The chemical composition of Marion Island soils, plants and vegetation

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Introduction

Marion Island (46°54'S, 37°45 E) is volcanic in origin and consists of a coastal plateau and a central mountainous region (highest peak 1230 m a.s.l.). The island is composed of two distinct lava types, a grey pre-glacial and a black post-glacial eruption. The coastal plain on the northern, eastern and south-eastern portions of the island forms an area 4–5 km wide rising gently from sea-level to the foot of the mountainous interior at about 300 m a.s.l. In this account the term eastern coastal plain describes this entire coastal region, distinguishing it from the western and southern coastal areas. These consist of a narrow, discontinuous plain of less than 100 m altitude and occupied largely by halophytic plant communities capable of withstanding the large amounts of sea-spray deposited onto the surface by the strong, predominantly westerly winds. Both black and grey lava flows are well represented on the eastern coastal plain, forming 73 and 27 per cent respectively of the area below 500 m (estimated by planimetry from the geological map of Verwoerd & Langenegger, 1971).

Situated in the sub-Antarctic region the island experiences low temperatures (annual mean 5,1 °C), high rainfall (> 2500 mm per annum) and a high incidence of gale-force winds (Schulze, 1971). Because of its geologically recent origin, its relative isolation and the rigorous environment the island's biota lacks in species diversity. Only 35 vascular plant species (all low-growing graminoids or dwarf-shrubs) occur in the island flora, of which only six are of importance in the overall standing crop of the vegetation (Smith, 1976a, 1977a). Bryophytes contribute significantly to the standing crops of some plant communities. Owing to the inclement weather only the lowland areas (below 500 m) support closed plant communities (Huntley, 1970). Despite the fact that the annual mean temperature is above zero the island possesses a tundra-type biome (*sensu* Wielgolaski, 1972). Detailed descriptions of this biome are provided in Van Zinderen Bakker, Sr., *et al.* (1971) and Smith (1977b).

Considerable information exists regarding the chemical composition of sub-Arctic and Arctic tundra plants and soils (Schultz, 1969; Rodin & Bazilevich, 1967, 1968; Chepurko, 1972; Ivanov, 1972; Small, 1972a, 1972b; Wielgolaski & Kjelvik, 1973; Haag, 1974; Chapin *et al.*, 1975; Chapin & Bloom, 1976). The major ash elements in herbaceous flowering plants of northern tundra areas are K and Ca but the content of the latter element is usually lower than in herbaceous flowering plants from more temperate latitudes. Perceptible amounts of Mg may accumulate, usually accompanied by high levels of Na and Cl. N content in tundra vascular plants varies widely between species but is least for dwarf-shrubs, grasses and sedges and greatest for forbs (Wielgolaski, *et al.*, 1975). According to the proportions of dominant elements involved in the annual cycle, Rodin & Bazilevich (1967) classify northern tundra biogeocoenoses as belonging to the Boreal-nitric group (low-ash content, poorly productive, nitrogen greatly predominates).

Data on the chemical composition of soils and plants from sub-Antarctic and maritime Antarctic regions are limited. Smith & Walton (1975), Smith & Stephenson (1975) and Walton & Smith (in press) provide estimates of the nutrient contents of leaves and shoots of the principal species on South Georgia. Piper (1938) and Taylor (1955) present pH values and PO_4, Cl and organic C contents of Macquarie Island soils, and Holdgate (1961) provides similar information on the soils of some South Chilean Islands. Their data agree with those obtained from the Ross Dependency, Antarctica (Claridge, 1965), Signy Island (Allen *et al.*, 1967; Northover & Allen, 1967; Collins *et al.*, 1975) and Elephant Island (Allison & Smith, 1973) and indicate that, except for those near seal wallows and penguin rookeries, soils of southern polar and sub-polar regions possess low contents of Ca, N and P but because of the predominant maritime influence they contain appreciable quantities of Na, K and Cl.

Huntley (1971) found the ionic order in some Marion Island soils to be Mg > Ca > K > Na > Cl but that this sequence depends on the proximity of the soil to the shore and that Na and Cl greatly predominate in the soils of the coastal region. Grobbelaar (1974) found that the ionic order in the soil solution of an area approximately 500 m inland on Marion Island was Cl > Na > Mg > Ca > K ~ Fe > SO_4 > Mn > Zn and corresponds closely with that in sea water surrounding the island. Croome (unpublished second expedition report) chemically analysed several guano, soil, soil-water and plant sap samples on Marion Island in an investigation into the effect of bird excreta on germination and growth of *Poa cookii*. From these investigations it is apparent that the major factors influencing the plant and soil nutrient statuses on Marion Island are the leaching effects of the high rainfall and chemical enrichment from the surrounding ocean, either in the form of sea-spray or as manuring by sea-birds and mammals. Cyanophytic nitrogen fixation (Croome, 1973) and slow decomposition of the vast reserves of organic matter are also mechanisms supplying nutrients for plant growth to the terrestrial ecosystem.

As ecologist to the second (1971/72) and third (1972/73) South African biological research expeditions to Marion Island, the author spent two summer seasons on the island involved in an investigation into the nutrient status of the island's plants and soils. Some of the results of this investigation are provided in an account of the standing crop of black lava vegetation (Smith, 1976a) and in a comparison of the chemical compositions of tussock grassland and non-tussock grassland plants (Smith, 1976b). This paper presents estimates of the amounts of mineral elements contained in the plants and soils of the island's eastern coastal plain.

Methods

Chemical analysis: soils

Soil samples representing the diagnostic horizons were removed from soil profiles examined under the various plant communities. Most soil samples, however, were collected from the surface using an 8-cm diameter steel core-borer which removed an intact core of earth. After removing the surface litter the core was separated into the various layers or, where these were absent or indistinguishable, cut into 5-cm lengths. The resultant samples were crumbled and allowed to dry in a heated (18–25 °C) room, sealed in polythene bags and returned to South Africa for chemical analysis. Subsamples of the freshly collected soil were immediately analysed for water content (drying at 105 °C to constant weight) and inorganic N (MgO–Devarda's alloy steam distillation of acidified KCl extracts of the soil (Bremner, 1965a). All other analyses were performed on air-dried, sieved (2 mm) soil samples except for organic C determinations, which utilized ground (< 0,2 mm) subsamples. The results of all determinations are expressed per unit oven-dry weight of soils.

Total nitrogen was measured according to the regular macro-Kjeldahl method of Bremner (1965b). Organic C was measured by the Walkley-Black method (Allison, 1965), modified slightly in that a 2N dichromate solution was employed, enabling a correspondingly larger amount of soil to be used in the determination and thereby reducing sampling errors. Total P was determined according to the method of Legg & Black (1955) except that the ignited soils were taken up in 10N HNO_3 rather than in concentrated HCl, and the concentration of P in the resultant extract determined according to the method of Kitson & Mellon (1944).

pH was measured in a suspension of 1 part soil : 2 parts 0,01 M $CaCl_2$ (w:w). Soil cation exchange capacity was determined by saturating the soils' adsorption complex with Ca^{2+} by equilibrating 5-g soil samples with 0,1 M $CaCl_2$. After removal of the free Ca^{2+} ions in the soil solution with rinses of isopropanol the saturating Ca^{2+} ions were displaced using 1N NH_4NO_3 in 60% ethanol solution and the concentrations of these ions in the leachate measured by atomic adsorption spectrophotometry after dilution with 0,2% $SrCl_2$ solution. Total exchangeable cations were determined on a 5-g soil sample which was first washed by filtering through small portions of 60% ethanol and the adsorbed cations then displaced using 1N NH_4Cl in 60% ethanol. The concentrations of Ca, Mg, Na and K in the leachate were measured by atomic absorption spectrophotometry.

