

# Seasonal changes in plant and soil chemical composition at Marion Island (sub-Antarctic): I — Mire-grasslands

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*The seasonal changes in concentrations of N, P, K, Ca, Mg and Na in the plants at two mire-grasslands on sub-Antarctic Marion Island (47°S, 38°E) are described. In general, N, P and K concentrations in the aboveground biomass decreased, and those of Ca (sometimes also Mg) increased as the season progressed. Concentrations of N, P and Mg in the aboveground biomass of graminoid species at the island are low compared with most graminoids at tundra mires and meadows or at montane grasslands, sedge-heaths and freshwater wetlands of more temperate latitudes. K concentrations in the island graminoids are similar to those at Arctic and sub-Arctic tundras but are greater than those for most sedges and grasses at more temperate moorland sites. Ca concentrations in all the island species considered in this study are markedly lower than for plants from tundra and tundra-like areas. There were no conspicuous seasonal variations in soil nutrient levels at the two mire-grasslands.*

*Die seisoenswisseling in die konsentrasie van N, P, K, Ca, Mg en Na by die plante van twee moerasagtige grasvelde op die sub-Antarktiese Marion-eiland (47°S, 38°O) word beskryf. Oor die algemeen het die konsentrasie van N, P en K in die bopgrondse biomassa afgeneem en het dié van Ca (in sommige gevalle ook van Mg) met verloop van die seisoen toegeneem. Die konsentrasie van N, P en Mg in die bopgrondse biomassa van die grasagtige spesies is laag in vergelyking met dié van die meeste grasagtiges van toendramoerasse en -vleie of van berggrasvelde, biesagtige heidevelde en varswatermoerasse van gematigder streke. Die kaliumkonsentrasie in die eiland se grasagtige stam ooreen met dié van Arktiese en sub-Arktiese toendras, maar is hoër as by die meeste biesies en grasse van gematigde heidevelde. Die kalsiumkonsentrasie is aansienlik laer by al die eilandspesies wat in hierdie ondersoek betrek is as by plante van die toendra en toendra-agtige gebiede. Daar was geen opvallende seisoenswisseling in grondvoedingstof-konsentrasies by die eiland se grasvelde nie.*

## Introduction

Due to the International Biological Programme's Tundra Biome Project much is known about the seasonal changes in plant nutrient status at northern hemisphere subpolar areas (e.g. Wielgolaski *et al.* 1975, Tieszen 1978, Chapin *et al.* 1980, Dowding *et al.* 1981, Van Cleve & Alexander 1981). There is much less information on plants from southern hemisphere subpolar areas (e.g. Lewis Smith 1985). Soil and plant chemical composition studies have enabled an assessment of the nutrient statuses of some vegetation types at Marion Island (47°S, 38°E), South Georgia (54-55°S, 36-38°W) and Signy Island (60°S, 45°W), but only in a few

instances did these studies include the seasonal trends in plant or soil chemical composition. This paper describes the seasonal changes in chemical composition of the dominant plant species at two mire-grasslands on Marion Island. Nutrient concentrations in the plants are compared with those for graminoid plants from other sub-Antarctic islands and from sub-Arctic, Arctic and alpine sites.

## Sites

Trees and woody shrubs are lacking in the Marion Island vegetation but extensive closed phanerogamic communities understored by bryophytes occur. The island climate is typically sub-Antarctic (Smith 1986), dominated by high wind, very high rainfall and the absence of a warm summer; the latter two features being conducive toward peat formation (French & Smith 1985).

Gremmen (1981) recognized six plant community complexes in the island vegetation, five of which are largely restricted to lowland areas less than 300 m above sea level. Communities of the *Juncus scheuchzerioides* - *Blepharidophyllum densifolium* complex form the vegetation of the island's bogs and mires, occurring on wet peat deposits of ill-drained basins and gentle slopes. Extremely wet peats support bog communities dominated by bryophytes. Where peat accumulation raises the surface above the watertable the importance of graminoid species is enhanced and a mire-grassland vegetation develops in which dicotyledons are rarely important. Physiognomically, these mire-grasslands are very similar to Arctic, sub-Arctic and subalpine sedge-moss meadows. On the island's eastern coastal plain bogs and mires occupy approximately 37 percent of the surface area of the unglaciated, younger lava flows (Smith 1976). On older lavas, which have been subjected to Pleistocene glaciation, bogs and mires occur on approximately 59 percent of the surface area (Smith 1977).

The two mire-grassland sites investigated in this study occurred within 50 m of each other, approximately 300 m west of the meteorological station on the island's eastern coastal plain. They are between 400 and 500 m from the coast and are at altitudes of 30 to 40 m a.s.l. Study mire 1 (approx. 1.5 ha) consists of a mosaic of closed canopy vegetation (closed stands) and parts where the vegetation (especially the bryophyte layer) has degraded to a more open type (open stands). Possible causes of this degradation are discussed by Gremmen (1981). No degradation had occurred at the other mire-grassland site (study mire 2; approx. 1 ha).

Details of the floristic composition and phytosociological classification of the two sites are provided in Smith (1987) so only brief descriptions are provided here. The main plant

community at study mire 1 is the association *Lycopodio magellanici* - *Jamesonielletum coloratae*, subassociation *ranunculetosum biternati* (Gremmen 1981), dominated by the grass *Agrostis magellanica* and sedge *Uncinia compacta*. *Juncus scheuchzerioides* is also common. *Jamesoniella colorata* is the dominant bryophyte species but at drier parts of the mire *Racomitrium lanuginosum* is co-dominant. At wetter areas, *Blepharidophyllum densifolium* and *Clasmatocolea humilis* occur but do not displace *J. colorata* as the dominant species. The fern *Blechnum penna-marina*, which reaches dominance at drier variants of the *ranunculetosum biternati* subassociation, is rare at this site, which represents the wet *Agrostis magellanica* variant (Gremmen 1981).

Study mire 2 consists of a well-developed mire-grassland vegetation dominated by a community similar to the *Blepharidophyllo densifolii* - *Clasmatocoleetum humilis* association (subassociation *ranunculetosum biternati*) of Gremmen (1981). However, *Juncus scheuchzerioides* is more common at study mire 2 than at typical stands of this community, especially at the wetter sites, where the vegetation is more typical of the *Juncus scheuchzerioides* - *Drepanocladetum uncinati* association (subassociation *clasmatoceletosum humilis*). *Agrostis magellanica* and *Uncinia compacta* dominate the herb layer. The dominant bryophyte species is *Blepharidophyllum densifolium*. At wetter parts, *Clasmatocolea humilis*, *Distichophyllum fasciculatum* and *Drepanocladus uncinatus* are co-dominant with *B. densifolium*.

## Methods

### Chemical analysis of peat/soil

Peat or soil samples were collected at fortnightly or monthly intervals to a depth of 25 cm using a soil corer (area, 50 cm<sup>2</sup>). Details of the sampling regime are provided by Smith (1987). At least four cores were sampled at each date. The cores were divided longitudinally into three subsamples and conspicuous roots removed from each. One subsample was weighed, dried at 105 °C and reweighed to assess water content. A second subsample was immediately used to determine NH<sub>4</sub>-N (on 0.5 M NaCl extracts by the phenolhypochlorite reaction; Solórzano 1969), NO<sub>2</sub> and NO<sub>3</sub>-N (Greiss-Ilosvay reaction on the same extracts, NO<sub>2</sub> being reduced to NO<sub>2</sub> with spongy cadmium; Mackereth *et al.* 1978) and pH (combination electrode immersed in a slurry of 10 g peat : 20 ml water). The remaining subsample was air-dried at 20 to 30 °C for the following analyses. Organic carbon was determined using the Walkley-Black procedure (Allison 1965). A 0.33 M (instead of 0.17 M) K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub> oxidizing solution was employed, enabling a larger subsample to be used in the analysis. The proportion of the total organic C oxidized was not determined and so the values are expressed here as "dichromate-oxidizable C". "Kjeldahl" N was determined by titration after steam distilling the NH<sub>4</sub>-N in H<sub>2</sub>SO<sub>4</sub>-K<sub>2</sub>SO<sub>4</sub>-CuSO<sub>4</sub>-Se digests of the peat into boric-acid/indicator solution. Exchangeable cations were determined by atomic absorption spectrophotometry on ammonium acetate (unbuffered, pH 7) extracts of the peat. The same samples were used to determine the cation exchange capacity (CEC). After washing out the excess NH<sub>4</sub>OAc with isopropanol, the adsorbed NH<sub>4</sub><sup>+</sup> was displaced (successive cycles of shaking and centrifugation) by Na<sup>+</sup> (as NaCl) and the amount of NH<sub>4</sub>-N in the displacement

solution determined by steam distillation. The CEC was calculated from these amounts. "Available" P levels in the soils was determined according to a resin-extraction procedure (Smith 1979a).

### Plant chemical analysis

The harvesting and sorting procedures whereby the plant samples were obtained are described in Smith (1987). Four to eight samples were harvested at each date. The sorted samples were rinsed briefly in distilled water, dried (105 °C), and ground (20 mesh). Subsamples ( $\pm 200$  mg, accurately weighed) of the dried, ground material were digested in HNO<sub>3</sub>-H<sub>2</sub>SO<sub>4</sub>-HClO<sub>4</sub> mixture (8:1:1, volume basis). Plant P content was determined on dilutions of the digest using a phosphomolybdate-blue procedure (Murphy & Riley 1962), the H<sup>+</sup> concentration of the colour-developing reagent being adjusted to compensate for the acidity in the digest. Ca, Mg, Na, and K concentrations were determined on suitable dilutions of the digest by atomic absorption spectrophotometry; lanthanum (in HCl) suppressant was added to the aliquots for Ca determination. Smith (1979b) assessed the reliability and sensitivity of this mixed-acid digestion procedure and compared it with alternative procedures.

Kjeldahl N was measured by digesting subsamples of the ground plant material in a H<sub>2</sub>SO<sub>4</sub>-K<sub>2</sub>SO<sub>4</sub>-CuSO<sub>4</sub>-Se mixture. NH<sub>4</sub>-N in the digest was either determined by steam distillation into boric acid indicator solution or by a modified phenol-hypochlorite reaction (Smith 1980).

## Results

### Peat chemical composition

Chemical parameters for the study mire peats are presented in Table 1. Except for pH at study mire 1 there were no conspicuous seasonal variations in these parameters and the values represent the ranges measured at study mire 1 between September 1979 and August 1980 and at study mire 2 from December 1973 to May 1974.

