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CHAPTER 8

TERRESTRIAL AND FRESHWATER PRIMARY PRODUCTION AND NUTRIENT CYCLING

VALDON R. SMITH

The first biological/geological research expedition to Marion Island in 1965/66 concentrated on the taxonomy of the island's biota and on the physiognomy and floristics of its vegetation (Van Zinderen Bakker *et al.* 1971). The next four expeditions (1971 to 1976) were mostly devoted to quantifying energy flow and nutrient pathways in the island ecosystem, particularly how the transfer of nutrients from the ocean to the island via saltspray, seabirds and seals influences the nutrient composition of freshwaters, soils and plants (Van Zinderen Bakker 1978). In the late 1970s and early 1980s, research at the island was heavily influenced by the systems approach of the International Biological Programme's Biome Project (Rosswall & Heal 1975), which at the time dominated ecological science efforts and had as it's chief objective "to measure net primary production of the main types of terrestrial ecosystems" and "to define the relationships between production and the main factors influencing it" (Heal 1981). Primary production and nutrient cycling of the most common plant communities on the island were investigated.

Subsequent research has focussed on factors that determine rates of the component processes of energy and nutrient flow in the island's ecosystem, such as photosynthesis, decomposition and nutrient interactions between

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plants, soils, micro organisms and soil invertebrates. This chapter describes production and nutrient cycling in the island's vegetation and the factors that influence both. Since most of the energy and nutrients incorporated in the vegetation go through a decomposition rather than a grazing chain, the factors that influence rates of decomposition and nutrient mineralization are discussed, including threats to these processes posed by an invasive alien organism. Finally, an account is given of the primary production and nutrient composition of the island's freshwaters.

8.1 Terrestrial communities

8.1.1 Vegetation standing crop and primary production

Production and nutrient cycling studies have been carried out in eight plant communities:

- A fellfield (dominated by the cushion plant *Azorella selago*).
- Two fernbrakes (an open type with *A. selago*, the fern *Blechnum penna-marina* and the grass *Agrostis magellanica*, and a closed type dominated by *B. penna-marina*).
- A drainage line on a slope (dominated by the dicot herb *Acaena magellanica*, *B. penna-marina* and the moss *Brachythecium rutabulum*).
- Two tussock (*Poa cookii*) grass communities; one a dense cover of *P. cookii*, *Acaena magellanica*, *B. penna-marina* and *B. rutabulum* on a slope occupied by burrowing birds and the other a narrow strip of *P. cookii* with an understory of *A. selago* cushions (some of which occurred over subterranean prion nests) on the crest of a slope.
- Two mire communities (dominated by the graminoids *Agrostis magellanica*, *Uncinia compacta* and *Juncus scheuchzerioides* and several bryophytes).

Together, these communities are representative of about 90% of the island's low altitude vegetation and are described in more detail by Gremmen & Smith (2008). Harvested quadrats were used to estimate standing crop and primary production. At each community, all the above- and belowground plant material in 0.1 m^2 or 0.25 m^2 quadrats was collected at approximately fortnightly intervals throughout the growing season and sorted into species, organ and, for the aboveground material, according to whether it was alive or dead. The plant material was dried at 105°C, weighed and chemically analysed. The dry masses were converted to biomass (the mass of living material per m^2) or necromass (the mass of dead material per m^2). Here, the maximum (biomass plus necromass) value found over the sampling period is reported as the standing crop of the particular community. Peak-trough analyses of the biomass and necromass dynamics (on a per-species basis) over the sampling period were carried out to estimate primary production for each community. The production values were corrected for decomposition

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using rates of disappearance of plant litter contained in nylon mesh bags. Nutrient concentrations in the biomass and necromass were converted to standing stocks, (g nutrient in the vegetation per m^2). Peak-trough analyses of the standing stock dynamics of a particular nutrient over the season yielded estimates of uptake of that nutrient at the particular community. Details of the harvest sampling procedures and computations of standing crop, primary production and nutrient uptake and losses are given by Smith (1987a, b).

8.1.1.1 Standing crop

Despite the low stature of their vegetation (there are no trees or even shrubs on the island, the tallest plants being the tussock grass), all the communities contain substantial amounts of plant matter. Vegetation standing crop (dry mass of living plus dead plant material) is 2 519 to 2 696 g m^{-2} in fellfield and mires, 4 406 to 5 269 g m^{-2} in fernbrakes and the drainage line, and 5 566 to 7 494 g m^{-2} in the tussock grass communities (Table 8.1). Substantial proportions (33% to 82%) of the standing crop occur belowground. Of the aboveground standing crop, much (32% to 82%) is dead plant material; this might also be true for the belowground standing crop but it was not possible to reliably distinguish living from dead roots.

Table 8.1 Vegetation standing crop, standing stocks and pool sizes of nutrients. All values are g m^{-2}. The contribution of bryophytes to the aboveground standing crop or nutrient standing stock is indicated in brackets. From Smith (1987b, 1988a, b) and unpublished data.

Community	Standing crop	Nutrient standing stock			
		N	P	K	Ca
	Tussock grassland				
In vegetation:					
Aboveground live	1 245 (340)	21.90 (6.59)	2.36 (0.71)	13.53 (2.96)	3.32 (1.16)
Aboveground dead	1 375	18.16	1.72	3.07	5.88
Aboveground total	2 620	40.06	4.08	16.60	9.20
Belowground	2 947	35.32	4.27	18.39	5.64
Total above- & belowground	5 566	75.37	8.35	34.99	14.84
In soil:					
Available pool		1.17	3.49	101.82	90.01
Organic pool		981.25	78.50	23.55	341.47
Total soil pool		982.42	81.99	125.37	431.48
Total pool (veg. plus soil):		1 057.79	90.34	160.36	446.32
Proportion of total pool in veg.		7%	9%	22%	3%

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Table 8.1 Continued.