Chemical analysis: plants

The harvest sampling technique employed in the estimation of the vegetation standing crop is described in Smith (1976a). The harvested, sorted plant material was rinsed briefly in distilled water, oven-dried at 105°C to constant weight and ground to pass a 40 mesh sieve using a micro-Wiley mill.

Ash elements. 1 g of dried, ground material was ashed at 450°C and the ash dissolved in hot, dilute HNO_3. The concentrations of Ca, Mg, Na, K and Fe in $SrCl_2$ dilutions of the ash extract were determined by atomic absorption spectrophotometry and the amount of P by the method of Kitson & Mellon (1944). Nitrogen was measured according to Bremner (1965b). No significant differences were found in the N contents of replicate samples of most Marion Island plant species dried at 60, 80 or 105°C but tissue inherently high in N exhibited lower measured N values when dried at 60°C rather than at 105°C (Smith, 1976c).

Sites, vegetation and soils

Two study sites of approximately 1,5 hectare each were chosen, one on black lava 1 km north-west of the meteorological station, 500 m from the shore at an average altitude of 30 m a.s.l. and another on grey lava at Skua Ridge, 750 m from the shore and 80 m a.s.l.

As might be expected of a young volcanic island the morphology of any particular area is strongly dependent on the geological structure and most of the island surface is of a primary constructional origin with no subsequent modification of landforms through fluvial erosion. There is, therefore, a striking contrast between the glaciated areas and those which have subsequently been covered by younger, black lava flows. These latter generally form a hummocky, well-vegetated mosaic of herbfield, mire and *fjaeldmark* while the smooth topography of the glaciated areas offers little protection from wind erosion and consequently supports a sparser vegetation, mostly open *fjaeldmark* on the ridges with mire vegetation occupying the numerous ill-drained basins. Slope plant communities similar to those prevalent in black lava areas are uncommon. Detailed physiognomic and floristic descriptions of many of the plant communities occurring on grey and black lava flows are presented in Huntley (1971).

Black lava study site

Topographically, morphologically and floristically this study site is typical of the younger lava flows of the eastern coastal plain, i.e. extremely hummocky and, except for the exposed rocky ridges and plateaux, well-vegetated. The plant communities occurring in this study site may be grouped into 3 categories: vegetation of the slope complex, mire vegetation, and *fjaeldmark*. A summary of the floristic composition of the plant communities is presented in Table 1.

(i) *The slope complex*

Five plant communities occupy the numerous slopes of the hummocks and ridges of the island's low-altitude black lava areas. A closed *Blechnum penna-marina* (Poir) Kuhn fernbrake occurs on slopes protected from the icy southern and south-western winds while on the less-protected slopes a stunted, open-fernbrake community, in which there is a greater importance of *Acaena magellanica* (Lam.) Vahl. and *Azorella selago* Hook. f., is found. Basal vegetation cover of open-fernbrake is lower than that of closed-fernbrake but the increased *A. magellanica* canopy over the Blechnum fronds and greater expanse of *A. selago* cushions, on which the other component species often occur epiphytically, cause open-fernbrake communities to exhibit an almost 100 per cent aerial cover (Table 1).

Soils under closed and open-fernbrake are similar in profile characteristics although open-fernbrake soils tend to be somewhat shallower. A dark-brown A_{litter} layer, 5–10 cm deep and consisting of a dark-brown very fibrous mat of *B. penna-marina* rhizomes, roots and fronds overlies a

Table 1

Percentage aerial cover values of component species in the plant communities occurring in the inland black lava study site

Plant community	*B. penna-marina*	*Poa cookii*	*A. selago*	*A. magellanica*^{1}	*A. magellanica*^{2}	Bryophytes	Algal mats	Other	Total
Slope complex									
Closed-fernbrake	79	9	15	3	tr.	tr.	nil	tr.	106
Open-fernbrake community	42	8	31	15	1	nil	nil	nil	97
A. magellanica^1 drainage-line	24	1	3	75	nil	80	nil	tr.	183
P. cookii, A. selago crest	11	57	36	2	2	tr.	nil	nil	108
P. cookii tussock grassland	11	37	11	43	nil	85	nil	2	189
Fjaeldmark									
A. selago fjaeldmark	9	nil	27	nil	16	1	nil	tr.	53
Mire complex									
A. magellanica^2 mire	nil	nil	tr.	nil	49	75–90	0,5–1	12^3	97

^{1}*Acaena magellanica;* ^{2}*Agrostis magellanica;* ^{3}Including *Uncinia dikei* (8%), *Juncus scheuchzerioides* (4%); tr. = trace (less than 0,5%).

Table 2

Percentage aerial cover values of component species in the plant communities occurring in the grey lava study site

Plant community	*B. penna-marina*	*Poa cookii*	*Azorella selago*	*A. mag-ellanica*[1]	*A. mag-ellanica*[2]	Bryo-phytes	Algal mats	Other	Total
Slope complex									
Closed-fernbrake	95	1	5	tr.	nil	nil	nil	tr.	96
Open-fernbrake	12	1	38	50	0,5	nil	nil	tr.	101
Slope-crest	50	60	20	nil	nil	tr.	nil	tr.	1
Tussock grassland	tr.	70	15	10	nil	30	nil	tr.	125
Fjaeldmark									
A. selago fjaeldmark	tr.	nil	16	tr.	4	1–2	nil	tr.	~ 22
Mire complex									
A. magellanica mire	nil	nil	0,5	nil	40	40–70	0–2	10[3]	~ 100

[1] *Acaena magellanica;* [2] *Agrostis magellanica;* [3] Including *Uncinia dikei* (3%), *Juncus scheuchzerioides* (5%), *Ranunculus biternatus* (2%).

5–15 cm deep dark-brown or brown A_0 horizon containing decaying plant remains and followed by a brown/light-brown B_h horizon, the upper parts of which are stained by the A_0. In shallower profiles a compact, light-brown/orange region occurs beneath the B_h, representing either a sesquioxide-enriched B_s horizon or a soft plinthic layer. Below this a light-brown/grey, amorphous sticky organic clay extends to bedrock. Deeper profiles under closed-fernbrake possess a well-developed red/orange hard plinthic layer beneath the B_h horizon underlayed by gravel-sized concretions of Fe and, below these, of Mn. These concretions either lie immediately above the parent rock and scoriae or over a gleyed horizon.

Depressions and drainage-lines in slope areas are occupied by a dense canopy of *Acaena magellanica* interspersed with long, etiolated fronds of *Blechnum penna-marina* and understoreyed by a luxuriant growth of the moss *Brachythecium rutabulum* (Hedw.) B.S.G. Soils of these areas are very wet and the water-table is seldom more than a few centimetres below the surface. The top 20–40 cm of the profile consists of an amorphous, dark-brown peat, the upper regions of which possess many roots, rhizomes and decaying *A. magellanica* fronds. A brown/light-brown B horizon occurs beneath this dark brown layer and overlies a soft or hard plinthic layer, usually containing black Mn nodules. Between this plinthic layer and parent rock (usually at 1–1½ m) a strongly gleyed horizon of grey/yellow-grey organic clay occurs. A second hard plinthic layer may occur immediately above the parent rock.

