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Seasonal changes in plant and soil chemical composition at Marion Island (sub-Antarctic): II – Fjaeldmark and fernbrakes

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Seasonal changes in concentrations of N, P, K, Ca, Mg and Na in the plants at a fjaeldmark and two fernbrake communities 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. Exceptions to this pattern are discussed. Seasonal changes in nutrient concentrations in reproductive organs, roots, rhizomes and in the aboveground necromass (dead plant material) differed between species. N, P and K concentrations in living leaves of dicotyledonous species (and of the fern Blechnum penna-marina, *which at the island behaves ecologically like a dwarf shrub) are similar to those for dwarf-shrubs and shrubs at northern hemisphere tundra and tundra-like communities; in many instances the K concentrations are higher than for tundra species. Mg and Na levels in the island dicots are greater than those generally reported for tundra plants. 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 three island communities.*

Die seisoenswisseling in die konsentrasie van N, P, K, Ca, Mg en Na by die plante van 'n fjaeldmark en twee varing-gedomineerde plantgemeenskappe 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 bogrondse biomassa afgeneem en het dié van Ca (in sommige gevalle ook van Mg) met verloop van die seisoen toegeneem. Uitsonderings op dié patroon word bespreek. Die seisoenswisseling in die voedingstofkonsentrasie in voortplantingsorgane, wortels, wortelstokke en die bogrondse nekromassa (dooie plantmateriaal) het tussen spesies verskil. Die konsentrasie van N, P en K in lewende blare van dikotielspesies (en in die varing Blechnum penna-marina *wat op die eiland ekologies soos 'n dwergstruik optree) is soortgelyk aan dié van dwergstruike en struike in die toendra en in toendra-agtige gemeenskappe van die Noordelike Halfrond. In baie gevalle is die K-konsentrasie van dié eilandplante hoër as by toendraspesies. Die konsentrasie van Mg en Na is by die dikotiele van die eiland hoër as by die meeste toendraplante. 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 grondvoedingstofkonsentrasies by die drie plantgemeenskappe op die eiland nie.*

Introduction

In another paper (Smith 1987a) I described the seasonal changes in peat and plant chemical composition at two mire-grasslands on Marion Island (46°54'S, 37°45'E). Mire-grasslands are dominated by graminoid and bryophyte species and represent an advanced stage of vegetation succession in areas where drainage is impeded. In this paper I present corresponding information for the soils and plants of three communities which represent a successional trend at drier sites on the island.

A sparse cover of bryophytes, lichens and low-growing (often cushion-forming) flowering plants occurs on exposed rocky ridges and plateaus. Similar vegetation formations in Arctic, sub-Arctic and alpine areas have been termed "rock tundra", "Schuttflur" "Felsenflur", "fjaeldmark" or "fellfield". The term fjaeldmark (or feldmark) has been adopted by most workers in the southern hemisphere subpolar region (e.g. Taylor 1955, Ashton & Gill 1965, Wace 1965, Huntley 1971, Gremmen 1981), although the English equivalent fellfield is often preferred (Lewis & Greene 1970, Lewis Smith & Walton 1975, Heilbronn & Walton 1984). Fjaeldmark was originally defined (Warming 1928) as "a formation where plants grow singly often with great intervals, though here and there denser spots of vegetation occur . . ." In a recent review, Lewis Smith (1984) described fjaeldmark as "Discontinuous patchy xerophytic vegetation dominated mainly by cushion-forming forbs, short grasses, cushion and turf-forming mosses and fruticose and crustose lichens; occurring on dry, windswept stony soils especially at higher altitudes".

Of the six plant community complexes defined for the Marion Island vegetation only fjaeldmark extends above 300 m a.s.l. (Gremmen 1981). Fjaeldmark is also common on exposed rocky areas at lower altitudes where it is dominated by cushions of *Azorella selago,* on which the grass *Agrostis magellanica* occurs epiphytically. At more sheltered areas, especially where peat accumulates, the number of vascular species increases. The additional species are most often the fern *Blechnum penna-marina*, the rosaceous suffruticose herb *Acaena magellanica* and the tussock-forming grass *Poa cookii.* This increased plant cover often represents a seral succession leading to the development of closed plant communities (Smith 1987b). Such seral communities have been termed "open scrub" (Smith 1976a) and "open fernbrake" (Smith 1977a), but are phytosociologically also part of the fjaeldmark complex defined by Gremmen (1981).

On well-drained slopes this successional sequence results in a "climax" closed fernbrake community dominated by *Blechnum penna-marina*, the short, hardy fronds of which form a dense carpet 10-15 cm high. Fernbrake is a conspicuous vegetation type covering many of the island's lowland slopes, especially those with northerly and easterly aspects. In contrast to fjaeldmark, fernbrakes are not ubiquitous throughout the sub-Antarctic. Although ferns are locally abundant in restricted areas at many sub-Antarctic (and southern cold-temperate) islands, it appears that only at Marion Island (and its nearby neighbour, Prince Edward Island) are fernbrakes an important component of the vegetation (Gremmen 1981).

Together, fjaeldmark, open and closed fernbrakes occupy approximately 60 per cent of the surface area of the unglaciated, younger lava flows of the island's eastern coastal plain (Smith 1976a). On the older lavas fjaeldmark occurs on approximately 40 per cent of the surface area, whereas open and closed fernbrakes are rare (Smith 1977a).

Sites

This study concentrated on plants from a fjaeldmark, an open fernbrake and a closed fernbrake approximately 300 m west of the meteorological station on the island's eastern coastal plain. They are approximately 500 m from the shore and between 30 and 40 m altitude. They occur within 50 m of each other and within 100 m of the mire-grasslands reported on by Smith (1987a). The areas of the communities are: fjaeldmark, *c.* 1700 m^2, open fernbrake, *c.* 1000 m^2 and closed fernbrake, *c.* 500 m^2. The floristic compositions of the three communities are described by Smith (1987c) in an account of their vegetation standing crop and primary production.

Methods

Harvesting and sorting procedures whereby the plant samples were obtained are described in Smith (1987c) and the chemical analyses performed on the samples in Smith (1987a). Soil collection and chemical analyses are also described in Smith (1987a).

Results

Soil chemical composition

There was a substantial amount of within-sampling date variability in the soil chemistry results from the three study sites and no consistent variations in soil nutrient levels were found during the sampling period. Values reported here (Table 1) are the ranges found for all the samples collected. Soil moisture contents reflected the amount of precipitation just prior to sampling and varied markedly between sampling dates; however, they were almost always highest at closed fernbrake and lowest at fjaeldmark. Fernbrake soils were more organic and more acid than those at fjaeldmark. Kjeldahl-N levels were also higher at the fernbrakes than at fjaeldmark. Low concentrations of inorganic N occurred at the three sites. At fjaeldmark, NH$_4$-N was rarely, and NO$_3$-N never, detected. At the two fernbrake sites, NH$_4$-N levels were mostly < 1 μg g^{-1}, but occasionally higher concentrations (up to *c.* 13 μg g^{-1}) were found. NO$_3$-N could also not be detected in most of the samples from the fernbrake sites but the occasional sample from closed fernbrake possessed fairly high (up to 11 μg g^{-1}) NO$_3$-N concentrations.

Fairly substantial total P levels occurred in the soils but concentrations of "available" P were generally low, especially at the fjaeldmark site.

Cation exchange capacities were high and decreased between the sites in the order closed fernbrake > open fernbrake > fjaeldmark. Linear regression indicated that 80 per cent ($P < 0.001$) of the variation in CEC at the three sites was explained by the variation in dichromate-oxidizable C levels. At the fjaeldmark site, Ca was the predominant exchangeable cation and Ca concentrations were most often

Table 1.

Soil chemistry at the fernbrake and fjaeldmark sites. All nutrient concentrations are per dry weight of soil

		% of dry weight				μg g^{-1}			milliequivalents 100 g^{-1}				
	pH	moisture	$Cr_2O_7^{2-}$ oxidiz. C	Kjeldahl N	Total P	NH_4^+ N	NO_3^- N	*Available P	C.E.C.	Exch. Ca	Exch. Mg	Exch. Na	Exch. K
Closed fernbrake	4.3-5.1	495-705	17-36	2.0-2.3	0.12-0.31	0-12.9 (2.6±5.8)*	0-11.0 (2.7±4.8)	4-48 (24±20)	109.4-161.8	1.7-12.6	2.9-14.1	0.3-1.3	0.1-1.2
Open fernbrake	4.6-4.9	349-586	17-32	1.2-2.6	0.11-0.21	0-4.5 (3.6±7.3)	0-0.5 (0.1±0.3)	5-36 (16±15)	91.7-121.5	7.9-13.0	2.1-8.1	0.4-0.7	0.1-0.5
Fjaeldmark	5.2-5.9	125-515	8-21	0.4-1.1	0.10-0.17	0-1.0 (0.1±0.3)	0 (0)	0-11 (3±4)	45.7-101.4	5.1-12.6	0.5-5.0	0.1-0.8	0-0.4

Mean ± standard deviation

Table 2

Mean (± standard deviation) percentage saturation of the CEC by Ca, Mg, Na and K for all soil samples from the three sites

	Ca	Mg	Na	K	Total
Closed fernbrake	4.1 ± 2.7	4.1 ± 3.1	0.5 ± 0.2	0.3 ± 0.3	9.1 ± 6.2
Open fernbrake	9.0 ± 1.2	4.8 ± 3.2	0.5 ± 0.1	0.2 ± 0.1	14.5 ± 3.9
Fjaeldmark	13.0 ± 4.4	3.8 ± 3.1	0.6 ± 0.5	0.2 ± 0.3	17.6 ± 5.5

more than twice those of Mg. At open fernbrake, Ca concentrations were also higher than those of Mg but the differences were much smaller, whereas at closed fernbrake exchangeable concentrations of the two elements were similar. These inter-site differences in the relative levels of Ca and Mg become especially conspicuous if the exchangeable concentrations are expressed on the basis of the mean percentage saturation of the corresponding CEC values (Table 2).

Low concentrations of Na and K occurred at the three sites and, for most samples, Na levels were approximately twice those of K. Only a small proportion of the CEC was accounted for by Ca + Mg + Na + K (Table 2).

Plant chemical composition

Azorella selago

Leaf nutrient levels for this cushion plant at the fjaeldmark, open fernbrake and closed fernbrake communities are depicted in Figure 1. N and P concentrations at closed fernbrake were consistently greater than at open fernbrake or fjaeldmark, but the differences were significant only during winter (i.e. from April onward). There were no consistent differences in leaf K concentrations between the three sites. N, P and K levels declined during the second half of summer but the decreases in N and P were small and only for K were the concentration values significantly ($P \leq 0.05$) lower in autumn than in midsummer. Concentrations of all three elements increased markedly throughout winter.

Throughout the sampling period, leaf Ca concentrations were lower at closed fernbrake than at open fernbrake or fjaeldmark and they increased markedly after March or April at all three sites. At closed fernbrake they declined again during July and August but at fjaeldmark they were highest in July, the last sampling date for this site. For all but the July sampling date leaf Mg concentrations were higher at fjaeldmark than at the two fernbrakes. Seasonal changes in this element were not as marked as those of Ca. Mg levels at fjaeldmark and open fernbrake increased slightly (but significantly, $P \leq 0.05$) throughout summer and then declined from March or April. At closed fernbrake, Mg levels increased throughout most of the sampling period.

Seasonal changes in leaf Na concentrations for *A. selago* were marked and were similar at the three communities. Values increased during the second half of summer and declined during autumn and winter. This decline was greatest at closed fernbrake so that whereas in summer Na concentrations were consistently higher at this community than at the others, during winter they resembled those at fjaeldmark.

Concentrations of N, P, K and Na in the aboveground necromass (consisting almost entirely of dead leaves) of *A. selago* (Fig. 2) were much lower than those in living leaves.

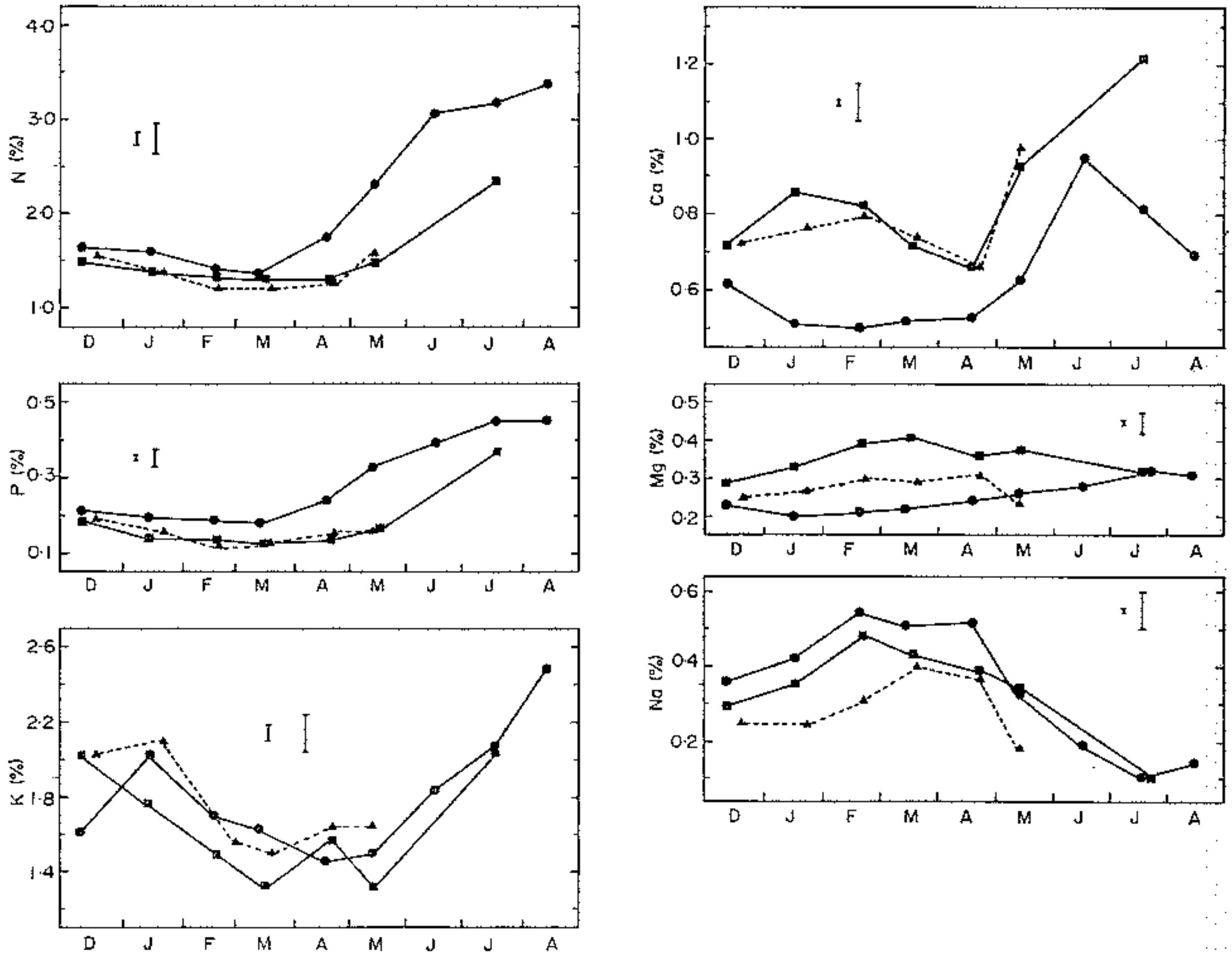


Fig. 1. Chemical composition of *Azorella selago* leaves at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

In contrast, Ca levels were greater in the necromass. Mg concentrations were similar in the two phytomass components. Not surprisingly, seasonal changes in necromass nutrient concentrations were much smaller than those for living leaves. At open fernbrake and fjaeldmark, N and P decreased throughout the second half of summer so that they were significantly ($P = 0.01$) lower in April than in December or January. Corresponding changes in necromass N and P levels did not occur at closed fernbrake but at all three sites they increased during winter. Ca and Mg concentrations increased slightly (but significantly, $P \leq 0.05$) during all (Ca) or most (Mg) of the sampling period at the fjaeldmark site but at the two fernbrakes they remained fairly constant.

At open fernbrake and fjaeldmark the necromass concentrations of K and Na were below the detection limit of the analytical procedure. At closed fernbrake, mean concentrations of both elements were also low (< 0.01 %) and were associated with high levels of uncertainty (standard deviations mostly 70 to 90 % of the mean values).

Flowering of *A. selago* occurred only at the open fernbrake site and the amount of flowering or fruit material in the harvest samples was too small for chemical analysis.

Seasonal nutrient concentration dynamics for *A. selago* live stems are shown in Figure 3. Stems possessed lower nutrient concentrations than did the leaves, except for Mg which was consistently higher in stems. As was the case with the leaves, N and P levels were consistently (and significantly, $P \leq 0.05$) higher, whereas Ca and Mg were always lower, at closed fernbrake than at the other two communities. No consistent inter-site differences occurred in stem K concentrations. Stem Na levels were very low (< 0.02 %) at fjaeldmark and closed fernbrake. Higher mean concentrations of this element (up to 0.12 %) were found for three of the sampling dates at open fernbrake, but these were associated with a high degree of variability and were possibly caused by contamination of one or more samples at these dates.

Stem N and K levels exhibited approximately similar seasonal trends and declined slightly during the second half of summer (except for K at fjaeldmark) and then increased markedly from February onwards. Stem K levels at fjaeldmark increased slowly during the sampling period.

Ca concentrations in *A. selago* stems at closed fernbrake declined between December and March and then increased during winter. A similar pattern was apparent for the stems at the fjaeldmark site but the late summer decrease was smaller and not significant at the 5 % level. Stem Ca concentrations at open fernbrake did not change in a consistent pattern during the sampling period. There were also no coherent or conspicuous changes in stem Mg concentrations at the three sites, but levels at closed fernbrake were slightly (but significantly, $P = 0.05$) lower in June and July than during summer.

Nutrient concentrations in the belowground standing crop of *A. selago* (mostly living, but some dead, roots) were very similar to those for the stems. Na levels were mostly higher (but still low, generally < 0.1 %) in roots than in stems but the differences were rarely significant because of a large degree of variability associated with the Na measurements.

Seasonal changes in belowground nutrient concentrations (Fig. 4) resembled those for the stems. At open fernbrake, root N levels increased from January to significantly ($P = 0.05$) higher levels in May. At closed fernbrake this increase started in March and continued until July. Changes in root N concentrations were much less marked at the fjaeldmark site but they also increased from April, so that values were significantly higher in winter than in late summer. The seasonal variations in belowground P and K levels at the

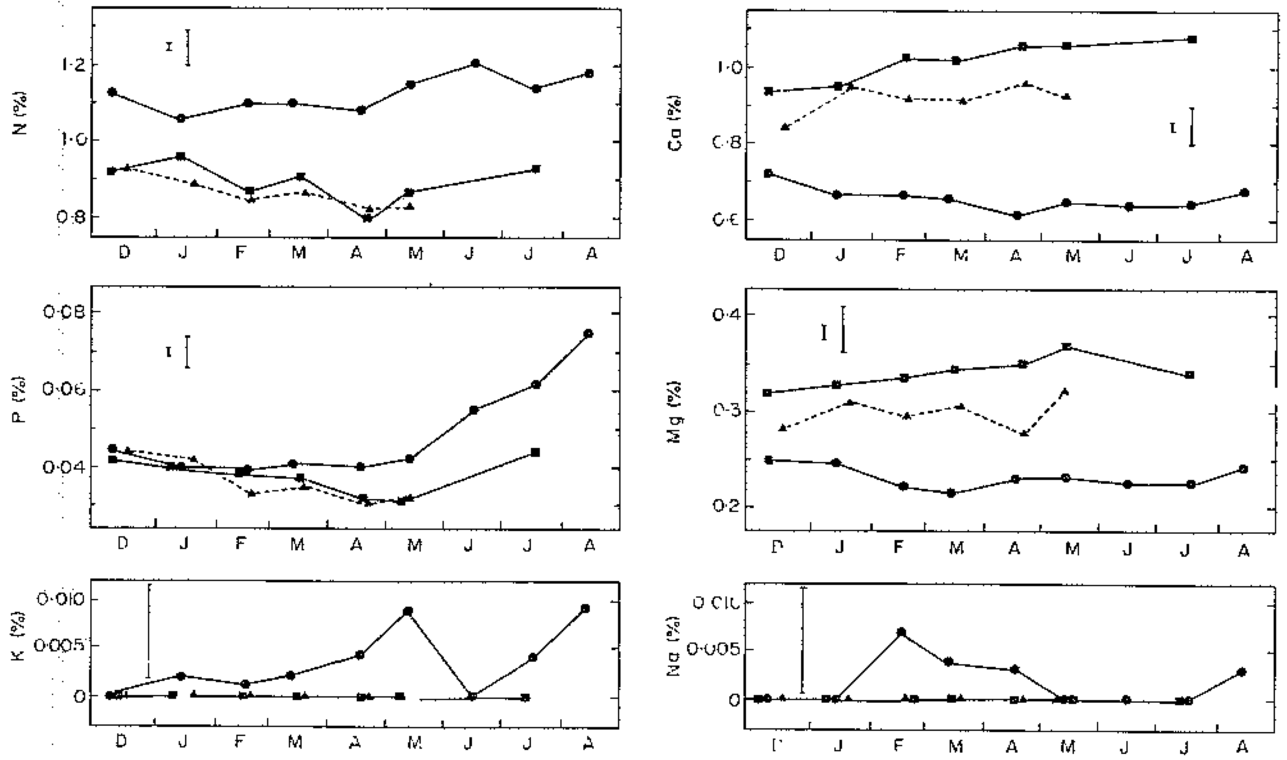


Fig. 2. Chemical composition of the aboveground necromass (mainly dead leaves) of *Azorella selago* at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