Peats from both sites were acid and very wet. Peat pH was not significantly ( $P \leq 0.05$ ) different between closed and open stands at study mire 1 but increased at both stands during summer, from  $4.7 \pm 0.1$  in September to  $5.3 \pm 0.2$  in February. Between February and June, pH varied erratically between sampling dates and then declined slowly until late August.

Peat water content reflected the intensity of precipitation prior to sampling. It therefore varied markedly between sampling dates and was not significantly different between closed and open stands. Peat samples from study mire 2 were mostly wetter than those from study mire 1. Because of the substantial organic matter contents, Kjeldahl N values were high. Cation exchange capacities (CEC) were fairly high, probably also related to the high contents of organic matter. Mg and Ca were the dominant exchangeable cations and the amount of exchangeable Na always exceeded that of K.

There were no consistent differences in the magnitudes of the chemical parameters depicted in Table 1 between study mires 1 and 2, except that exchangeable Mg and Na tended to be higher at study mire 2, especially if expressed on the basis of their percentage saturation of the CEC. "Available" P levels under closed vegetation stands at study mire 1 were also mostly lower than those at open stands or at study mire 2.

Table 1.  
Soil chemistry at the two mire-grasslands. All nutrient concentrations are on a dry weight basis

	n*	pH	% of dry weight			µg g <sup>-1</sup>			millicivalents 100 g <sup>-1</sup>					
			moisture	Cr <sub>2</sub> O <sub>7</sub> <sup>-2</sup> oxidiz. C	Kjeldahl N	Total P	NH <sub>4</sub> <sup>+</sup> N	NO <sub>3</sub> <sup>-</sup> N	"Available" P	C.E.C.	Exch. Ca	Exch. Mg	Exch. Na	Exch. K
Study mire 1														
closed stands	76	4.6-5.3	1100-1650	32-37	1.6-2.3	0.08-0.13	5.1-114.0	0-35.7	9-45	82-91	6.2-9.1	5.0-6.4	0.8-1.9	0.4-1.0
open stands	80	4.6-5.3	1050-1750	31-36	2.0-2.7	0.09-0.15	9.5-136.0	0-14.6	18-99	79-87	4.7-6.9	4.9-6.4	0.8-1.8	0.7-1.4
Study mire 2	28	4.3-5.3	1250-2150	30-36	1.7-2.3	0.08-0.14	0-23.0**	0-5.0**	17-62	49-94	2.1-5.2	5.0-7.1	1.0-2.6	0.7-1.8

\* n = number of samples

\*\* n = 12

Inorganic forms of N at study mire 2 were only determined on three occasions (four replicates each) during 1973/74 and ranged from 0 to 23 µg NH<sub>4</sub>-N and 0 to 5 µg NO<sub>3</sub>-N per g dry peat. There were no significant differences in the concentrations of either NH<sub>4</sub>-N or NO<sub>3</sub>-N between sampling dates and NO<sub>3</sub>-N was never detected. At study mire 1, peat NH<sub>4</sub>-N contents under both closed and open vegetation were remarkably consistent within, but varied markedly between, sampling dates. Within sampling dates there was also seldom any significant difference in inorganic N contents between closed and open stands but NO<sub>3</sub>-N at open stands never reached the peak levels attained at closed stands. NH<sub>4</sub>-N was the predominant form of inorganic N in the mire peat and increased markedly from low values during three periods; early November to mid December, early January to early March and mid April to late June. All

these increases were highly significant ( $P < 0.001$ ). Highest NH<sub>4</sub>-N concentrations occurred during late June but values then decreased five-fold by August. NO<sub>3</sub>-N contents, also fairly consistent within sampling dates, varied markedly between dates, with striking increases during periods when NH<sub>4</sub>-N values were low or were decreasing from high levels.

#### Plant chemical composition

Seasonal changes in plant nutrient concentrations for the various phytomass components of the mire-grassland species are depicted in Figures 1 to 8. Each data point is the mean of 4 to 8 replicate samples collected at each harvest date.

Aboveground vascular plant vegetative biomass at study mire 1 consisted mainly of living *Agrostis magellanica* shoots, with smaller proportions of *Uncinia compacta* and

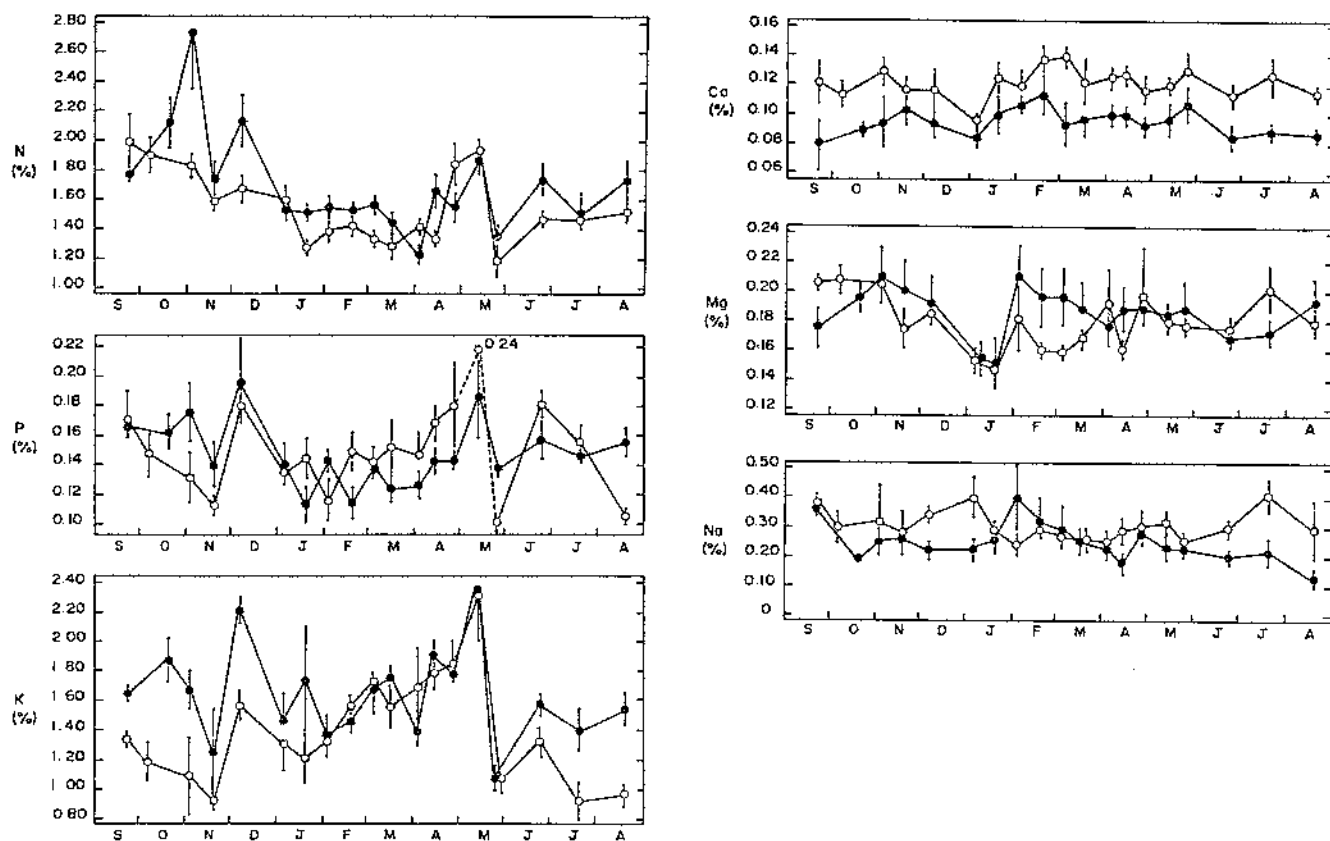


Fig. 1. Chemical composition of aboveground vascular plant vegetation biomass at closed (●) and open (○) stands at study mire 1. Vertical lines indicate the standard errors of the mean values.

*Juncus scheuchzerioides* shoots. Highest concentrations of N and P in the aboveground vegetative biomass at closed stands of vegetation occurred in November/December and at open stands in September (Fig. 1). At both closed and open vegetation the concentrations of N decreased markedly after the early season peaks. P concentrations also tended to decline from high early summer levels, except for inexplicably high values for material harvested early in December. Between April and May there were marked increases in N and P concentrations in the aboveground vascular vegetative biomass at both stand types. This preceded, with approximately a fortnight overlap, a substantial early winter appearance of aboveground biomass at study mire 1 (Smith 1987).

K concentrations in the aerial vascular plant biomass varied markedly, both within and between sampling dates and no seasonal pattern could be discerned. Very low Ca concentrations occurred in the aboveground vascular plant material and the values were consistently lower at closed (0.08 to 0.11 %) than at open (0.10 to 0.14 %) stands. No seasonal trend in Ca concentration was noted. Mg levels were greater than those of Ca and they decreased during early summer, followed by a rapid increase in late January/early February. Na concentrations in the aboveground biomass did not vary seasonally and, except for

a short period just after midsummer, were slightly lower at closed than at open stands.

Harvest samples from study mire 1 were not sorted according to species and the observed temporal changes in the chemical composition of the total vascular plant biomass only reflected the net effect of the changes in the component species. Because of successive growth and senescence amongst them, this net effect was "buffered", obscuring the timing and magnitude of changes in plant mineral composition which may have occurred in the vegetation.