Community	Standing crop	Nutrient standing stock			
		N	P	K	Ca
Drainage line					
In vegetation:					
Aboveground live	1 170 (358)	15.95 (5.20)	1.81 (0.78)	7.60 (2.61)	5.80 (2.42)
Aboveground dead	549	8.70	0.83	1.50	5.69
Aboveground total	1 719	24.65	2.64	9.10	11.49
Belowground	2 687	22.51	2.95	11.97	4.38
Total above- & belowground	4 406	47.16	5.59	21.07	15.87
In soil:					
Available pool		0.33	0.67	12.98	65.67
Organic pool		722.00	41.80	30.40	570.00
Total soil pool		722.33	42.47	43.38	635.67
Total pool (veg. plus soil):		769.49	48.06	64.45	651.54
Proportion of total pool in veg.		6%	11%	32%	2%
Slope crest					
In vegetation:					
Aboveground live	1 121	16.77	2.03	13.23	2.23
Aboveground dead	3 504	35.10	3.27	4.80	16.35
Aboveground total	4 625	51.87	5.30	18.02	18.58
Belowground	2 868	34.09	3.81	15.04	6.91
Total above- & belowground	7 494	85.96	9.11	33.06	25.49
In soil:					
Available pool		0.47	1.03	21.78	7.61
Organic pool		856.75	30.17	37.25	525.22
Total soil pool		857.22	31.20	59.03	532.83
Total pool (veg. plus soil):		943.18	40.31	92.09	558.32
Proportion of total pool in veg.		9%	23%	36%	5%
Closed fernbrake					
In vegetation:					
Aboveground live	592	9.29	1.49	10.22	2.62
Aboveground dead	1 487	20.08	1.18	1.59	11.49
Aboveground total	2 079	29.37	2.67	11.81	14.11
Belowground	3 190	34.62	5.39	19.25	10.08
Total above- & belowground	5 269	63.99	8.06	31.06	24.19
In soil:					
Available pool		0.20	0.89	5.92	42.85
Organic pool		793.28	78.42	14.42	310.50
Total soil pool		793.48	79.31	20.34	353.35
Total pool (veg. plus soil):		857.47	87.37	51.40	377.54
Proportion of total pool in veg.		8%	9%	60%	6%

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Table 8.1 Continued.

Community	Standing crop	Nutrient standing stock			
		N	P	K	Ca
Open fernbrake					
In vegetation:					
Aboveground live	580	7.55	0.81	6.67	3.11
Aboveground dead	1 839	17.68	0.83	0.61	15.65
Aboveground total	2 419	25.23	1.64	7.28	18.76
Belowground	2 036	20.03	2.08	13.23	7.99
Total above- & belowground	4 455	45.26	3.72	20.51	26.75
In soil:					
Available pool		0.15	0.64	3.25	75.33
Organic pool		679.58	59.62	27.32	285.16
Total soil pool		679.73	60.26	30.57	360.49
Total pool (veg. plus soil):		724.99	63.98	51.08	387.24
Proportion of total pool in veg.		6%	6%	40%	7%
Fellfield					
In vegetation:					
Aboveground live	330 (15)	3.86 (0.10)	0.43 (0.01)	4.17 (0.02)	1.95 (0.03)
Aboveground dead	1 483	12.81	0.57	0.13	14.42
Aboveground total	1 813	16.67	1.00	4.30	16.37
Belowground	883	8.38	0.59	6.32	4.85
Total above- & belowground	2 696	25.05	1.59	10.62	21.22
In soil:					
Available pool		<0.01	0.10	1.32	66.97
Organic pool		237.10	42.83	16.17	551.75
Total soil pool		237.10	42.93	17.49	618.72
Total pool (veg. plus soil):		262.15	44.52	28.11	639.94
Proportion of total pool in veg.		10%	4%	38%	3%
Mire 1					
In vegetation:					
Aboveground live	173 (34)	2.25 (0.46)	0.22 (0.03)	2.03 (0.11)	0.23 (0.09)
Aboveground dead	282	2.22	0.15	0.35	0.39
Aboveground total	455	4.47	0.37	2.38	0.62
Belowground	2 064	30.58	2.05	2.57	2.60
Total above- & belowground	2 519	35.05	2.42	4.95	3.22
In soil:					
Available pool		0.69	0.67	5.11	26.66
Organic pool		386.85	18.54	10.40	37.59
Total soil pool		387.54	19.21	15.51	64.25
Total pool (veg. plus soil):		422.59	21.63	20.46	67.47
Proportion of total pool in veg.		8%	11%	24%	5%

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Table 8.1 Continued.

Community	Standing crop	Nutrient standing stock			
		N	P	K	Ca
	Mire 2				
In vegetation:					
Aboveground live	457 (279)	4.04 (2.22)	0.26 (0.11)	5.37 (3.33)	1.16 (1.00)
Aboveground dead	332	2.49	0.15	0.12	0.40
Aboveground total	789	6.53	0.41	5.49	1.56
Belowground	1 759	11.73	0.95	6.46	0.97
Total above- & belowground	2 548	18.26	1.36	11.95	2.53
In soil:					
Available pool		0.26	0.84	6.81	14.09
Organic pool		326.31	18.03	10.33	56.77
Total soil pool		326.57	18.87	17.14	70.86
Total pool (veg. plus soil):		344.83	20.23	29.09	73.39
Proportion of total pool in veg.		5%	7%	41%	3%

High vegetation standing crops have also been reported for other sub-Antarctic islands. On South Georgia, *Festuca contracta*-dominated mires and meadows (which are physiognomically similar to the Marion Island mires) have standing crops of 3 930 to 4 317 g m^{-2} (Greene *et al.* 1973; Lewis Smith & Stephenson 1975), and an *Acaena magellanica* herbfield (very similar to the Marion Island drainage line community) a standing crop of 9 578 g m^{-2} (Lewis Smith & Walton 1975). On Macquarie Island, a *Pleurophyllum hookeri-Stilbocarpa polaris* herbfield 235 m above sea level had a total standing crop of 2 727 g m^{-2}; a similar community at lower altitude had 2 343 g plant material m^{-2} aboveground alone (Jenkin 1975). Like at Marion Island, however, it is the tussock grass-dominated communities that possess the highest standing crops – 8 411 g m^{-2} for *Poa foliosa* tussock at Macquarie (Jenkin 1975) and 17 785 g m^{-2} for *Poa flabellata* tussock at South Georgia (Lewis Smith & Walton 1975).

Sub-Antarctic island vegetation has most often been described as "tundra" since it shows strong physiognomic similarities to Northern Hemisphere tundra vegetation (low-growing, dominated by cryptogams, cushion plants, small shrubs, herbs and graminoids, mostly occurring on wet organic soils or peats). Aboveground standing crops of the Marion Island plant communities (455 to 4 625 g m^{-2}) are mostly higher than values reported for physiognomically-similar vegetation types in Northern Hemisphere tundra (< 100 to 2 500 g m^{-2}), but belowground standing crops at the island are in the range of tundra values. Bryophytes are an important component in many of the island's communities and actually contribute more to the standing crop than is suggested in Table 8.1. The table shows standing crops at the time of peak aboveground mass of living plant material (late March/early April, i.e. late summer/

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autumn). This corresponds to the time of maximum vascular plant live mass but not maximum bryomass, which is in winter and spring. Peak bryomasses are 451 g m^{-2} in the tussock grassland, 482 g m^{-2} in the drainage line and 245 g m^{-2} at mire 1, considerably higher than the values in Table 8.1. However, even these peak values are in the lower part of the range (40 to 1 682 g m^{-2}) of bryomasses found in Northern Hemisphere tundras.