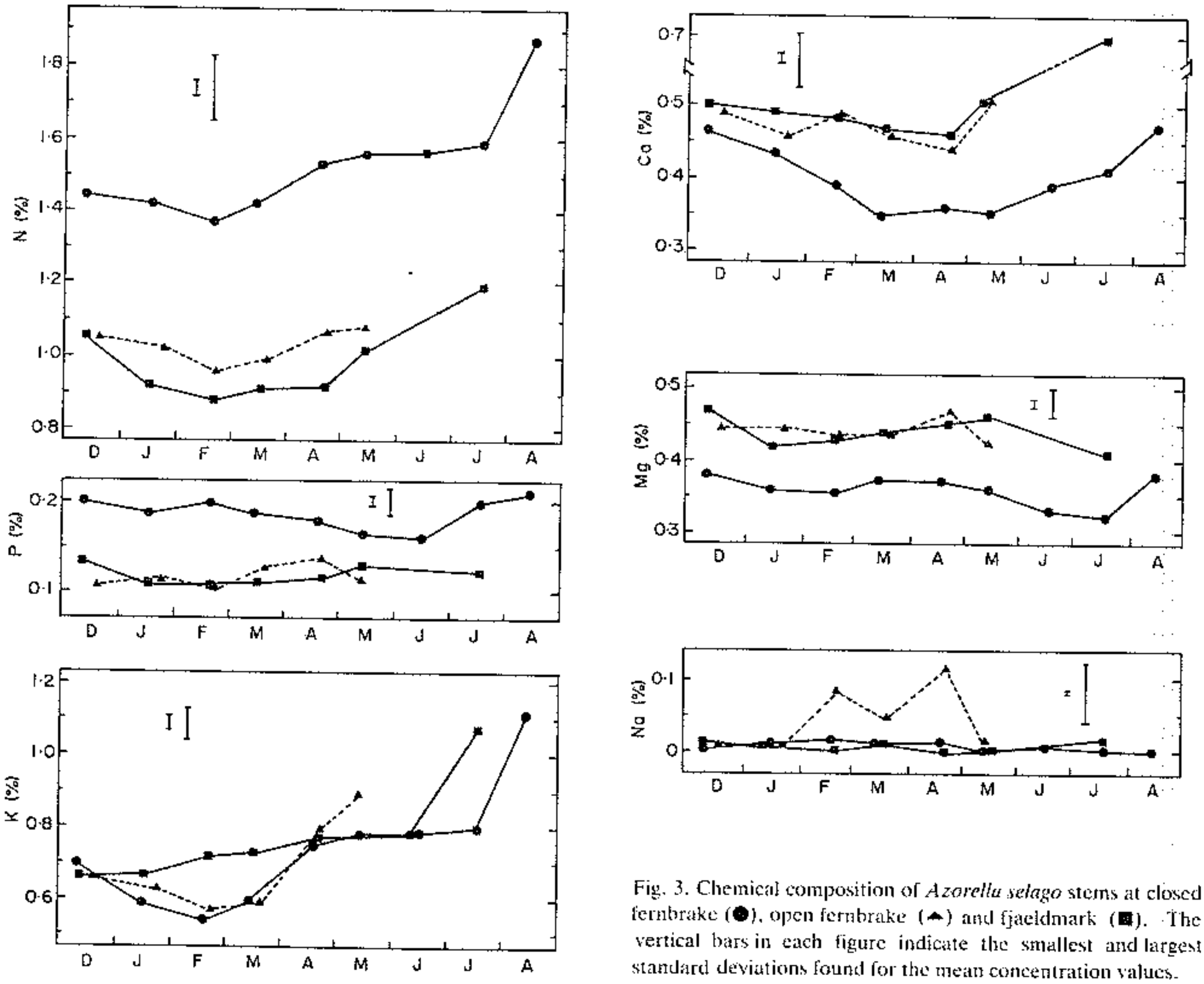


Fig. 3. Chemical composition of *Azorella selago* stems at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

three sites closely resembled those for N but the winter increases at fjaeldmark were greater (and started earlier) than was the case with N. Ca concentrations in the *A. selago* roots declined after December or January at the fernbrake communities but exhibited no consistent pattern at fjaeldmark. Root Mg and Na levels at the three sites varied inconsistently throughout the sampling period.

Blechnum penna-marina

Nutrient concentrations in the aboveground vegetative biomass (living non-reproductive fronds) of the fern *Blechnum penna-marina* at the three sites during December 1973 to December 1974 are presented in Figure 5.

Significantly ($P \leq 0.05$) higher N, P and K concentrations occurred in fronds from closed fernbrake than in those from the other two sites and for most sampling dates levels of the three nutrients were higher at open fernbrake than at fjaeldmark. N, P and K concentrations exhibited similar trends, declining from January (fernbrakes) or February (fjaeldmark) until May/June. Levels remained low through winter, except that N in fronds from open fernbrake increased significantly between May and August. The mean K concentration in fronds from open fernbrake was *c.* 80 % higher in March than for the other sampling dates and this cannot be explained. N, P and K concentrations in fronds at closed fernbrake were significantly higher in December 1973 than in December 1974. This is also difficult to explain but may reflect a higher proportion of young leaves in the biomass at the sites in December 1973. There were no corresponding differences at the other two sites, except for frond K concentrations at fjaeldmark, which were also significantly higher in December 1973 than December 1974.

Concentrations of Ca, Mg and Na were higher in *B. penna-marina* fronds at fjaelmark than those at the fernbrakes. Although Mg and Na levels were generally greater at open- than at closed fernbrake, the differences were mostly not significant at $P < 0.05$. Frond Ca concentrations increased at all three sites from December or January to maximum values just before midwinter. They then decreased markedly to low levels in early spring. Mg and Na concentrations increased from January or February to peak values at midwinter (Mg) or early summer (Na). Na concentrations in fronds from open fernbrake and fjaeldmark were significantly higher in December 1974 than December 1973.

Nutrient concentrations depicted in Figure 5 are those in the total biomass of sterile fronds at each community (i.e. those produced in the current season plus those which overwintered) so they do not reflect the high N, P and K levels, or the low Ca, Mg and Na levels which occur in young sterile fronds in early and midsummer. The figure also does not show the concentrations in reproductive (sporulating) fronds which occur in the aboveground biomass from December to June/July. Nutrient

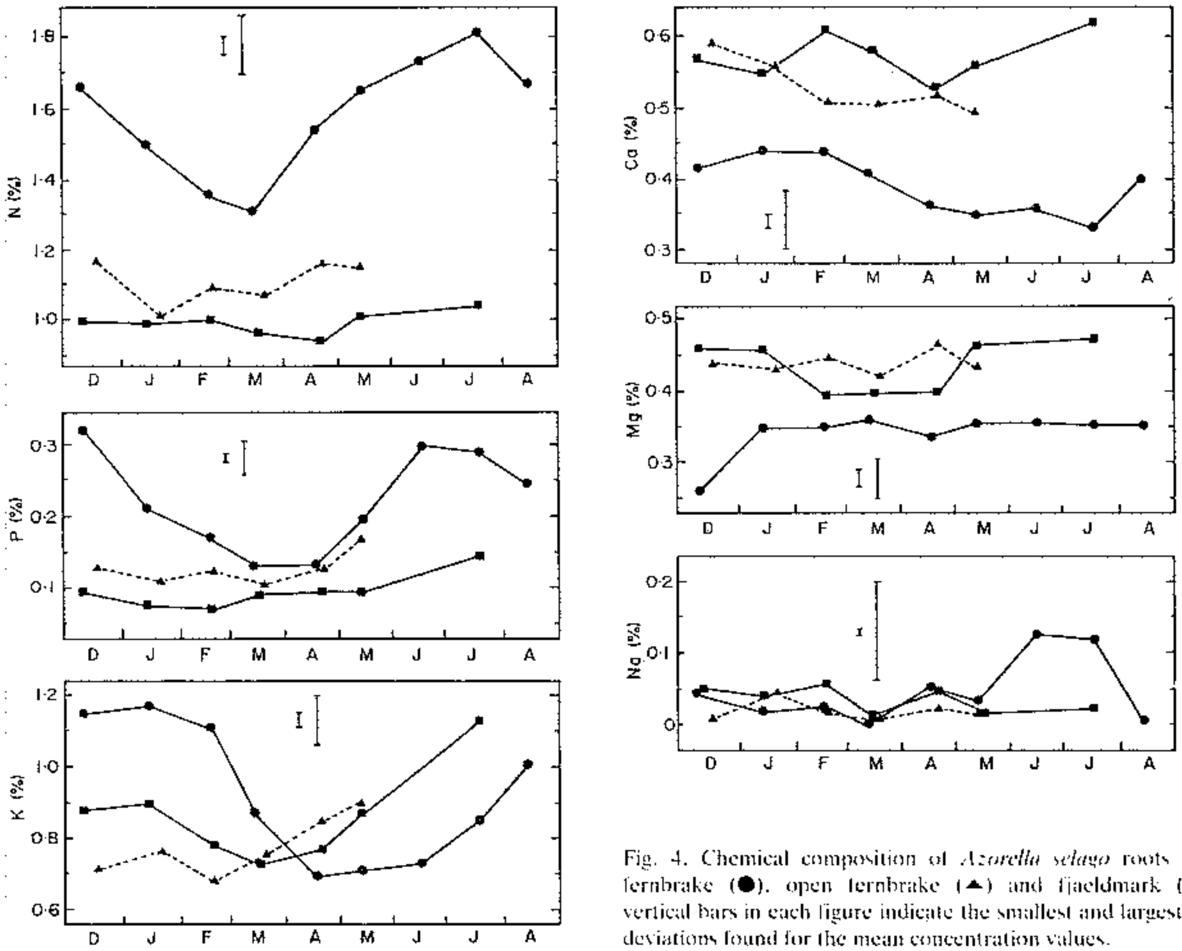


Fig. 4. Chemical composition of *Azorella selago* roots at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

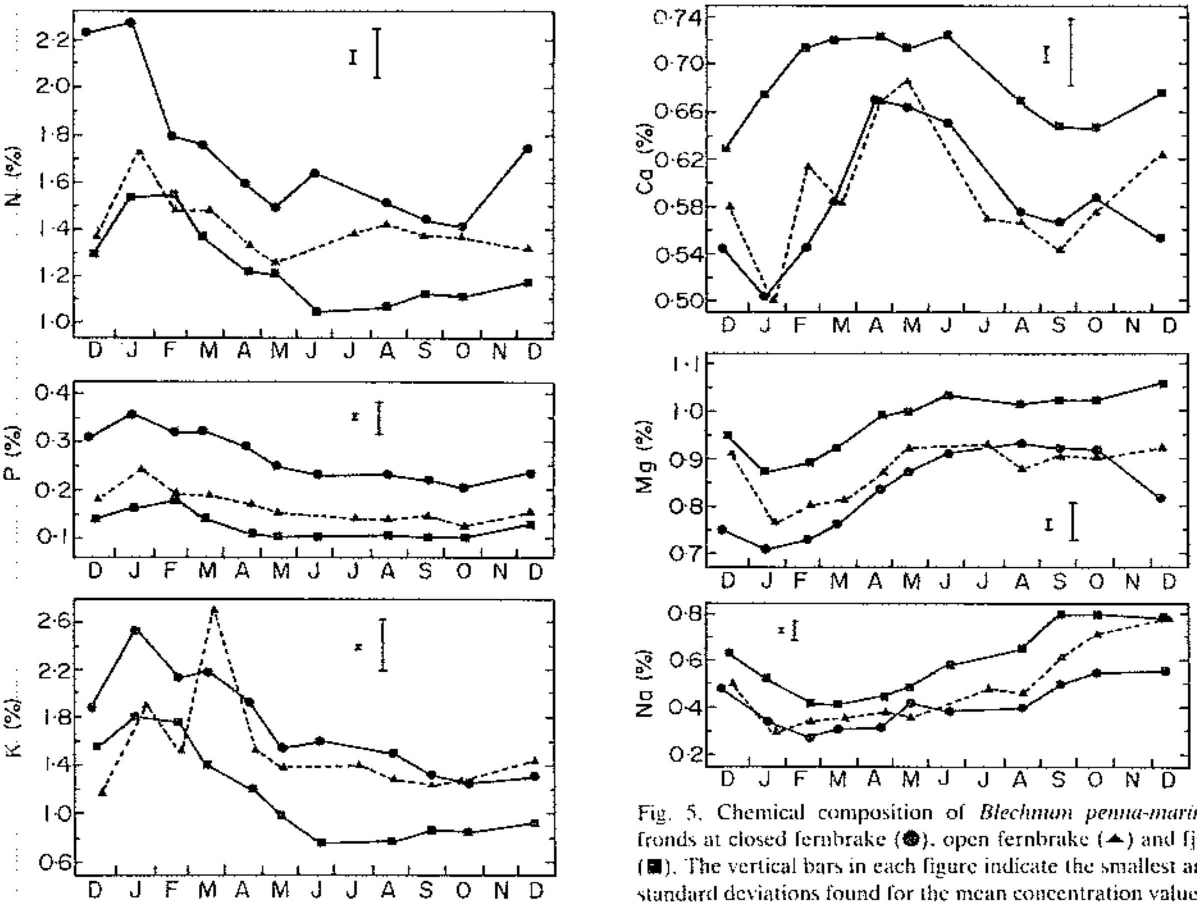


Fig. 5. Chemical composition of *Blechnum penna-marina* sterile fronds at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

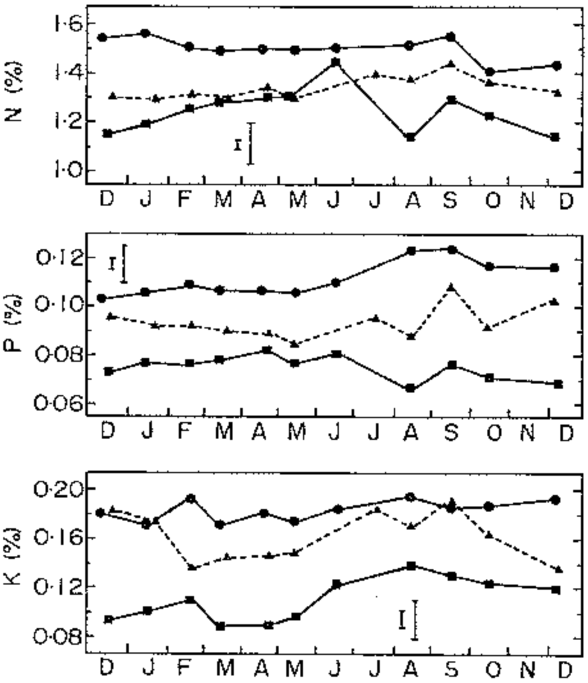
Table 3

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 and in sterile and sporulating *Blechnum penna-marina* fronds

Site and species	N	P	K	Ca	Mg	Na
Blechnum penna-marina						
Sterile fronds						
Closed fernbrake	3.37 - 1.42	0.46 - 0.20	3.39 - 1.26	0.36 - 0.67	0.57 - 0.93	0.25 - 0.56
Open fernbrake	2.98 - 1.32	0.43 - 0.13	2.93 - 1.24	0.30 - 0.62	0.59 - 0.92	0.18 - 0.79
Fjaeldmark	2.70 - 1.11	0.33 - 0.10	2.28 - 0.77	0.48 - 0.72	0.69 - 1.06	0.36 - 0.79
Sporulating fronds						
Closed fernbrake	2.35 - 1.52	0.41 - 0.34	2.66 - 1.82	0.26 - 0.46	0.46 - 0.65	0.12 - 0.32
Open fernbrake	1.63 - 1.35	0.32 - 0.25	2.29 - 1.69	0.32 - 0.48	0.59 - 0.69	0.24 - 0.41
Fjaeldmark	1.74 - 1.38	0.33 - 0.18	1.84 - 1.42	0.34 - 0.48	0.52 - 0.74	0.30 - 0.46
Acaena magellanica						
Closed fernbrake	3.25 - 2.46	0.27 - 0.21	1.76 - 0.65	0.27 - 0.32	0.23 - 0.18	0.38 - 0.16
Open fernbrake	2.77 - 2.36	0.26 - 0.20	1.69 - 0.55	0.19 - 0.34	0.16 - 0.23	0.22 - 0.10
Poa cookii						
Closed fernbrake	2.17 - 1.47	0.25 - 0.16	1.01 - 0.19	0.08 - 0.09	0.09 - 0.10	0.14 - 0.36*
Open fernbrake	1.97 - 1.50	0.24 - 0.16	1.16 - 0.15	0.10 - 0.09	0.10 - 0.09	0.12 - 0.33*
Agrostis magellanica						
Fjaeldmark	2.66 - 2.74*	0.33 - 0.20	1.15 - 0.37	0.08 - 0.10*	0.11 - 0.14	0.08 - 0.17*
Mire-grassland**	2.29 - 2.00	0.26 - 0.17	1.02 - 0.29	0.08 - 0.10*	0.12 - 0.14*	0.15 - 0.25*

* Order does not reflect the seasonal progression

** From Smith (1987a)



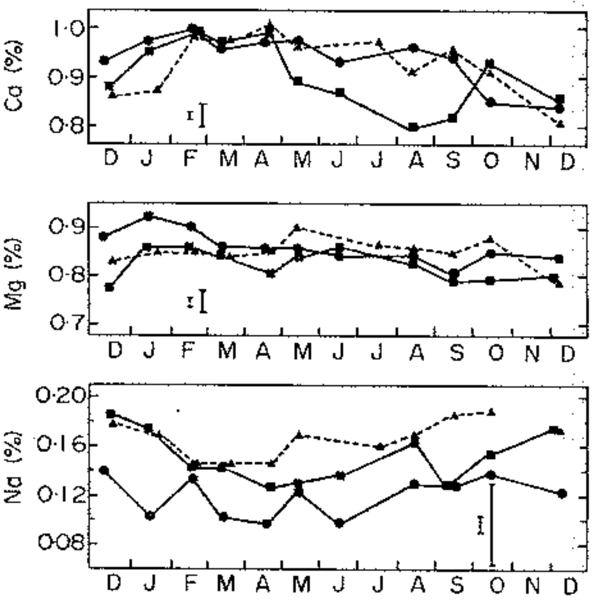


Fig. 6. Chemical composition of dead *Blechnum penna-marina* fronds at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

concentrations, approximately in the order of their seasonal variation, in current-season sterile and sporulating fronds are given in Table 3. Age-related changes in nutrient concentrations were the same for sterile and sporulating fronds; N, P and K decreased markedly, whereas Ca, Mg and Na increased. Peak levels of N, P and K in young tissue were higher for sterile than for sporulating fronds, with the single exception of P for material from fjaeldmark. For fully expanded mature fronds P and K concentrations were higher in sporulating than in sterile material, whereas N levels were similer in the two types. At equivalent stages of frond development, Ca, Mg and Na were higher in sterile than in fertile material.

As was the case for living fronds, concentrations of N, P and, at most sampling dates, of K in dead fronds were higher at closed fernbrake than at the other two sites (Fig. 6). Necromass P and K concentrations were consistently higher at open fernbrake than at fjaeldmark. During late

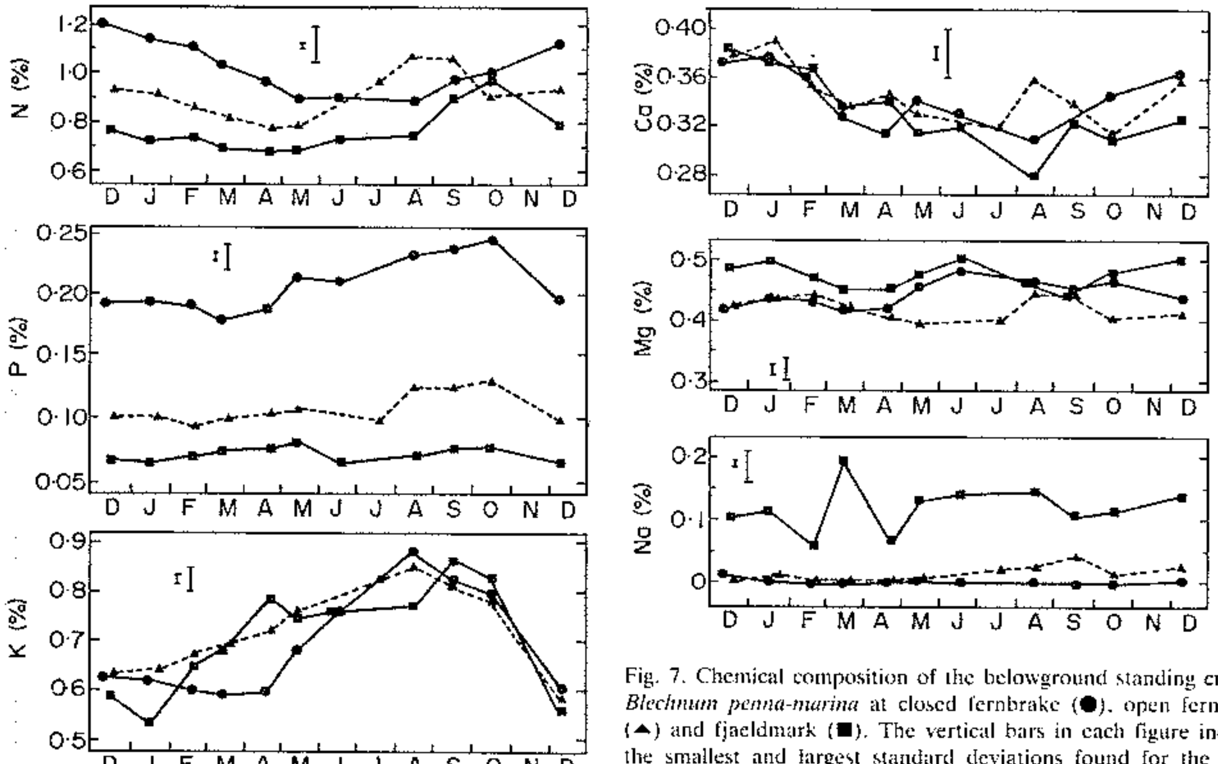


Fig. 7. Chemical composition of the belowground standing crop of *Blechnum penna-marina* at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

winter and summer N concentrations at open fernbrake were also higher than at fjaeldmark. Na levels were invariably lower (but not always significantly so) at closed fernbrake than at the other two communities. There were no consistent inter-site differences in Ca or Mg.