Vascular plant material harvested from study mire 2 was sorted to species, of which three occurred; *Agrostis magellanica*, *Uncinia compacta* and *Juncus scheuchzerioides*. The seasonal changes in nutrient concentration in the aboveground vegetative vascular plant biomass of these three species are presented in Figure 2. Highest N concentrations occurred in the leaves and stems of *J. scheuchzerioides* and the lowest in those of *U. compacta*. N concentrations in *A. magellanica* increased from September to November, before the midsummer increase in the biomass, indicating that new leaf material was being produced earlier in the growing season than could be observed from the biomass data. N concentrations then declined markedly during the second half of summer and in early winter. In living aboveground material of *J.*

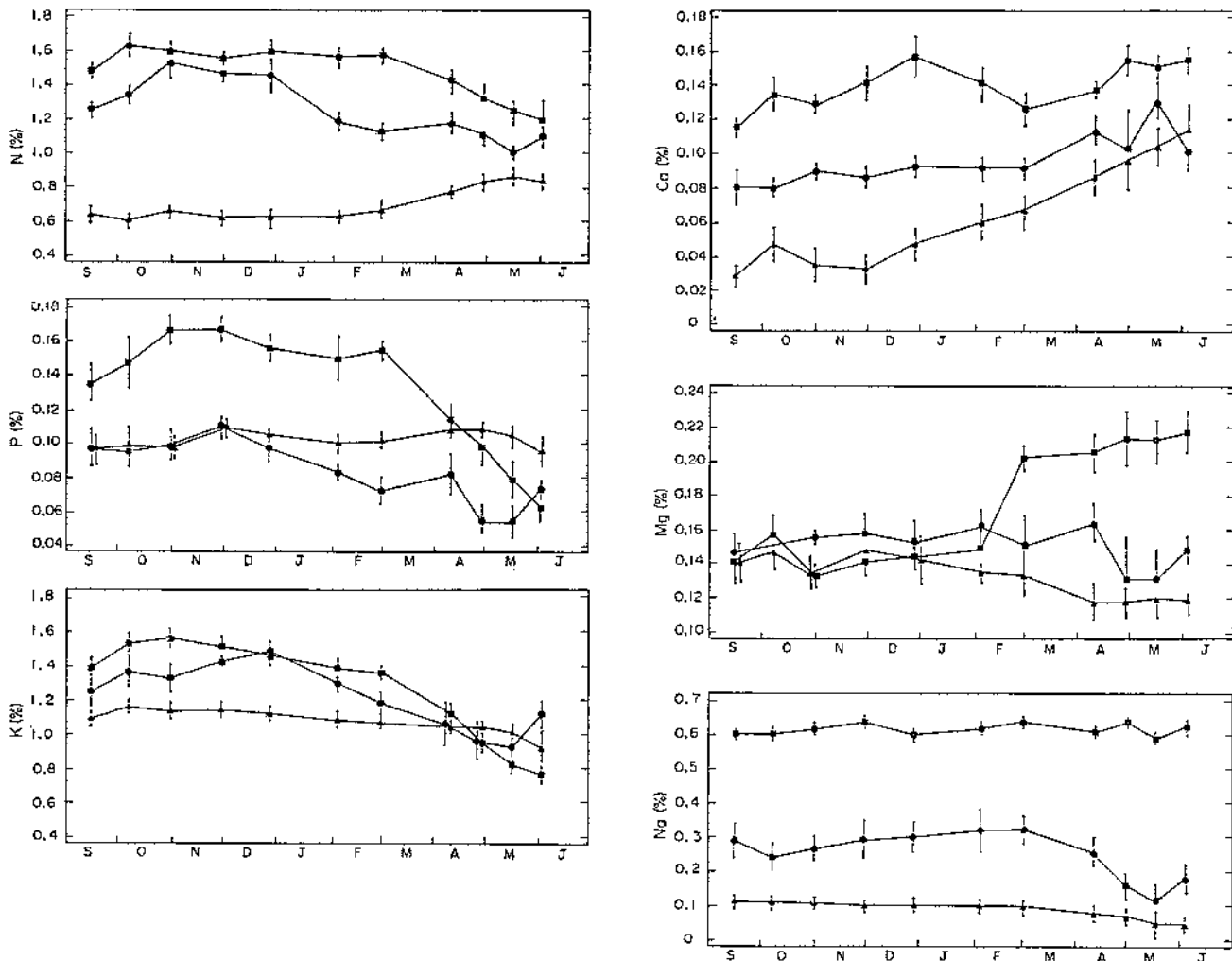


Fig. 2. Chemical composition of the aboveground vegetative biomass of *Agrostis magellanica* (●), *Uncinia compacta* (▲) and *Juncus scheuchzerioides* (■) at study mire 2. Vertical lines indicate the standard errors of the mean values.

*scheuchzerioides*, N concentrations were consistent throughout summer but decreased markedly in early winter. N levels in *U. compacta* did not change during summer, but increased in autumn. This pattern, which contrasts with that observed for the other two species, may be due to the fact that, from late February, a substantial proportion of the *U. compacta* aerial biomass consisted of green inflorescence stalks which possessed higher N levels than did the stem bases and mature leaves.

Seasonal patterns of P concentrations in the aboveground vegetative biomass of *A. magellanica* and *J. scheuchzerioides* were similar to those of N; however, for *J. scheuchzerioides* the autumn decrease in P concentration was even more marked than that of N. P levels in *U. compacta* material were fairly constant throughout the sampling period.

Changes in the K concentrations of the aerial biomasses of *A. magellanica* and *J. scheuchzerioides* paralleled those of N and P, i.e. increased early in summer and declined to low levels in winter. *U. compacta* biomass exhibited low K concentrations which, however, declined only slightly (but significantly;  $P = 0.01$ ) during the summer so that during early winter the values were not significantly different to those for *A. magellanica* and *J. scheuchzerioides*.

Ca concentrations in aboveground living material of *J. scheuchzerioides* were consistently higher than those for *A. magellanica* which were, in turn (except for early winter),

substantially higher than those for *U. compacta*. For *A. magellanica* and *U. compacta*, Ca concentrations increased throughout summer. A midsummer peak for Ca was observed in *J. scheuchzerioides*, followed by a decline until March and an increase in autumn. Mg concentrations in the aboveground biomass of *A. magellanica* and *U. compacta* remained fairly consistent throughout the sampling period; a slight decline occurred during summer for the latter species but the difference between the highest (late November) and lowest (April) value was not significant at  $P \leq 0.05$ . *J. scheuchzerioides* living shoots exhibited much higher Mg levels in autumn and early winter than in summer.

Na concentrations in aboveground living plant material were highest for *J. scheuchzerioides* and lowest for *U. compacta*. In *A. magellanica* and *U. compacta*, Na values declined significantly in autumn. Hence, for these two species the seasonal variation in Na concentration was similar to those for N, P and K. Na concentrations in the aboveground biomass of *J. scheuchzerioides* remained consistently high throughout the sampling period.

Concentrations of Ca, Mg and Na in the aboveground vascular vegetative biomass at study mire 1 were within the ranges of those measured for the three graminoid species at study mire 2. Although peak concentrations of N, P and K were greater at study mire 1, for most of the season the levels of these three elements were similar to those in *A.*

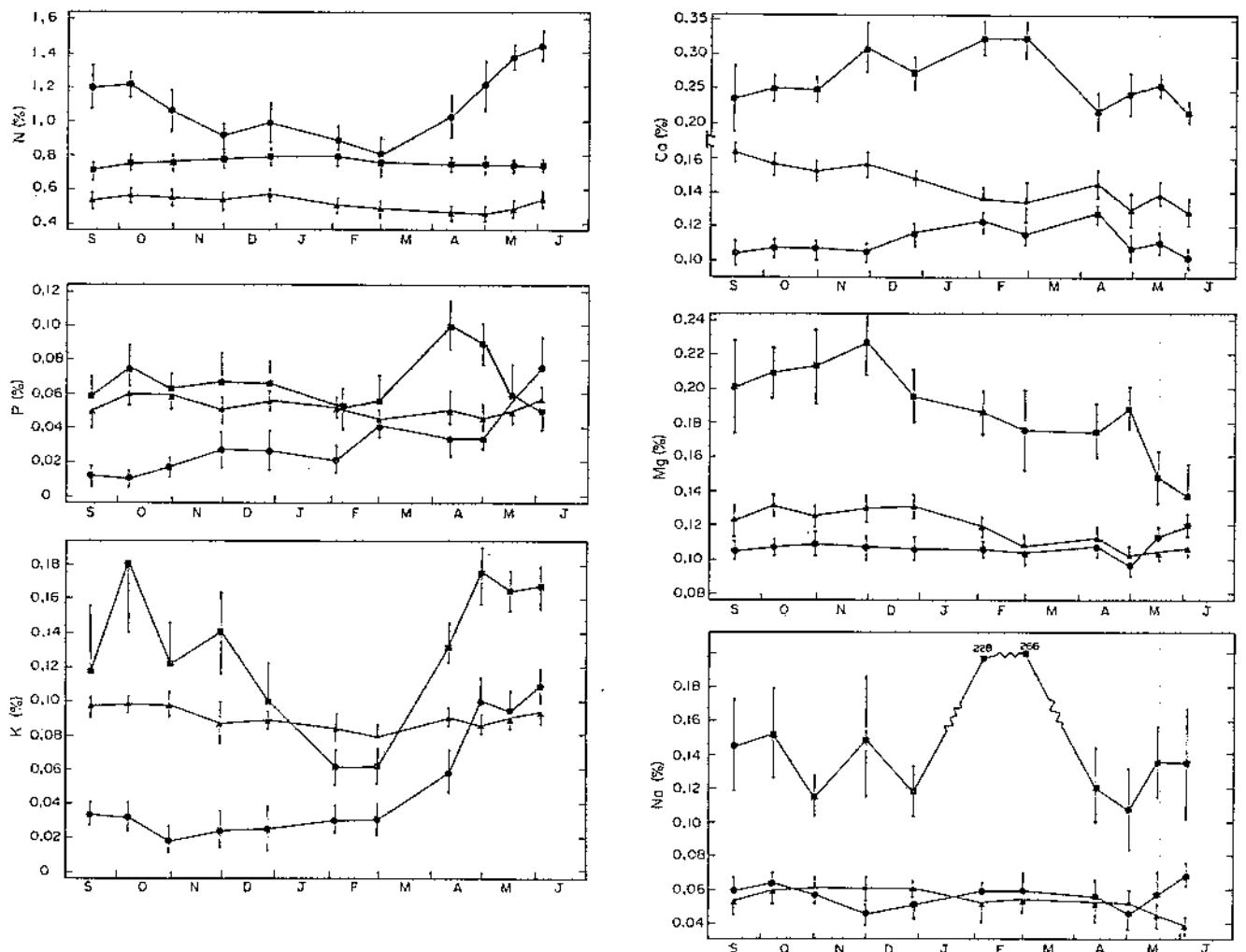


Fig. 3. Chemical composition of the aboveground necromass of *Agrostis magellanica* (●), *Uncinia compacta* (▲) and *Juncus scheuchzerioides* (■) at study mire 2. Vertical lines indicate the standard errors of the mean values.

Table 2

Range of mean nutrient concentrations (percent of dry weight), approximately in the order of their seasonal variation, in the reproductive biomass (flowers and seed-heads) of the vascular plants at the two mire-grasslands.