8.1.1.2 Primary production

Annual net primary production (ANP) of all the island's communities is high – from 685 g m^{-2} y^{-1} at fellfield to 2 178 g m^{-2} y^{-1} at one of the mires, and belowground production contributes between 41 and 68% to the ANP (Table 8.2). High ANP values have also been reported from other sub-Antarctic islands; 1 014 g m^{-2} y^{-1} for a herbfield on Macquarie Island (Jenkin 1975) and 842 g m^{-2} y^{-1} and 1 605 g m^{-2} y^{-1} for a *F. contracta* meadow and *Acaena magellanica* herbfield, respectively, on South Georgia (Clarke *et al.* 1971; Lewis Smith & Walton 1975). Very much higher ANPs have been reported for *Poa* tussock grasslands on these two islands – 5 581 g m^{-2} y^{-1} at Macquarie and 6 025 g m-2 y-1 at South Georgia (Jenkin 1975; Lewis Smith & Walton 1975). It is thus somewhat surprising that the two tussock communities on Marion Island (1 982, 1 936 g m^{-2} y^{-1}) were not the most productive of the Marion Island communities.

Excepting for the fellfield, total ANPs of the island communities are higher than those (7 to 885 g m^{-2} y^{-1}) reported for the 52 Northern Hemisphere sites investigated as part of the IBP Tundra Biome Study (Wielgolaski *et al.* 1981). Bryophyte ANPs at the island (172 to 307 g m^{-2} y^{-1}) are in the upper part of the range shown by Northern Hemisphere tundra; e.g. 9 to 350 g m^{-2} y^{-1} at Arctic and sub-Arctic mires and sedge-moss meadows and 5 to 210 g m^{-2} y^{-1} at shrub, dwarf shrub and sedge-heath communities. Even compared with temperate plant communities, ANPs of the island's plant communities are high; for instance, total ANPs at mire 1 (2 178 g m^{-2} y^{-1}), tussock grassland (1 982 g m^{-2} y^{-1}) and slope crest community (1 936 g m-2 y-1) are greater than the maximum (1 425 g m-2 y-1) found for temperate North America grasslands by the IBP Grassland Biome Study (Sims & Singh 1978). They are very much in the upper part of the range reported for temperate wetlands and marshes – vegetation types considered to be particularly productive; e.g. 918 to 1 741 for sedge wetlands (Bernard & Gorham 1978), 1 539 g m^{-2} y^{-1} for bog marshes (Reader 1978) and 2 187 g m^{-2} y^{-1} for a freshwater tidal wetland (Whigham *et al.* 1978).

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Table 8.2 Annual net primary production (ANP) and cycling of nutrients at the plant communities. All values are g m^{-2} y^{-1}. The contribution of bryophytes to the aboveground production is given in brackets. The percentage contribution of belowground to the total ANP is shown in italics. From Smith (1987a, b, c; 1988a, b) and unpublished data.

Community	ANP	N	P	K	Ca
Tussock grassland					
Aboveground	949 (172)				
Belowground	1 033 *52%*				
Total	1 982				
Uptake into aboveground		18.93 (3.34)	2.38 (0.36)	10.36 (1.50)	4.91 (0.60)
Backtranslocated		3.38	0.82	6.55	0
Lost in litterfall		15.55	1.56	3.81	4.91
Uptake into belowground		11.80	1.50	6.34	1.55
Total net uptake for ANP		27.35	3.06	10.15	6.46
Drainage line					
Aboveground	891 (274)				
Belowground	612 *41%*				
Total	1 503				
Uptake into aboveground		17.11 (3.98)	1.94 (0.60)	8.78 (2.00)	8.89 (1.86)
Backtranslocated		2.98	0.41	5.01	0
Lost in litterfall		14.13	1.53	3.77	8.89
Uptake into belowground		4.77	0.73	2.95	1.22
Total net uptake for ANP		18.90	2.26	6.72	10.11
Slope crest					
Aboveground	809				
Belowground	1 127 *58%*				
Total	1 936				
Uptake into aboveground		12.48	1.66	9.55	3.64
Backtranslocated		3.86	0.88	8.33	0
Lost in litterfall		8.62	0.78	1.22	3.64
Uptake into belowground		12.14	1.34	6.12	3.05
Total net uptake for ANP		20.76	2.12	7.34	6.69
Closed fernbrake					
Aboveground	728				
Belowground	1 230 *63%*				
Total	1 958				
Uptake into aboveground		12.05	1.33	8.06	5.71
Backtranslocated		1.64	0.62	6.89	0
Lost in litterfall		10.41	0.71	1.17	5.71
Uptake into belowground		13.94	2.47	8.68	4.01
Total net uptake for ANP		24.35	3.18	9.85	9.72

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Table 8.2 Continued.

Community	ANP	N	P	K	Ca
Open fernbrake					
Aboveground	502				
Belowground	1 076 *68%*				
Total	1 578				
Uptake into aboveground		6.34	0.61	6.34	3.99
Backtranslocated		0.70	0.30	5.82	0
Lost in litterfall		5.64	0.31	0.52	3.99
Uptake into belowground		11.08	1.25	7.70	4.57
Total net uptake for ANP		16.72	1.56	8.22	8.56
Fellfield					
Aboveground	266 (4)				
Belowground	419 *61%*				
Total	685				
Uptake into aboveground		3.54 (0.03)	0.32 (0.004)	3.26 (0.005)	2.14 (0.008)
Backtranslocated		1.04	0.22	3.13	0
Lost in litterfall		2.50	0.10	0.13	2.14
Uptake into belowground		4.04	0.36	3.40	2.24
Total net uptake for ANP		6.54	0.46	3.53	4.38
Mire 1					
Aboveground	883 (307)				
Belowground	1 295 *59%*				
Total	2 178				
Uptake into aboveground		8.97 (3.41)	0.72 (0.15)	4.41 (1.47)	1.85 (0.89)
Backtranslocated		0.69	0.22	2.09	0.03
Lost in litterfall		8.28	0.50	2.32	1.82
Uptake into belowground		16.55	1.29	3.00	2.10
Total net uptake for ANP		24.83	1.79	5.32	3.92
Mire 2					
Aboveground	570 (253)				
Belowground	547 *49%*				
Total	1 117				
Uptake into aboveground		6.17 (1.75)	0.56 (0.13)	5.78 (3.85)	1.35 (0.98)
Backtranslocated		1.06	0.31	1.76	0
Lost in litterfall		5.11	0.25	4.02	1.35
Uptake into belowground		4.38	0.31	2.29	0.35
Total net uptake for ANP		9.49	0.56	6.31	1.70

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8.1.1.3 Growth season duration, primary productivity and production efficiency