The aboveground necromass of *B. penna-marina* was large and accounted for over 75 per cent of the total aboveground standing crop of the species (Smith 1987c). Not surprisingly, therefore, the seasonal changes in nutrient concentrations for this component were not marked. Necromass P concentrations increased slightly during winter at both fernbrakes so that in September they were significantly ($P = 0.01$) higher than in April or May. K levels at fjaeldmark and open fernbrake also increased in winter but only for fjaeldmark was the increase significant at $P < 0.05$. Necromass Ca levels declined at fjaeldmark during winter.

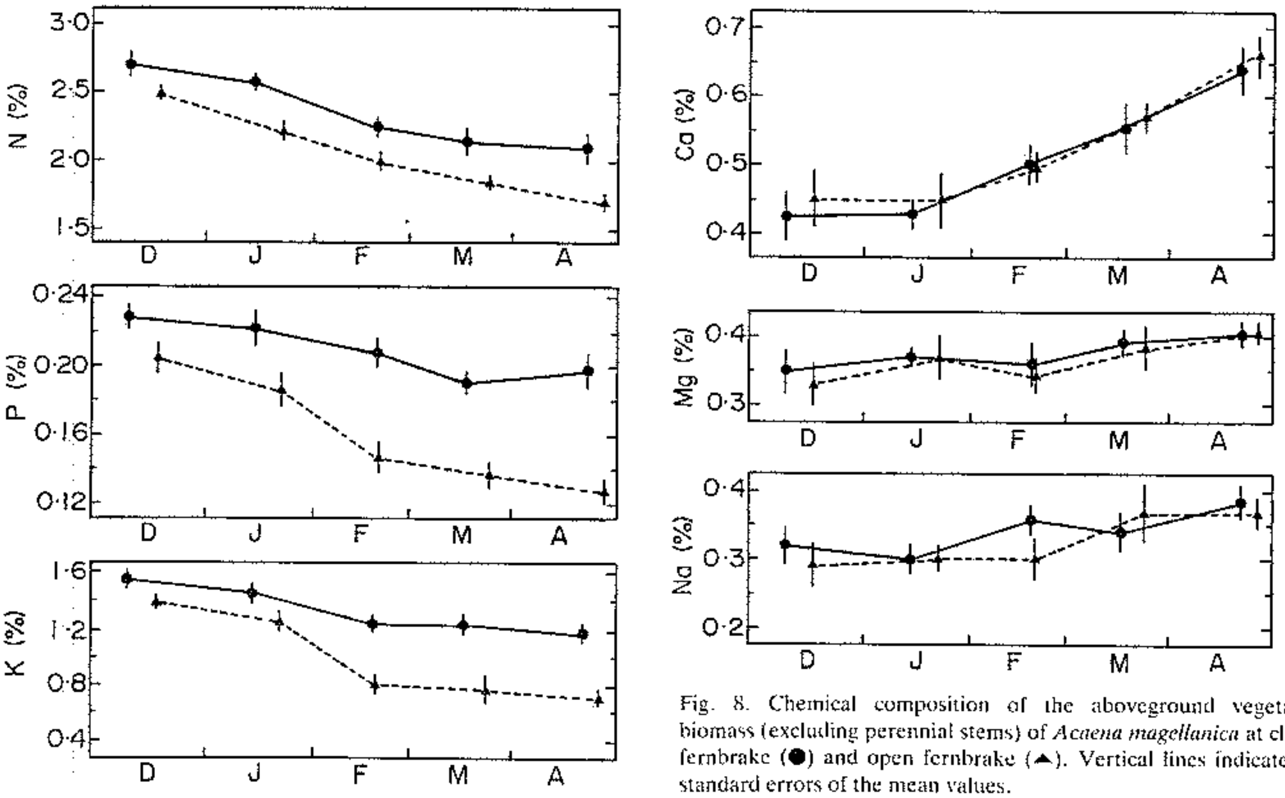


Fig. 8. Chemical composition of the aboveground vegetative biomass (excluding perennial stems) of *Acaena magellanica* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

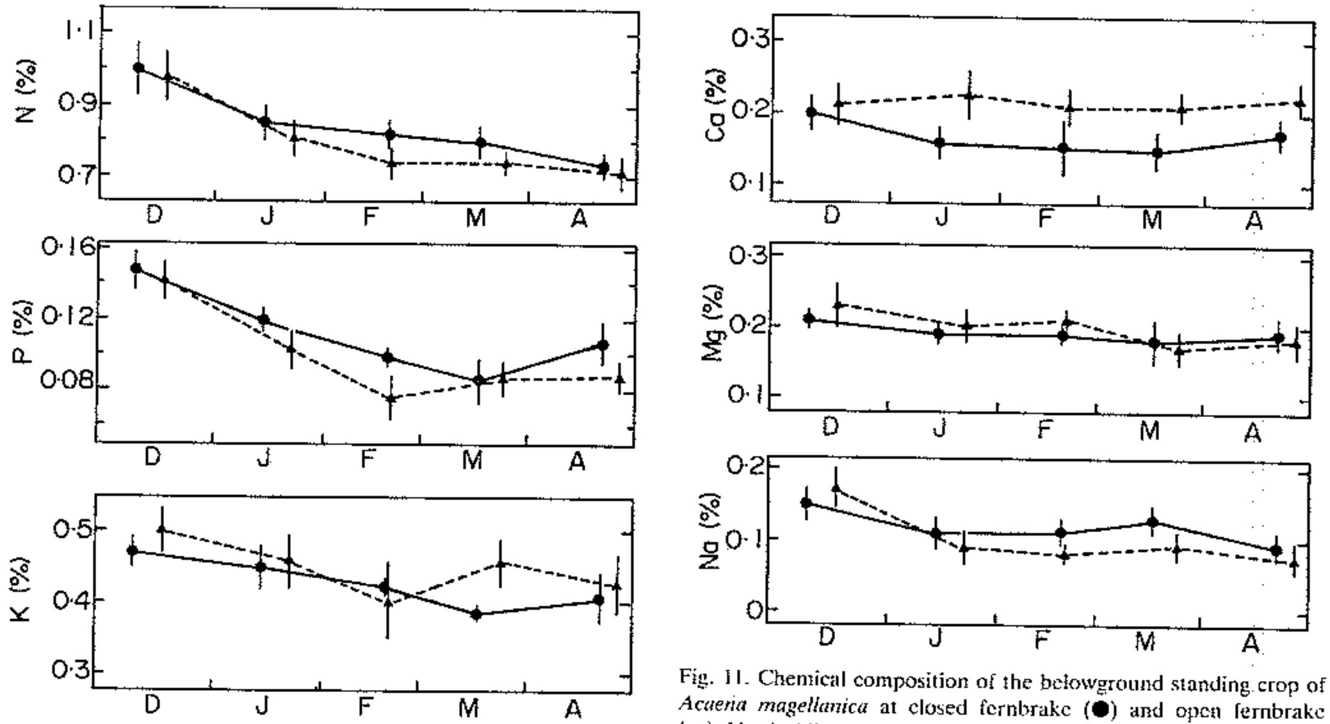


Fig. 11. Chemical composition of the belowground standing crop of *Acaena magellanica* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

Changes in belowground phytomass concentrations of N, P and K for *Acaena* during the sampling period (Fig. 11) were generally more marked than those in the aboveground stems (Fig. 10). Belowground N concentrations declined throughout the sampling period at both sites. P and K also decreased from December but increased again from February (open fernbrake) or March (closed fernbrake). At both sites there were no conspicuous changes in belowground concentrations of Ca, Mg or Na.

Poa cookii

Concentrations of P and Mg in aboveground living shoots of *Poa cookii* at the two fernbrakes decreased during the sampling period (December to April), whereas those of the other nutrients did not change in any coherent pattern (Fig. 12). There were no consistent inter-site differences in shoot concentrations of N, P, K or Ca. Mg and Na levels were consistently (but not always significantly) lower at open- than at closed fernbrake.

P. cookii flowered at both sites in September and October and some capitula remained on the plants until March or April. Nutrient concentrations in the reproductive biomass of this species, approximately in the order of their seasonal variation, are given in Table 3. No significant inter-site

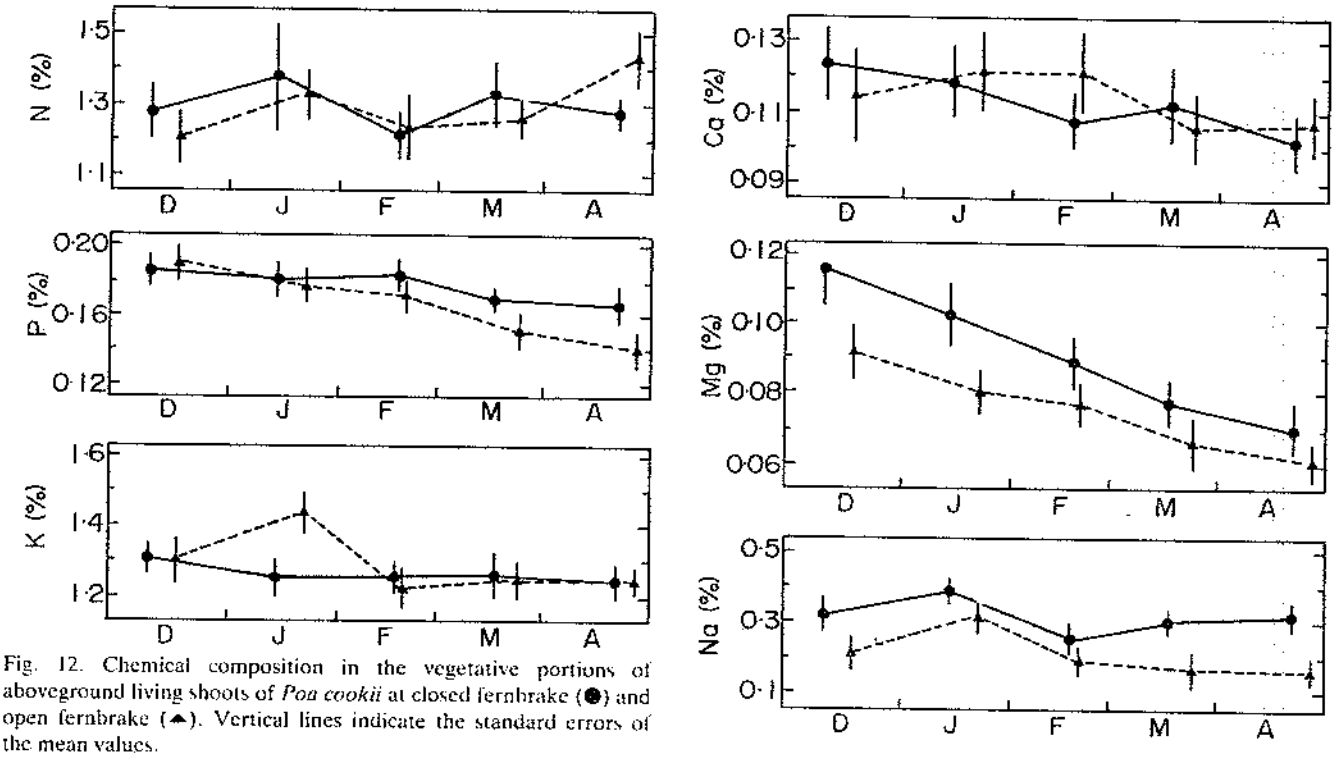


Fig. 12. Chemical composition in the vegetative portions of aboveground living shoots of *Poa cookii* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

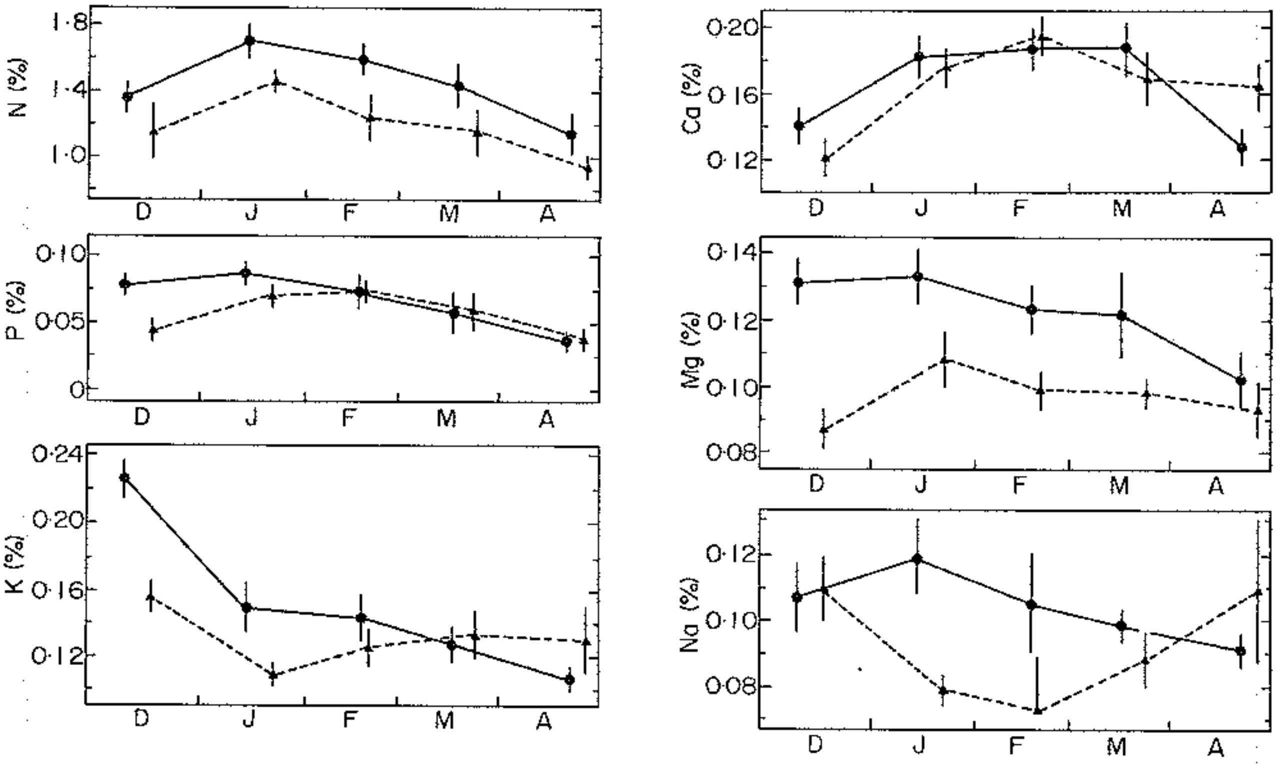


Fig. 13. Chemical composition of the aboveground necromass of *Poa cookii* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

differences occurred in these concentrations. Age-specific decreases in N, P and, especially, K in the reproductive biomass were marked. Ca and Mg levels were very low and did not change significantly during the sampling period. Na concentrations were higher than those of Ca or Mg and, at both sites, decreased markedly from December to February and then increased to April.

Concentrations of N and Mg in the aboveground necromass (dead leaves and stems) of *P. cookii* at closed fernbrake were consistently higher than those at open fernbrake (Fig. 13). P and K levels were also higher at the closed community during December and January but were similar at the two sites later in the season. No significant inter-site differences occurred in necromass Ca concentrations, which were highest during January to March. N, P and K concentrations decreased from high

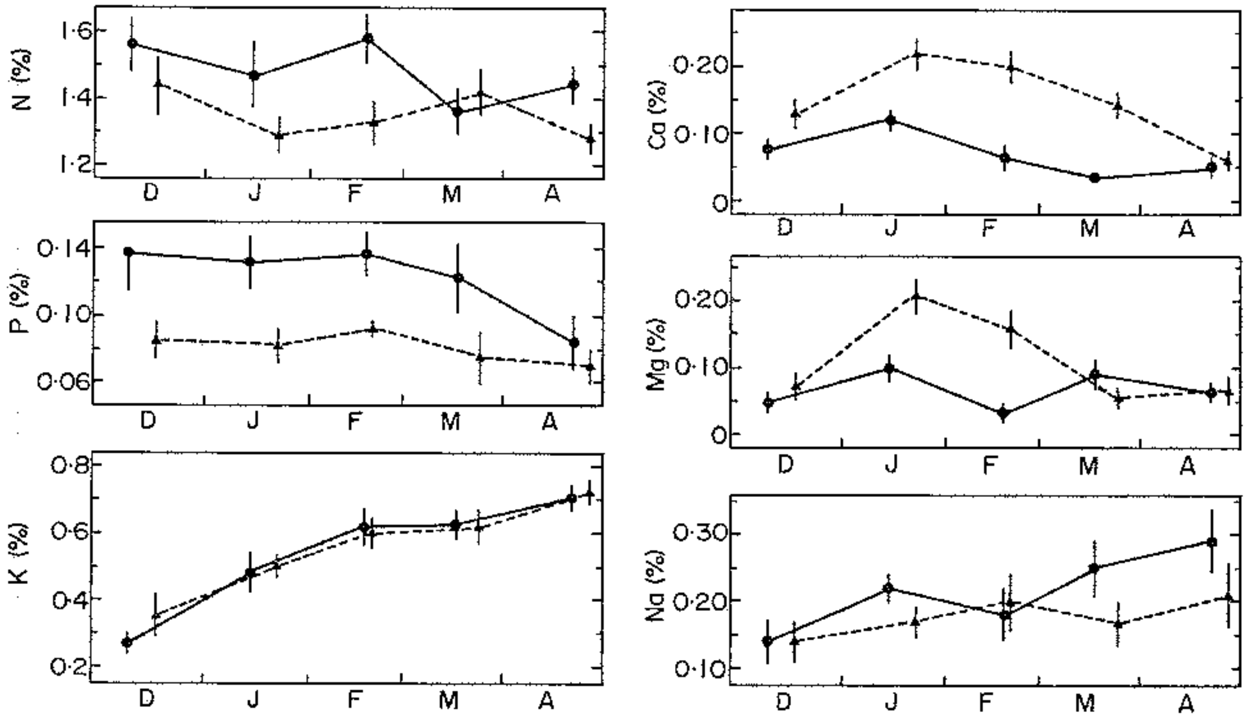
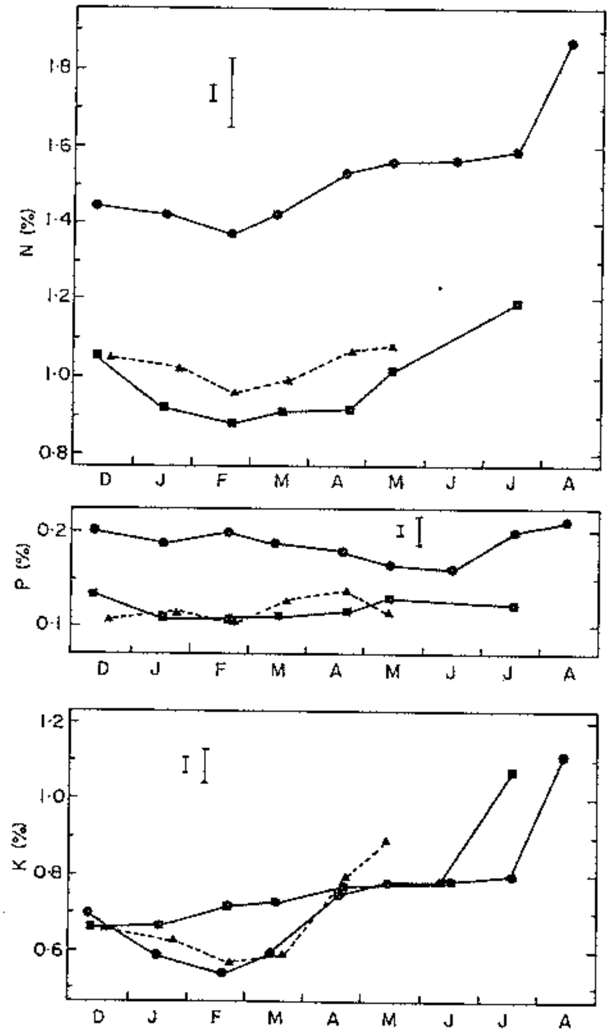


Fig. 14. Chemical composition of the belowground standing crop of *Poa cookii* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.



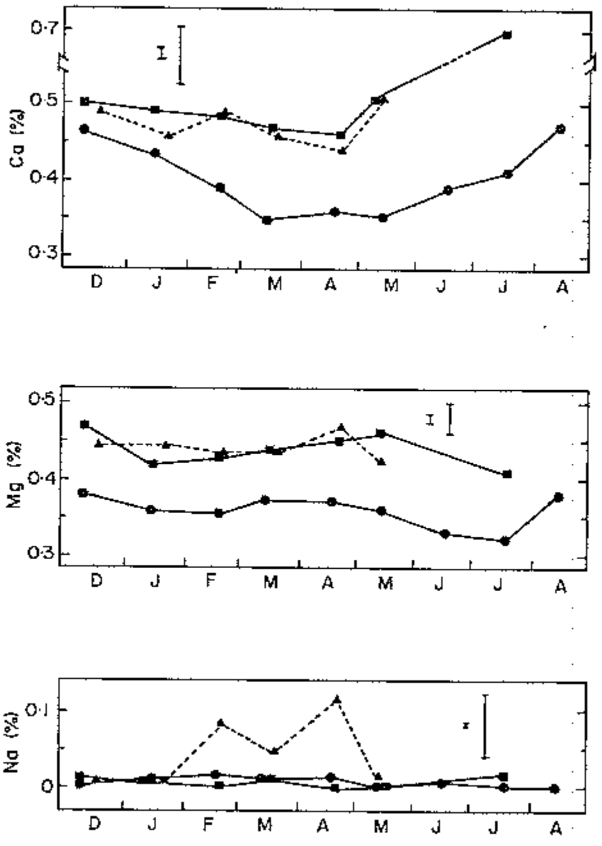


Fig. 3. Chemical composition of *Azorella selago* stems at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

three sites closely resembled those for N but the winter increases at fjaeldmark were greater (and started earlier) than was the case with N. Ca concentrations in the *A. selago* roots declined after December or January at the fernbrake communities but exhibited no consistent pattern at fjaeldmark. Root Mg and Na levels at the three sites varied inconsistently throughout the sampling period.