Site and species	N	P	K	Ca	Mg	Na
<b>Study mire 1</b>						
Closed stands	2.53-0.72	0.32-0.03	1.64-0.20	0.06-0.12	0.09-0.21*	0.01-0.21
Open stands	2.61-1.39	0.39-0.14	1.97-0.24	0.10-0.15	0.14-0.19*	0.01-0.21
<b>Study mire 2</b>						
<i>Agrostis magellanica</i>	2.29-2.00	0.26-0.17	1.02-0.29	0.08-0.10**	0.12-0.14**	0.15-0.25**
<i>Ucinia compacta</i>	1.88-0.82	0.19-0.09	1.57-0.40	0.13-0.17**	0.12-0.19**	0.12-0.18**

\* Concentrations increased from January to March/April and then decreased.

\*\* Order does not reflect the seasonal progression.

*magellanica* and *J. scheuchzerioides* material from study mire 2.

Nutrient concentrations in vascular reproductive material at the two mire-grassland sites are presented in Table 2. This material consisted of inflorescences which, later in the season, contained seed. Old flowering heads which had shed their seed were also included in the "reproductive" component. *Juncus scheuchzerioides* reproductive material contributed very little to the overall standing crop at both study mires (Smith 1987) and not enough of this material was obtained from the harvest samples for chemical analysis. Almost all of the reproductive material at study mire 1 consisted of *A. magellanica* flowers and seeds.

For *A. magellanica* and *U. compacta*, concentrations of N and P in the reproductive material were higher than, and those of Mg and K similar to, the corresponding concentrations in the vegetative material. Ca concentrations in *A. magellanica* reproductive tissue were also similar to, whereas Na levels were lower than, those in the vegetative material. For *U. compacta*, the concentrations of both these

elements were higher in reproductive than in vegetative material.

The substantial ranges of nutrient concentrations depicted in Table 2 for reproductive material of *A. magellanica* at study mire 2 and of the bulked vascular vegetation at study mire 1 are due to marked seasonal variations in these concentrations. Flowering in *A. magellanica* commenced in January at both mires and by May most of the seed had been shed. However, standing reproductive material occurred at both communities (as empty flowering heads) throughout most of winter. At study mire 2, concentrations of N and P in *A. magellanica* reproductive material were highest between February and late March, after which they declined very markedly to low values, presumably reflecting the loss of seeds from the flowering heads. Ca and Na concentrations increased throughout summer, then also declined in autumn. K concentrations were highest in very young flowers. By late February K levels had decreased to approximately 60 per cent of these early high values and thereafter declined slowly throughout the rest of summer. Mg concentrations in *A.*

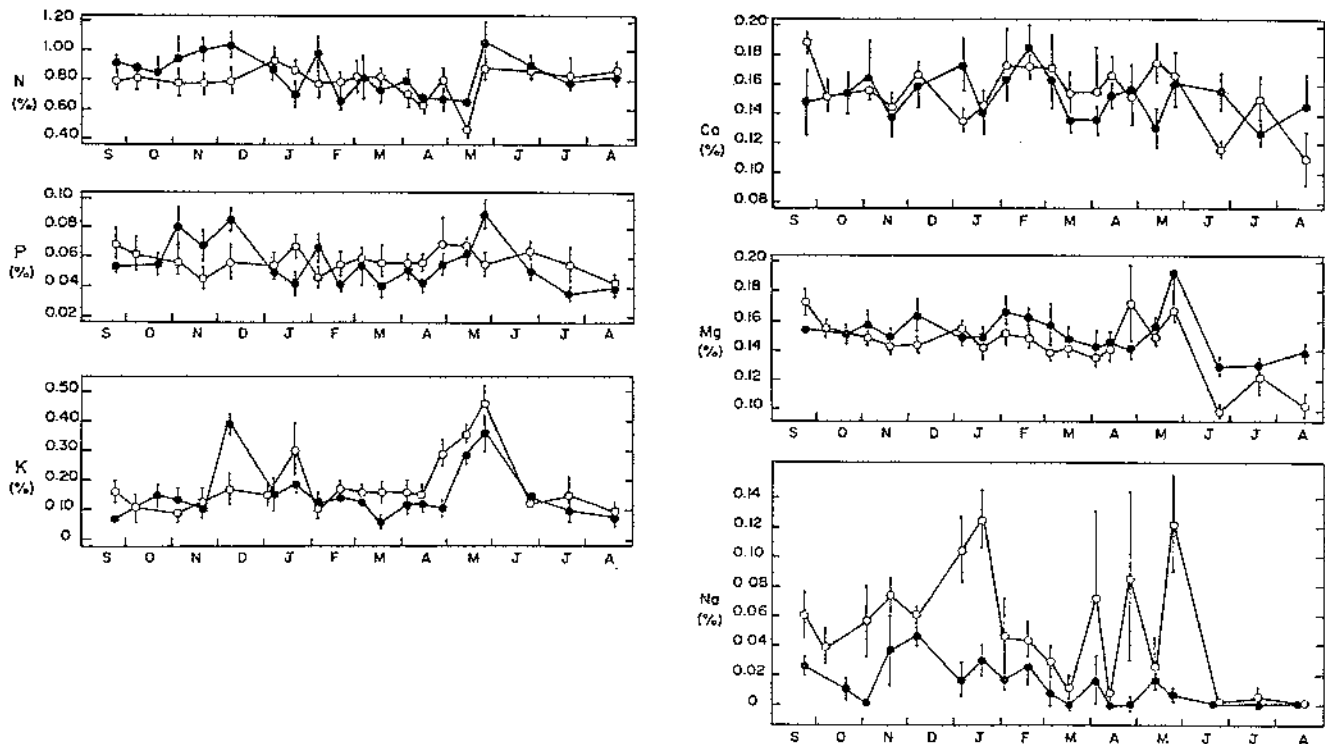


Fig. 4. Chemical composition of the aboveground vascular plant necromass at closed (●) and open (○) stands at study mire 1. Vertical lines indicate the standard errors of the mean values.

*magellanica* reproductive material did not vary in a consistent pattern throughout the sampling period. Age-related changes in nutrient concentrations in the reproductive biomass of *U. compacta* resembled those for *A. magellanica*.

Concentrations of N, P, K and Ca in vascular reproductive material at study mire 1 were generally higher (especially at open stands) than in the corresponding *A. magellanica* material at study mire 2. However, the seasonal trends in concentration of all elements in the study mire 1 material were identical to those described for *A. magellanica* at study mire 2. Reproductive plant tissue possessed higher concentrations of N, P, K and Ca at open than at closed stands.

Aboveground vascular plant necromass consisted mainly of standing dead leaves, stem bases and flowering culms without inflorescences. The changes in chemical composition of this dead material during the season are depicted in Figure 3. For all three species the concentrations of N, P, Na and, especially, of K were lower in the necromass than in the biomass, although in early winter the N concentrations in dead material of *A. magellanica* were similar to, or even higher than those in the living shoots. Necromass Ca concentrations were higher than in the biomass. Necromass of *A. magellanica* possessed lower concentrations of Mg than did the biomass, whereas in *U. compacta* similar Mg levels

were found in the two components. Mg concentrations in dead leaves of *J. scheuchzerioides* declined sharply throughout the season, in contrast to the trend shown by this element in the shoot biomass (compare Fig. 2 and 3), so that in summer dead material possessed lower concentrations than did the living material whereas in autumn and early winter the converse was true.

Concentrations of N and P in dead aboveground material of *U. compacta* and *J. scheuchzerioides* were fairly constant throughout the season, except for high P concentrations in *J. scheuchzerioides* during April and May. Necromass of this species also increased very sharply in April (Smith 1987) and the enhancement in P levels was possibly due to the contribution of recently senesced leaves possessing relatively high P concentrations. For *A. magellanica*, concentrations of N were lowest in dead material collected in summer, whereas P and K concentrations increased throughout the growing season, possibly also reflecting the increasing importance of recently senesced material in the necromass as the season progressed. K concentrations in *U. compacta* dead material remained fairly constant but in the case of *J. scheuchzerioides* declined throughout the first half of summer and then increased sharply in autumn.

Ca levels in the aboveground necromass were fairly consistent throughout the season for *A. magellanica* and *J. scheuchzerioides* but decreased significantly for *U. compacta*