The island's hyperoceanic climate results in small seasonal and diurnal variations in temperature and in rain falling throughout the year (le Roux 2008). On temperature and moisture considerations, the growing season for the vegetation is potentially long. From the harvest quadrat data and phenological observations (Huntley 1970, 1972), the growing season for vascular plants at low altitudes (< 300 m) is mid-August to mid-June, or about 10 months. Bryophytes carry out most of their growth during the same period but there is some bryomass production even in midwinter (Smith 1987a). Long growing seasons have also been suggested for other sub-Antarctic islands (Wielgolaski *et al.* 1981). By contrast, the Northern Hemisphere tundra communities mentioned in the comparisons above have much shorter growing seasons, from a few weeks at high Arctic sites to about 6 months for sub-Arctic and alpine tundras. It is the long growing season that allows such high annual primary productions at sub-Antarctic islands, rather than any intrinsic capability of the vegetation to grow fast. In fact, production rates (termed here *productivity*, and considering only the aboveground ANP) are between 0.9 g m^{-2} day^{-1} for fellfield and 3.1 g m^{-2} day^{-1} for tussock grassland, lower than aboveground productivities of most sub-Arctic shrub- or dwarf shrub-dominated tundras (3 to 10 g m^{-2} day^{-1}; Wielgolaski *et al.* 1981) where the growing season is thermally more favourable for plant growth. They are more similar to the productivities (2.2 to 3.3 g m^{-2} day^{-1}; Wielgolaski *et al.* 1981) of sedge-moss and grass-herb communities at higher latitude Arctic regions, which also have cool summers.

The low productivities are also related to low radiation levels at the island. The oceanic climate results in incessant cloudiness and the daily radiation receipt in the growing season is only about 50% of that at the top of the atmosphere. This is lower than at polar and sub-polar regions of the Northern Hemisphere. Production efficiencies of the island's plant communities, based on the radiation receipt for the seasons when the production studies were carried out (mean, 409 x 10^4 kJ m^{-2}) and the energy contents of the plants (Smith 1987c), and considering both above- and belowground components, are between 0.7% (fellfield) and 2.1% (mire 1), similar to values (0.7% to 2.4%) for sub-Arctic and Arctic tundras (Wielgolaski *et al.* 1981). This shows that although the island vegetation grows more slowly during the growing season, it uses the incident radiation as effectively as do the Northern Hemisphere tundras.

Various regression models relating primary production to temperature, precipitation or evapotranspiration have been proposed (Whittaker 1970; Lieth 1972, 1974; Lieth & Box 1972; Lauenroth 1979; Walter 1979). They all predict higher ANPs at Marion Island than what are actually found. For instance, Lieth's model (Lieth 1974), which is reasonably successful across a range of other vegetations, from tundra to tropical, predicts an aboveground ANP of 990 g m^{-2} y^{-1} based on temperature and 1 968 g m^{-2} y^{-1} based on precipitation. Both predictions are higher than any of the measured values (266 to 949 g m^{-2} y^{-1}, Table 8.2), suggesting that, in addition to temperature and

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precipitation, other factors are important in determining primary production at the island. The role of light has been mentioned above. Wind is another factor that has long been considered an important, even dominant, factor for the vegetation of sub-Antarctic islands (Skottsberg 1912; Taylor 1955; Löffler 1983). The almost incessant high wind is a strong determinant of vegetation structure at Marion Island (Huntley 1971; Gremmen 1981) and it probably also influences vegetation function through its chill-factor effect and by depressing stomatal conductance. A similar suggestion was made by French & Smith (1985), based on multivariate ordination comparisons of microclimatic, edaphic and vegetation parameters from sub-Antarctic, Northern Hemisphere tundra and oceanic moorland ecosystems. In the ordinations based on climate only, sub-Antarctic plant communities linked with Northern Hemisphere tundra communities at a higher latitude than their own. Including vegetation and soil parameters in the ordinations increases the latitudinal shift, so that the vegetation and its variation at sub-Antarctic islands is more typical of the most climatically-extreme high-latitude Arctic sites than of sub-Arctic tundras or oceanic moorlands. French & Smith (1985) concluded that abiotic factors other than those included in the ordination analyses must be having a marked effect on the vegetation of sub-Antarctic islands and suggested that the most important one is wind. Smith and Steenkamp (2001; see also Gremmen & Smith 2008) showed that the most widespread vegetation type on Marion Island, that of mid-to-high altitude regions exposed to exceptionally strong winds, is structurally (an extremely sparse vegetation made up only of mosses and lichens on a barren unstable surface caused by active periglacial activity) and functionally (ecosystem processes controlled by abiotic rather than biotic factors) typical of high Arctic polar deserts, the most climatically-extreme type of tundra.

8.1.2 Nutrient cycling

8.1.2.1 Nutrient pool sizes

Nutrient pool sizes in the communities are given in Table 8.1. The total N pool (N in the vegetation and the soil) is low in fellfield (262 g N m^{-2}) due to shallow soils with low N concentrations. N and P pools in the mires (345 to 423 g N m^{-2}, 20 to 22 g P m^{-2}) are lower than at the slope communities (725 to 1 058 g N m^{-2}, 40 to 90 g P m^{-2}). This is due to lower peat bulk densities at the mires rather than lower gravimetric N or P concentrations, which are actually similar to those of the slope communities. Ca pools are largest in the communities dominated by dicotyledonous plants or on mineral soils (e.g. the drainage line and fellfield with > 600 g Ca m^{-2}) and lowest in communities dominated by graminoids and bryophytes and on peats (e.g. the mires with *c*.70 g Ca m^{-2}).

The pattern of K pool size across the communities is less clear and does not follow a simple differentiation between slope/mire or dicot/graminoid-

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bryophyte vegetation. K pool size is closely related ($r^2 = 0.71$, $P < 0.001$) to the amount of aboveground living plant material (especially living leaves), which contains much higher concentrations of K than does dead or belowground plant material. It also correlates strongly with soil K concentration ($r^2 = 0.94$; $P < 0.001$). Hence, tussock grassland, with a large proportion of living leaf material and enriched in soil K by burrowing birds (Smith 1976), has the largest K pool (160 g K m^{-2}) of all the communities. For all the communities, 22 to 60% of the total K pool is contained in the vegetation. Only 3 to 11% of the total pools of N, P or Ca occur in the vegetation, except for P at the slope crest community, where the vegetation contains 23% of the total P pool.

Total N pools at the island (262 to 1 058 g N m^{-2}) are similar to those found for other sub-Antarctic and Maritime Antarctic plant communities (426 to 1 164 g N m^{-2}), Northern Hemisphere tundras (330 to 1 014 g N m^{-2}) and oceanic moorlands, bogs and montane grasslands (309 to 1 075 g N m^{-2}; all these non-Marion Island values are from collations of nutrient pool size information by Smith 1987b, 1988a). P pools at the island (20 to 90 g m^{-2}) are lower than for most Northern Hemisphere tundras (42 to 461 g P m^{-2}) and are more similar to those (9 to 85 g P m^{-2}) for oceanic bogs, heaths and grasslands. As is the case at Marion Island, soils at these oceanic sites are highly organic peats with low total P concentrations. K pools of the island's communities (20 to 160 g K m^{-2}) are in the lower part of the range of values (16 to 474 g K m^{-2}) reported for Northern Hemisphere tundras and similar to those (17 to 160 g K m^{-2}) for oceanic bogs, heaths and grasslands. The strong distinction in Ca pool size between graminoid/bryophyte-dominated vegetation and dicot-dominated vegetation is also shown in Northern Hemisphere tundra. Within the two types, Ca pools at the island are smaller than in the Northern Hemisphere communities. The two mires possessed 67 to 73 g Ca m^{-2}, compared with 134 to 750 g Ca m^{-2} for tundra sedge meadows and tundra grasslands, and the fellfield and slope communities have Ca pools of 378 to 652 g Ca m^{-2}, compared with 537 to 1 219 g Ca m^{-2} for shrub and heath tundras. In summary, the island communities have total N pools that are similar to, but total P, K and Ca pools that are lower than, their counterparts in Northern Hemisphere tundra.