Blechnum penna-marina

Nutrient concentrations in the aboveground vegetative biomass (living non-reproductive fronds) of the fern *Blechnum penna-marina* at the three sites during December 1973 to December 1974 are presented in Figure 5.

Significantly ($P \leq 0.05$) higher N, P and K concentrations occurred in fronds from closed fernbrake than in those from the other two sites and for most sampling dates levels of the three nutrients were higher at open fernbrake than at fjaeldmark. N, P and K concentrations exhibited similar trends, declining from January (fernbrakes) or February (fjaeldmark) until May/June. Levels remained low through winter, except that N in fronds from open fernbrake increased significantly between May and August. The mean K concentration in fronds from open fernbrake was *c.* 80 % higher in March than for the other sampling dates and this cannot be explained. N, P and K concentrations in fronds at closed fernbrake were significantly higher in December 1973 than in December 1974. This is also difficult to explain but may reflect a higher proportion of young leaves in the biomass at the sites in December 1973. There were no corresponding differences at the other two sites, except for frond K concentrations at fjaeldmark, which were also significantly higher in December 1973 than December 1974.

Concentrations of Ca, Mg and Na were higher in *B. penna-marina* fronds at fjaelmark than those at the fernbrakes. Although Mg and Na levels were generally greater at open- than at closed fernbrake, the differences were mostly not significant at $P \leq 0.05$. Frond Ca concentrations increased at all three sites from December or January to maximum values just before midwinter. They then decreased markedly to low levels in early spring. Mg and Na concentrations increased from January or February to peak values at midwinter (Mg) or early summer (Na). Na concentrations in fronds from open fernbrake and fjaeldmark were significantly higher in December 1974 than December 1973.

Nutrient concentrations depicted in Figure 5 are those in the total biomass of sterile fronds at each community (i.e. those produced in the current season plus those which overwintered) so they do not reflect the high N, P and K levels, or the low Ca, Mg and Na levels which occur in young sterile fronds in early and midsummer. The figure also does not show the concentrations in reproductive (sporulating) fronds which occur in the aboveground biomass from December to June/July. Nutrient

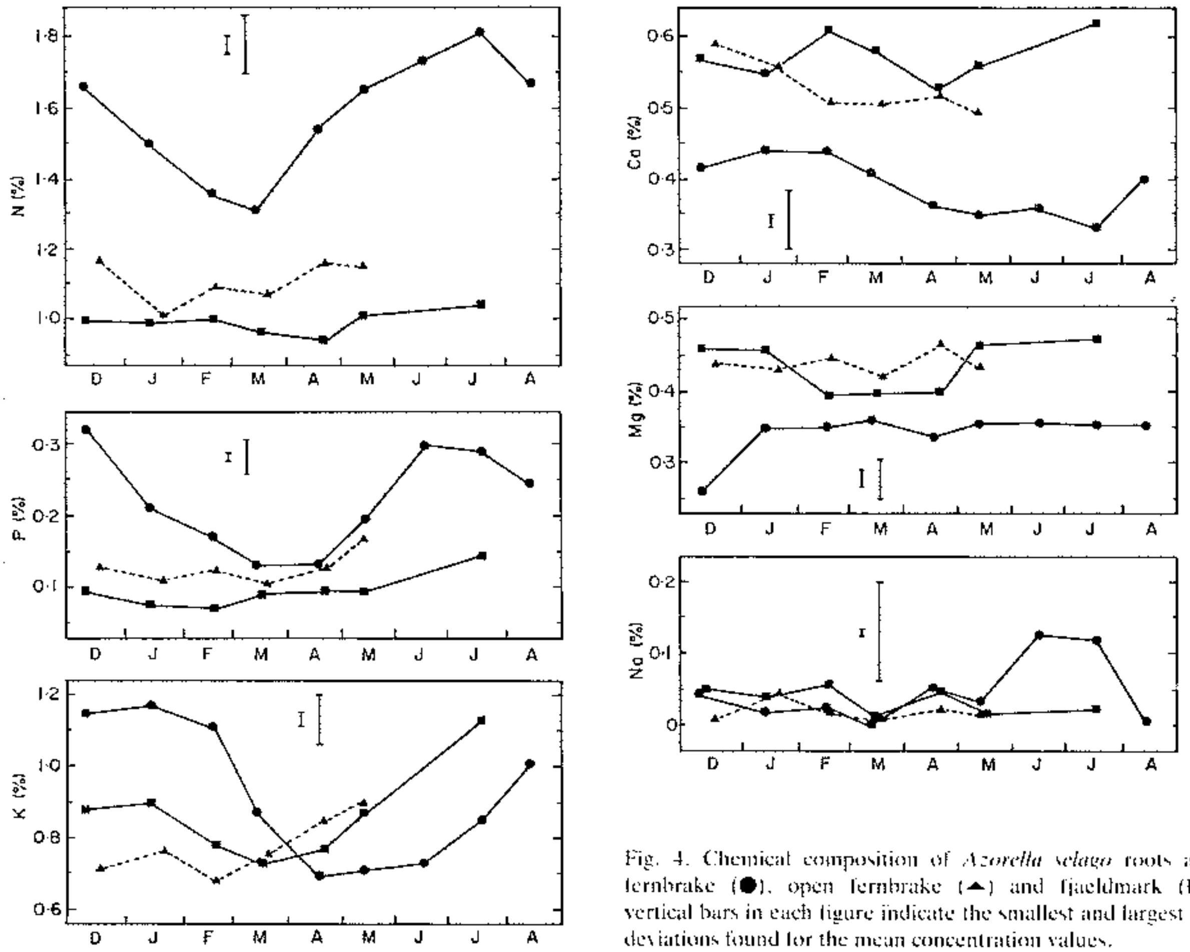


Fig. 4. Chemical composition of *Azorella selago* roots at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

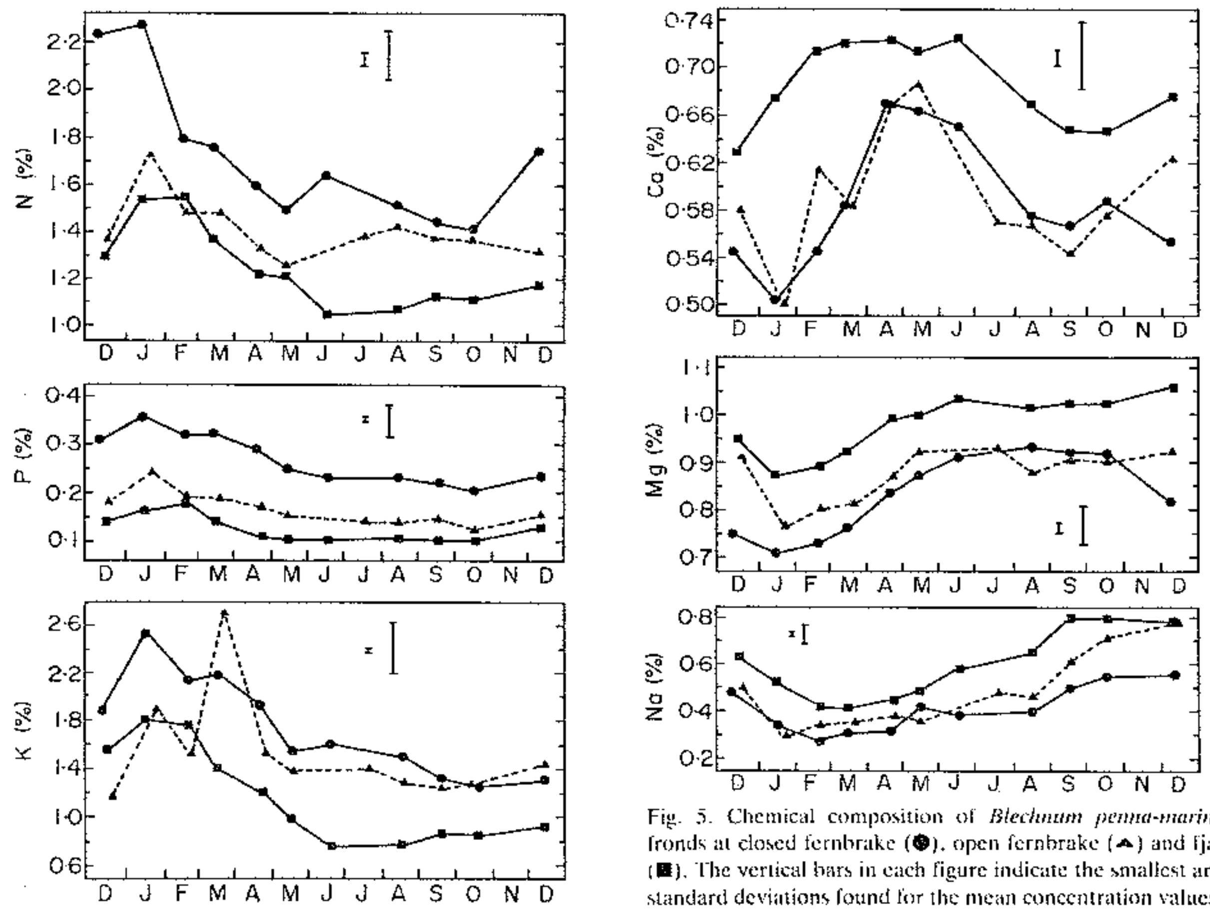
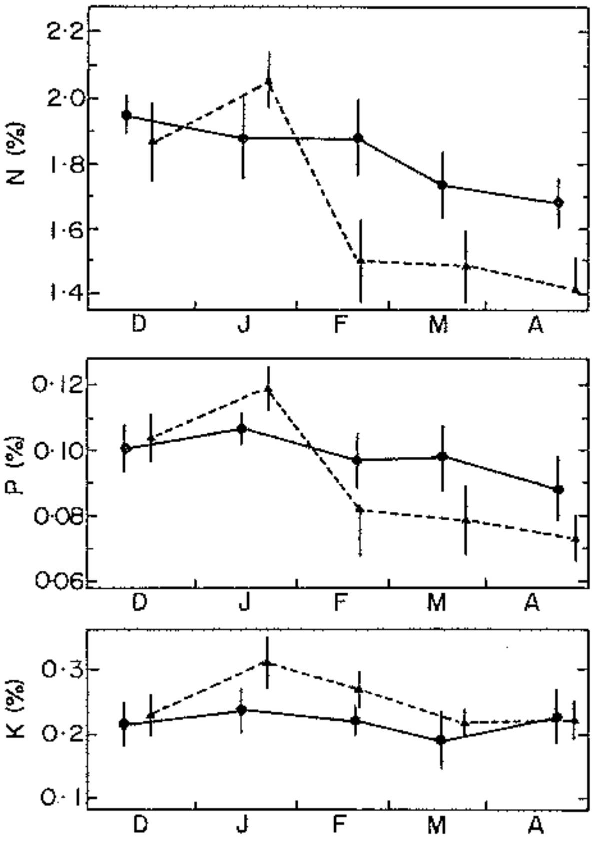


Fig. 5. Chemical composition of *Blechnum penna-marina* sterile fronds at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.



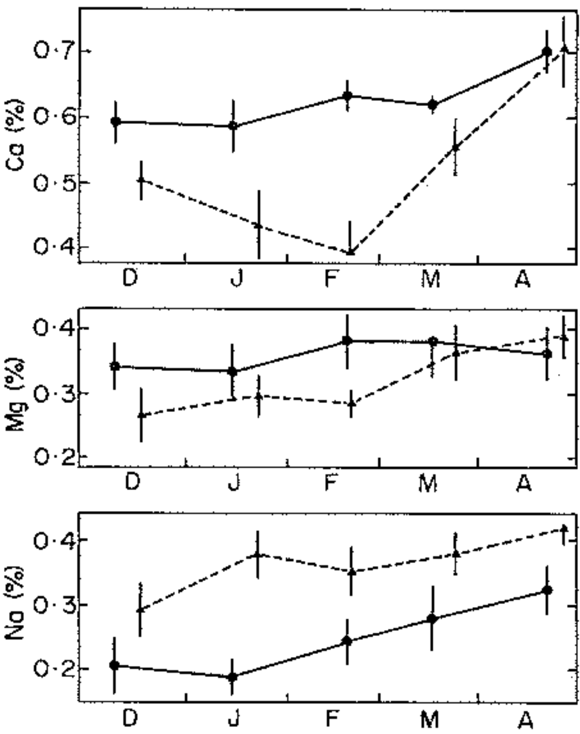


Fig. 9. Chemical composition of the aboveground necromass of *Acaena magellanica* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

There were no conspicuous seasonal changes for Mg or Na.

P concentrations in the belowground standing crop of *B. penna-marina* (roots and rhizomes) were consistently highest at closed fernbrake and lowest at fjaeldmark (Fig. 7). At most sampling dates similar inter-site differences occurred for N, but during winter and spring the N levels were similar at the two fernbrakes. Na levels were highest at fjaeldmark and so were those of Mg during summer. Na concentrations in *B. penna-marina* roots and rhizomes were especially low at the two fernbrake sites, generally < 0.02 per cent. There were no consistent inter-site differences in the concentrations of K or Ca.

N concentrations in the belowground standing crop of *B. penna-marina* declined during summer at all three sites. This decline continued until April at open fernbrake and fjaeldmark and until May at closed fernbrake. At the two open communities, N levels then increased during winter but at closed fernbrake they remained low throughout winter and only increased in spring. Belowground P concentrations for *B. penna-marina* showed no discernible seasonal pattern at fjaeldmark; at the two fernbrake sites they increased slightly during winter so that values were significantly ($P = 0.05$) higher in spring than in autumn. Seasonal changes in belowground K concentrations were marked and were similar at the three sites. At open fernbrake and fjaeldmark they increased from December/January to maximum levels in August/September. At closed fernbrake this increase started later (April) but maximum values were also attained in August. At all three sites, belowground K concentrations declined sharply during spring and early summer. Contrary to what was found for the leaves, the concentrations of N, P and K in *B. penna-marina* roots and rhizomes were not significantly different between the two December sampling dates.

Belowground Ca concentrations in *B. penna-marina* exhibited a well-defined seasonal pattern. Values declined from December/January until August and then increased in spring and early summer. At open fernbrake the August value was high and inconsistent with this general trend. However, the differences between the value in August and minimum concentrations in July and October were not significant at the 5 per cent level. No discernible seasonal pattern occurred in belowground concentrations of Mg or Na for *B. penna-marina*.

Acaena magellanica

Nutrient concentrations in the living vegetative parts of current-season *Acaena* shoots (leaves, petioles and current-season stems but excluding flowers, seed-heads or scapes) at the fernbrake sites from December 1973 to April 1974 are depicted in Figure 8. Shoot N, P and K concentrations were consistently higher ($P \leq 0.05$) at closed fernbrake, whereas those of Ca, Mg and Na did not differ between the two sites. N, P and K decreased, and Ca increased, throughout the sampling period. Mg and Na concentrations also increased slightly during this period but values in April were not significantly higher than those in December.

Inflorescences and/or seed heads of *Acaena* were present at both study sites throughout the sampling period. Nutrient levels in the reproductive biomass (inflorescences and scapes) are given in Table 3. N and P levels were higher, and Ca, Mg and Na levels lower, than in the vegetative shoot biomass. K concentrations were similar in the two components. The age-related concentration changes in the reproductive material were the same as those for the vegetative biomass, i.e. N, P and K decreased, whereas Ca, Mg and Na increased with age although, as was the case with the shoot concentrations, the increases in Mg and Na were

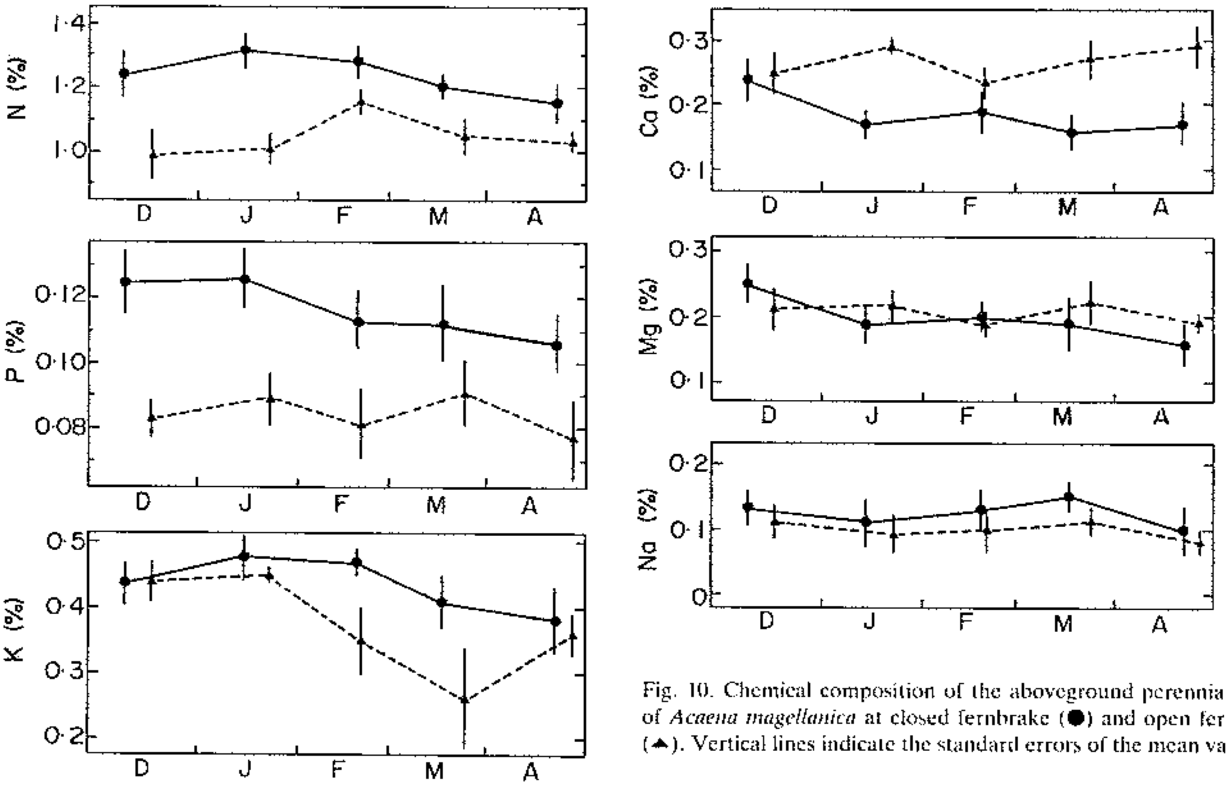


Fig. 10. Chemical composition of the aboveground perennial stems of *Acaena magellanica* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

small.

Nutrient concentrations in the aboveground necromass of *Acaena* (dead leaves and petioles, occasionally dead stems) are given in Figure 9. Concentrations of N, P and, especially, of K were lower in the necromass than in living shoots. Mg levels were similar in the two phytomass components. At closed fernbrake, necromass Ca concentrations were consistently higher, and Na concentrations lower, than those in living shoots. For most sampling dates these differences were significant at $P \leq 0.05$. Corresponding differences did not occur at the open fernbrake site. Within sampling dates, a substantial amount of variability was associated with the nutrient concentration estimates for the aboveground necromass of *Acaena*. Inter-site differences in necromass N, P and K concentrations were therefore not as marked, or as significant, as those in the shoot biomass. Necromass N and P levels were most often higher, and K levels lower, at closed fernbrake than at open fernbrake but for most sampling dates the differences were not significant at the 5 per cent level. Ca and Mg concentrations were generally greater at closed fernbrake but the differences were only significant in the case of Ca. Necromass Na levels were consistently lower at closed fernbrake.

Because of the large within-sampling-date variability in the *Acaena* necromass nutrient data, the concentration changes during the sampling period (Fig. 9) were not as conspicuous as those which occurred in the live shoots. Necromass N and P concentrations declined after December or January at both fernbrakes, but the changes were only significant at open fernbrake. No consistent changes in K levels occurred at either site. Ca and Na increased from January (closed fernbrake) or February (open fernbrake) to significantly higher values in April. Necromass Mg values were also significantly higher in April than in midsummer for open fernbrake but not for closed fernbrake.

Living aboveground perennial stems formed the largest component in the aboveground biomass of *Acaena* (Smith 1987c). Concentrations of N, P, Ca and Mg in the current-year shoots were commonly double, and those of K and Na 3 to 4-fold, those in stems. Intersite differences in stem nutrient concentrations (Fig. 10) were similar to those for current season shoots. *Acaena* stems at closed fernbrake possessed significantly greater concentrations of N and P than those at open fernbrake. Stem K levels were also higher at closed- than at open fernbrake but, at most sampling dates, the differences were not significant at $P \leq 0.05$. At closed fernbrake stem N, P and K concentrations declined consistently from January to April but the overall changes were not significant at the 5 per cent level. Stem N and P levels at open fernbrake did not vary in a consistent pattern but K concentrations declined significantly between January and March. At both sites there were no consistent changes in the stem concentrations of Ca, Mg or Na during the sampling period. Unlike the shoots, stem Ca concentrations were lower at closed fernbrake than at open fernbrake. Stem Na levels were consistently slightly lower at open fernbrake but the differences were not significant. There were no consistent inter-site differences in stem Mg concentrations.