The exposed crests of slopes often support a narrow band of *Poa cookii* understoreyed by large cushions of *Azorella selago*. Both these species are tolerant of cold air and cold soil (Huntley, 1971) and this may be the reason for their association in this distinctive band, which is seldom more than 3–5 m wide, on the exposed crests of the slopes. Profiles under slope-crest communities are similar to those under fernbrake. A black/dark-brown litter layer overlies a shallow A_0 layer, which usually contains small (1–5 cm) pieces of scoriae. A purplish-brown layer occurs under this, possibly representing the A_f region of the A_0. An orange-brown B_h horizon beneath this A_f region overlies an orange-red B_s horizon (or soft plinthic layer). A semi-gleyed grey/light-brown horizon occurs between this B_s and the parent rock or scoriae. In many cases a hard plinthic layer immediately overlies the parent rock, in which case a red sesquioxide *skin* coats the uppermost rocks.

On many well-drained, protected slope areas the *Blechnum penna-marina* carpet is replaced by a dense plant cover comprising *Acaena magellanica* codominant with luxuriant swards of *Poa cookii*. A dense understorey of *Brachythecium rutabulum* occurs and *Azorella selago* and *B. penna-marina* are common throughout this community, which has been termed inland tussock grassland by Huntley (1971) and which is invariably undermined by numerous burrows of small petrel and prion species.

The lowermost duff portions of the grass tussocks and dead *A. magellanica* stems and *B. rutabulum* fronds form a dark-brown A_{litter} layer overlying a red-brown horizon 20–50 cm deep and stained black in the upper and lower regions. Beneath this a dark-brown black organic clay occurs above a hard plinthic layer. Between this plinthic layer and parent rock a grey, gleyed horizon with ochrous mottles occurs.

(ii) *The exposed rocky plateaux:* fjaeldmark *communities*

Exposure to wind limits the growth of most plant species on the rocky plateaux. *Azorella selago, Agrostis magellanica* Lam. and a few scattered, stunted individuals of *Blechnum penna-marina* form the vegetation cover of these areas (Table 1). In areas completely exposed to the wind the total plant cover seldom exceeds 5 per cent. These are the true *fjaeldmark* or wind desert communities and occur mainly above the 200 m contour (Huntley, 1971). On the rocky plateaux of lower-lying areas, however, the cushions of *A. selago* are large and very numerous, supporting many epiphytic individuals of *Agrostis magellanica.* The percentage aerial cover of the vegetation in such areas is between 50 and 60 per cent and basal cover may be as high as 50 per cent.

Soils under *fjaeldmark* vegetation are skeletal, gravelly loams of a shallow nature. An A_{litter} horizon occurs beneath the *Azorella selago* cushions but, where no plants are growing, the soil surface is either bare or covered by a layer of scattered, gravel-sized scoriae. Beneath the surface a brown, gravelly loam, becoming orange-brown with depth and containing much scoriae, extends to parent rock.

(iii) *The mire complex*

The topography formed by the younger lavas as well as the extremely porous and *blocky* structure of these lavas is of such a nature that very few stream courses exist in areas covered by them. Considering the high rainfall, considerable amounts of water must reach the sea via underground drainage. A characteristic feature of the hummocky topography is, in fact, the numerous small bogs between the humps in which subsurface drainage from the surrounding slopes is ponded.

In many such areas the bogs have been succeeded by soligenous mires. The dominant vascular plant cover of these mires is an open canopy of the grass *Agrostis magellanica* under which *Uncinia dikei* Nelmes and *Juncus scheuchzerioides* Gaud. usually occur. Several bryophyte species also often form a dense carpet under the *A. magellanica* canopy; the most common of these are *Drepanocladus uncinatus* (Hedw.) Wernst., *Rhacomitrium lanuginosum* (Hedw.) Brid. and *Plagiochila crozetensis* Kaal. In extremely wet regions a dense carpet of *Blepharidophyllum densifolium* (Hook.) Angstr. Arnell develops.

The water-table is almost continuously at the surface within the mire areas. Peat formed under mire vegetation is deep and amorphous and mineral horizons seldom occur within the

Table 3

Chemical status of the horizons containing living roots in the soils under black and grey lava plant communities

Plant community	N	Depth (cm)	pH	Water (%)	% saturation of C.E.C.					Org. C (%)	Total N (%)	Total P (%)	mg/100 g soil	
					Ca	Mg	Na	K	Total				NH_4	NO_3
Black lava														
Closed-fernbrake	8	0–18	4,3	715 ± 67,0	21 ± 5,2	40 ± 2,2	4 ± 0,8	7 ± 2,1	72 ± 5,4	43,8 ± 1,33	2,18 ± 0,161	0,74 ± 0,195	tr.–1,6	0,0–tr.
Open-fernbrake	4	0–10	4,3–4,5	325 ± 45,9	13 ± 2,9	14 ± 2,1	4 ± 0,9	1 ± 0,5	31 ± 5,4	12,7 ± 3,16	1,24 ± 0,310	0,52 ± 0,093	tr.–0,9	0,0–tr.
*A.*** *magellanica* drainage-line	6	0–45	4,2–4,7	1002 ± 275,0	26 ± 1,1	32 ± 9,0	4 ± 1,9	2 ± 1,0	65 ± 10,8	42,9 ± 10,66	2,50 ± 0,442	0,66 ± 0,224	tr.–2,9	0,0–tr.
Poa cookii, *A. selago* crest	4	0–17	4,3–4,4	450 ± 328,8	11 ± 4,5	14 ± 6,8	5 ± 2,3	2 ± 2,3	31 ± 15,8	23,9 ± 16,20	1,63 ± 0,733	0,56 ± 0,480	tr.–1,7	0,0–tr.
Poa cookii tussock grassland	8	0–50	4,0–4,1	360 ± 23,2	14 ± 1,2	13 ± 3,0	5 ± 2,2	1 ± 0,5	34 ± 4,1	25,0 ± 4,73	1,66 ± 0,298	1,55 ± 0,456	0,9–8,4	0,0–1,0
A. selago fjaeldmark	4	0–10	5,2*	217 ± 168,4	3 ± 2,1	9 ± 3,4	3 ± 1,9	2 ± 3,3	17 ± 5,9	6,0*	0,73*	0,42*	0,0–0,5	0,0–tr.
Agrostis magellanica mire	10	0–20	4,2–4,3	1667 ± 199,1	5 ± 1,5	13 ± 0,5	5 ± 0,7	3 ± 1,0	26 ± 1,5	48,1 ± 4,93	2,34 ± 0,420	0,60 ± 0,491	2,4–6,5	0,0–0,7
Grey lava														
Closed-fernbrake	4	0–32	4,3–4,5	484 ± 93,4	10 ± 3,3	11 ± 2,1	5 ± 1,6	1 ± 0,5	27 ± 4,4	25,3 ± 4,52	2,49 ± 0,320	0,68 ± 0,184	tr.–0,7	0,0–tr.
Open-fernbrake	4	0–28	4,6–4,8	238 ± 104,0	11 ± 2,0	14 ± 3,3	5 ± 0,8	1 ± 0,2	30 ± 5,8	15,2 ± 2,04	0,90 ± 0,416	0,64 ± 0,121	tr.	0,0–tr.
Tussock grassland	5	0–48	3,8–4,4	355 ± 16,5	3 ± 1,2	3 ± 1,4	2 ± 0,3	1 ± 0,3	9 ± 2,6	18,5 ± 6,08	1,50 ± 0,471	0,86 ± 0,114	tr.–1,5	tr.
Fjaeldmark	6	0–20	4,9–5,0	219 ± 62,8	3 ± 1,0	5 ± 1,3	4 ± 0,9	2 ± 0,8	14 ± 2,0	9,4 ± 2,39	0,68 ± 0,096	0,55 ± 0,093	0,0	0,0
Mire	5	0–30	4,2–4,4	725 ± 162,9	6 ± 1,1	5 ± 0,7	5 ± 1,3	1 ± 0,2	17 ± 2,5	34,8 ± 4,62	2,08 ± 0,265	0,6 ± 0,165	tr.	0,0–tr.