Despite the fact that most of the total nutrient pool occurs in the soil, rather than the plants, the island vegetation actually supports larger N, P and K standing stocks (quantity of nutrients contained in plant material; Table 8.1) than most Northern Hemisphere tundras, especially if only the aboveground vegetation is considered. This reflects the higher vegetation standing crops on the island and the fact that the island's climate allows for greater aboveground plant growth than in Northern Hemisphere tundra, which is more climatically-extreme and where a greater proportion of nutrient standing stocks are maintained in belowground plant parts. In contrast to the larger N, P and K, standing stocks, Ca standing stocks at the island are lower than in most tundra vegetations.

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8.1.2.2 Nutrient uptake, nutrient turnover times and nutrient costs of the ANP

The high ANP means that the vegetation takes up substantial amounts of nutrients; 7 to 27 g N m^{-2} y^{-1}, 0.5 to 3 g P m^{-2} y^{-1}, 5 to 10 g K m^{-2} y^{-1} and 2 to 10 g Ca m^{-2} y^{-1} (Table 8.2). In some instances the quantity taken up annually is greater than the standing stock of the particular nutrient in the vegetation (Table 8.1), suggesting fast circulation rates. Nutrient turnover times in the vegetation (Table 8.3) are, in fact, short (1.4 to 4.1 years for N, 1.4 to 4.3 y for P, 0.9 to 4.5 y for K and 0.8 to 4.8 y for Ca), in the lower part of the range reported for Northern Hemisphere tundra vegetation (1.1 to 17.5 y for N, 1.0 to 14.0 y for P, 0.9 to 15.0 y for K and 1.5 to 17.0 y for Ca; Dowding *et al.* 1981; Van Cleve & Alexander 1981). However, despite the large amounts of nutrients taken up in the ANP, and the fast circulation rates through the vegetation, only a small fraction (1 to 8%) of the total pools of N, P or Ca circulates annually through the vegetation (Table 8.3). A larger proportion (6 to 26%) of the total K pool circulates through the vegetation.

Nutrient costs (the amounts of nutrient required to produce one g of plant material) are given in Table 8.3. For particular nutrients, the difference in cost between communities is mostly related to differences in the type of plant material (species, organ) that form the predominant component of the ANP. Hence, the amount of Ca taken up per g ANP is low for the mires (1.5 to 1.8 mg Ca g^{-1}), where monocotyledon plants and bryophytes (with a low Ca requirement) contribute solely to the ANP, and high for the fellfield, fernbrakes and drainage line (5.0 to 6.7 mg Ca g^{-1}), where dicotyledon plants and *B. penna-marina* (with a substantial requirement for Ca) predominate in the ANP. Intermediate Ca costs are shown by the tussock grassland and slope crest communities, where monocotyledon and dicotyledon plants both contribute to the ANP. *Blechnum penna-marina* fronds also have a high growth requirement for K and contribute a substantial proportion of the ANP at the tussock grassland, fellfield and fernbrakes, accounting for the high K cost of the ANP at these communities. ANP at mire 2 also carries a high K cost, and, interestingly, there is a different relationship between the N and K costs of the two mire communities. N cost is greater at mire 1 than at mire 2, whereas the opposite is true for K cost. This is because the bryophyte layer at mire 1 comprises mainly *Jamesoniella colorata* and *Racomitrium lanuginosum* which, like most of the other bryophytes on the island, accumulate more N than K. Mire 2 is dominated by two bryophytes (*Blepharidophyllum densifolium* and *Clasmatocolea humilis*) that are unusual in that they accumulate more K than N (Smith 1987d).

There is no information on the costs of individual nutrients to the ANP of Northern Hemisphere tundra, but Swift *et al.* (1979) reported the *total nutrient costs* (i.e. the sum of the costs of N, P, K, Ca, Mg Na, Si, Fe and Mn) of the aboveground ANP for 18 vegetation types, ranging from tundra to tropical forest. Total nutrient costs for the island's communities (17 to 40 mg nutrients g^{-1} aboveground ANP; Table 8.3) are very much in the lower part of the range (18 to 135 mg g^{-1}) for the vegetations considered by Swift *et al.* (1979). Boreal

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Table 8.3 Nutrient cycling parameters for the communities. From Smith (1987b, 1988a, b) and unpublished data.

Community	N	P	K	Ca	N	P	K	Ca
	Turnover time in vegetation (years)				Percentage of total nutrient pool that circulates through the vegetation annually (%)			
Tussock grassland	2.8	2.7	3.4	2.3	3	3	6	1
Drainage line	2.5	2.5	3.1	1.6	3	5	10	2
Slope crest	4.1	4.3	4.5	3.8	2	5	8	1
Closed fernbrake	2.6	2.5	3.2	2.5	3	4	19	3
Open fernbrake	2.7	2.4	2.5	3.1	2	2	16	2
Fellfield	3.8	3.5	3.0	4.8	3	1	13	1
Mire 1	1.4	1.4	0.9	0.8	6	8	26	6
Mire 2	1.9	2.4	1.9	1.5	3	3	22	2
Community	**N**	**P**	**K**	**Ca**	**Total nutrients**			
	Nutrient "cost" of the above- and belowground ANP (mg nutrient taken up per g ANP)				Total nutrient cost of the aboveground ANP only (mg g^{-1})			
Tussock grassland	13.8	1.5	5.1	3.3	34.0			
Drainage line	12.6	1.5	4.5	6.7	40.1			
Slope crest	10.7	1.1	3.8	3.5	21.9			
Closed fernbrake	12.4	1.6	5.0	5.0	33.1			
Open fernbrake	10.6	1.0	5.2	5.4	27.9			
Fellfield	9.5	0.7	5.1	6.4	23.9			
Mire 1	11.4	0.8	2.4	1.8	17.4			
Mire 2	8.5	0.5	5.6	1.5	22.1			
Community	**N**	**P**	**K**	**Ca**	**N**	**P**	**K**	**Ca**
	Percentage of amount taken up aboveground by vascular vegetation that is backtranslocated (%)				Replenishment of available nutrient pool needed to meet the vegetation's requirements (times per year)			
Tussock grassland	22	40	74	0	23	0.9	0.1	0.1
Drainage line	23	31	74	0	57	3.4	0.5	0.2
Slope crest	31	53	87	0	44	2.1	0.3	0.9
Closed fernbrake	14	47	85	0	122	3.6	1.7	0.2
Open fernbrake	11	49	92	0	111	2.4	2.5	0.1
Fellfield	30	71	96	0	2 179	4.6	2.7	0.1
Mire 1	12	39	71	3	36	2.7	1.0	0.1
Mire 2	24	71	92	0	36	0.7	0.9	0.1

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forests are generally regarded as being extremely efficient at maintaining appreciable primary production levels under severe nutrient limitation and the lowest nutrient costs (18 to 25 mg nutrients g^{-1}) given by Swift *et al.* (1979) were, in fact, for three boreal forests. The island's fellfield (24 mg nutrients g^{-1}) and mires (17 and 22 mg g^{-1}) are as efficient in maintaining their productivity at a low unit nutrient uptake.