Nutrient concentrations in the belowground standing crop of *Acaena* (mainly roots, but including buried stems) are given in Figure 11. Belowground N and Ca concentrations were slightly lower than in aboveground stems, whereas concentrations of the other nutrients were similar in the two standing crop components. There were no significant inter-site differences in the belowground nutrient concentrations for *Acaena*, but Ca levels were consistently higher at open fernbrake than at closed fernbrake. This might have been due to a greater proportion of buried stems in the belowground standing crop at the open fernbrake site (Smith 1987c).

Table 3

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 and in sterile and sporulating *Blechnum penna-marina* fronds

Site and species	N	P	K	Ca	Mg	Na
Blechnum penna-marina						
Sterile fronds						
Closed fernbrake	3.37 - 1.42	0.46 - 0.20	3.39 - 1.26	0.36 - 0.67	0.57 - 0.93	0.25 - 0.56
Open fernbrake	2.98 - 1.32	0.43 - 0.13	2.93 - 1.24	0.30 - 0.62	0.59 - 0.92	0.18 - 0.79
Fjaeldmark	2.70 - 1.11	0.33 - 0.10	2.28 - 0.77	0.48 - 0.72	0.69 - 1.06	0.36 - 0.79
Sporulating fronds						
Closed fernbrake	2.35 - 1.52	0.41 - 0.34	2.66 - 1.82	0.26 - 0.46	0.46 - 0.65	0.12 - 0.32
Open fernbrake	1.63 - 1.35	0.32 - 0.25	2.29 - 1.69	0.32 - 0.48	0.59 - 0.69	0.24 - 0.41
Fjaeldmark	1.74 - 1.38	0.33 - 0.18	1.84 - 1.42	0.34 - 0.48	0.52 - 0.74	0.30 - 0.46
Acaena magellanica						
Closed fernbrake	3.25 - 2.46	0.27 - 0.21	1.76 - 0.65	0.27 - 0.32	0.23 - 0.18	0.38 - 0.16
Open fernbrake	2.77 - 2.36	0.26 - 0.20	1.69 - 0.55	0.19 - 0.34	0.16 - 0.23	0.22 - 0.10
Poa cookii						
Closed fernbrake	2.17 - 1.47	0.25 - 0.16	1.01 - 0.19	0.08 - 0.09	0.09 - 0.10	0.14 - 0.36*
Open fernbrake	1.97 - 1.50	0.24 - 0.16	1.16 - 0.15	0.10 - 0.09	0.10 - 0.09	0.12 - 0.33*
Agrostis magellanica						
Fjaeldmark	2.66 - 2.74*	0.33 - 0.20	1.15 - 0.37	0.08 - 0.10*	0.11 - 0.14	0.08 - 0.17*
Mire-grassland**	2.29 - 2.00	0.26 - 0.17	1.02 - 0.29	0.08 - 0.10*	0.12 - 0.14*	0.15 - 0.25*

Order does not reflect the seasonal progression

** From Smith (1987a)

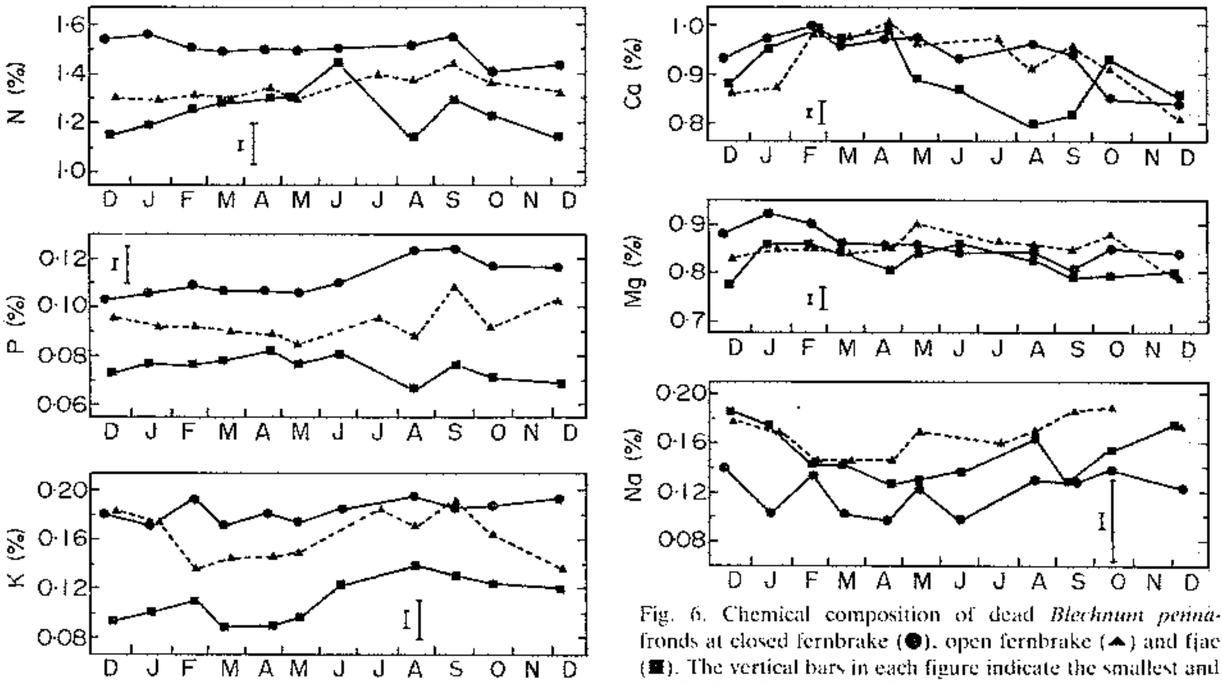


Fig. 6. Chemical composition of dead *Blechnum penna-marina* fronds at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

concentrations, approximately in the order of their seasonal variation, in current-season sterile and sporulating fronds are given in Table 3. Age-related changes in nutrient concentrations were the same for sterile and sporulating fronds: N, P and K decreased markedly, whereas Ca, Mg and Na increased. Peak levels of N, P and K in young tissue were higher for sterile than for sporulating fronds, with the single exception of P for material from fjaeldmark. For fully expanded mature fronds P and K concentrations were higher in sporulating than in sterile material, whereas N levels were similer in the two types. At equivalent stages of frond development, Ca, Mg and Na were higher in sterile than in fertile material.

As was the case for living fronds, concentrations of N, P and, at most sampling dates, of K in dead fronds were higher at closed fernbrake than at the other two sites (Fig. 6). Necromass P and K concentrations were consistently higher at open fernbrake than at fjaeldmark. During late

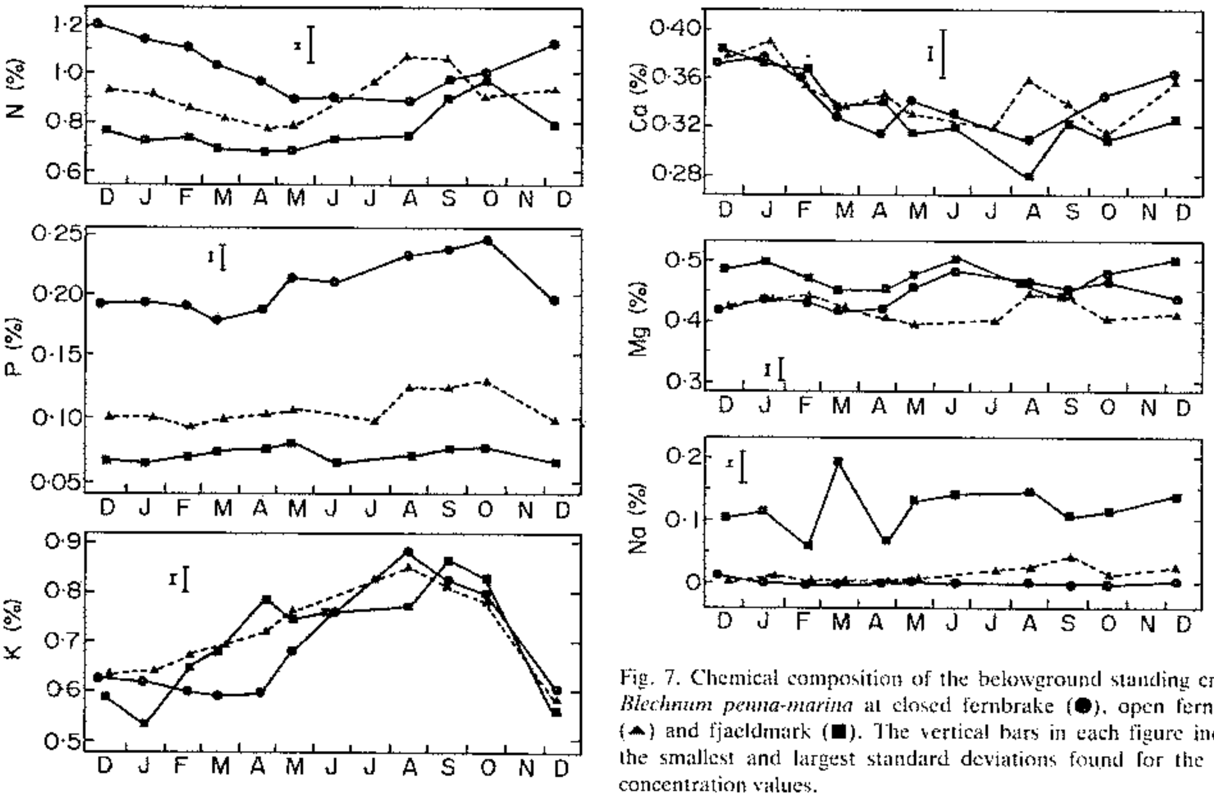


Fig. 7. Chemical composition of the belowground standing crop of *Blechnum penna-marina* at closed fernbrake (●), open fernbrake (▲) and fjaeldmark (■). The vertical bars in each figure indicate the smallest and largest standard deviations found for the mean concentration values.

winter and summer N concentrations at open fernbrake were also higher than at fjaeldmark. Na levels were invariably lower (but not always significantly so) at closed fernbrake than at the other two communities. There were no consistent inter-site differences in Ca or Mg.

The aboveground necromass of *B. penna-marina* was large and accounted for over 75 per cent of the total aboveground standing crop of the species (Smith 1987c). Not surprisingly, therefore, the seasonal changes in nutrient concentrations for this component were not marked. Necromass P concentrations increased slightly during winter at both fernbrakes so that in September they were significantly ($P = 0.01$) higher than in April or May. K levels at fjaeldmark and open fernbrake also increased in winter but only for fjaeldmark was the increase significant at $P < 0.05$. Necromass Ca levels declined at fjaeldmark during winter.

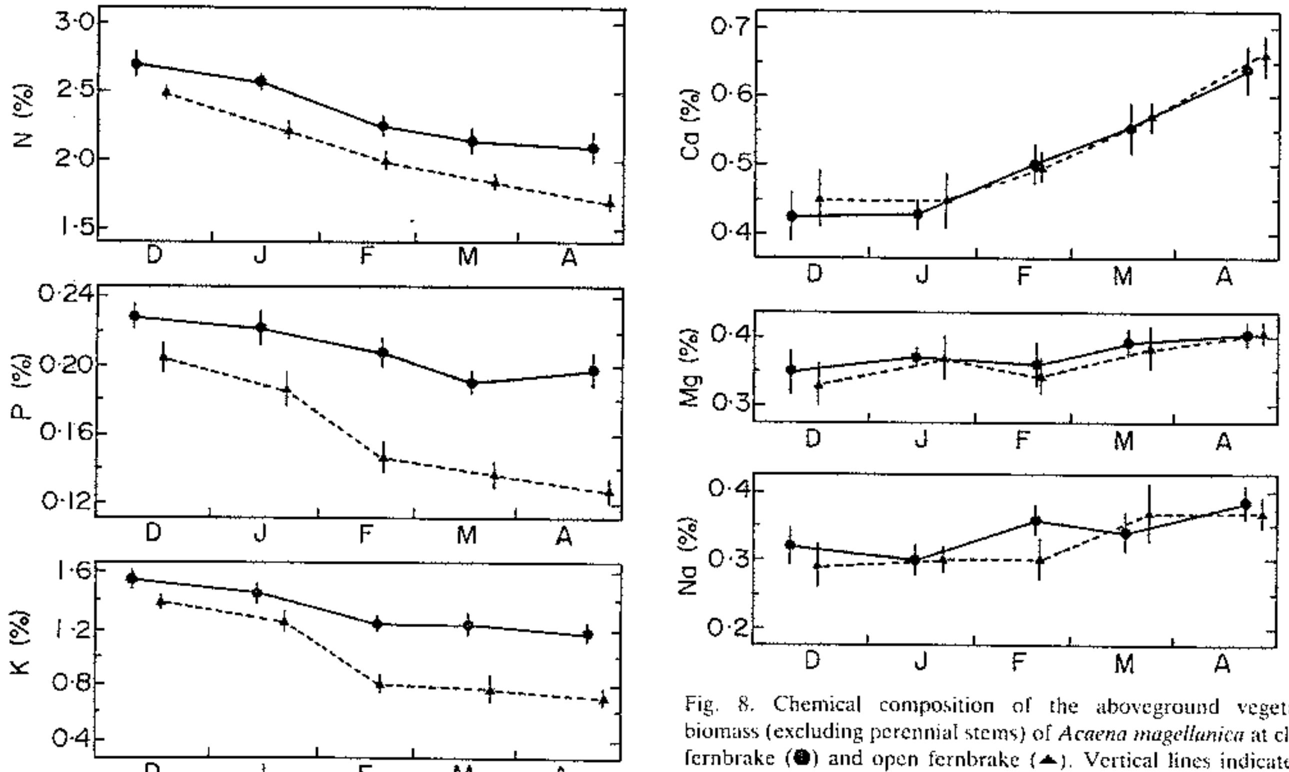
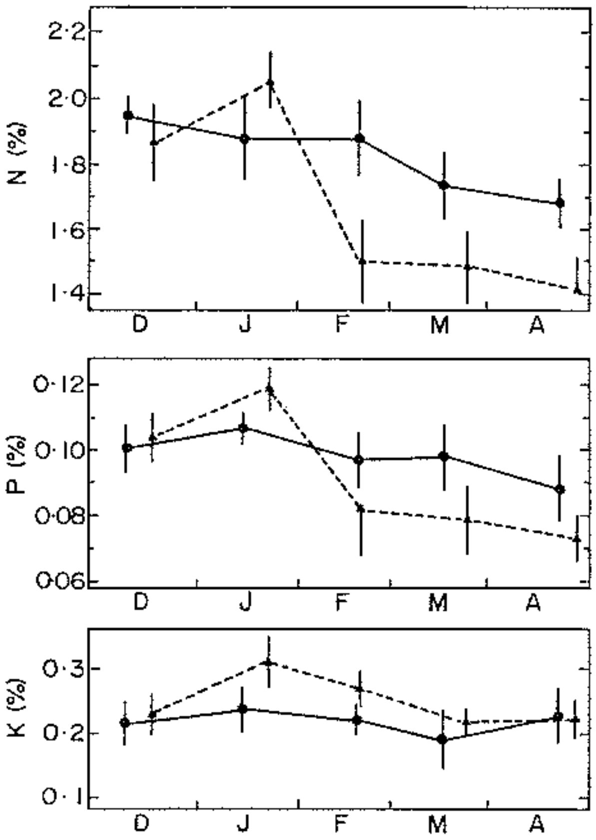


Fig. 8. Chemical composition of the aboveground vegetative biomass (excluding perennial stems) of *Acaena magellanica* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.



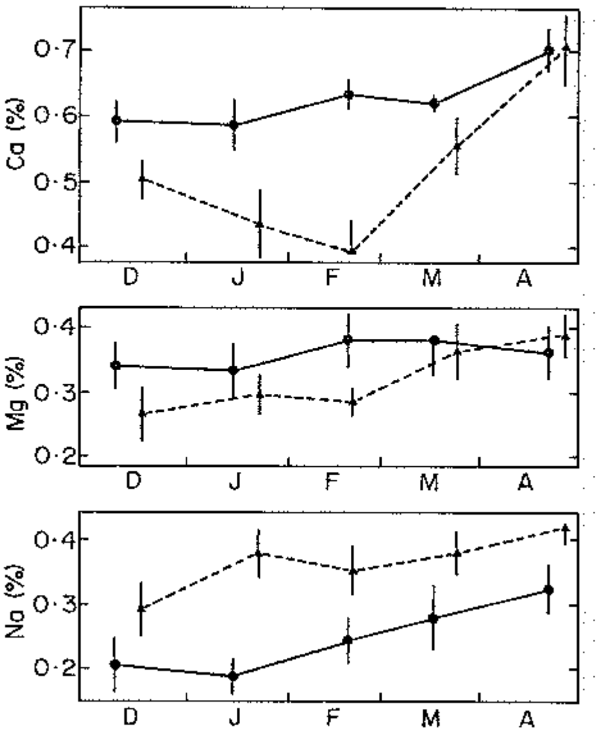


Fig. 9. Chemical composition of the aboveground necromass of *Acaena magellanica* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

There were no conspicuous seasonal changes for Mg or Na.

P concentrations in the belowground standing crop of *B. penna-marina* (roots and rhizomes) were consistently highest at closed fernbrake and lowest at fjaeldmark (Fig. 7). At most sampling dates similar inter-site differences occurred for N, but during winter and spring the N levels were similar at the two fernbrakes. Na levels were highest at fjaeldmark and so were those of Mg during summer. Na concentrations in *B. penna-marina* roots and rhizomes were especially low at the two fernbrake sites, generally < 0.02 per cent. There were no consistent inter-site differences in the concentrations of K or Ca.

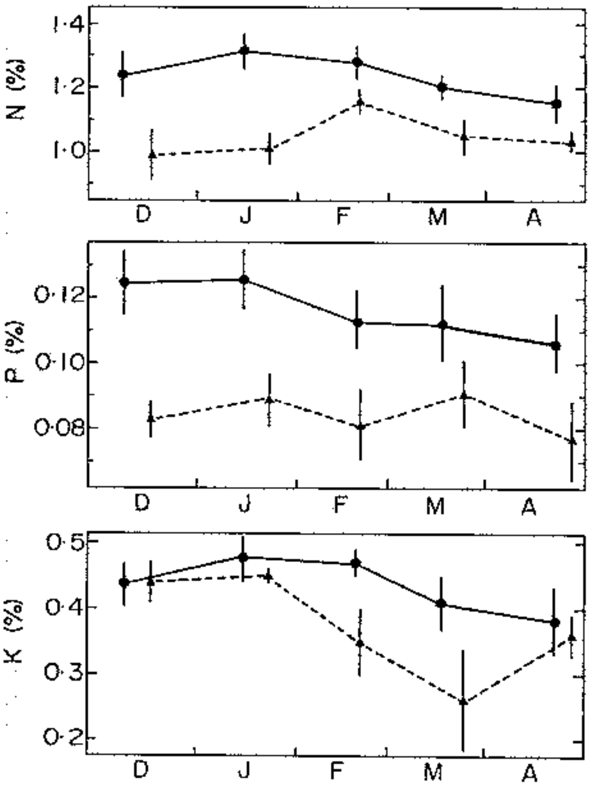
N concentrations in the belowground standing crop of *B. penna-marina* declined during summer at all three sites. This decline continued until April at open fernbrake and fjaeldmark and until May at closed fernbrake. At the two open communities, N levels then increased during winter but at closed fernbrake they remained low throughout winter and only increased in spring. Belowground P concentrations for *B. penna-marina* showed no discernible seasonal pattern at fjaeldmark; at the two fernbrake sites they increased slightly during winter so that values were significantly ($P = 0.05$) higher in spring than in autumn. Seasonal changes in belowground K concentrations were marked and were similar at the three sites. At open fernbrake and fjaeldmark they increased from December/January to maximum levels in August/September. At closed fernbrake this increase started later (April) but maximum values were also attained in August. At all three sites, belowground K concentrations declined sharply during spring and early summer. Contrary to what was found for the leaves, the concentrations of N, P and K in *B. penna-marina* roots and rhizomes were not significantly different between the two December sampling dates.

Belowground Ca concentrations in *B. penna-marina* exhibited a well-defined seasonal pattern. Values declined from December/January until August and then increased in spring and early summer. At open fernbrake the August value was high and inconsistent with this general trend. However, the differences between the value in August and minimum concentrations in July and October were not significant at the 5 per cent level. No discernible seasonal pattern occurred in belowground concentrations of Mg or Na for *B. penna-marina*.

Acaena magellanica

Nutrient concentrations in the living vegetative parts of current-season *Acaena* shoots (leaves, petioles and current-season stems but excluding flowers, seed-heads or scapes) at the fernbrake sites from December 1973 to April 1974 are depicted in Figure 8. Shoot N, P and K concentrations were consistently higher ($P \leq 0.05$) at closed fernbrake, whereas those of Ca, Mg and Na did not differ between the two sites. N, P and K decreased, and Ca increased, throughout the sampling period. Mg and Na concentrations also increased slightly during this period but values in April were not significantly higher than those in December.