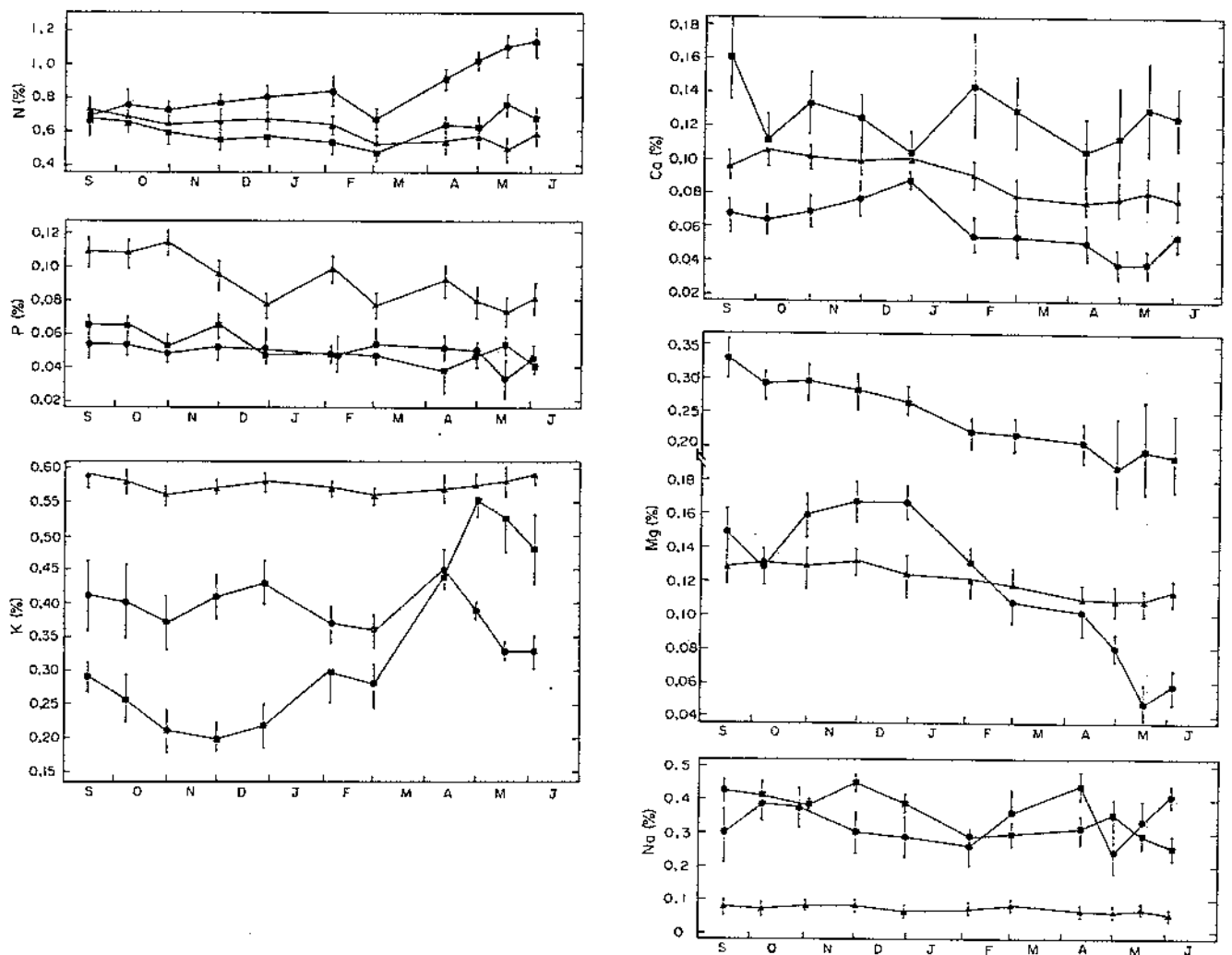


Fig. 5. Chemical composition of the belowground standing crop of *Agrostis magellanica* (●), *Uncinia compacta* (▲) and *Juncus scheuchzerioides* (■) at study mire 2. Vertical lines indicate the standard errors of the mean values.

between December and April. Necromass Mg concentrations remained constant for *A. magellanica* but decreased during the second half of summer for *U. compacta* and *J. scheuchzerioides*. Na concentrations in both *A. magellanica* and *U. compacta* necromasses were low and showed no conspicuous seasonal variation. For *J. scheuchzerioides* the necromass Na concentrations were high and showed large variations within sampling dates. Especially high Na levels were found for material collected in February and March; however, because of the variability of these estimates they were not significantly different ( $P \leq 0.05$ ) from the values measured at other sampling dates.

Concentrations of N, P, K and Na in the aboveground dead vascular material at closed and open stands at study mire 1 (Fig. 4) were similar to those of *A. magellanica* material at study mire 2. Ca and Mg concentrations were higher in the study mire 1 material. Conspicuous seasonal variations in necromass chemical composition were not apparent at either closed or open stands of study mire 1; however, there were substantial increases in N, P and K concentrations at both stands during April and May, during which time the necromass levels were also increasing (Smith 1987). Very sharp declines in necromass Mg concentrations occurred at study mire 1 just before midwinter. Na concentrations were very variable both within and between harvest dates and showed no consistent seasonal pattern at either closed or open stands of vegetation.

Nutrient concentrations in the belowground standing crop (living plus dead roots and stem bases) at study mire 2 are depicted in Figure 5. Of the three species, *U. compacta* consistently possessed the highest P and K (and the lowest Na) concentrations in the belowground material. *J. scheuchzerioides* belowground material exhibited the highest concentrations of Ca and Mg, while N concentrations were generally greatest in roots of *A. magellanica*.

The belowground component was not separated into living and dead categories. Seasonal trends in chemical composition shown by the total belowground component might be expected to be less marked than those of the living

roots only. N concentrations in belowground *A. magellanica* material remained approximately constant throughout summer and then increased between March and June. In *J. scheuchzerioides*, N concentrations declined during summer, before increasing in early winter. Belowground N levels in *U. compacta* declined throughout the study period. P concentrations in *A. magellanica* and *J. scheuchzerioides* did not vary significantly over the season whereas in *U. compacta* they declined between early November and late December. K concentrations in belowground material of *A. magellanica* and *U. compacta* also showed no conspicuous or consistent patterns throughout summer; in the former species they varied markedly between and within sampling dates. In contrast, a very marked seasonal pattern was exhibited by K concentrations in belowground material of *J. scheuchzerioides*. Values declined during the first half of summer and then increased markedly between December and April. This contrasted with the pattern exhibited by K concentrations in the aboveground biomass of this species (Fig. 2)

Belowground Ca concentrations for *J. scheuchzerioides* varied inconsistently throughout the season and also exhibited large within-harvest variability. For *U. compacta*, Ca levels declined significantly throughout summer and then remained at fairly constant values during autumn and early winter. Ca concentrations in *A. magellanica* belowground material increased significantly ( $P = 0.05$ ) between October and late December and then declined sharply until February, after which the mean concentrations did not vary significantly between harvest dates.

The trend of Mg concentrations in the belowground phytomass of all three species was one of declining values throughout summer, except that in *A. magellanica* levels first increased in early summer. Na concentrations in *U. compacta* roots varied very little within and between sampling dates. A larger variability in Na concentration was exhibited by *A. magellanica* roots but no consistent seasonal pattern could be discerned. Na in *J. scheuchzerioides* roots decreased significantly ( $P = 0.05$ ) during December and January and then remained approximately constant

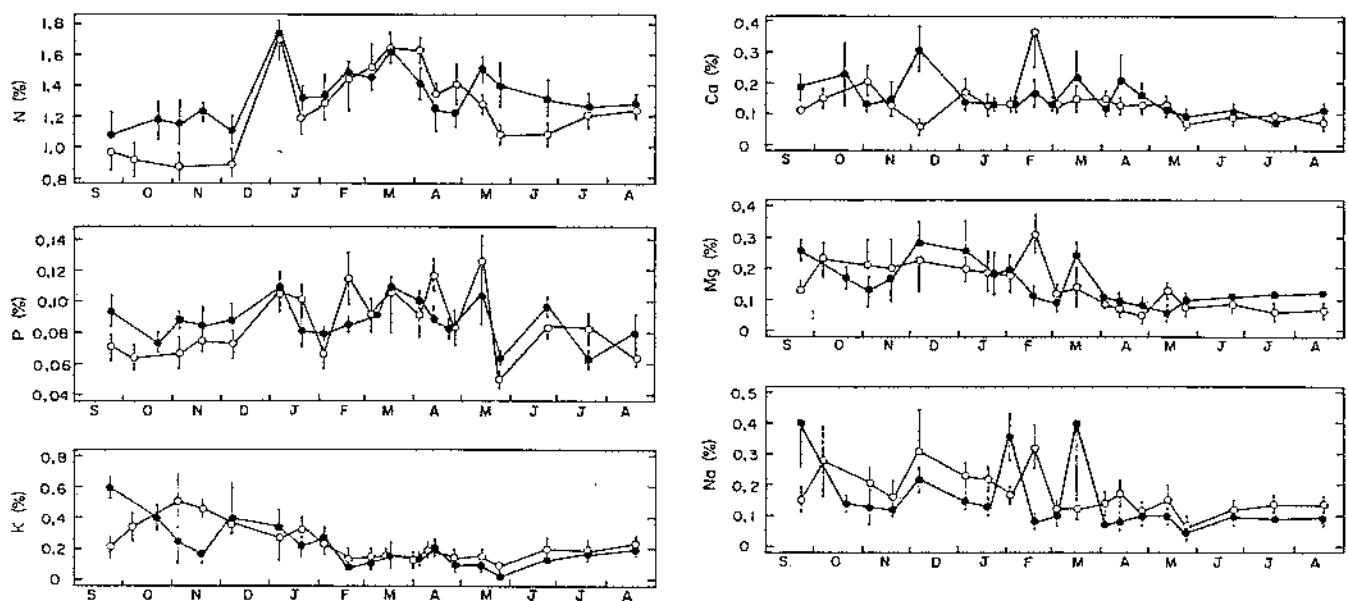


Fig. 6. Chemical composition of the belowground standing crop at closed (●) and open (○) stands at study mire 1. Vertical lines indicate the standard errors of the mean values.



throughout the rest of summer and autumn.

Concentrations of N, P, Ca and Mg in belowground plant material at study mire 1 (Fig. 6) were consistently higher than those in *A. magellanica* roots from study mire 2, while the converse was true for Na. During summer, belowground K concentrations at study mire 1 were similar to those for *A. magellanica* roots from study mire 2 but they fell to very low values in early winter. N concentrations in the belowground standing crop at study mire 1 increased throughout summer, whereas those of P, Ca and Na showed no conspicuous seasonal pattern. Mg levels were substantially lower in winter than in spring and early summer. Mean concentrations of Ca, Mg and, to a lesser extent, of K in the

belowground phytomass were unusually high at closed stands in December 1979 and at open stands in February 1980. In both instances this was due to the occurrence of substantial quantities of *Azorella selago* roots in some of the core samples. As shown later, roots of this dicotyledonous, cushion-forming species contain much higher concentrations of Ca, Mg and K than do roots of the graminoid species dominating the mire-grasslands.

Very high concentrations of Na (up to 1.2%) were found for some root samples collected in early February and mid-March at closed stands and early December and late February at open stands. These high concentrations are thought to be spurious and may possibly be due to