This efficiency is achieved mainly by having plant tissue with low nutrient concentrations (N, P and Ca concentrations in the mire graminoid plants and bryophytes are considerably lower than in tundra graminoids and bryophytes; Smith 1987b), rather than by conserving nutrients through efficient backtranslocation of nutrients from senescing tissue into perennial organs. This is apparent from the short turnover times of all the nutrients in the vegetation, but also from estimates of the amounts of nutrients taken up into the aboveground vascular vegetation that are retranslocated to storage organs (mainly leaf sheaths, stem bases, rhizomes and roots) before senescence (Table 8.3). Only 12 to 31% of the N taken up into the aboveground vascular vegetation is retranslocated, the rest is lost in the litterfall. For P, less than half of the amount taken up is retranslocated, except for the fellfield and one of the mires, where 71% of the P is retranslocated. In tundra vegetation commonly more than 50%, and up to 90%, of the aboveground N and P is retranslocated before senescence (Berendse & Jonasson 1992). Between 71 and 96% of K taken up by the island vegetation is retranslocated. This is in the upper part of the range for tundra plants but might be an overestimate due to possible leaching of K from senescing tissue. Almost all the Ca taken up into the aboveground vascular vegetation is lost in the litterfall.

8.1.2.3 Plant-available nutrient pools and their replenishment rates

The communities considered in this chapter possess low soil levels of plant-available forms of P, and exceptionally low levels of plant-available N. Pools of available N (NH_4-N + NO_2-N + NO_3-N) were between < 0.01 and 1.2 g N m^{-2} (Table 8.1), corresponding to volumetric soil concentrations of between 0.004 and 4.68 μg N cm^{-3}. Even the most ultra-oligotrophic sub-Arctic and Arctic tundra mire peats possess much higher concentrations of inorganic N (17 to 43 μg N cm^{-3}; Gersper *et al.* 1980; Rosswall & Granhall 1980). Similarly, available P pools in the island's communities (0.1 to 3.5 g P m^{-2}; Table 8.1) equate to volumetric concentrations of 0.4 to 14 μg P cm^{-3}, in the lower part of the range for tundra soils (0.1 to 101.4 μg P cm^{-3}; Brown & Veum 1974; Everett *et al.* 1981). There is a close correlation between N and P concentrations in plant litter and the amounts of available N and P in the soils (Figs 8.1a, b). Likewise, N and P concentrations in the bryomass (which in some communities form the main input into the decomposer system, but for which dead shoots cannot be distinguished from live ones) are also positively related to available N and P levels (Figs 8.1c, d). The significance of the positive relationship between plant litter or bryomass N and P concentrations and soil levels of available N and P will become apparent later.

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The available N pool needs to be replenished from 23 to 2 179 times per year to meet the vegetation's annual requirement for N (Table 8.3). The P pool needs to be replenished 0.7 to 4.6 times per year. The available Ca pool at all the communities is larger than the vegetation's annual requirement and needs to be replenished only every 1.1 to 10 years. Available K pools need to be replenished 1.7 to 2.7 times per year at the fernbrakes and fellfield (where *B. penna-marina* fronds take up substantial amounts of K), but K pools at the other communities are at least as large as the annual requirement.

8.1.2.4 Nutrient inputs

The fact that the available N pools need to be turned over much more rapidly (from four hours at fellfield to 16 days at the tussock grassland) than the pools of available P, K or Ca (80 days to 10 years) suggests that N might be the element most likely to limit primary production. Only the tussock grassland (possibly also the slope crest community) is directly influenced through manuring of birds (Smith 1976), but ammonia from penguin rookeries in the nearby shore zone reaches the communities via precipitation and dry deposition. However, as a source for replenishing the N pool, this is insignificant, bringing in only 0.21 g N m^{-2} y^{-1} (Smith 1987e), or 1 to 3% of the annual requirement for N by the vegetations of the various communities. Precipitation also supplies only 4 to 11% of the K, and 4 to 22% of the Ca, needed for plant growth. No P occurs in the precipitation. None of the island's plants form associations with N-fixing rhizobia, but nitrogen is fixed by heterotrophic soil bacteria (Smith 1985) and cyanobacteria (the latter in algal mats on the soil surface and as epiphytes on mosses; Smith 1984). For five of the eight communities considered here the amounts of N fixed heterotrophically- and autotrophically were determined. In total, a maximum of 0.1 g N m^{-2} y^{-1} is added to the communities by N fixation (Smith 1988b), a negligible amount compared with the needs of the vegetation.

By contrast with the very small pools of plant-available (inorganic) N, the island's soils contain appreciable reserves of organic N (237-981 g N m^{-2}; Table 8.1). This is also true of the other nutrients (e.g. 18-79 g P m^{-2} and 10-39 g K m^{-2}) and is because the low level of herbivory leads to most of the plant material produced in the ANP becoming incorporated into the soil. Decomposition, with its concomitant mineralization of nutrients from organic matter, is the chief process by which the available nutrient pools in the soil are replenished. However, the same oceanicity of climate (no warm periods and high, recurrent precipitation) leads to cold, waterlogged, acid, leached soils, all of which are expected to restrict soil microbial activity. It has been shown that decomposition, with the concomitant release of nutrients, is the main bottleneck in nutrient cycling and primary production for most of the island's plant communities (Smith 1988b; Smith & Steenkamp 1992a). Consequently, much research has focussed on understanding decomposition of plant litter and soil organic matter at the island.

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8.1.3 Decomposition and nutrient mineralization

8.1.3.1 Decomposition and soil heterotrophic activity

Vascular plant leaf litter enclosed in mesh bags shows a 33 to 59% mass loss over the first year (excepting for *B. penna-marina* fronds which lose only 13% of mass, possibly because they contain high concentrations of polyphenols; unpublished data). This is higher than mostly found from litter bag studies at Arctic (10 to 20%; Widden 1977) or sub-Arctic (4 to 42%; Rosswall *et al.* 1975) tundras and is more similar to loss rates of litters in warm oceanic bogs, mires and moorlands (16 to 57%; Heal *et al.* 1981).