Inflorescences and/or seed heads of *Acaena* were present at both study sites throughout the sampling period. Nutrient levels in the reproductive biomass (inflorescences and scapes) are given in Table 3. N and P levels were higher, and Ca, Mg and Na levels lower, than in the vegetative shoot biomass. K concentrations were similar in the two components. The age-related concentration changes in the reproductive material were the same as those for the vegetative biomass, i.e. N, P and K decreased, whereas Ca, Mg and Na increased with age although, as was the case with the shoot concentrations, the increases in Mg and Na were



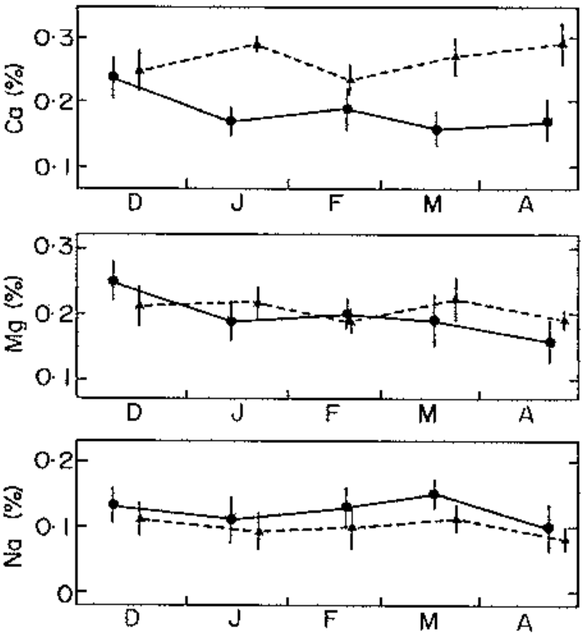


Fig. 10. Chemical composition of the aboveground perennial stems of *Acaena magellanica* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

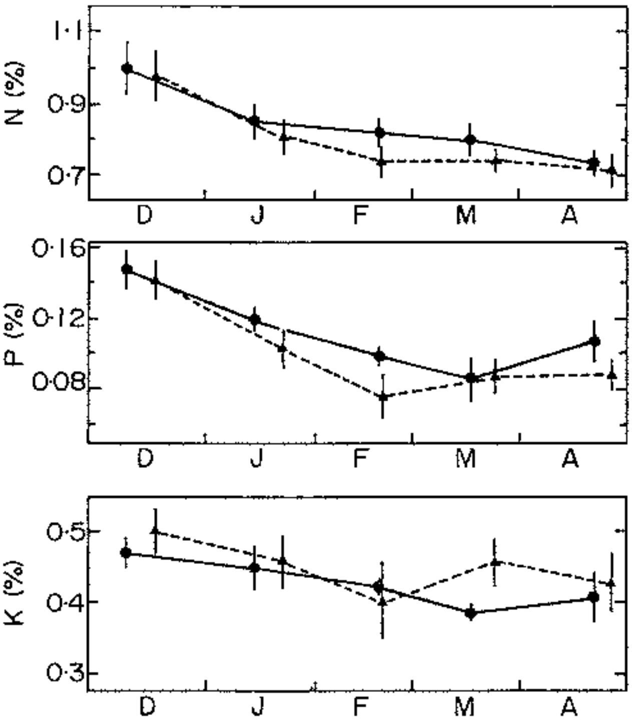
small.

Nutrient concentrations in the aboveground necromass of *Acaena* (dead leaves and petioles, occasionally dead stems) are given in Figure 9. Concentrations of N, P and, especially, of K were lower in the necromass than in living shoots. Mg levels were similar in the two phytomass components. At closed fernbrake, necromass Ca concentrations were consistently higher, and Na concentrations lower, than those in living shoots. For most sampling dates these differences were significant at $P \leq 0.05$. Corresponding differences did not occur at the open fernbrake site. Within sampling dates, a substantial amount of variability was associated with the nutrient concentration estimates for the aboveground necromass of *Acaena*. Intersite differences in necromass N, P and K concentrations were therefore not as marked, or as significant, as those in the shoot biomass. Necromass N and P levels were most often higher, and K levels lower, at closed fernbrake than at open fernbrake but for most sampling dates the differences were not significant at the 5 per cent level. Ca and Mg concentrations were generally greater at closed fernbrake but the differences were only significant in the case of Ca. Necromass Na levels were consistently lower at closed fernbrake.

Because of the large within-sampling-date variability in the *Acaena* necromass nutrient data, the concentration changes during the sampling period (Fig. 9) were not as conspicuous as those which occurred in the live shoots. Necromass N and P concentrations declined after December or January at both fernbrakes, but the changes were only significant at open fernbrake. No consistent changes in K levels occurred at either site. Ca and Na increased from January (closed fernbrake) or February (open fernbrake) to significantly higher values in April. Necromass Mg values were also significantly higher in April than in midsummer for open fernbrake but not for closed fernbrake.

Living aboveground perennial stems formed the largest component in the aboveground biomass of *Acaena* (Smith 1987c). Concentrations of N, P, Ca and Mg in the current-year shoots were commonly double, and those of K and Na 3 to 4-fold, those in stems. Intersite differences in stem nutrient concentrations (Fig. 10) were similar to those for current season shoots. *Acaena* stems at closed fernbrake possessed significantly greater concentrations of N and P than those at open fernbrake. Stem K levels were also higher at closed- than at open fernbrake but, at most sampling dates, the differences were not significant at $P \leq 0.05$. At closed fernbrake stem N, P and K concentrations declined consistently from January to April but the overall changes were not significant at the 5 per cent level. Stem N and P levels at open fernbrake did not vary in a consistent pattern but K concentrations declined significantly between January and March. At both sites there were no consistent changes in the stem concentrations of Ca, Mg or Na during the sampling period. Unlike the shoots, stem Ca concentrations were lower at closed fernbrake than at open fernbrake. Stem Na levels were consistently slightly lower at open fernbrake but the differences were not significant. There were no consistent inter-site differences in stem Mg concentrations.

Nutrient concentrations in the belowground standing crop of *Acaena* (mainly roots, but including buried stems) are given in Figure 11. Belowground N and Ca concentrations were slightly lower than in aboveground stems, whereas concentrations of the other nutrients were similar in the two standing crop components. There were no significant inter-site differences in the belowground nutrient concentrations for *Acaena*, but Ca levels were consistently higher at open fernbrake than at closed fernbrake. This might have been due to a greater proportion of buried stems in the belowground standing crop at the open fernbrake site (Smith 1987c).



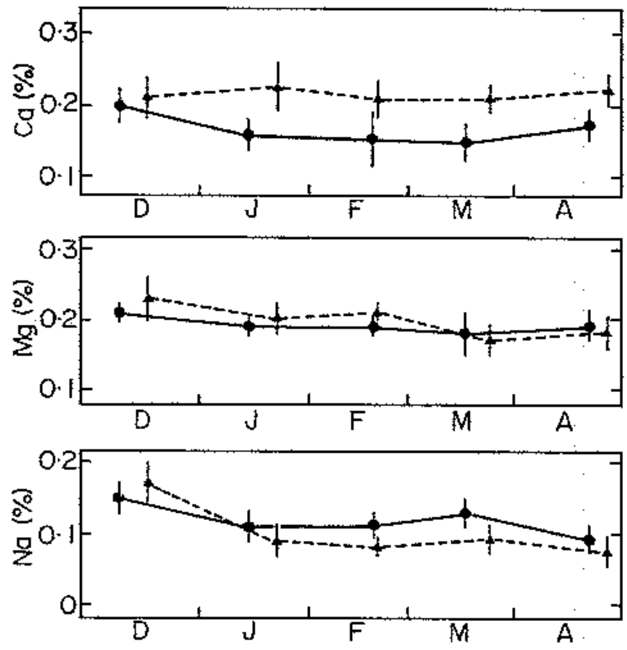


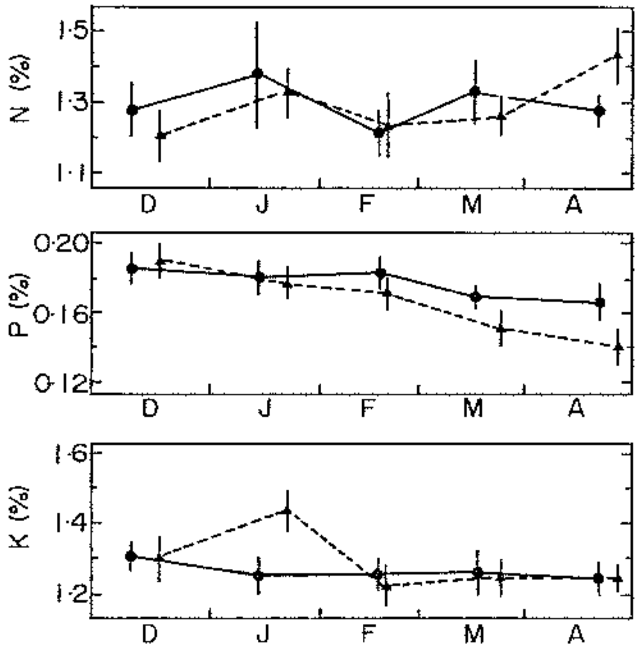
Fig. 11. Chemical composition of the belowground standing crop of *Acaena magellanica* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

Changes in belowground phytomass concentrations of N, P and K for *Acaena* during the sampling period (Fig. 11) were generally more marked than those in the aboveground stems (Fig. 10). Belowground N concentrations declined throughout the sampling period at both sites. P and K also decreased from December but increased again from February (open fernbrake) or March (closed fernbrake). At both sites there were no conspicuous changes in belowground concentrations of Ca, Mg or Na.

Poa cookii

Concentrations of P and Mg in aboveground living shoots of *Poa cookii* at the two fernbrakes decreased during the sampling period (December to April), whereas those of the other nutrients did not change in any coherent pattern (Fig. 12). There were no consistent inter-site differences in shoot concentrations of N, P, K or Ca. Mg and Na levels were consistently (but not always significantly) lower at open- than at closed fernbrake.

P. cookii flowered at both sites in September and October and some capitula remained on the plants until March or April. Nutrient concentrations in the reproductive biomass of this species, approximately in the order of their seasonal variation, are given in Table 3. No significant inter-site



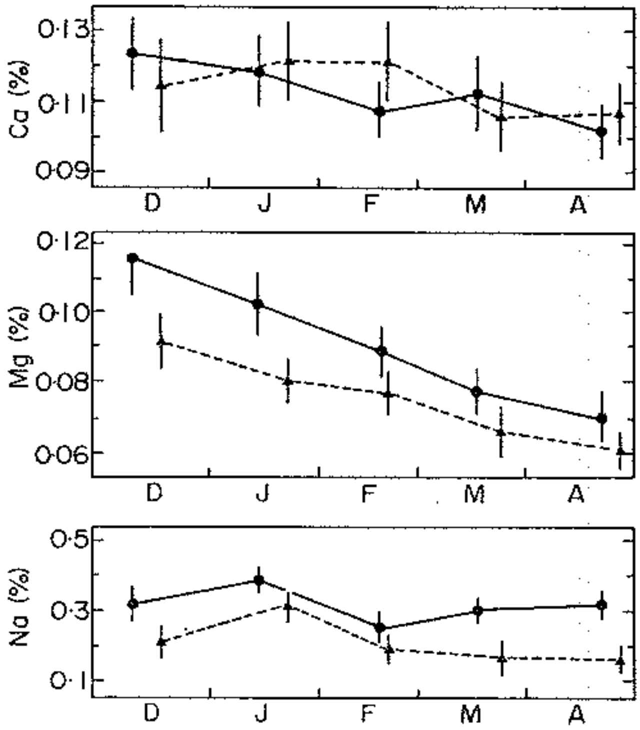


Fig. 12. Chemical composition in the vegetative portions of aboveground living shoots of *Poa cookii* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

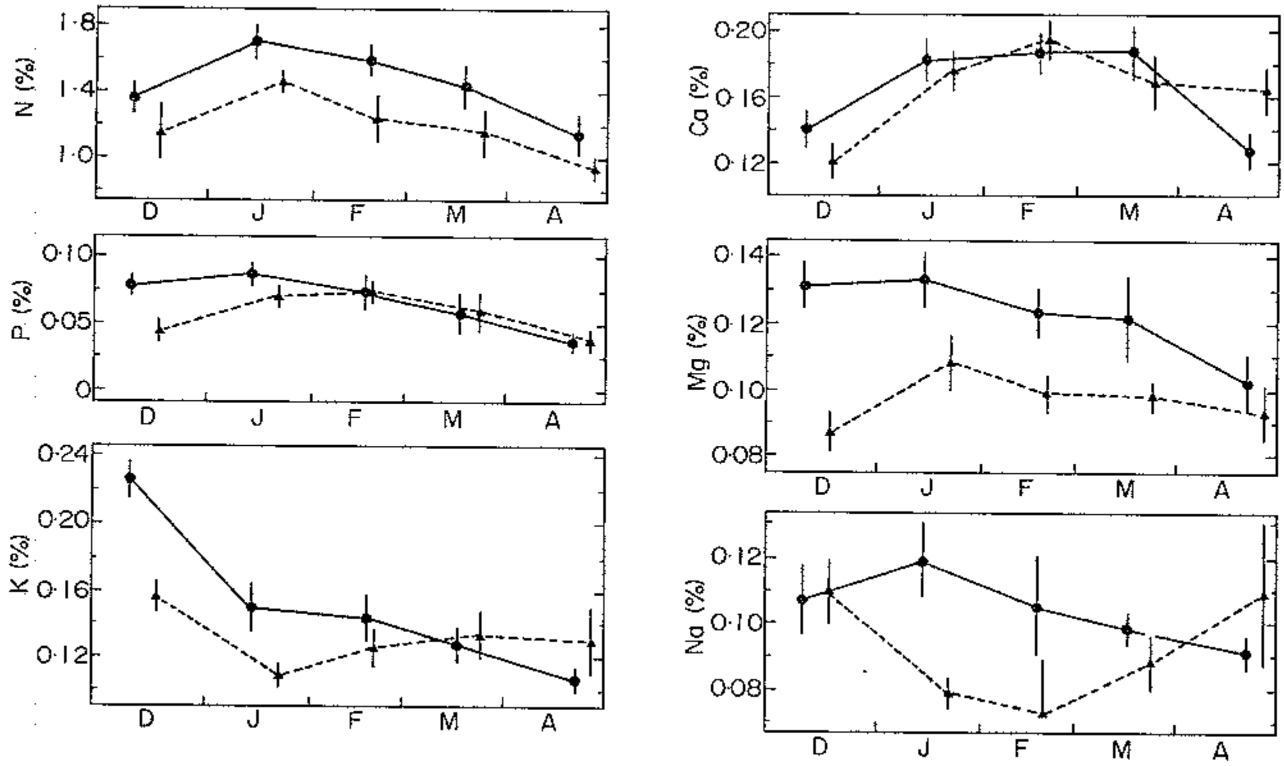


Fig. 13. Chemical composition of the aboveground necromass of *Poa cookii* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

differences occurred in these concentrations. Age-specific decreases in N, P and, especially, K in the reproductive biomass were marked. Ca and Mg levels were very low and did not change significantly during the sampling period. Na concentrations were higher than those of Ca or Mg and, at both sites, decreased markedly from December to February and then increased to April.

Concentrations of N and Mg in the aboveground necromass (dead leaves and stems) of *P. cookii* at closed fernbrake were consistently higher than those at open fernbrake (Fig. 13). P and K levels were also higher at the closed community during December and January but were similar at the two sites later in the season. No significant inter-site differences occurred in necromass Ca concentrations, which were highest during January to March. N, P and K concentrations decreased from high

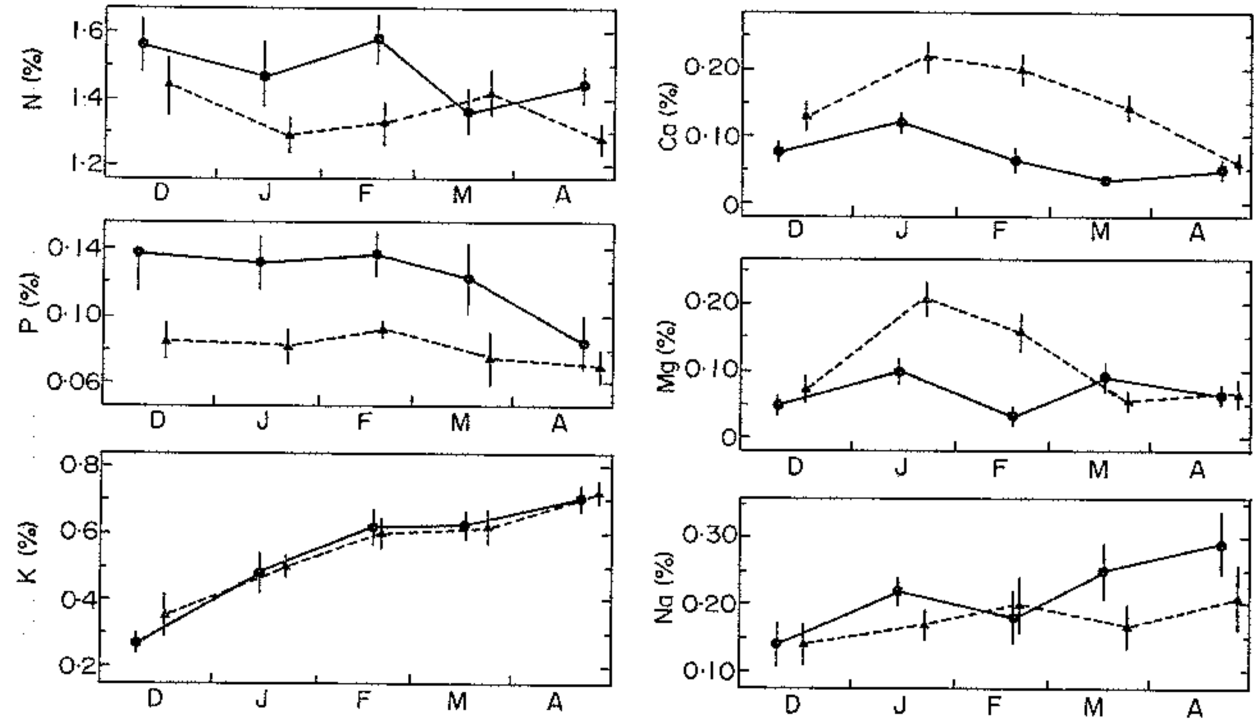


Fig. 14. Chemical composition of the belowground standing crop of *Poa cookii* at closed fernbrake (●) and open fernbrake (▲). Vertical lines indicate the standard errors of the mean values.

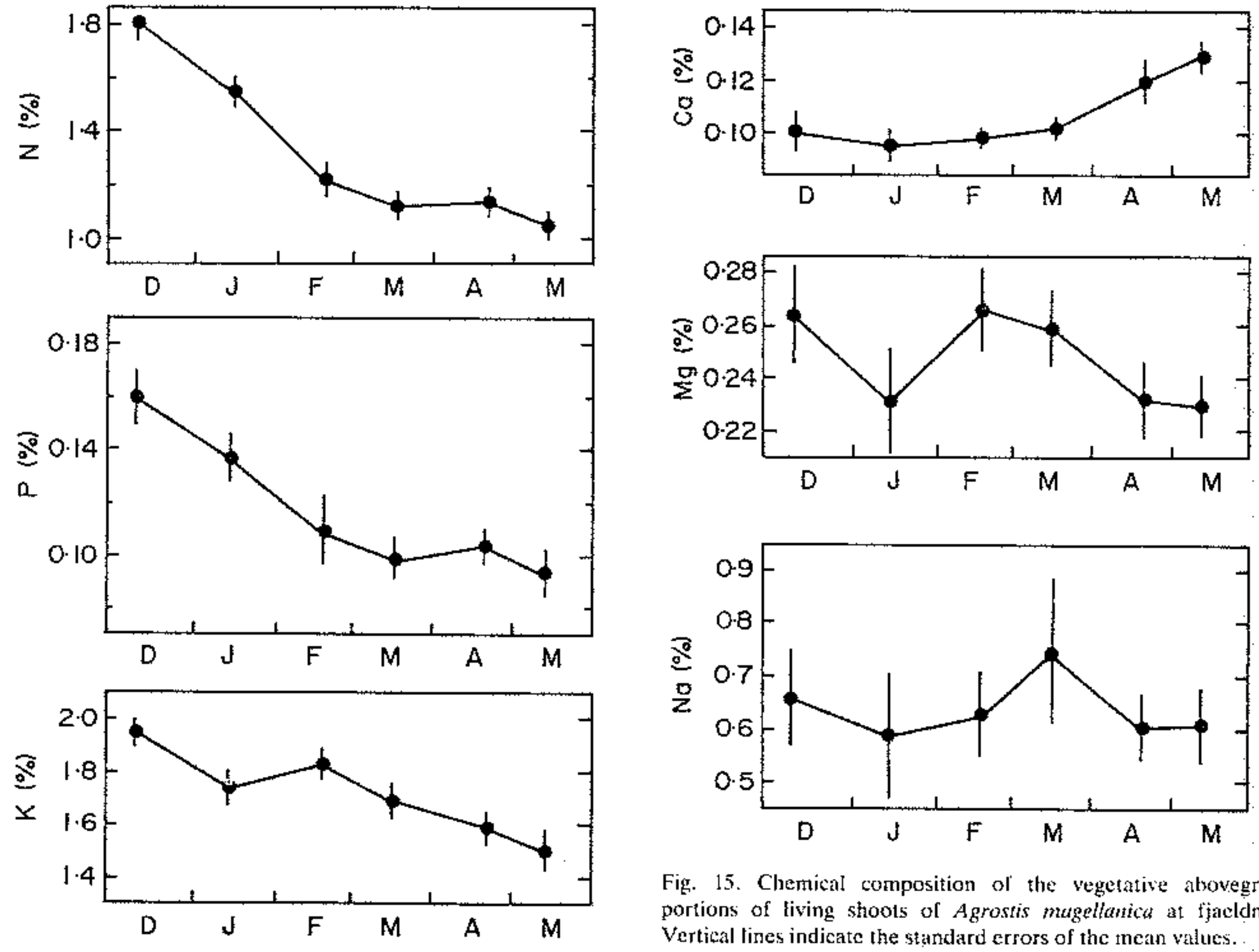


Fig. 15. Chemical composition of the vegetative aboveground portions of living shoots of *Agrostis magellanica* at fjaeldmark. Vertical lines indicate the standard errors of the mean values.

values in December or January. Mg and Na declined at closed fernbrake from January maxima to significantly lower values in April. At open fernbrake, necromass Mg levels did not change significantly during the sampling period, whereas Na levels decreased from December to February and then increased to April. However, because of the large standard errors associated with the necromass Na concentration measurements, these changes were not significant at the 5 per cent level, nor were the inter-site differences in Na significant, except at the February sampling date.