N = number of determinations; values expressed as ranges or as means ± standard deviations; tr. = trace (< 0,5 mg/100 g soil); *single determination; ***Acaena magellanica*.

Table 4

Chemical composition of the plant species

Species	Organ	N	Calcium	Magnesium	Sodium	Potassium	Iron	Nitrogen	Phosphorus
Blechnum penna-marina	leaf	19	0,44 ± 0,080	0,73 ± 0,100	0,29 ± 0,101	1,54 ± 0,207	0,006 ± 0,010	2,36 ± 0,343	0,24 ± 0,034
	litter	18	0,79 ± 0,163	0,89 ± 0,038	0,11 ± 0,052	0,20 ± 0,049	0,019 ± 0,012	1,85 ± 0,221	0,18 ± 0,037
	rhizome	12	0,33 ± 0,030	0,13 ± 0,059	0,17 ± 0,082	0,92 ± 0,228	0,024 ± 0,015	1,30 ± 0,221	0,24 ± 0,096
Acaena magellanica	leaf	10	0,68 ± 0,108	0,51 ± 0,068	0,41 ± 0,087	1,40 ± 0,252	0,017 ± 0,012	2,01 ± 0,140	0,21 ± 0,055
	litter	9	0,91 ± 0,176	0,54 ± 0,040	0,16 ± 0,048	0,34 ± 0,079	0,031 ± 0,024	1,99 ± 0,255	0,18 ± 0,021
	root	10	0,18 ± 0,042	0,24 ± 0,048	0,08 ± 0,057	0,56 ± 0,082	0,028 ± 0,035	0,78 ± 0,075	0,11 ± 0,032
Poa cookii	leaf	27	0,11 ± 0,031	0,08 ± 0,027	0,23 ± 0,101	1,23 ± 0,178	0,009 ± 0,008	1,67 ± 0,269	0,16 ± 0,041
	litter	10	0,15 ± 0,062	0,11 ± 0,015	0,09 ± 0,039	0,15 ± 0,087	0,024 ± 0,014	1,13 ± 0,187	0,11 ± 0,024
	root	9	0,14 ± 0,058	0,13 ± 0,030	0,25 ± 0,083	0,40 ± 0,071	0,072 ± 0,010	1,19 ± 0,148	0,10 ± 0,025
Azorella selago	leaf	16	0,46 ± 0,115	0,33 ± 0,080	0,85 ± 0,228	1,45 ± 0,318	0,017 ± 0,008	1,42 ± 0,215	0,13 ± 0,024
	litter	15	0,53 ± 0,082	0,30 ± 0,080	0,04 ± 0,029	0,08 ± 0,022	0,111 ± 0,085	1,09 ± 0,161	0,10 ± 0,023
	root	11	0,41 ± 0,079	0,37 ± 0,049	0,17 ± 0,046	0,87 ± 0,123	0,017 ± 0,006	1,30 ± 0,098	0,13 ± 0,030
Agrostis magellanica	leaf	8	0,13 ± 0,024	0,20 ± 0,033	0,41 ± 0,253	1,11 ± 0,465	0,007 ± 0,004	1,76 ± 0,631	0,15 ± 0,054
	litter	7	0,15 ± 0,046	0,14 ± 0,012	0,12 ± 0,044	0,17 ± 0,152	0,019 ± 0,010	0,89 ± 0,212	0,07 ± 0,030
	root	3	0,18 ± 0,166	0,25 ± 0,108	0,25 ± 0,138	0,48 ± 0,227	0,013 ± 0,005	0,76 ± 0,283	0,16 ± 0,163
Brachythecium rutabulum	living frond	7	0,39 ± 0,103	0,36 ± 0,049	0,13 ± 0,046	0,83 ± 0,054	0,045 ± 0,026	1,81 ± 0,180	0,17 ± 0,058
Juncus scheuchzerioides	leaf	3	0,13 ± 0,011	0,18 ± 0,063	0,62 ± 0,049	1,39 ± 0,041	0,027 ± 0,018	1,34 ± 0,333	0,15 ± 0,026
	litter	3	0,37 ± 0,190	0,18 ± 0,026	0,24 ± 0,141	0,09 ± 0,039	0,056 ± 0,018	0,80 ± 0,071	0,07 ± 0,017
Uncinia dikei	leaf	3	0,08 ± 0,024	0,12 ± 0,023	0,09 ± 0,017	1,01 ± 0,059	0,006 ± 0,001	0,76 ± 0,115	0,10 ± 0,006
	litter	3	0,13 ± 0,024	0,11 ± 0,004	0,04 ± 0,016	0,08 ± 0,011	0,028 ± 0,009	0,52 ± 0,096	0,05 ± 0,016
Agrostis bergiana	leaf	4	0,19 ± 0,049	0,23 ± 0,097	0,52 ± 0,032	1,72 ± 0,697	0,004 ± 0,001	2,77 ± 1,030	0,22 ± 0,054
Montia fontana	leaf	2	0,21 ± 0,010	0,42 ± 0,045	0,76 ± 0,132	4,49 ± 0,127	0,068 ± 0,081	2,91 ± 0,510	0,25 ± 0,001

Values expressed as means ± standard deviations. N = number of determinations.

profile. A shallow, dark-brown/brown surface horizon (A_0?) overlies a light-brown, featureless peat which becomes orange-brown with depth. This may extend unaltered to bed-rock or a dark organic pan may occur, usually at 40–70 cm depth. Lateral drainage of fresh water across the surface of the underlying bed-rock occurs through many mire peats.

Grey lava study site

(i) *The slope complex*

Few slopes steep enough to support slope-plant communities similar to those in black lava occur in grey lava areas. However, two such slopes do occur in the Skua Ridge study site. These are covered by a closed *Blechnum penna-marina* fernbrake and, on more exposed aspects, by a stunted open-fernbrake community. A small area on one slope is occupied by burrowing birds and supports a dense *Poa cookii–Acaena magellanica* tussock grassland similar to that on black lava. A summary of the floristic compositions of the plant communities is presented in Table 2. The aerial cover values of *A. magellanica* and *Azorella selago* are greater, and that of *B. penna-marina* smaller, in open-fernbrake on grey lava than on black lava.

Soils under both closed and open-fernbrake in the grey lava study site exhibit poorly developed profile characteristics and approximate those occurring under open-fernbrake in black lava areas. A dark-coloured A horizon of decomposing plant material overlies a brown/light-brown, clayey B horizon which is usually only poorly differentiated into an organic B_h and lighter B_s region and often contains gravel-sized pieces of rock. A hard plinthic layer frequently occurs beneath this B_s, followed by a gleyed horizon and parent rock at 100–140 cm depth. In many cases the B_s overlies a soft plinthic layer followed immediately by parent rock.

Soils under tussock grassland on grey lava generally consist of an A_{litter} layer of *Acaena magellanica* and *Poa cookii* followed by a dark-brown A_0 horizon which overlies a B horizon approximately 60 cm deep. The lower regions of this horizon possess gravel-sized pieces of lava. Below this a semi-gleyed horizon free of gravel extends to the parent rock at 120 cm.