The most intensive and extensive study of decomposition at the island has been an assessment of soil decomposition potential using the so-called "cotton strip" technique (Harrison *et al.* 1988) which is based on the tensile strength loss (TSL) of standardised cotton strips buried in soil. There are strong correlations between TSL and other measures of decomposition, such as plant litter mass loss (Heal *et al.* 1974) and nutrient mineralization (French 1988). The cotton strip technique has been shown to be useful for comparing soil decomposition potentials between different communities and even ecosystems, especially in cold temperate and sub-polar regions (Heal *et al.* 1981; Walton 1988; Wynn-Williams 1988). TSL rates of the island's non-manured soils are at the upper extreme of the range found for tundra, largely due to the relatively greater warmth of the island's soils (Smith *et al.* 1993). Soil nutrient status is the most important determinant of TSL, so that the island's manured soils have TSL rates up to an order of magnitude greater than those in tundra.

Soil respiration rate (as measured by the efflux of CO_2) in the unmanured communities considered in this chapter ranges from 0.9 μmol CO_2 g^{-1} h^{-1} (fellfield, to 6.3 μmol CO_2 g^{-1} h^{-1} (mire) (Smith 2003), very similar to those reported for arctic and sub-arctic tundra soils (0.2 to 6.0 μmol CO_2 g^{-1} h^{-1}; Nadelhoffer *et al.* 1991; Vanhala *et al.* 1996; Vance & Chapin 2001). However, these comparisons are based on respiration rates at 10°C. For most of the year tundra soils are much colder, mostly frozen, and soil activity will be low. By contrast, soil temperature under closed vegetation on the island is much more stable throughout the year (Blake 1997) and freezing does not occur. Like TSL, soil respiration is also very markedly enhanced by animal manuring, due to inorganic nutrient enrichment (Smith 2003) as well as an enhanced input of labile organic C substrate in the form of excreta (Smith 2005). Mean respiration rate of tussock grassland soils is 9.4 μmol CO2 g^{-1} h^{-1} at 10°C; soils more heavily influenced by birds or seals have up to three times higher rates.

The importance of seabirds and seals has also been shown for other decomposition-related soil characteristics. For instance, 48% of the variation in plate-count numbers of soil aerobic bacteria is explained by differences in soil inorganic N content, related to the manuring influence of seabirds or seals (Smith & Steyn 1982). Direct (epifluorescence microscopy) counts of soil

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bacteria are also significantly positively related to soil N and P levels (French & Smith 1986). From information on bacterial cell numbers, types (shapes and sizes) and total volumes, French & Smith (1986) predicted the growth and metabolic activities of soil bacteria in relation to site conditions. Grobler *et al.* (1987) subsequently showed that bacterial metabolic activity (^{14}C-glucose kinetics and dehydrogenase activity) varied across communities in the manner predicted: manured soils have higher bacterial activity than unmanured soils, but within these two groups there is a clear effect of altitude (taken to indicate climatic severity). The pattern of TSL across the plant communities is also entirely consistent with the soil heterotrophic activity data of Grobler *et al.* (1987).

8.1.3.2 Nutrient mineralization and the role of soil fauna

Detailed investigations of nutrient mineralization rates have only been carried out at one of the communities (mire 1) and only N has been considered. From changes in peat inorganic N concentrations and concomitant uptake rates by the mire vegetation, it has been calculated that mineralization rates are 178 mg N m^{-2} d^{-1} in summer and 55 mg N m^{-2} d^{-1} in winter (Smith & Steenkamp 1992a). In mid-summer, when the vegetation is growing most actively, the rate of uptake by the vegetation is 336 mg N m^{-2} d^{-1}, equivalent to a mineralisation of 0.1% of the organic reserve of N per day. Laboratory and field measurements, by several techniques, of N mineralization in the mire peat all yield values that are too low to account for these estimated rates of N release, or for the requirements of the vegetation. For instance, at the maximum measured mineralisation rate (48 mg N m^{-2} d^{-1}; Smith & Steenkamp 1992a), uptake by the vegetation in summer would have led to depletion of the available N pool in about seven days.

These mineralization results are limited by the usual ambiguities associated with simplistic N transformation studies that consider small soil samples and where the fate of some of the inorganic forms of N are uncertain (e.g. it is not known how important denitrification is at the island). However, their main shortcoming is that they reflected N release by microbial organisms on their own, ignoring the effect of soil fauna. The island's soils contain large numbers of meso- and macrofauna (e.g., nematodes, springtails, mites, earthworms and insect larvae (Burger 1978; Gabriel *et al.* 2001; Barendse *et al.* 2002), most of which are detritivores and/or microbivores, and which account for a substantial proportion of energy flow at the island. For instance, Crafford (1990a) estimated that the larvae of one moth species alone consumes about 150 g plant litter m^{-2} y^{-1} and also processes large quantities of peat.

Soil fauna stimulate decomposition rate by comminuting the decomposing substrate, by chemically altering it so that it is more amenable to microbial action, and by enlarging the suite of microorganisms acting on it (Anderson *et al.* 1981). Microcosm studies have confirmed that this is true for the island's soil fauna (Smith & Steenkamp 1992b, 1993). The release of inorganic nutrients from decomposing plant litter and peat in the microcosms, with or without

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macroinvertebrates, is shown in Table 8.4. Moth larvae (*Pringleophaga marioni*) and earthworms (*Microscolex kerguelarum*) significantly enhance mineralization rates of N, P and K from litter. The effect is even more marked with peat, where N release is up to 30 times faster in the presence of moth larvae, earthworms or weevil larvae. No inorganic P release can be detected in microcosms containing only peat but there is substantial release when moth larvae or earthworms were present.

Table 8.4 Release rates of nutrients from plant litter or peat in microcosms (μg nutrient g^{-1} litter or peat d^{-1}, ± standard error). "Control" indicates microcosms without macroinvertebrates. Otherwise the microcosms contained either two moth larvae, two earthworms or five weevil larvae. Four plant (species) litters were tested with moth larvae and three with earthworms. Asterisks indicate that the difference between the animal and control microcosms is significant at ***P = 0.001 or **P = 0.01. From Steenkamp (1991).