N and P concentrations in the belowground standing crop (roots, rhizomes and stem bases) of *P. cookii* (Fig. 14) were higher at closed- than at open fernbrake, except in the case of N at one sampling date. N concentrations did not change significantly or consistently at either site during the sampling period. At closed fernbrake, P levels declined significantly between February and April. A smaller decrease in P also occurred at open fernbrake during the same period but it was not significant at $P \leq 0.05$. Belowground K concentrations were similar at the two sites and increased markedly during the sampling period. Ca values were greater at open fernbrake and at both sites they decreased from maxima in January to significantly lower levels in March and April. A similar pattern occurred for Mg at open fernbrake but not at closed fernbrake. Belowground Na concentrations in *P. cookii* were similar at the two sites for the first three sampling dates but levels then increased significantly in March and April at closed fernbrake.

Agrostis magellanica

Nutrient concentrations in aboveground live shoots (leaves and stems) of *Agrostis magellanica* at the fjaeldmark site between December 1973 and May 1974 are given in Figure 15. Changes in shoot nutrient levels were very similar to those observed at a mire-grassland for the same period (Smith 1987a), i.e. N, P and K decreased and Ca increased with time. No consistent changes occurred for Mg and Na during the sampling period but, as at the mire-grassland, the amount of within-harvest variability associated with the shoot concentration estimates of these two elements was greater than for the other nutrients.

Flowers and seed-heads (reproductive biomass) represented a greater proportion of the aboveground biomass of *A. magellanica* at fjaeldmark than at the mire-grassland. N, P and K concentrations in the reproductive biomass were also consistently higher at fjaeldmark than at the mire-grassland (Table 3 and Smith 1987a). There were no age-related changes in N levels in the reproductive biomass but concentrations of P and, especially, of K declined during the season. Ca levels remained fairly constant, whereas those of Mg increased during the sampling period. Ca and Mg concentrations were not different between the fjaeldmark and the mire-grassland site. Na levels in the reproductive biomass were higher at fjaeldmark and did not change in any consistent pattern during the sampling period.

Concentrations of N, Mg, Na and, especially, P and K were substantially lower in the necromass (Fig. 16) than in the biomass (Fig. 15) of *A. magellanica*. Necromass P levels were below the detection limit of the analytical procedure, with the exception of some samples in December. Ca concentrations in the necromass were higher than in the

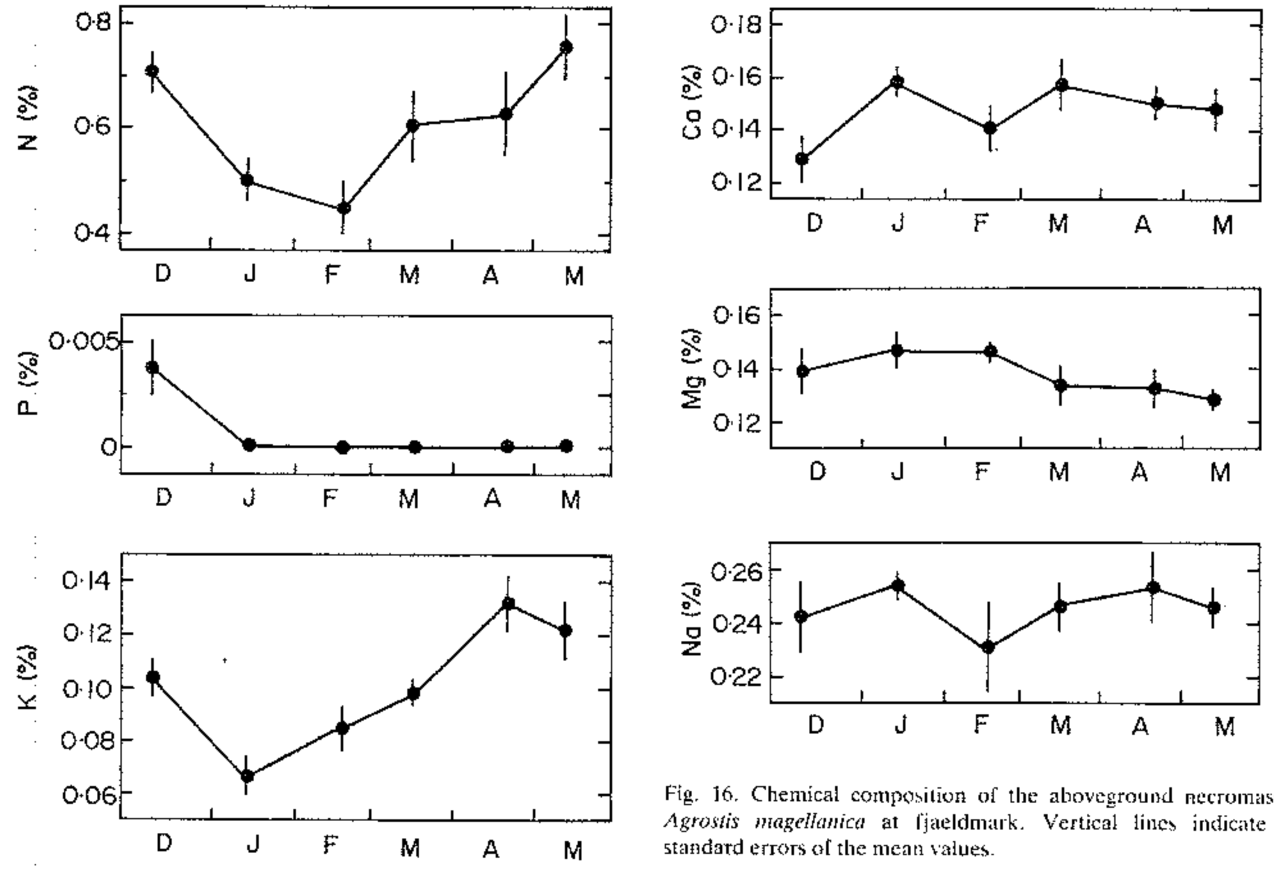


Fig. 16. Chemical composition of the aboveground necromass of *Agrostis magellanica* at fjaeldmark. Vertical lines indicate the standard errors of the mean values.

biomass. These differences between living and dead shoots were the same as those found for this species at the mire-grassland. The seasonal patterns of necromass nutrient concentrations at fjaeldmark (Fig. 16) were also similar to those at the mire-grassland site. N declined between December and February and then increased markedly. A similar pattern occurred for K, except that values started increasing earlier (January). There were no consistent changes in necromass concentrations of Ca, Mg or Na during the sampling period.

N, P and K concentrations in the belowground standing crop (roots and rhizomes) of *Agrostis magellanica* at the fjaeldmark site did not change in any coherent pattern between December and May, whereas concentrations of Ca, Mg and Na declined sharply from maximum levels in December (Fig. 17). Belowground P concentrations for *A. magellanica* at fjaeldmark were much lower (5 to 10 times), and Ca, Mg and Na concentrations much higher (up to 10 times) than at the mire-grassland (Smith 1987a). Maximum N and K values were higher at the study mire but, for most sampling dates, there were no significant intersite differences in concentrations of these two elements.

Discussion

Soil nutrients

Soil nutrient concentrations at the fjaeldmark and fernbrake sites during the 1973/74 summer (Table 1) were very similar to those found there in the summers of 1971/72 and 1972/73 (Smith 1976b, 1977b). In the earlier studies CEC was determined by Ca^{2+} (as $CaCl_2$) saturation, which yields much lower (50 to 75 %) values for the island soils than does the ammonium acetate procedure. The CEC estimates in Table 1 are therefore greater than reported previously for the three sites (Smith 1976b) and consequently the percentage cation saturation values (Table 2) are higher than those given before (Smith 1977b, 1978a, 1978b). The ranges in soil pH values presented in Table 1 are shifted upward by 0.4 to 0.5 units compared to those reported before (e.g. Smith 1976b, 1977b). Earlier determinations were made on 0.01 M $CaCl_2$ suspensions of the soils, which are known to yield lower (by approximately 0.5 units) pH estimates than do soil-water suspensions (e.g. Peech 1965).

Soils at the three sites were fairly organic and maximum organic (dichromate-oxidizable) C contents at the two fernbrakes were similar to those at the mire-grasslands (Smith 1987a). Organic (Kjeldahl) N levels were also fairly high (0.4 to 2.6 %), but inorganic N concentrations were even lower than at the mire-grasslands, which have been shown to be exceptionally poor in NH_4-N and NO_3-N. Loach (1966) considered 0.04 per cent total P to be the minimum level for P sufficiency in organic soils. Nearly all of the samples from the fjaeldmark and fernbrake sites possessed higher levels than this. Total and "available" concentrations of N and P decreased between the sites in the order closed fernbrake > open fernbrake > fjaeldmark.

Exchangeable K concentrations (0 to 1.2 mequiv 100 g^{-1}) at the three study sites were in the lower part of the range of values (0.38 to 2.54 mequiv 100 g^{-1}) reported for soils from Macquarie, Kerguelen and Heard Islands (Piper 1938), South Georgia (0.2 – 3.8 mequiv 100 g^{-1}; Lewis Smith & Walton 1975) and a variety of tundra sites (Brown & Veum 1974). They were similar to those reported for wet heaths and bogs in England and Ireland (Boatman 1961, Loach 1966). For the majority (78 %) of samples collected at the three Marion Island sites during 1971 to 1974, exchangeable K values were < 0.4 mequiv 100 g^{-1} which, even for peaty

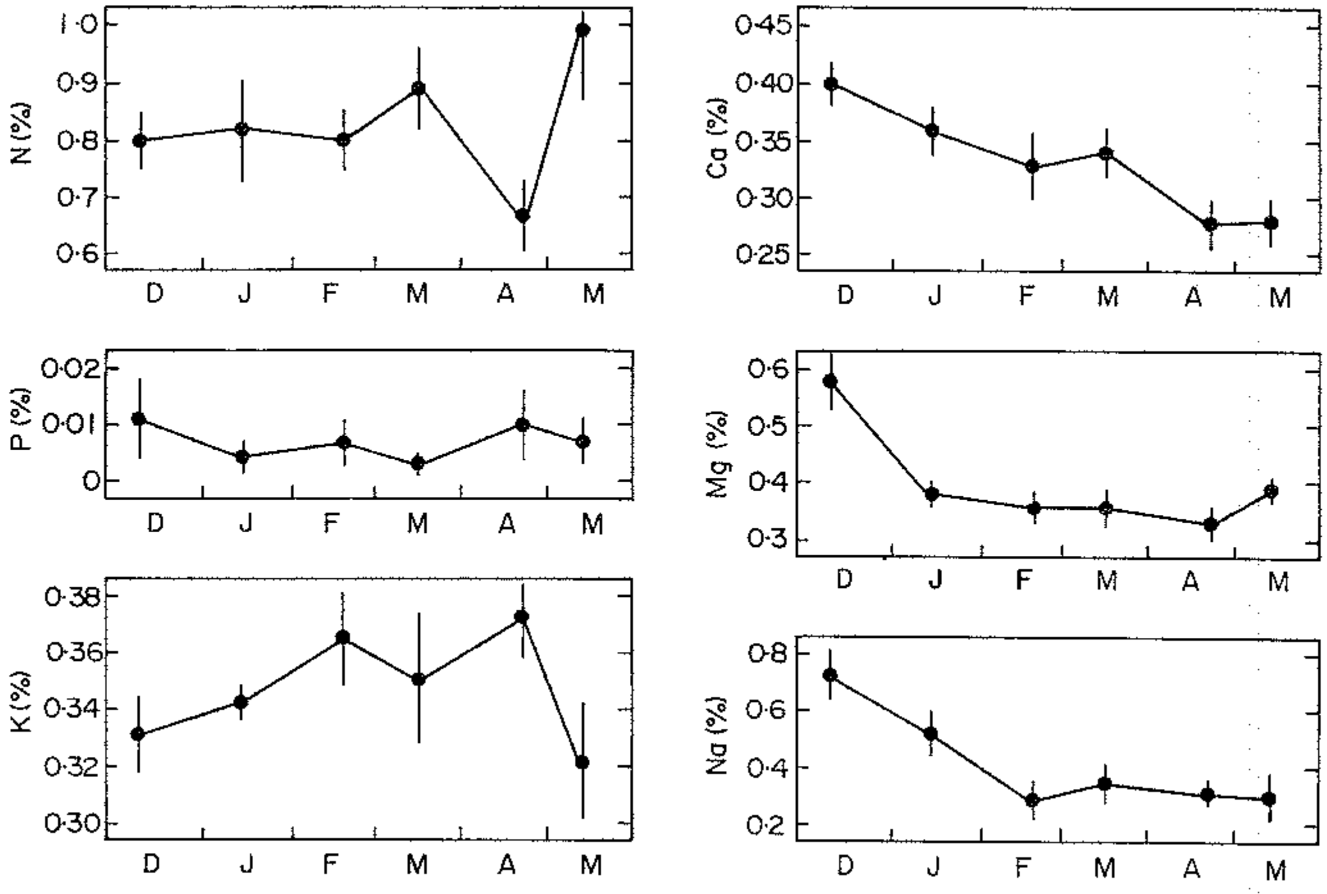


Fig. 17. Chemical composition of the belowground standing crop of *Agrostis magellanica* at fjaeldmark. Vertical lines indicate the standard errors of the mean values.

soils, is low. Considering that K is the cation taken up in the largest quantities by the plants, the island soils were suspected of being deficient in this element (Smith 1976c). However, Smith (1978c) showed that application of NPK fertilizer at an open fernbrake site did not cause an increase in leaf K concentrations for *Poa cookii, Blechnum penna-marina* or *Acaena magellanica.* Exchangeable K levels were mostly highest at closed fernbrake and lowest at fjaeldmark (Table 1). They were mostly slightly lower at the open fernbrake and fjaeldmark sites than at the mire-grasslands (Smith 1987a).

Concentrations of exchangeable Ca (1.7 to 13.0 mequiv 100 g^{-1}) and Mg (2.1 to 14.1 mequiv 100 g^{-1}) at fjaeldmark and the two fernbrakes resembled those at the mire-grasslands and were also similar to values reported for other sub-Antarctic islands (1.0 to 15.2 mequiv Ca 100 g^{-1}, 2.2 to 10.7 mequiv Mg 100 g^{-1}; Piper 1938). They were within the range of values found for organic soils at northern hemisphere subpolar areas (Brown & Veum 1974). However, for the sub-Antarctic soils generally, there is a greater importance of Mg, relative to Ca, than at northern hemisphere tundra sites, especially the more continental ones.

Exchangeable Ca concentrations, expressed on the basis of their percentage saturation of the CEC (Table 2), increased in the order, closed fernbrake < open fernbrake < fjaeldmark. Expressed on the same basis, there were no significant, or consistent, differences in exchangeable Mg, Na or K levels between the three sites. Absolute values of exchangeable Mg were mostly lower at fjaeldmark than at the two fernbrakes and those of K were generally highest at closed fernbrake and lowest at fjaeldmark (Table 1).

No consistent or coherent trends in soil nutrient concentrations occurred at the three sites during the sampling period, which did not include midwinter or spring. However, it is considered unlikely that significant changes in nutrient levels occurred during winter or spring since none were shown at the nearby mire-grassland communities (Smith 1987a) and soil freezing has not been observed at the closed- or open fernbrake site. At the fjaeldmark site the top 2 or 3 cm freeze for short periods in winter, as at the mire-grasslands.

Plant nutrients

Intersite comparisons and comparison with previously reported nutrient concentration values for the island plants

Nutrient concentrations presented here for the leaves and shoots (as well as the aboveground necromass and belowground organs) of species occurring at the fjaeldmark and fernbrake sites were very similar to those reported previously for the same species at a wider range of plant communities at the island (Smith 1977b). Main exceptions are the higher mean N and P (and lower Mg) levels previously reported for *B. penna-marina* and higher Na, but lower Ca, levels for *Azorella selago.* Earlier mean values for *B. penna-marina* were influenced by the inclusion of samples from sites manured by animals (e.g. tussock grasslands). The differences for *A. selago* cannot readily be explained but may reflect the fact that more samples from non-rocky sites (e.g. closed fernbrake, tussock grassland, drainage lines, slope crests and mires) were represented in the earlier mean estimates and these samples had lower Ca and higher Na concentrations than did samples from fjaeldmarks and open fernbrakes. The lower Ca concentrations reported earlier than presented here for *A. selago* might also have resulted from the inclusion of samples from grey lava areas, where soil exchangeable Ca levels were approximately half those at the black lava sites considered in this investigation (Smith 1977b).

Differences in plant nutrient concentrations between the fjaeldmark, closed- and open fernbrake sites were fairly consistent for the various species, as well as for the different phytomass components within species. N, P and K concentrations mostly decreased in the order closed fernbrake > open fernbrake > fjaeldmark. Notable exceptions were the shoot biomass of *P. cookii*, for which concentrations of all three elements were similar at closed- and open fernbrake, and similar K concentrations at all three sites for the leaves, stems and roots of *A. selago*. Ca and Mg concentrations were generally higher in plant tissue from fjaeldmark and open fernbrake than from closed fernbrake, excepting for the shoot biomass and necromass of *Acaena magellanica* and shoots of *P. cookii*. Although total soil levels of N and P indicate neither the amount nor rate of release of available forms of these elements, and even the instantaneous values of the inorganic forms are unlikely to be correlated with the total amounts available to the plants during the growing season, to some extent the inter-site differences in N, P, K and Ca concentrations in the phytomass resemble the corresponding differences, discussed previously, in the soil levels of these nutrients.

P, K, Mg and Na concentrations in aboveground living shoots of *Agrostis magellanica* at the fjaeldmark site (Fig. 15) were 50 to 100 per cent greater than the same species in a mire-grassland (Smith 1987a). For most sampling dates, shoot N and Ca levels were also slightly higher at fjaeldmark. N, K, Mg and Na levels in *Agrostis* shoots at fjaeldmark were higher, and P levels lower, than in shoots of *P. cookii*, the other grass species considered in this study. Mg concentrations were similar in the two grass species.

Comparison between life-forms

N, P, Ca and Mg concentrations in *A. selago* and *B. penna-marina* leaves, and in the green portions of aboveground *Acaena magellanica* shoots, were considerably higher than those in aboveground shoots of *Agrostis magellanica* and *P. cookii*, or of *Uncinia compacta* and *Juncus scheuchzerioides* at a mire-grassland. *B. penna-marina* and *A. selago* also exhibited much higher leaf concentrations than did the four graminaceous species. These observations accord with those from South Georgia (Walton & Lewis Smith 1980) and most nothern hemisphere tundras (Rodin & Bazilevich 1967, Chapin *et al.* 1975, Wielgolaski *et al*, 1975, Dowding *et al.* 1981) that the green portions of forbs and decidous shrubs generally have considerably higher N, K, Ca and Mg levels than do those of monocotyledonous (especially graminoid) species.

Differences in P concentrations between the two plant-types are less consistent. At South Georgia, as at Marion Island, *Acaena magellanica* and other dicotyledonous species (e.g. *Callitriche antarctica*, *Galium antarcticum* and *Ranunculus biternatus*) possess higher leaf P concentrations than do most of the graminoid species (Walton & Lewis Smith 1980). At wet heaths in England Loach (1968) found higher P concentrations in *Erica tetralix* and *Calluna vulgaris* shoots than in *Molinia caerulea* shoots, but data presented by Kilfeather (1973) for the Glenamoy (Ireland) blanket bog showed no corresponding differences between the photosynthetic parts of shrubs (mainly *C. vulgaris* and *Erica* spp.) and those of *M. caerulea* or *Schoenus nigricans*. Similarly, no significant or consistent differences in P concentrations were found between dicotyledon and monocotyledon leaves at the Fennoscandian tundras (Wielgolaski *et al.* 1975), alpine tundras of the Khibini Mountains, Kola Peninsula (Chepurko 1972) or a variety of other tundra sites (e.g. data in Rodin & Bazilevich 1967). In contrast, at the Arctic tundra at Barrow (Alaska), Chapin *et al.* (1975) observed substantially higher P levels in dicotyledonous than in monocotyledonous shoots and ascribed this to a greater incidence of mycorrhizal infections in the dicotyledonous plants. At Marion Island, vesicular-arbuscular mycorrhizae have been found for all of the plant species considered in this study (Smith & Newton, 1986). The frequency of infection (i.e. the proportion of plants infected) ranged from 50 per cent for *U. compacta* and *J. scheuchzerioides* to 100 per cent for *Acaena magellanica*. However, there were no consistent differences between monocotyledonous and dicotyledonous species in the proportion of roots infected per plant.

Comparison between plant parts

Concentrations of almost all nutrients (but especially K) were higher in the green parts than in the stems or roots of the non-graminaceous species considered in this study. The only exception was for the stems and roots of *A. selago*, which consistently possessed slightly higher Mg concentrations than did the leaves. For this species, and *Acaena magellanica*, nutrient concentrations in the stems resembled those in the roots, except that N and Ca levels in *Acaena* stems were generally slightly higher than those in the roots. For *Agrostis magellanica*, aboveground N, P and K levels were higher aboveground than belowground. Shoots P and K concentrations in *P. cookii* were also higher, but N concentrations lower, than those in the roots. Ca *(Poa)* or both Ca and Mg *(Agrostis)* concentrations were often higher belowground than aboveground. A similar situation occurred for the other two graminoid species at a mire-grassland (Smith 1987a), where either Ca (for *Uncinia compacta*) or Mg (for *Juncus scheuchzerioides*) was generally higher in roots than in shoots. In both cases the level of the other element was similar in the two components. However, much weight cannot be given to these above – belowground comparisons since they consider living aboveground tissue, but a mixture of living and dead belowground material.

Aboveground concentrations of N, P, K and Na were higher in the biomass than in the necromass of the island species, except for *P. cookii*, in which necromass N levels were similar to, and often slightly higher than, those in the biomass. This is difficult to explain since leaf N declines with age in this species (Bate & Smith 1983) and earlier studies (e.g. Smith 1977b) showed that there were significantly greater N concentrations in living than in dead leaves of *P. cookii*. In the study reported on here the comparison was between living shoots (leaves and stems) and necromass (almost entirely leaves). The inclusion of stem material in the estimate of N concentrations in the biomass component possibly caused the similarity observed between the concentration values for this element in the biomass and necromass of this species.