(ii) Fjaeldmark *vegetation*

Fjaeldmark vegetation on grey lava generally exhibits a lower percentage aerial plant cover than does black lava *fjaeldmark* and consists almost entirely of *Azorella selago* cushions scattered within a loose aggregation of rocks and pebbles forming a *hamada* pavement. The underlying soils are very similar in profile characteristics to those under black lava *fjaeldmark*. An A_{litter} layer of undecomposed *A. selago* stems and leaves overlies a brown/light-brown horizon containing pieces of rock and extending to the parent lava at 40–75 cm below the soil surface.

(iii) *The mire complex*

Grey and black lava mire vegetation are similar in species composition, being dominated by *Agrostis magellanica* and several bryophyte species (the most important in grey lava mires being *Jamesoniella colorata* (Lehm). Schiffn. and *Rhacomitrium lanuginosum*.

Only one peat profile was investigated under mire vegetation on grey lava. A shallow A_{litter} layer of decomposing bryophytes and *A. magellanica* litter occurred above a brown/light-brown amorphous organic horizon similar to the corresponding horizon in black lava mire profiles. At 70 cm depth, however, a well-defined layer of scattered, flat rocks similar in appearance to those at the surface of *fjaeldmark* areas occurred. Beneath these rocks a brown/light-brown organic clay containing a substantial amount of partly-decomposed plant material occurred at 70–104 cm depth, above a semi-gleyed, yellow/grey clay. Below this gleyed horizon a light-brown/brown clayey layer containing small pieces of stoney material was present. This stoney material increased in size and number in the lower regions of this layer, which rested on parent rock at 180 cm depth.

Results and discussion

Soil chemical composition

Chemical data for the horizons containing the majority of living roots in soils under the plant communities on black and grey lava are presented in Table 3. The concentrations of adsorbed cations in black lava soils decrease in the sequence $Mg > Ca > Na > K$. In grey lava soils the importance of Mg relative to Ca is reduced and the contents of K are especially low. Smith (1976c) presents evidence that the intensity of sea-spray deposition at the grey lava site is less than at the black lava site and that differences also occur between the two sites in the ability of the parent rock to influence the chemical composition of the overlying soils. These factors may be partly responsible for the observed differences in the adsorbed cation concentrations of black and grey lava soils.

Closed-fernbrake soils on black lava possess greater amounts of Ca, Mg and K than do open-fernbrake soils whereas no such difference occurs between soils of these two communities in grey lava areas. The enhanced Ca saturation of drainage-line soils is reflected by increases in the content of this element in leaves of *Acaena magellanica* plants growing in these soils (Smith, 1976b). The contents of organic C, total N, total P and adsorbed cations of soils under slope-crest plant communities are lower than those of closed-fernbrake soils but are similar to those of open-fernbrake soils.

The high inorganic N, total N and total P contents of tussock grassland soils, compared with other soils of the slope complex, evidences the importance of manuring by burrowing bird species on the nutrient status of these soils. This is substantiated by the effects which these birds have on the chemical composition of plants growing in inland tussock grassland communities (Smith, 1976b). Tussock grassland soils possess lower amounts of adsorbed cations and are more acid than most other soils of the slope complex.

All slope soils not influenced by manuring contain low amounts of inorganic N, predominantly in the NH_4^+ form. Negligible concentrations of NO_3^- occur, as might be expected under the low temperature, low pH soil regime. The NH_4^+ content of black lava mire peat is higher than those of other, non-manured, island soils. All mire peat samples exhibiting the higher values in the range of NH_4^+ contents reported in Table 3 occurred under a gelatinous algal mat containing *Nostoc commune* Vaucher (Smith, 1976a). Croome (1973) showed that *N. commune* fixes significant quantities of atmospheric N in mires of the black lava study site and this enriches these mires in reduced N. No peat samples from under algal mats containing *N. commune* in grey lava mires were analysed for inorganic N, probably explaining the low NH_4^+ values reported for peats of these areas in Table 3. The poor N status of Marion Island mire peats is illustrated by the fact that even the enhanced levels of NH_4^+ under *N. commune* (up to 6,5 mg/100 g soil) are much lower than that in a surface peat of similar bulk density from a wet tundra meadow at Barrow, Alaska (14,1 mg/100 g soil; Flint & Gersper, 1974).

Fjaeldmark soils possess especially low concentrations of plant nutrients, possibly due to the poor water-retention capacity of these soils caused by the low organic matter contents allowing for enhanced leaching by the incoming rainfall.

Plant chemical composition

The concentrations of mineral elements at the time of maximum above-ground biomass in leaves, leaf litter and roots of the plant species dominating the eastern coastal plain are presented in Table 4. Small differences in plant

Table 5

Concentrations of N, P, K and Na in the leaf litter of mire and non-mire plants as a percentage of their concentrations in living leaf material

	N	P	K	Na
Non-mire species	80 ± 13,5	78 ± 5,7	14 ± 7,5	30 ± 16,4
Mire species	59 ± 10,1	49 ± 1,7	10 ± 5,9	37 ± 7,6

chemical composition do occur within species between the two study sites as well as between communities within each study site (notably between tussock grassland and non-tussock grassland plants; Smith, 1976b). No significance can be ascribed to many of these differences owing to insufficient replicate determinations so that the plant chemical data from all the communities have been combined in Table 4.

The concentrations of N and P in Marion Island plants are similar to those in most northern hemisphere tundra plant species (Rodin & Bazilevich, 1967; Wielgolaski & Kjelvik, 1973; Chapin *et al.*, 1975). In common with plants of northern hemisphere tundra areas, K is the most predominant ash element in the leaves and roots of the island plants. The Ca content is lower than in more temperate herbaceous plant species but substantial concentrations of Mg occur, probably due to the low soil Ca status and to influx of Mg from the surrounding ocean. Heavy influx of Na also occurs from this source and the plants characteristically contain high concentrations of this element. Smith (1976a) suggests that the importance of Na in the leaves of *Agrostis magellanica*, *Juncus scheuchzerioides*, *Agrostis bergiana* and *Montia fontana* represents an adaptation enabling these plants to occur predominantly in the nutrient-poor mire areas. Grobbelaar (1975, unpublished DSc thesis) has demonstrated that the mire soil solution contains more than 6 times as much Na than any other cation.

Dead leaf material possesses higher concentrations of Ca, Mg and Fe and lower concentrations of the more mobile elements Na, K, N and P. It is not known how much of this decrease in N, P, K and Na in dead leaf tissue is attributable to translocation of these nutrients to the roots preceding leaf senescence and how much is due to leaching from dying and dead leaves by the high rainfall. It is of interest, however, that the concentrations of N, P and K in the leaf litter, expressed as a percentage of their concentrations in living leaf material, of plants listed above as occurring predominantly in mire areas are significantly lower than the corresponding values for non-mire plant species (Table 5), supporting the proposal (Small, 1972a, 1972b) that bog plants subsist on relatively smaller amounts of nutrients than do plants in other habitats and that this is related to the ability of the bog species to reabsorb a greater proportion of nutrients from their leaves preceeding leaf-fall than do non-bog species.

Standing crops of the vegetation

Standing crop values of the various plant communities at the time of maximum above-ground biomass are presented in Table 6. *Biomass* refers to living, and *dead organic matter* (o.m.) to dead, plant material. The latter does not include the decomposed or humified organic constituents of the soils. *Standing crop* is the sum of living and dead material. Because of difficulty in distinguishing below-ground living and dead material, these two components are not reported separately but rather the composite figure (below-ground standing crop) is presented.

