is much slower than in similar temperate grasslands. Haag (1974) has pointed out that the re-translocation of N and P back to the stems and roots before leaf fall is of considerable importance in Arctic ecosystems. Recent ^{14}C studies on several South Georgian species have shown that material previously classified as dead on the basis of appearance may still show evidence of translocation. The high nutrient levels in the standing dead of *Festuca* and *Poa* grasslands might then act as a nutrient pool which is at least partly available to the plant. Conversely, the deciduous nature of *Acaena magellanica* and the rapid rate of decay of its leaves (Walton, 1973) suggests a comparatively rapid re-cycling of nutrients in the dwarf-shrub ecosystem. Thus, although re-cycling via the soil may be much slower in *Festuca* grassland than in an *Acaena* sward, an important proportion of the nutrient requirements of the plant may be met by the standing dead acting as a temporary buffer store.

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