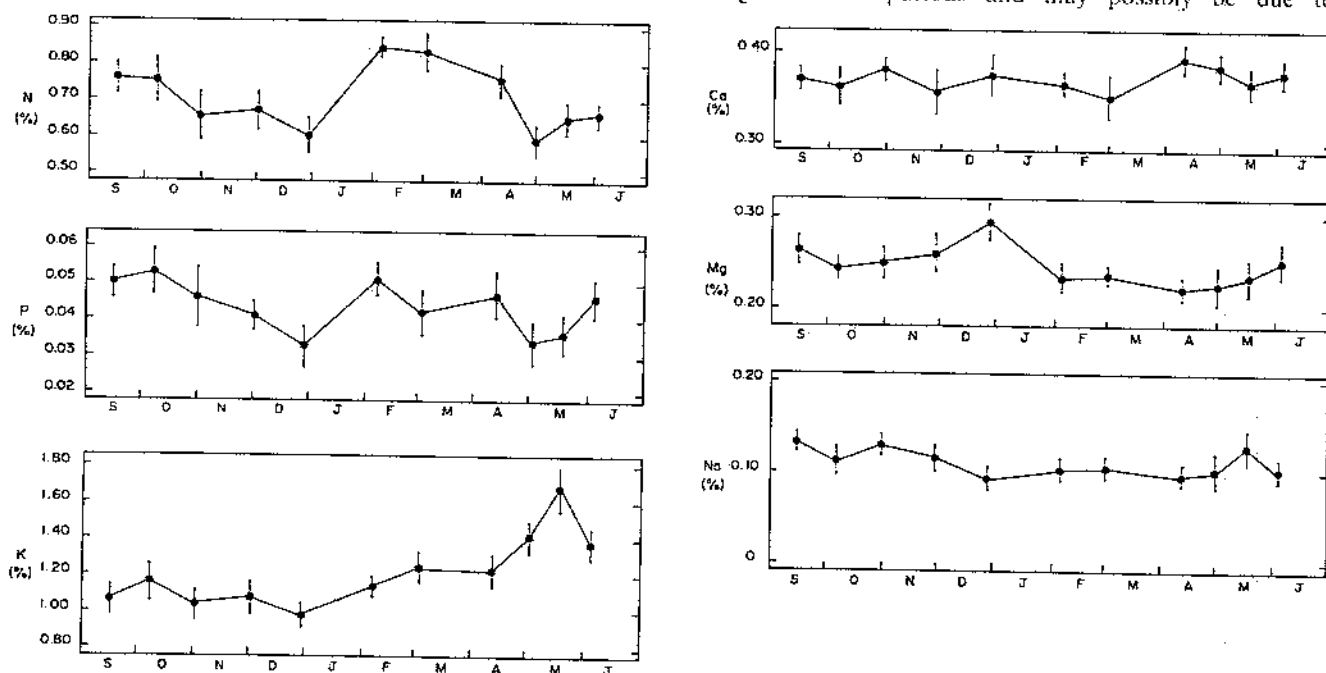


Fig. 7. Chemical composition of the bryomass at study mire 2. Vertical lines indicate the standard errors of the mean values.

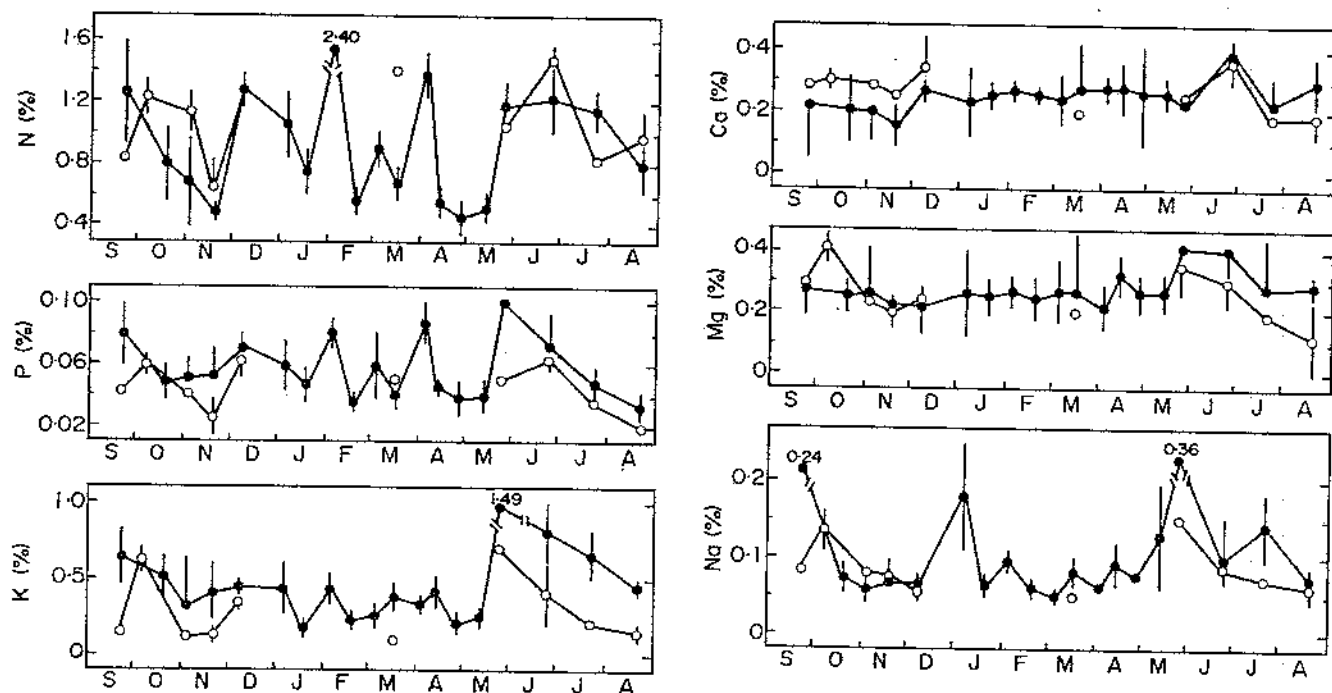


Fig. 8. Chemical composition of the bryomass at closed (●) and open (○) stands at study mire 1. Vertical lines indicate the standard errors of the mean values.

contamination of the samples during processing.

The harvested bryophyte material was not sorted into species so that the nutrient concentrations presented here (Fig. 7 and 8) for both study mires are those in the bryomass as a whole. *Blepharidophyllum densifolium* dominated the bryophyte stratum at study mire 2 and formed the bulk of the bryomass collected in most harvest samples. Nutrient levels for the bryophyte material for this mire (Fig. 7) therefore probably closely reflect those in this species. Bryomass at study mire 2 declined very sharply in early summer (September – January) and then increased as sharply between February and June (Smith 1987). N, P and K concentrations in bryophyte material also declined in early summer and then showed a significant increase during January, when standing crop values were lowest. This suggests that the flush of bryophyte growth indicated for February by the bryomass dynamics actually started earlier, with the appearance of young tissue rich in N, P and K. Between February and April, N and P concentrations decreased. However, K continued increasing throughout late summer until May. Ca, Mg and Na levels were fairly constant throughout the season except for a significantly ( $P = 0.05$ ) higher Mg concentration in December than later in the season.

Several other bryophytes occurred along with the dominant species, *Jamesoniella colorata*, at study mire 1. Although most of the harvested bryomass consisted of this species and *Racomitrium lanuginosum*, varying proportions of other bryophytes (mainly *B. densifolium*, *Clasmatocolea humilis* and *Lepidozia laevifolia*) occurred in most of the harvest samples. Hence, bryomass nutrient concentrations for this community (Fig. 8) probably do not reflect as closely the concentrations in the dominant bryophyte to the same extent as at study mire 2. Also, differences in species composition between the harvest samples caused substantial variations in the bryomass nutrient concentration data from study mire 1, both within and between sampling dates. Because of this variability, distinct seasonal patterns in bryomass nutrient concentrations did not occur at study mire 1. However, bryophyte material collected late in May and in June at both closed and open stands possessed substantially higher concentrations of N, P, K, Mg and Na than did material collected earlier in summer and autumn. This period of high nutrient values preceded, and overlapped, a period (June to August) of major appearance of bryophyte material at study mire 1 (Smith 1987). Between January and May bryomass at open stands was either zero or so low that sufficient material could not be collected for chemical analysis.

N and P concentrations in the bryomass at study mire 1 were generally higher, but those of K and Ca considerably lower, than at study mire 2. Mg and Na levels were similar at the two communities. The most conspicuous difference in bryomass chemical composition between them was in the relative proportions of N and K. N concentrations were up to twice as high as the K concentrations in bryophyte material from study mire 1, whereas at study mire 2 the K concentrations were always higher than those of N. In a recent, more detailed investigation into the production and nutrient ecology of Marion Island bryophytes, *B. densifolium*, the dominant species at study mire 2 and *C. humilis*, also a common species there, have been shown to possess much lower (approximately half) concentrations of N than of K (Russell 1987). In contrast, for the dominant

species at study mire 1 (*J. colorata* and *R. lanuginosum*, and also for most of the other bryophytes at the island, concentrations of N are substantially greater than those of K: in *R. lanuginosum* they are approximately six times as great.

## Discussion

### Peat chemical composition

Peat concentrations of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  at study mire 1 (Table 1) appear to be fairly high when expressed on a dry peat-weight basis (up to c.  $136 \mu\text{g NH}_4\text{-N g}^{-1}$  and up to c.  $36 \mu\text{g NO}_3\text{-N g}^{-1}$ ). However, as pointed out by Harmsen & Kolenbrander (1965), expressing inorganic N contents on a dry weight basis is unrealistic in terms of their availability for plant growth in peat soils of low bulk density and high water holding capacity. Bulk densities for the mire-grassland peats ranged between  $0.044$  and  $0.075 \text{ g cm}^{-3}$  (with mean values of  $0.070 \text{ g cm}^{-3}$  at study mire 1 and  $0.068 \text{ g cm}^{-3}$  at study mire 2). From these mean bulk densities, maximum inorganic N concentrations on a volume basis were  $9.1 \mu\text{g NH}_4\text{-N cm}^{-3}$  and  $2.5 \mu\text{g NO}_3\text{-N cm}^{-3}$  and mean values were less than a third of these maxima. The poor inorganic N status of the island mire peats is demonstrated by the fact that even the maximum inorganic N concentrations were lower than mean values found for surface peats from a tundra mire at Stordalen, Sweden (mean for 0–30 cm depth, c.  $17 \mu\text{g cm}^{-3}$ ; Rosswall & Granhall 1980) and a wet tundra meadow at Barrow (mean for 0–25 cm depth, c.  $43 \mu\text{g cm}^{-3}$ ; Gersper *et al.* 1980). These values were considered to indicate a low soil inorganic N status at the two sites.

Cation exchange capacities for the Marion Island mire-grassland peats were between 49 and 94 mequiv  $100 \text{ g}^{-1}$ , with 80 per cent of the values falling between 70 and 90 mequiv  $100 \text{ g}^{-1}$ . This is in the lower part of the range of CEC values reported for organic soils at tundra meadows and mires of the northern hemisphere (Brown & Veum 1974) and for a large variety of mid and high latitude wetlands (Richardson *et al.* 1978). Exchangeable Ca concentrations in the mire-grassland peats (2.1 to  $9.1 \text{ mequiv } 100 \text{ g}^{-1}$ ) were lower than those for wet meadows at Barrow, Devon Island and Hardangervidda, similar to those for mires at Stordalen and bogs at Moor House and Glenamoy (Brown & Veum 1974) and higher than those in soils under montane grasslands at Snowdonia (Ball 1978). They were also similar to exchangeable Ca levels reported for Macquarie, Kerguelen and Heard Islands (Piper 1938) but in the lower part of the range of values found for peats at South Georgia (Lewis Smith & Walton 1975, Lawson 1985). Exchangeable Mg concentrations at the mire-grasslands ( $4.9$  to  $7.1 \text{ mequiv } 100 \text{ g}^{-1}$ ) were similar to those found at these other sub-Antarctic islands and were within the ranges of values exhibited at most northern hemisphere tundra sites. However, they were much lower than exchangeable Mg levels in the blanket bog peats at Glenamoy (Kilfeather 1973). Exchangeable Na levels ( $0.8$  to  $2.6 \text{ mequiv } 100 \text{ g}^{-1}$ ) in the mire-grassland peats were higher than those at most northern hemisphere tundra and tundra-like sites, again with the exception of the Glenamoy bog, at which slightly higher Na levels occur. Exchangeable K levels ( $0.4$ – $1.8 \text{ mequiv } 100 \text{ g}^{-1}$ ) at the two Marion Island mire sites were similar to those in organic soils at all these northern hemisphere sites and also to those reported for other sub-Antarctic soils.