Plant communities on grey lava exhibit markedly lower standing crop values than do the corresponding black lava communities, probably due to the higher altitude of the grey lava area and its greater exposure to wind due to the flat topography (Smith, 1977). Within lava types, slope communities support higher standing crops than do mire and *fjaeldmark* communities.

A considerable amount of dead plant material accumulates in the *Poa cookii* swards of the tussock grassland and slope-crest communities, supporting previous observations on sub-Antarctic and Antarctic grasslands (Davies, 1939; Jenkin & Ashton, 1970; Edwards, 1973; Greene *et al.*, 1973; Smith & Stephenson, 1975). The importance of this dead material as a nutrient reserve in the Marion Island grassland communities is demonstrated in the next section.

The percentage surface area occupied by each plant community on the two lava types (estimated using a modified stop-point method; Smith, 1976a) and the contribution of each community to the total standing crop of an average

Table 6

Standing crops (g/m²) of the plant communities

	Above-ground					Below-ground s. crop	Total stand. crop
	Biomass			Dead o.m.	Total s. crop		
	Vasc.	Cryp.	Total				
Black lava							
Slope complex							
Closed-fernbrake community	568±79	tr.	568	1557±322	2125	3984±684	6109
Open-fernbrake community	438±63	tr.	438	1580±208	2018	2462±441	4480
Acaena drainage-line	727±92	224±94	951	528±107	1479	3607±572	5086
P. cookii, *A. selago* crest	804±117	tr.	804	3654±1086	4458	2001±227	6459
P. cookii tussock grassland	778±134	230±49	1008	1649±225	2657	3988±898	6645
Fjaeldmark							
Azorella selago fjaeldmark	238±36	tr.	238	1541±183	1779	963±224	2742
Mire complex							
Agrostis magellanica mire	117±29	219±82	336	303±69	639	2024±421	2663
Grey lava							
Slope complex							
Closed-fernbrake	310±16	—	310±16	872±85	1182	3156±310	4338
Open-fernbrake	439±16	—	439±16	1260±106	1699	1238±83	2937
Tussock grassland	735±29	70±23	805	1871±53	2676	2687±211	5363
Fjaeldmark							
Azorella selago fjaeldmark	111±12	—	111±12	645±38	756	418±61	1174
Mire complex							
Agrostis magellanica mire	97±18	147±76	244	242±63	486	1778±313	2264

Table 7

Percentage surface area occupied by the various plant communities on black and grey lava and the contribution of these communities to the standing crop (kg/ha) of the vegetation occupying these lava types.

	Black lava		Grey lava	
Community	Area occup.	S.c. in ave. ha	Area occup.	S.c. in ave. ha
Slope Complex				
Closed-fernbrake	18,0	10996	0,04	17
Open-fernbrake	21,6	9677	1,10	323
Drainage-line	0,3	153	nil	nil
Slope-crest	1,0	646	nil	nil
Tussock grassland	0,6	399	0,43	230
Fjaeldmark				
Azorella fjaeldmark	20,9	5731	39,30	4614
Mire Complex				
Agrostis mire	37,4	9960	59,00	13358

hectare of the particular lava type are provided in Table 7. Despite their higher standing crops, slope plant communities do not contribute markedly to the total standing crop of grey lava vegetation. Fernbrake communities, however, form an important component in the standing crop of black lava vegetation.

The total standing crops of black and grey lava vegetations and a combined value for the eastern coastal plain as a whole, based on the proportionate representation of the two lava types in this area, are presented in Table 8. The contribution of closed-fernbrake (< 0,1 per cent) to the standing crop of the grey lava vegetation is ignored in the table.

The standing crop components of black lava vegetation are 2 to 2½ times greater than those of grey lava vegetation due to the greater luxuriance of black lava plant communities and to the relative importance of closed slope communities, rather than mire and *fjaeldmark*, on black lava. The below-ground contribution to the total standing crop of the island vegetation is of less importance than in comparable northern hemisphere tundra vegetation (Scott & Billings, 1964; Bliss, 1966; Dennis & Johnson, 1970; Webber, 1974), probably owing to more favourable conditions for plant growth on the island (warmer soils, higher air temperatures, longer growing season; Smith, 1976a). The percentage contribution of below-ground material to the total standing crop increases in the sequence *fjaeldmark* (36 ± 0,7 per cent), slope communities (56 ± 14,5 per cent), mire (78 ± 2,1 per cent). Detailed accounts of the island vegetation standing crop and a comparison of this standing crop with those of other tundra vegetations are provided in Smith (1976a, 1977a).

Standing stocks of mineral elements

By applying the chemical analysis data used in compiling Table 4 to the appropriate standing crop values of the component species in each plant community, the amounts (standing stocks) of mineral elements in the plant matter of the various communities have been determined (Tables 9–20). These quantities are approximately proportional to the community standing crops. However, the low concentrations of mineral elements in the litter of mire plant species and the importance of the below-ground component causes mire vegetation to exhibit a disproportionately low standing stock of nutrients in relation to the standing crop. The nutrient standing stocks in the above-ground vascular biomass of black and grey lava mire vegetations (4,5 and 3,4 g/m^2 respectively) are approximately similar to that (3,2 g/m^2) of a wet tundra meadow community at Barrow, Alaska, at the time of maximum above-ground biomass (Chapin *et al.*, 1975). The concentrations of nutrients (in mg elements per g plant matter) in the above-ground standing crop of black and grey lava mire vegetations (32 mg/g and 25 mg/g respectively) also agrees closely with that (32 mg/g) of the Barrow community.

Table 8

Standing crops (kg/ha) of vegetation on the island's eastern coastal plain.

	Above-ground					Below-ground total	Total stand. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Black lava	3060	840	3900	11050	14950	22620	37570
Grey lava	1088	870	1959	4182	6140	12389	18525
Eastern coastal plain	2528	848	3376	9196	12571	19858	32428

Dead *Poa cookii* material contains between 35 and 60 per cent of the above-ground standing stock of nutrients in tussock grasslands and slope-crest communities on Marion Island. Greene *et al.* (1973) and Smith & Stephenson (1975) emphasize the importance of litter and standing dead material as a nutrient reserve in *Festuca contracta* T. Kirk (= *F. erecta* D'Urv) tussock grasslands on South Georgia, where dead material accounts for 40–60 per cent of the total above-ground nutrient standing stock. The total amounts of mineral elements in the living above-ground component of these South Georgian communities (11,0 to 21,9 g/m^2; Smith & Stephenson, 1975) are substantially lower than in black and grey lava tussock grasslands on Marion Island (46,5 and 27,7 g/m^2 respectively) due to the higher aerial biomasses of these latter communities. The above-ground biomass in climax tussock grassland dominated by 2-m tall tussocks of *Poa flabellata* (Lam.) Hook. f. on South Georgia possesses exceptionally high mineral element standing stocks (259–373 g/m^2; Walton & Smith, in press), more than 5 times greater than the corresponding values for any Marion Island tussock grasslands. In relation to their standing crops, Marion Island grasslands are disproportionately richer in K and N and poorer in Ca than are those of South Georgia.

The standing stock of mineral elements (41,9 g/m^2) in the above-ground biomass of the *Acaena magellanica* drainage-line community agrees closely with that of a similar community on South Georgia (43,4 g/m^2; Walton & Smith, in press).