Differences in mineral content between living and dead material for the island plants were greatest for K; on a weight basis 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 plants from tundra (Wielgolaski *et al.* 1975, Chapin *et al.* 1975, Dowding *et al.* 1981) and sub-Antarctic (Walton & Lewis Smith 1980) regions.

Ca concentrations were always higher in the aboveground necromass than in living shoots of the island plants. Mg levels were similar in the two phytomass components, except that for *P. cookii* they were higher, and for *Agrostis magellanica* they were lower, in the necromass than in the biomass.

Comparison with plants from tundra and tundra-like sites

N, P, K and Ca concentrations in leaves of *A. selago* and *B. penna-marina* and current year shoots of *Acaena magellanica* at the three Marion Island sites were in the lower part of the ranges reported for dicotyledonous species at South Georgia (Table 4). Maximum concentrations of all nutrients found for *Acaena magellanica* at South Georgia were higher than those exhibited by the same species at Marion Island. For N, P and K, the differences between the two islands might be due to an earlier commencement of sampling at South Georgia (November) than at Marion Island (December). Taken into consideration with the possibility that vegetative activity starts later in the season at the colder South Georgia Island this means that the ranges of plant nutrient concentrations reported for that island included values for much younger tissue than was sampled in this study.

There were substantial inter-site differences in plant Ca concentrations at South Georgia (Pratt & Lewis Smith 1982, Lawson 1985), mainly related to corresponding differences in soil Ca levels, which ranged from the low values found at Marion Island to high values (up to 52 mequiv 100 g^{-1}) for eutrophic seepage slopes (Brown & Veum 1974). The higher Ca levels reported for the South Georgia plant species, compared to those in the Marion Island plants, probably reflect the higher Ca status of some of the South Georgia soils.

Maximum N, P and K concentrations in fronds of the fern *B. penna-marina* were considerably higher than those in fronds of *Polystichum mohrioides* at South Georgia. In both instances the concentration maxima were determined on young fronds. Mg and Na concentrations were also higher for *B. penna-marina* than for *P. mohrioides* fronds.

Shoot N concentrations for *P. cookii* and *Agrostis magellanica* at Marion Island were lower than for *Deschampsia antarctica*, *Juncus scheuchzerioides* and *Phleum alpinum* at South Georgia but were similar to concentrations in the other graminoid species at that island. P concentrations in the two Marion Island grasses were in the lower part of the range exhibited by grasses at South Georgia. Shoot K and Ca levels resembled those of the South Georgia graminoids, except for the high concentrations in *J. scheuchzerioides* at a eutrophic seepage slope. *P. cookii* exhibited similar, but *Agrostis magellanica* higher, Na levels to those in the South Georgia species, again with the exception of high Na concentration in *J. scheuchzerioides* at the eutrophic site.

Concentrations of N and P found for the green portions of the Marion Island dicotyledonous species (and *B. penna-marina*) were similar to those reported for *Betula* and *Salix* species and ericaceous dwarf shrubs at Scandinavian sub-Arctic tundras, dwarf shrub tundras of the Khibini Mountains (Kola Peninsula) and western Siberia and at the Barrow Arctic tundra (Table 4). They were also within the range of N and P values reported for a wide variety of other tundra and forest tundra sites (Rodin & Bazilevich 1967). Leaf (or shoot) K concentrations for the island dicotyledonous species were, in many instances, higher than for shrubs and forbs at these northern hemisphere tundras. In contrast, Ca levels were mostly lower in the island plants. Mg concentrations were higher than those generally found in northern tundra plants but were similar to concentrations reported for dicotyledonous species at Barrow and for *Vaccinium myrtillus* at the Khibini Mountains. Na levels in the Marion Island species were higher than those generally found for northern hemisphere tundra plants.

Shoot nutrient levels in *Acaena magellanica*, *A. selago* and *B. penna-marina* were higher than those reported for *Calluna vulgaris* and *Erica tetralix* at ericaceous bogs and wet heaths in England. Shoot P and Ca concentrations in the island species were higher than, but N, K and Mg concentrations were similar to, those in dwarf-shrubs (mainly *C. vulgaris* and *Erica* spp.) at the Glenamoy blanket bog.

N and P concentrations in the aboveground parts of living shoots of *Agrostis magellanica* at the fjaeldmark site and of *P. cookii* at the two fernbrakes were in the lower part of the range reported for graminoid species from northern hemisphere subpolar regions. Shoot N levels in the two island grasses were similar to, but P greater than, those for *Molinia caerulea*, *Schoenus nigricans* and *Eriophorum vaginatum* from British bogs and heaths. K levels in *P. cookii* and *Agrostis magellanica* were higher than those in monocotyledonous species at northern hemisphere tundra and tundra-like areas, except for the eutrophic Fennoscandian tundra mires. Shoot Ca levels in both grasses were substantially lower than for most monocotyledonous species at Fennoscandian tundras, for graminoids at the alpine tundra at the Khibini Mountains or for grasses at the montane grassland at Snowdonia. They were similar to values reported for grasses and sedges at Barrow, Devon Island and heaths and bogs in England but were greater than the Ca concentrations in *S. nigricans* or *M. caerulea* at Glenamoy. Shoot Mg concentrations for the two island grasses were within the range of those exhibited by graminoids from these various tundra and tundra-like sites.

Ca:K ratios in the shoots of *P. cookii* (0.08-0.10) and *Agrostis magellanica* (0.05-0.08) were much lower than for shoots of *Acaena magellanica* (0.27-0.89) or leaves of *A. selago* (0.25-0.71) or *B. penna-marina* (0.20-0.96); a similar difference has generally been observed between monocotyledonous and dicotyledonous species at many tundra, temperate and tropical areas (Rodin & Bazilevich 1967, Allen *et al.* 1974, Wielgolaski *et al.* 1975). However Ca:K ratios for the island species were mostly lower than for plants of similar life-forms at these areas. They were similar to those in plants of British bogs and heaths and the high Arctic tundras at Devon Island and Barrow but were in the lower part of the range exhibited at the Fennoscandian and Agapa sub-Arctic sites and at most of the sites represented in the data presented by Rodin & Bazilevich (1967).

Because of the greater importance of K relative to N in the Marion Island species, low N:K concentration ratios

Table 4

Nutrient concentrations (percentage of dry weight) in photosynthetic parts of 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
Marion Island (sub-Antarctic)								
Azorella selago, leaves	1.3-3.3 (1.8)	0.12-0.45 (0.22)	1.3-2.5 (1.7)	0.5-1.2 (0.7)	0.2-0.4 (0.3)	0.1-0.5 (0.3)	Fjaeldmark and fernbrakes, range during sampling period	
Blechnum penna-marina, fronds	1.1-3.4 (1.5)	0.10-0.46 (0.19)	0.8-3.4 (1.5)	0.3-0.7 (0.6)	0.6-1.1 (0.9)	0.2-0.8 (0.5)		
Acaena magellanica, current-season shoots	1.7-2.7 (2.2)	0.12-0.23 (0.19)	0.7-1.6 (1.2)	0.4-0.7 (0.5)	0.3-0.4 (0.4)	0.3-0.4 (0.3)	Fernbrakes, range during sampling period	This account
Poa cookii, shoots	1.2-1.4 (1.3)	0.14-0.19 (0.17)	1.2-1.4 (1.3)	0.10-0.13 (0.11)	0.06-0.12 (0.08)	0.1-0.4 (0.24)		
Agrostis magellanica, shoots	1.0-1.8 (1.3)	0.10-0.18 (0.12)	1.5-2.0 (1.7)	0.10-0.14 (0.11)	0.23-0.27 (0.25)	0.6-0.7 (0.64)	Fjaeldmark, range during sampling period	
South Georgia (sub-Antarctic)								
Acaena magellanica, leaves[a]	1.5-4.0	0.3-0.6	1.3-3.1	1.1-3.1	0.4-0.6	0.1-0.8		[a]Walton and Lewis Smith (1980), Figures 1, 7 & 8
Acaena magellanica, shoots[c]	1.8-3.6	0.2-0.6	0.6-2.6	0.3-2.2	0.4-0.8	—	Bogs and dry grasslands	
Galium antarcticum, shoots[c]	2.2-4.0	0.3-0.5	3.0-5.0	0.8-0.9	0.2-0.35	0.05-0.10	Community on mineral soils	[b]Pratt and Lewis Smith (1982), Figures 4 to 8.
Ranunculus biternatus, shoots[a]	1.9-3.5	0.3-0.7	2.8-4.0	0.7-0.8	0.1-0.2	0.4-1.0	"Flushed habitat"	
Polystichum mohrioides, fronds[a]	1.5-2.2	0.2-0.3	1.5-2.5	0.3-0.6	0.3-0.4	0.1-0.3		Ranges for season
Festuca contracta, shoots[b]	1.0-2.0	0.11-0.32	1.0-2.0	0.05-0.12	0.08-0.15	—	Open and dense grasslands	[c]Lawson (1985), seasonal means, estimated by weighting the means in Table 2
Deschampsia antarctica, shoots[b]	2.1-3.6	0.23-0.37	0.4-1.2	0.09-0.16	0.11-0.26	—	Mesic meadow	
Phleum alpinum, leaves[a]	1.2-2.8	0.28-0.51	1.2-2.6	0.03-0.05	0.09-0.14	0.01-0.04	Fjaeldmark	
Poa flabellata, shoots[b]	1.1-1.7	0.10-0.27	0.6-0.9	0.09-0.14	0.07-0.10	—	Tussock grassland	
Juncus scheuchzerioides, leaves[a]	1.7-2.9	0.21-0.58	2.7-4.3	0.30-0.65	0.17-0.34	0.28-0.35	Eutrophic mire	
Rostkovia magellanica, shoots[c]	1.2	0.16	0.86	0.23	0.08	0.17	Eutrophic slope	
Barrow (High Arctic)								
Petasites frigidus, shoots	2.3(3.2)	0.22(0.41)	2.3(2.7)	0.6	0.4	—	Wet tundra meadow, values at time of peak aboveground standing crop. Values in parenthesis are maximum levels reached during the season	Chapin *et al.* (1975), Table 2
Salix phlebophylla, shoots	2.6	0.24	0.8	0.4	0.4	—		
S. rotundifolia,	1.6	0.22	1.1	0.7	0.7	—		
Saxifraga cernua	1.0	0.18	0.7	1.0	0.5	—		
S. punctata	1.6	0.22	1.2	0.7	0.6	—		
Stellaria laeta	2.0	0.23	1.8	0.3	0.4	—		
Average for monocot shoots	1.9-0.07	0.13±0.01	0.9±0.04	0.16±0.01	0.20±0.02	—		
Devon Island (High Arctic)								
Carex stans	3.1	0.33	1.9	0.23	—	—	Hummocky sedge-moss meadow; seasonal mean	Muc (1977), Table 8

Table 4 (continued)

Site and species	N	P	K	Ca	Mg	Na	Community and nature of reported values	Reference
Khibini Mountains (sub-Arctic)								
Dwarf shrubs (mainly *Betula, Empetrum, Vaccinium*), green parts	1.2-1.6	0.09-0.14	—	0.2-0.7	0.1-0.2	0.01-0.04	Alpine dwarf shrub tundra, mean for season	Chepurko (1972), Table 1
Vaccinium myrtillus	2.10	0.26	—	1.03	0.35	0.23		
Average for grasses	2.3	0.23	—	0.9	1.8	—		
Agapa (Siberian sub-Arctic)								
Betula and *Salix* spp. leaves	1.3-2.0	0.12-0.20	0.6-1.0	0.5-1.1	0.4-0.6	0.02-0.04	Shrub tundra, range of seasonal mean values for each species	Vassiljevskaya *et al.* (1975), Table 5
Fennoscandian Tundras								
Betula spp., green parts	0.8-2.2	0.10-0.30	0.3-0.9	0.4-0.7	0.2-0.3	0.02	Willow thickets, mires and wet and dry meadows, seasonal range	Wielgolaski *et al.* (1975), Table 1
Salix spp., green parts	1.6-2.8	0.15-0.30	0.6-1.0	1.1-1.4	0.2	0.03		
Deciduous ericaceous dwarf shrubs (mainly *Vaccinium* and *Empetrum* spp.) green parts	1.0-1.9	0.15-2.05	0.4-0.9	0.4-0.6	0.15	0.02		
Non-N fixing forbs	1.8-2.4	0.17-0.26	1.4-2.2	1.0-1.16	0.30	0.04		
Eutrophic monocotyledons, green parts	1.4-2.5	0.15-0.25	1.0-2.1	0.4	0.13	0.03		
Other monocotyledons	1.7-2.3	0.13-0.20	0.9-1.6	0.3	0.12	0.03		
United Kingdom Bogs, heaths and montane grasslands								
Calluna vulgaris, green parts[d]	1.35	0.13	0.6	0.3	0.2	0.06	[d]Moorhouse blanket bog, mean for 10 sites	[d]Heal & Smith (1978), Table 3
Calluna vulgaris, shoots[e]	1.3-1.4	0.06-0.09	0.5-0.7	0.4	0.1-0.2	—	[e]English wet heaths, range of September means for 3 sites	
Ericacious species (mainly C. vulgaris and *Erica* spp.), photosynthetic parts[f]	0.8-2.4 (1.7)	0.04-0.08 (0.05)	0.3-0.7 (0.21)	0.2-0.8 (0.20)	0.2-0.4 (0.22)	—	[f]Glenamog bog, Ireland, range for season and (mean for season)	[e]Loach (1968), Table 4
Erica tetralix, shoots[e]	1.0-1.3	0.05-0.08	0.7-0.9	0.3-0.4	0.1	—		[f]Kilfeather (1973), Figures 11, 12 & 13
Eriophorum vaginatum, green leaves[d]	1.8	0.17	0.64	0.15	0.16	0.01		
Molinia caerulea, shoots[e]	1-1.2	0.03-0.06	0.6-1.1	0.08-0.12	0.03-0.04	—		
Molinia caerulea, leaves[g]	0.5-1.7	0.02-0.08	0-1.0	0.05-0.20	0.01-0.02	—		
Molinia caerulea, photosynthetic parts[f]	1.5-3.2	0.04-0.12	0.7	0.01-0.02	0.05-0.16	—	[g]Molinietum, Southern England, Range during winter	[g]Morton (1977), Figures 1 & 2
Molinia caerulea, photosynthetic parts[h]	(2.6)	(0.08)	(0.6)	(0.02)	(0.09)	—		
Schoenus nigricans, photosynthetie parts[f]	0.8-2.4	0.04-0.08	0.4-0.7	0.02-0.08	0.2-0.4	—		[h]Moore *et al.* (1975)
Schoenus nigricans, photosynthetic parts[h]	(1.6)	(0.06)	(0.5)	(0.05)	(0.2)	—		
Agrostis tenuis, shoots[i]	2.2	0.18	1.13	0.17	0.34	—		
Festuca ovina, shoots[i]	1.3	0.19	1.29	0.14	0.28	—	[i]Mesotrophic montane grassland, Snowdonia, Wales. Means for season	[i]Perkins *et al.* (1978), Table 6
Anthoxanthum odoratum, shoots[i]	2.7	0.26	1.47	0.19	0.45	—		
Other grasses, shoots[i]	2.0	0.21	1.45	0.21	0.43	—		

were found in their leaves and shoots. N:K ratios were mostly < 1 for the two grasses and 1 to 2 for the dicotyledonous species and *B. penna-marina*. The latter values are lower than the N:K ratios observed for most shrub and dwarf-shrub species at tundra and tundra-like ecosystems but are within the range of those found for Arctic and sub-Arctic forb species (e.g. Chapin *et al.* 1975, Vassiljevskaya *et al.* 1975, Wielgolaski *et al.* 1975). Aboveground N:K concentration ratios in the two grass species at the fjaeldmark and fernbrake sites were mostly lower than for grasses from northern tundras.

Seasonal changes

Three of the five species occurring at the fjaeldmark and fernbrake sites were sampled only from December to April (or May) so the full seasonal variation in their nutrient concentrations was not observed. Overall, however, age-related changes in the aerial plant biomasses at the fjaeldmark and fernbrake sites were the same as those observed at the mire-grasslands (Smith 1987a), South Georgia (Walton & Lewis Smith 1980, Pratt & Lewis Smith 1982) and temperate and subpolar sites of the northern hemisphere (Wielgolaski *et al.* 1975, Chapin *et al.* 1975, Dowding *et al.* 1981), i.e. N, P and K decreased and Ca (in some cases also Mg) increased as the season progressed.

There were a few exceptions to this pattern. A conspicuous one was the marked increase in N, P and K concentrations in leaves, stems and roots of *A. selago* during late summer and winter (Fig. 1, 3 and 4), when growth in this species had ceased (Smith 1986). This suggests that late summer and winter, when demand for nutrients by growth is declining or absent, is a period of active uptake and accumulation of nutrients in *A. selago*. This accords with the hypothesis put forward by Dowding *et al.* (1981) that the end of the growing season, when the aboveground plant parts are senescing, forms an important period of nutrient acquisition for tundra plants.

K concentrations in the belowground standing crop of *B. penna-marina* increased during late summer and winter at all three sites (Fig. 7). *P. cookii* roots and stem bases showed a similar trend of increasing K concentrations during late summer and early winter (Fig. 14). Accompanying increases in N or P, where they occurred, were insignificant. This may indicate either that K is more readily available than N and P in the soils during winter or that during the earlier part of the season, when there is a greater rate of growth (and a higher leaf biomass), the demand for K is greater than that of N and P. The demand for K may also be high because of a need to replace that lost by leaching in the high-rainfall environment. *In situ* leaching studies have not been performed for any of the island species but soaking green *B. penna-marina* fronds in distilled water causes an immediate increase in Na concentrations in the water, followed by slow increases in K concentrations. Very small amounts of NH_4^+-N were detected in the water after 12 hours but inorganic P was not found even after 24 hours of soaking. Organic N and P were not tested for. If it is assumed that during spring and summer the demand for K by *B. penna-marina* (and *P. cookii*) greatly exceeded that for N and P (as suggested by their low N:K ratios) then, in winter, when this demand decreased (or ceased altogether), K levels could be expected to accumulate in the roots and rhizomes, the major storage organs in both species. This implies a rapid decrease in belowground K levels when aboveground demand increases in spring and early summer. An exceptionally marked decrease in K concentration was, in fact shown by the roots and rhizomes of *B. penna-marina* between September and December. Nutrient data was not collected for *P. cookii* during that period.

Ca concentrations in *B. penna-marina* fronds increased with age (Table 3) but Ca concentrations in the leaf biomass as a whole for this species decreased during winter (especially late winter) at all three study sites (Fig. 5). This is difficult to explain and suggests that new leaves were produced in winter. However, this is not supported by the leaf biomass dynamics (Smith 1987c) or by observations made during leaf-tagging studies. Assuming that the average frond age in the biomass actually decreased in the biomass during winter due to senescence of older fronds (which have the highest Ca concentrations) does not account for the extent of the decrease in biomass Ca concentrations, although it might explain why the sharp decline in biomass N, P and K levels in the second half of summer and during autumn did not continue into winter (Fig. 5).

Conclusions

There were no conspicuous seasonal patterns in the concentrations of any of the soil nutrients considered in this study. The fjaeldmark soils were less organic, had a higher pH and possessed higher levels of exchangeable Ca but lower levels of available K, N or P than the two fernbrakes. This accords with the relative positions of the Marion Island fjaeldmark and fernbrake sites along Principal Component Analysis gradients based on microclimate, soil and vegetation data for a wide variety of sub-Antarctic and northern hemisphere tundra and tundra-like sites (cf. Figures 6, 7 and 8 in French & Smith 1985). There, the fernbrakes were placed further toward the positive ends of vector I (warm, wet, organic, acid, high N to cold, dry, mineral, alkaline, low N gradient) and vector II (wet, organic, eutrophic to dry, mineral, oligotrophic) than were the fjaeldmarks.

Differences in plant nutrient concentrations between the fjaeldmark, open- and closed fernbrake sites were fairly consistent. N, P and K concentrations mostly decreased in the order, closed fernbrake > open fernbrake > fjaeldmark. Ca and Mg concentrations were generally higher in plant tissue from fjaeldmark and open fernbrake than from closed fernbrake. These differences reflected the "relative availability" of soil nutrients, as indicated by their exchangeable concentrations, at the three sites. Tissue concentrations of most nutrients in plants from the fjaeldmark and fernbrake communities were higher than in plants from the island's mire-grasslands. Mostly, this may be ascribed to differences in life-forms (i.e. dicots versus monocots) at the two groups of sites. However, P, K, Mg and Na concentrations in the grass *Agrostis magellanica* were considerably higher at fjaeldmark than at mire-grasslands.

N, P and K concentrations in the photosynthetic parts of the two dicotyledonous species at the fjaeldmark and fernbrake sites (and the fern *Blechnum penna-marina*, which at these sites behaves ecologically like a dwarf-shrub) are similar to those in dwarf-shrubs and shrubs at northern hemisphere tundra and tundra-like communities; K concentrations in the island species are in many instances higher than those in tundra species. Mg and Na levels in the dicotyledonous species (and the fern) are greater than those generally reported for tundra plants. In contrast, Ca concentrations in all of the island species considered in this study are markedly lower than for most plants from tundra and tundra-like areas.

For most of the species studied, a substantial proportion of the early-season aboveground biomass consisted of leaves which had overwintered so the nutrient concentrations in the biomass at that time did not reflect those in young tissue and the true magnitudes of age-related nutrient concentration changes could not be assessed. However, seasonal changes in nutrient concentrations of the aboveground biomass of the fjaeldmark and fernbrake species generally reflected the age-related changes and were similar to those for the mire-grassland plants and for plants from other subpolar and more temperate vegetation types, i.e. N, P and K decreased and Ca (sometimes also Mg) increased as the season progressed.

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