Other than the fluctuations described for inorganic N

levels, there were no conspicuous temporal changes, and certainly no coherent seasonal patterns, in nutrient levels in the mire-grassland peats. Freeze-thaw activity which occurred in the top few cm of the peats during winter was also not associated with changes in peat nutrient concentrations. At the much colder island of South Georgia, observations at four different communities (including a mire) over a 30 month period also revealed no coherent seasonal trends in soil nutrient levels (Lewis Smith 1985) and even at the maritime Antarctic Signy Island the freeze-thaw cycles which occur frequently throughout the year were shown not to affect exchangeable levels of N, P, K or Ca (Northover & Grimshaw 1967). These, admittedly few, observations from Southern Ocean islands are contrary to those from subpolar areas of the northern hemisphere where soil nutrients fluctuate in response to seasonal changes in climatic and hydrological regimes, an especially important feature being the nutrient flux associated with the spring melt-off (Flint & Gersper 1974, Everett *et al* 1981).

#### Seasonal variations in plant chemical composition

It is well known that leaf concentrations of N, P and K in plants from temperate, sub-Arctic and Arctic areas are highest in young green material and decline throughout the season. This has also been shown for many of the graminoid species at South Georgia (Walton & Lewis Smith 1980, Pratt & Lewis Smith 1982) and appears to be the trend for aboveground live shoots of *Agrostis magellanica* and *Juncus scheuchzerioides*, but not for *Ucinia compacta* at Marion Island (Fig. 2). That the seasonal changes in nutrient concentrations for these species were not very marked was due to the fact that the concentration values were for whole shoots. At South Georgia, Lawson (1985) demonstrated the importance of leaf (or organ) age in relation to nutrient concentrations in *Rostkovia magellanica* throughout the year. While the mean whole-shoot values indicated the overall seasonal trend, it was only when individual leaf age classes were analysed that the patterns of nutrient allocation during the season, and the major differences between nutrients, became apparent. For the Marion Island mire species, concentrations of N, P and K in newly-formed, early season leaves were much greater than those in the overall biomass at that time (Table 3). A substantial proportion of the live green foliage of these species overwintered and died back only slowly in early summer, so that in spring a large part of the biomass consisted of mature or senescing material which masked the high concentrations of N, P and K in the young leaves.

Shoot Ca concentrations in the mire-grassland species increased markedly throughout the season, agreeing with observations from tundra and tundra-like sites of the northern hemisphere (Dowding *et al* 1981) and from South Georgia (Walton & Lewis Smith 1980). In *J. scheuchzerioides* Mg levels increased as the season progressed, whereas they remained unchanged in *A. magellanica* and decreased in *U. compacta*. At South Georgia, Mg levels in graminoids remained unchanged, or decreased slightly, throughout the growing season (Walton & Lewis Smith 1980).

#### Comparison of the mire-grassland vascular plants with other graminoid species

Nutrient concentrations in aboveground live shoots of the three dominant mire vascular species at Marion Island are

compared with those of graminoid plants from bogs, mires and wet meadows at other subpolar, montane and oceanic moorland sites in Table 3. Also provided in the table are the ranges of nutrient concentration values reported for a variety of temperate freshwater wetland plants. Where possible, the seasonal range of nutrient concentrations is presented, but for some sites only the seasonal means, or else the values at the time of peak aboveground standing crop, are available.

Aboveground shoots of *Juncus scheuchzerioides* contained higher concentrations of N, Ca, Na and, for much of the season, of P, K and Mg than did shoots of *A. magellanica* or *U. compacta*. *U. compacta* shoots possessed lower concentrations of N than did those of *A. magellanica*, in contrast to most northern hemisphere tundra sites where sedges generally have appreciably higher N contents than do grasses (Dowding *et al* 1981), except for early in the growing season when peak N concentrations are often higher in grasses (Chapin *et al* 1975).

Aboveground concentrations of N, P and K in the Marion Island species appear to be lower than those reported for grasses and rushes at South Georgia by Lewis Smith & Walton (1975) and Walton & Lewis Smith (1980). However, those authors analysed green leaf, rather than total living shoot, material. Values presented by Pratt & Lewis Smith (1982) for shoots of the South Georgia graminoids are more similar to those found in the Marion Island species, especially if *A. magellanica* is compared with the grasses and *J. scheuchzerioides* with the rushes. Recent information (Lawson 1985) indicates that the nutrient concentrations in *Rostkovia magellanica* shoots from two contrasting sites at South Georgia are similar to those in *J. scheuchzerioides* at study mire 2, except for higher Ca levels in *R. magellanica* from a eutrophic seepage slope. *J. scheuchzerioides* also contained much higher concentrations of Na than did any of the species at South Georgia. *Deschampsia antarctica* at South Georgia and at Signy Island possessed higher concentrations of N and P, but similar concentrations of K, to the three Marion Island mire species.

N concentrations in the aboveground vegetative biomass of the Marion Island mire-grassland plants are lower than those in graminoids from the northern hemisphere tundra and montane sites included in Table 3, although the seasonal range of concentrations in *A. magellanica* spans the values for grasses at an Arctic tundra at Barrow, Alaska. N levels in the island species are also in the lower part of the range reported for a variety of temperate freshwater wetland plants. Shoot P concentrations for the island mire plants are low compared with those of graminoids at most of the northern hemisphere sites, especially the Fennoscandian mires and Devon Island meadows and the Snowdonia montane grassland. P levels at the time of maximum aboveground biomass of the Arctic tundra species at Barrow are in the upper limit of the seasonal range exhibited by *A. magellanica*, *U. compacta* and *J. scheuchzerioides*. Maximum P concentrations in the Barrow species were attained before the time of peak aboveground biomass (Chapin 1978), hence it is likely that these species possess higher P levels on a seasonal basis than do the Marion Island mire plants. P concentrations in the island species are in the lower part of the range reported for temperate wetland species but are similar to those in graminoids at Moor House and Glenamoy.

Shoot K concentrations in the island mire species are

Table 3  
Nutrient concentrations (percentage of dry weight) in photosynthetic parts of graminoid plants from sub-Antarctic, tundra, bog and heath sites

Site and species	N	P	K	Ca	Mg	Na	Community and nature of reported values	Reference
<b>Marion Island (sub-Antarctic)</b>								
<i>Agrostis magellanica</i> , living shoot	0.99-1.53 1.25 (2.66)	0.05-0.11 0.08 (0.26)	0.93-1.47 1.21 (2.74)	0.08-0.13 0.10	0.13-0.16 0.15	0.12-0.32 0.25	Seasonal range Seasonal mean Max. value in young leaves	
<i>Ulexia compacta</i> , living shoot	0.60-0.87 0.70 (1.67)	0.10-0.11 0.10 (0.28)	0.92-1.16 1.08 (2.44)	0.03-0.11 0.07	0.12-0.15 0.13	0.04-0.11 0.09	Seasonal range Seasonal mean Max. value in young leaves	This account
<i>Juncus schenck-zeroides</i> , living shoot	1.20-1.63 1.47 (2.74)	0.06-0.17 0.13 (0.31)	0.76-1.56 1.26 (2.92)	0.12-0.16 0.14	0.13-0.22 0.17	0.59-0.64 0.62	Seasonal range Seasonal mean Max. value in young leaves	
<b>South Georgia Island (sub-Antarctic)</b>								
<i>Festuca contracta</i> , living leaves*	1.3-1.7	0.17-0.25	1.3-2.0	0.06-0.12	0.09-0.10	0.01-0.02	Dry meadow, seasonal range	*Lewis Smith & Walton (1975), Table 4, and Walton & Lewis Smith (1980), Figures 2-5
<i>Festuca contracta</i> , living shoot**	1.0-2.0	0.11-0.32	1.0-2.0	0.05-0.12	0.08-0.15	—	Open and dense grasslands, seasonal range	**Pratt & Lewis Smith (1982), Figures 4-8
<i>Deschampsia antarctica</i> , living leaves*	3.5-4.9	0.39-0.47	1.4-1.8	0.02-0.13	0.02-0.26	0.05-0.23	Mesic meadow, seasonal range	**Lawson (1985), estimated by weighting the means in Table 2
<i>Deschampsia antarctica</i> , living shoot**	2.1-3.6	0.23-0.37	0.4-1.2	0.09-0.16	0.11-0.26	—	Mesic meadow, seasonal range	
<i>Rostkovia magellanica</i> , living leaves*	2.0-2.4	0.25-0.39	1.6-1.8	0.22-0.31	0.09	0.04-0.05	Oligotrophic mire, seasonal range	
<i>Rostkovia magellanica</i> , living shoot**	1.5-2.1	0.10-0.18	0.7-1.0	0.19-0.26	0.12-0.15	—	Mesotrophic bog, seasonal range	
<i>Rostkovia magellanica</i> , living shoot***	1.1	0.15	0.72	0.06	0.12	0.21	Mesotrophic basin bog, seasonal mean	
<i>Rostkovia magellanica</i> , living shoot***	1.2	0.16	0.86	0.23	0.08	0.17	Eutrophic slope, seasonal mean	
<i>Juncus schenck-zeroides</i> , living leaves*	1.7-2.9	0.20-0.58	2.7-4.3	0.30-0.65	0.17-0.34	0.28-0.35	Eutrophic mire, seasonal range	
<i>Phleum alpinum</i> , living leaves*	1.2-2.8	0.28-0.51	1.2-2.6	0.03-0.05	0.09-0.14	0.01-0.04	<i>Fiechtmark</i> , seasonal range	
<i>Phleum alpinum</i> , living shoot**	1.2-2.6	0.10-0.33	0.5-2.1	0.06-0.34	0.12-0.24	—	Mesotrophic bog and <i>Festuca</i> grasslands, seasonal range	
<i>Poa flabellata</i> , current season foliage*	1.0	0.14	1.2	0.05	0.06	0.13	Tussock grassland, mid-season value	
<i>Poa flabellata</i> , living shoot**	1.1-1.7	0.10-0.27	0.6-0.9	0.09-0.14	0.07-0.10	—	Tussock grassland, seasonal range	
<b>Macquarie Island (sub-Antarctic)</b>								
<i>Poa foliosa</i> , leaf blade	1.78	—	—	—	—	—	Tussock grassland, senescing material	Jenkin (1972), Table 4.10
<b>Signy Island (maritime Antarctic)</b>								
<i>Deschampsia antarctica</i> , green foliage	2.22	0.29	0.48	0.47	0.51	0.11	Grass sward, "summer" value	Collins <i>et al.</i> (1975), Table 7
<i>Deschampsia antarctica</i> , living leaves	2.90(2.40)	0.43(0.43)	1.0(1.4)	0.15(0.21)	0.26(0.24)	0.24(0.23)	Closed sward, early and (late) season	Edwards (1974), Table 26
<b>Hardangervidda, Norway and Kevo, Finland</b>								
("Fennoscandian" sub-Arctic and low alpine tundra)								
"Eutrophic" monocotyledons, green parts	2.5-1.4	0.25-0.15	2.1-1.0	0.4	0.13	0.03	Mires, order of seasonal variation in mean contents for the groups	Wiegolaski <i>et al.</i> (1975), Table 1
Other monocotyledons, green parts	2.3-1.7	0.20-0.13	1.6-0.9	0.3	0.12	0.03	Seasonal means	Dowding <i>et al.</i> (1981), Table 21.4
<i>Carex nigra</i> , green parts	2.4	0.24	0.9	0.53	—	—		