Standing stock data for each community are multiplied by the percentage surface area occupied by these communities to yield an estimate of the amounts of nutrients contained in the vegetation occupying the two lava types (Table 21). Standing stocks of Ca, Mg and Na in the various standing crop components of black lava vegetation are 3 to 4 times greater, and those of K, Fe, P and N, 2 to 3 times greater than the corresponding values for grey lava vegetation. The total mineral element standing stock in black lava vegetation is 2½ times higher than that in grey lava vegetation. This cannot be ascribed to differences in nutrient concentration between plants growing on the two lava types and is due to the lower standing crop of the grey lava vegetation as well as to the importance of nutrient-poor communities (mire and *fjaeldmark*) on grey lava flows.

An estimate of the standing stocks of minerals in the vegetation of the island eastern coastal plain is provided by combining the data in Table 21 according to the proportional representation of the two lava types in this area (Table 22).

A total of 913 kg/ha of mineral elements accumulates in the plant matter of the island vegetation. The living above-ground component possesses 154 kg/ha of mineral elements, more than those contained in a mosaic low-Arctic tundra of sedges, lichens, mosses and shrubs of the Koryak National

Table 9

Amounts of mineral elements (g/m²) contained in the standing crop components of closed-fernbrake communities on black lava

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	2,35	—	2,35	9,97	12,32	12,71	25,03
Mg	2,96	—	2,96	8,75	11,71	16,04	27,75
Na	2,35	—	2,35	1,32	3,67	7,90	11,57
K	7,59	—	7,59	2,14	9,73	30,12	39,85
Fe	0,03	—	0,03	0,61	0,64	1,16	1,80
P	1,19	—	1,19	2,11	3,30	7,87	11,17
Total ash elements	16,47	—	16,47	24,90	41,37	75,80	117,17
N	11,48	—	11,48	20,76	32,24	52,17	84,41
Total mineral elements	27,95	—	27,95	45,66	73,61	127,97	201,58

Table 10

Amounts of mineral elements (g/m²) contained in the standing crop components of open-fernbrake communities on black lava

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	2,18	—	2,18	9,02	11,20	7,99	19,19
Mg	2,01	—	2,01	6,63	8,64	8,38	17,02
Na	2,36	—	2,36	1,14	3,50	4,32	7,82
K	5,63	—	5,63	1,88	7,51	17,63	25,14
Fe	0,04	—	0,04	0,75	0,79	0,69	1,48
P	0,84	—	0,84	1,80	2,64	3,87	6,51
Total ash elements	13,06	—	13,06	21,22	34,28	42,88	77,16
N	7,96	—	7,96	19,25	27,21	30,88	58,09
Total mineral elements	21,02	—	21,02	40,47	61,49	73,76	135,25

Table 11

Amounts of mineral elements (g/m²) contained in the standing crop components of drainage-line communities on black lava

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	4,73	0,93	5,66	4,67	10,33	5,63	15,96
Mg	3,53	0,77	4,30	3,30	7,60	7,03	14,63
Na	2,43	0,23	2,66	0,80	3,46	2,23	5,69
K	8,43	1,80	10,23	1,47	11,70	15,33	27,03
Fe	0,07	0,07	0,14	0,07	0,21	0,60	0,81
P	1,47	0,30	1,77	0,93	2,70	3,33	6,03
Total ash elements	20,66	4,10	24,76	11,24	36,00	34,15	70,15
N	13,30	3,83	17,13	9,70	16,83	16,23	53,06
Total mineral elements	33,96	7,93	41,89	20,94	62,83	60,38	123,21

Table 12

Amounts of mineral elements (g/m²) contained in the standing crop components of slope-crest communities on black lava

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	1,88	—	1,88	15,32	17,20	5,19	22,39
Mg	1,34	—	1,34	9,00	10,34	4,59	14,93
Na	3,83	—	3,83	2,16	5,99	3,96	9,95
K	9,67	—	9,67	3,44	13,11	13,35	24,46
Fe	0,06	—	0,06	1,81	1,87	1,07	2,94
P	1,19	—	1,19	3,34	4,53	2,59	7,12
Total ash elements	17,97	—	17,97	35,07	53,04	28,75	81,79
N	12,32	—	12,32	38,13	50,45	25,66	76,11
Total mineral elements	30,29	—	30,29	73,20	103,49	54,41	157,90

Table 13

Amounts of mineral elements (g/m²) contained in the standing crop components of inland tussock grasslands on black lava

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	2,72	0,82	3,54	7,28	10,82	6,30	17,12
Mg	2,17	0,85	3,02	4,32	7,34	7,55	14,89
Na	3,12	0,37	3,49	1,63	5,12	9,25	14,37
K	12,26	2,00	14,26	3,87	18,13	22,23	40,36
Fe	0,17	0,15	0,32	1,52	1,84	1,95	3,79
P	1,55	0,48	2,03	2,38	4,41	4,93	9,34
Total ash elements	21,99	4,67	26,66	21,00	47,66	52,21	99,87
N	15,38	4,47	19,85	25,41	45,26	43,87	89,13
Total mineral elements	37,37	9,14	46,51	46,41	92,92	96,08	189,00

Table 14

Amounts of mineral elements (g/m²) contained in the standing crop components of fjaeldmark on black lava

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	0,99	—	0,99	8,62	9,61	3,69	13,30
Mg	0,86	—	0,86	5,21	6,07	3,65	9,72
Na	1,87	—	1,87	0,89	2,76	1,95	4,71
K	2,95	—	2,95	1,59	4,54	7,45	11,99
Fe	0,03	—	0,03	1,00	1,03	0,17	1,20
P	0,37	—	0,37	1,43	1,80	1,50	3,30
Total ash elements	7,07	—	7,97	18,74	25,81	18,41	44,22
N	3,76	—	3,76	16,21	19,97	12,23	32,20
Total mineral elements	10,83	—	10,83	34,95	45,78	30,64	76,42

Table 15

Amounts of mineral elements (g/m^3) contained in the standing crop components of black lava mire vegetation

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	0,15	1,35	1,50	0,47	1,97	4,46	6,43
Mg	0,22	1,12	1,34	0,41	1,75	5,65	7,40
Na	0,53	0,32	0,85	0,35	1,20	5,48	6,68
K	1,19	2,60	3,79	0,53	4,32	10,32	14,64
Fe	0,01	0,10	0,11	0,07	0,18	N.D.	0,18
P	0,19	0,45	0,64	0,24	0,88	3,44	4,32
Total ash elements	2,29	5,94	8,23	2,07	10,30	29,35	39,65
N	2,24	5,22	7,46	2,80	10,26	17,40	27,66
Total mineral elements	4,53	11,16	15,69	4,87	20,56	46,75	67,31

Table 16

Amounts of mineral elements (g/m^2) contained in the standing crop components of closed-fernbrake on grey lava

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	1,23	—	1,23	5,28	6,51	10,10	16,61
Mg	2,11	—	2,11	6,25	8,36	4,12	12,48
Na	1,01	—	1,01	0,40	1,41	5,23	6,64
K	5,15	—	5,15	1,20	6,35	27,96	34,31
Fe	0,05	—	0,05	0,37	0,42	0,82	1,24
P	0,59	—	0,59	0,93	1,52	6,16	7,68
Total ash elements	10,14	—	10,14	14,43	24,57	54,39	78,96
N	5,37	—	5,37	13,21	18,58	37,53	56,11
Total mineral elements	15,51	—	15,51	27,64	43,15	91,92	135,07

Table 17

Amounts of mineral elements (g/m^2) contained in the standing crop components of open-fernbrake on grey lava

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	1,80	—	1,80	6,16	7,96	4,03	11,99
Mg	1,77	—	1,77	4,43	6,20	3,42	9,62
Na	1,74	—	1,74	0,46	2,20	1,79	3,99
K	5,56	—	5,56	1,04	6,60	10,05	16,65
Fe	0,17	—	0,17	1,16	1,33	0,31	1,64
P	0,61	—	0,61	1,17	1,78	1,32	3,10
Total ash elements	11,65	—	11,65	14,42	26,07	20,92	46,99
N	6,52	—	6,52	13,54	20,06	13,72	33,78
Total mineral elements	18,17	—	18,17	27,96	46,13	34,64	80,77

Table 18

Amounts of mineral elements (g/m^2) contained in the standing crop components of tussock grasslands on grey lava

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	1,38	0,27	1,65	4,71	6,36	3,84	10,20
Mg	1,01	0,25	1,26	3,31	4,57	4,16	8,73
Na	2,13	0,09	2,22	1,47	3,69	6,41	10,10
K	8,14	0,58	8,72	2,25	10,97	10,37	21,34
Fe	0,10	0,03	0,13	0,64	0,77	1,53	2,30
P	0,83	0,12	0,95	1,70	2,65	2,20	4,85
Total ash elements	13,59	1,34	14,93	14,08	29,01	28,51	57,52
N	11,53	1,27	12,80	19,58	32,38	28,99	61,37
Total mineral elements	25,12	2,61	27,73	33,66	61,39	57,50	118,89

Table 19

Amounts of mineral elements (g/m^2) contained in the standing crop components of grey lava fjaeldmark

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	0,43	—	0,43	2,97	3,40	1,52	4,92
Mg	0,35	—	0,35	2,03	2,38	1,34	3,72
Na	0,54	—	0,54	0,21	0,75	0,68	1,43
K	1,29	—	1,29	0,47	1,76	3,55	5,31
Fe	0,02	—	0,02	0,56	0,58	0,06	0,64
P	0,12	—	0,12	0,57	0,69	0,39	1,08
Total ash elements	2,75	—	2,75	6,81	9,56	7,54	17,10
N	1,42	—	1,42	6,48	7,90	4,77	12,67
Total mineral elements	4,17	—	4,17	13,29	17,46	12,31	29,77

Table 20

Amounts of mineral elements (g/m^2) contained in the standing crop components of grey lava mire vegetation

Element	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Ca	0,12	0,47	0,59	0,30	0,89	3,20	4,09
Mg	0,19	0,46	0,65	0,31	0,94	4,20	5,14
Na	0,37	0,17	0,54	0,29	0,83	4,50	5,33
K	0,98	1,22	2,20	0,39	2,59	8,53	11,12
Fe	0,01	0,04	0,05	0,04	0,09	0,23	0,32
P	0,11	0,25	0,36	0,15	0,51	2,89	3,40
Total ash elements	1,78	2,61	4,39	1,48	5,87	23,55	29,42
N	1,60	2,93	4,53	1,92	6,45	13,10	19,55
Total mineral elements	3,38	5,54	8,92	3,40	12,32	36,65	48,97

Territory, U.S.S.R. (136 kg/ha, Rheder, 1976) and in a dwarf-shrub tundra of the Kola Peninsula (104 kg/ha, Chepurko, 1972), despite the higher aerial biomasses (4900 and 4747 kg/ha respectively) of these northern hemisphere tundra vegetations.

The contribution of N to the standing stock of mineral elements in the above-ground biomass of the island vegetation is 42 per cent, slightly lower than that reported in the literature (45–56 per cent) for comparable northern hemisphere tundra vegetations. K predominates amongst the ash elements in the above-ground plant biomass on the island, followed by approximately equal amounts of Ca, Na and Mg and much lower quantities of P and Fe. This contrasts with most other tundra and subpolar vegetations where the content of Ca is usually substantially higher than that of Mg (Rodin & Bazilevich, 1967; Wielgolaski & Kjelvik, 1973; Walton & Smith, in press) and the standing stocks of Na are especially low, usually below those of Fe. In contrast to herbaceous plant species, low-shrub leaves often contain more Ca than K so that in some dwarf-shrub tundra ecosystems the standing stock of Ca may be markedly greater than that of K. (Chepurko, 1972).

There is a substantial accumulation of Ca, Mg and Fe in the dead above-ground component of the island vegetation. Owing to the relatively low below-ground standing crop only. 59 per cent of the mineral elements incorporated in the island vegetation are located underground whereas in typical northern hemisphere tundras more than 80 per cent of the nutrient standing stock is contained in the below-ground sphere (Rodin & Bazilevich, 1967).

Conclusion

Conditions are less severe for plant growth in sub-Antarctic regions than at northern hemisphere tundra sites (Wielgolaski, 1972; Walton *et al*., 1975; Smith, 1977a) and this is reflected in the development of high above-ground standing crops in sub-Antatctic vegetation (Jenkin & Ashton, 1970; Huntley, 1972; Walton, 1973). The high above-ground biomass of the Marion Island vegetation and the predominance of green material in this biomass as well as the influence of sea-spray causes the above-ground component of this vegetation to contain a disproportionately large amount of mineral elements compared to most other tundra vegetation types.

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Table 21

Standing stocks of mineral elements (kg/ha) contained in black and grey lava vegetations

	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
	Vasc.	Cryp.	Total				
Black lava							
Ca	12,06	5,13	17,19	59,13	76,32	65,55	141,87
Mg	12,60	4,26	16,86	43,75	60,61	74,92	135,53
Na	15,86	1,23	17,09	8,35	25,44	49,09	74,53
K	38,40	9,90	48,30	13,83	62,13	149,38	211,51
Fe	0,26	0,39	0,65	5,34	5,99	4,16	10,15
P	5,70	1,72	7,42	12,08	19,50	39,18	58,68
Total ash elements	84,88	22,63	107,51	142,48	249,99	382,28	632,27
N	56,65	19,92	76,57	128,93	205,50	257,24	462,74
Total mineral elements	141,53	42,55	184,08	271,41	455,49	639,52	1095,01
Grey lava							
Ca	2,66	2,79	5,44	14,32	19,76	25,46	45,23
Mg	2,74	2,73	5,46	10,44	15,90	30,60	46,50
Na	4,59	1,01	5,59	2,65	8,25	29,70	37,94
K	11,81	7,22	19,03	4,36	23,40	65,83	89,23
Fe	0,16	0,24	0,40	2,59	2,99	1,69	4,68
P	1,22	1,48	2,70	3,33	6,03	18,82	24,85
Total ash elements	23,18	15,47	38,62	37,69	76,33	172,10	248,43
N	16,23	17,34	33,58	39,13	72,70	98,79	171,49
Total mineral elements	39,41	32,81	72,20	76,82	149,03	270,89	419,92

Table 22

Standing stock of mineral elements (kg/ha) contained in the vegetation of the island's eastern coastal plain

	Above-ground					Below-ground total	Total in s. crop
	Biomass			Dead o.m.	Total above		
Element	Vasc.	Cryp.	Total				
Ca	9,52	4,50	14,02	47,03	61,05	54,73	115,78
Mg	9,94	3,85	13,78	34,76	48,54	62,95	111,49
Na	12,82	1,17	13,99	6,81	20,80	43,85	64,65
K	31,22	9,18	40,40	11,27	51,67	126,82	178,49
Fe	0,23	0,35	0,58	4,60	5,18	3,49	8,67
P	4,49	1,66	6,15	9,72	15,86	33,68	49,55
Total ash elements	68,22	20,70	88,91	114,19	203,10	325,53	528,63
N	45,74	19,22	64,96	104,68	169,64	214,46	384,10
Total mineral elements	113,96	39,92	153,87	218,87	372,75	539,99	912,74

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