Table 3 (continued)

Site and species	N	P	K	Ca	Mg	Na	Community and nature of reported values	Reference
<b>True-love Lowland, Devon Island (Arctic)</b>								
Graminoid leaves	3.12	0.30	—	—	—	—	Hummocky sedge-moss meadow	Babb & Whitfield (1977), Table 3
<i>Carex stands</i> , aboveground biomass	3.05	0.35	1.88	0.23	—	—	Hummocky sedge-moss meadow, seasonal means	Muc (1977), Table 8
<b>Barrow, Alaska (Arctic)</b>								
<i>Calluna vulgaris</i> , aboveground biomass	1.44	0.12	0.91	0.26	0.22	—		
<i>Carex aquatilis</i> , aboveground biomass	2.18	0.15	1.24	0.08	0.20	—	Wet sedge meadow, values at time of peak aboveground standing crop for each species	Chapin <i>et al.</i> (1975), Table 2
<i>Drosera rotundifolia</i> , aboveground biomass	1.60	0.09	0.80	0.10	0.12	—		
<i>Eriophorum angustifolium</i> , aboveground biomass	2.10	0.11	0.88	0.19	0.29	—		
<i>E. schrecheri</i> , aboveground biomass	2.13	0.18	0.77	0.15	0.11	—		
<i>Poa arctica</i> , aboveground biomass	1.25	0.12	0.97	0.27	0.27	—		
<i>Luzula arctica</i>	1.15	0.20	1.33	0.10	0.15	—		
<b>Moorhouse (Cool temperate montane vegetation)</b>								
<i>Lophophorum angustifolium</i> , green leaves	1.52	0.10	0.49	0.16	0.13	0.07		
<i>Eriophorum vaginatum</i> , green leaves	1.83	0.17	0.64	0.15	0.16	0.01	Blanket bog vegetation, seasonal means	Heal & Smith (1978), Table 3
<i>Trichophorum cespitosum</i>	1.53	0.11	1.02	0.13	0.18	0.22		
<b>Llyn Llydaw (Snowdonia, Wales; cool-temperate montane grassland)</b>								
<i>Agrostis tenuis</i> , aboveground biomass	2.21	0.18	1.13	0.17	0.34	—		
<i>Festuca ovina</i> , aboveground biomass	1.32	0.19	1.29	0.14	0.28	—		
<i>Anthoxanthum odoratum</i> , aboveground biomass	2.69	0.26	1.47	0.19	0.45	—	Mesotrophic montane grassland, seasonal means	Perkins <i>et al.</i> (1978), Table 6
Other grasses, aboveground biomass	2.04	0.21	1.45	0.21	0.43	—		
Sedges, rushes and herbs	2.04	0.16	1.17	0.44	0.53	—		
<b>Glenny (Cool temperate bog)</b>								
<i>Molinia caerulea</i> , green foliage	2.64	0.08	0.57	0.02	0.09	—	Blanket bog vegetation, seasonal means	Kilfeather (1973), Table 3
<i>Schoenus nigricans</i> , green foliage	1.55	0.06	0.45	0.05	0.20	—		
<b>Temperate Freshwater Wetlands (glacial marshes, prairie wetlands, freshwater estuarine marshes)</b>								
Typical wetland species	1.46-3.95	0.08-0.65	0.42-4.56	0.20-8.03	0.08-0.95	0.07-1.52	Range of values for "lush green plants" of 35 species	Boyd (1978), Table 3

similar to those in graminoid plants at the Fennoscandian tundra sites. K concentrations in *A. magellanica* are similar to those of montane grasses at Snowdonia whereas the seasonal ranges in K concentration for *U. compacta* and *J. scheuchzerioides* span the seasonal mean values reported for "sedges, rushes and herbs" at that site. K levels in *A. magellanica* and *U. compacta* are also substantially greater than the seasonal mean values found for graminoids at Moor House and Glenamoy but are in the lower part of the range of concentrations reported for temperate freshwater wetland species.

Rodin & Bazilevich (1967) reported that tundra plants typically have much greater concentrations of N than any other element, although K predominates amongst the ash elements. Those authors were referring principally to dicotyledonous species; monocots characteristically have lower N:K ratios. However, even the monocots from northern hemisphere subpolar and montane sites possess larger (mostly > 1.5) N:K ratios in the above-ground biomass than do the island mire species (< 1 for *U. compacta*, c. 1 for *A. magellanica* and 1 to 1.5 for *J. scheuchzerioides*). For *U. compacta* and *J. scheuchzerioides* N:K ratios increased during the season, indicating that K was removed faster than N from maturing leaves, either through translocation or leaching. N:K ratios in the South Georgia monocots (Walton & Lewis Smith 1980) are similar to those of the Marion Island species.

Shoot Mg concentrations in the three Marion Island mire plants are mostly lower than in graminoid species from Snowdonia and are in the lower part of the range of concentrations exhibited by the Barrow graminoids. *U. compacta* shoots contain lower concentrations of Mg than does *Schoenus nigricans* at Glenamoy but similar levels to two *Eriophorum* species at Moor House. Na concentrations in the Marion Island mire species are substantially higher than those reported for graminoids in the Fennoscandian tundra and cool temperate bogs at Moor House.

Ca concentrations in the aboveground shoots of the Marion Island mire species are substantially lower than in graminoids from Devon Island, the Fennoscandian tundra sites, Moor House and Snowdonia. They are in the lower part of the range of concentrations exhibited by graminoids at Barrow and are much lower than the concentrations in temperate freshwater wetland species. However, the two graminoids at Glenamoy contain substantially lower Ca concentrations than do the Marion Island species.

Because of their low Ca and relatively high K concentrations, especially low Ca:K ratios are found in the island plants; this is in general agreement with observations on monocots from South Georgia (Walton & Lewis Smith 1980), the USSR tundra (Rodin & Bazilevich 1967), Fennoscandian tundra (Wielgolaski *et al.* 1975), Arctic tundra at Devon Island (Babb & Whitfield 1977) and at Barrow (Chapin *et al.* 1975) and also montane moorlands and grasslands in Britain (Heal & Smith 1978, Perkins *et al.* 1978).

Concentrations of K, N, P and Na were lower in the aboveground necromass than in the biomass of the three mire species, excepting for late season material of *A. magellanica* where N and P concentrations in the necromass were similar to, or even higher than, those in living shoots. Differences in mineral content between living and dead material were greatest for K: much more (2-8 times) K than N was removed from senescing leaves, presumably by both

retranslocation and leaching. This is similar to observations on graminoids from tundra (Wielgolaski *et al.* 1975, Chapin *et al.* 1975, Dowding *et al.* 1981) and sub-Antarctic (Walton & Lewis Smith 1980) regions.

Belowground parts of the Marion Island mire plants contained lower concentrations of P, K and, except for *U. compacta*, of N than did the aerial biomass. This agrees with observations on tundra and alpine graminoids (Rehder 1976, Malmer & Nihlgard 1980, Dowding *et al.* 1981). Belowground Ca concentrations in *J. scheuchzerioides* were similar to those aboveground but were lower belowground than aboveground for *A. magellanica*. For *U. compacta*, concentrations of Ca were higher in belowground than aboveground material except in early winter, when they were similar. Mg and Na concentrations in *A. magellanica* and *U. compacta* were similar between above and belowground components but for *J. scheuchzerioides* higher Mg, and lower Na, concentrations occurred belowground. However, because the belowground material was not sorted into living and dead categories these comparisons are circumspect, e.g. low levels of N, P and K in the belowground component are probably a consequence of the presence of dead roots which might be expected to contain low levels of these soluble nutrients.

## Conclusions

Shoot concentrations of N, P, Mg and (especially) Ca for the graminoid species at the mire-grasslands are low compared with most graminoids at tundra mires and meadows or those at montane grasslands, sedge-heaths and freshwater wetlands of more temperate latitudes. K concentrations in the island graminoids are similar to those at Arctic and sub-Arctic tundras and are greater than those for most sedge and grass species from more southerly sites such as Glenamoy and Moor House. Na concentrations in the island graminoids are substantially higher than for northern hemisphere tundra graminoids.

For *Agrostis magellanica* and *Uncinia compacta* a substantial proportion of the early season aboveground biomass consisted of living leaves which had overwintered. Nutrient concentrations for the biomass at this time therefore do not reflect those in young, early season tissue and so the true magnitudes of age-related nutrient concentration changes were not detected by the sampling and sample-sorting strategies employed. Overall, however, the seasonal nutrient concentration changes in aerial plant biomasses for the mire-grassland species reflected the age-related changes and were similar to those observed for other subpolar and more temperate vegetation types, i.e. N, P and K decreased, whereas Ca (in some cases also Mg) increased, as the season progressed.

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