Plant litters	N	P	K	Ca
Control	0.7 ± 0.06	0.3 ± 0.05	2.8 ± 0.27	1.3 ± 0.22
Moth larva	3.8 ± 0.68***	1.1 ± 0.19***	5.0 ± 0.12***	2.2 ± 0.20***
Control	0.7 ± 0.04	0.4 ± 0.04	3.3 ± 0.17	0.9 ± 0.13
Earthworm	1.8 ± 0.17***	0.7 ± 0.10**	4.0 ± 0.25**	0.9 ± 0.12
Peat	**N**	**P**	**K**	**Ca**
Control	1.5 ± 0.26	0	0.8 ± 0.09	2.2 ± 0.03
Moth larva	42.1 ± 2.45***	8.4 ± 0.69***	7.4 ± 0.99***	2.5 ± 0.16
Earthworm	29.9 ± 1.50***	8.0 ± 0.79***	2.0 ± 0.05***	2.3 ± 0.33
Weevil larva	10.2 ± 1.07**	0	2.4 ± 0.18***	1.4 ± 0.06***

Smith & Steenkamp (1992c) used the microcosm results in a model to estimate rates of N cycling at mire 1. The model considered macroinvertebrate densities, peat:macroinvertebrate mass ratios, microorganism biomasses, N pool sizes of the soil microorganisms and of the macroinvertebrates, temporal changes in soil inorganic N concentration and rates of N uptake by the vegetation. Of specific interest here is the contribution of macroinvertebrates to N mineralization. Earthworms cause the release in the mire peat of 265 mg N m^{-2} d^{-1}, moth larvae 67 mg N m^{-2} d^{-1}, weevil larvae 8 mg N m^{-2} d^{-1}, snails 0.7 mg N m^{-2} d^{-1} and slugs 4.3 mg N m^{-2} d^{-1}. To this combined total of 345 mg N m^{-2} d^{-1}, due to the macroinvertebrates, must be added the 48 mg N m^{-2} d^{-1} caused by microbes alone. This gives a total mineralization rate of 393 mg N m^{-2} d^{-1}, sufficient to account for the maximum daily requirement for N by the vegetation plus the observed concomitant changes in peat inorganic N in midsummer (336 mg N m^{-2} d^{-1}). A mineralization of 393 mg N m^{-2} d^{-1} means that soil macroinvertebrates and microorganisms together release an amount of N equivalent to that contained in their combined biomasses (1.2 g N m^{-2}) at mire 1 in three days. This indicates a very short turnover time of N in the two components (more correctly, it is a "pseudo-residence time"; Frissel 1981)

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and clearly shows that although soil macroinvertebrates and soil microflora constitute only a small fraction of the total N pool (0.3% at mire 1), their interaction is a crucial determinant of N mobilization.

The contribution of soil fauna to the release of nutrients besides N has not been quantified since no field studies have been carried out to parameterise the model. A simple extrapolation of the enhancements of P, K and Ca release from peat in microcosms (Table 8.4), using invertebrate densities at mire 1 given by Smith & Steenkamp (1992c), suggests a mineralization of 5.5 g P y^{-1} through the combined action of moth larvae, earthworms and weevil larvae, or about three times the annual requirement of the mire vegetation (1.8 g m^{-2} y^{-1}; Table 8.2). For K, the three invertebrate species cause a release of about 1.5 g m^{-2} y^{-1}, which is only a third of the vegetation's requirement. However, as shown in Table 8.3 there is substantial recirculation of K within the vegetation and the mean pool size of plant-available K in the soil is equal to the annual requirement. None of the three invertebrate species significantly stimulate release rate of Ca from peat over that caused by microorganisms alone. In fact, weevil larvae cause a net immobilization of Ca (Table 8.4). Microbially-mediated Ca mineralization is probably fast enough to replenish the available Ca pool, which at mire 1 is about 10 times larger than the amount taken up annually by the vegetation.

8.1.3.3 Impact of invasive biota on nutrient cycling

Factors detrimental to the soil macroinvertebrate populations will impact on nutrient cycling and hence on vegetation production at the island. One such factor that has been identified is the introduced House Mouse (*Mus musculus*) which has become feral on the island (Matthewson *et al.* 1994). Smith *et al.* (2002) investigated the diet of mice at three sites near the communities at which production and nutrient cycling studies were carried out. They showed that, on average over the year, moth larvae and adults, weevil larvae and adults and earthworms together contribute between 51% and 81% to the volume of stomach contents of the mice. Mice daily consume between 45 and 184 g (dry mass) ha^{-1} of those invertebrates; daily consumption of moth larvae alone is between 30 and 107 g ha^{-1}. These values agree with those from earlier studies. For instance, Rowe-Rowe *et al.* (1989) estimated that mice consume 108 g macroinvertebrates ha^{-1} d^{-1} on the island's coastal plain as a whole, 65 g ha^{-1} d^{-1} being moth larvae (Crafford 1990a). The species-specific consumption rates found by Smith *et al.* (2002) and Crafford (1990a) imply that mice annually remove between a third and six times the instantaneous biomass of the macroinvertebrate prey species in the particular study areas. This must severely impact on the macroinvertebrates, especially since most have long life cycles (e.g. the moth larvae take 2-10 years to mature; Crafford 1990b; see also Barendse & Chown 2000), and confirms conclusions from other studies that mice are cardinal determinants of macroinvertebrate population dynamics on the island (Crafford & Scholtz 1987; Chown 1990;

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Chown & Smith 1993). It offers an explanation for the decline in densities of the preferred macroinvertebrate prey (moth larvae, weevil larva and adults, and spiders; Hänel 1999).

In the context of this chapter, predation by mice on terrestrial macroinvertebrates causes decreased rates of nutrient mineralization, quantitatively and qualitatively affecting vegetation production. A lowered nutrient availability will not only lower primary production, but the plant material which is produced will have a lower nutrient concentration (Fig. 8.1), resulting in a lower quality litter that will decompose even more slowly. Ultimately, this will change the balance between peat accumulation and decay, which is the most important factor governing vegetation succession at the island (Smith *et al.* 2001). This, along with the more direct effects of mice on the vegetation (e.g. granivory; Chown & Smith 1993), is a striking example of how insidious the effects of an alien invasive species may be on ecosystem structure and function at an oceanic island, especially when the invader is in a functional group or groups (in this instance, terrestrial herbivore and insectivore) poorly represented or absent at the island.

The limacid European slug *Deroceras panormitanum* was inadvertently introduced to the island in the mid- to late 1960s (Smith 1992). Since then it has spread throughout the low altitude regions of the island and in some habitats occurs in greater numbers than any indigenous macroinvertebrate. Slugs do not appear to be preyed on regularly by mice since their remains are seldom found in mouse stomach contents and captured starved mice refuse offered slugs (Smith *et al.* 2002). Like the indigenous macroinvertebrates, slugs markedly stimulate rates of nutrient release from plant litter (Smith & Steenkamp 1992b). However, they cause inorganic nutrient release rates that, relative to rates of carbon release, are different to those caused by indigenous invertebrates. This leads to different carbon:nutrient ratios in the decomposing substrate, ultimately affecting peat nutrient quality and hence primary production (Smith 2007) and suggesting that slugs cannot simply replace indigenous macroinvertebrates as nutrient recyclers without consequences for ecosystem structure and functioning on the island.

8.1.3.4 Climate change and nutrient cycling

The island's climate has changed significantly over the past 40 years, having become warmer and drier (Smith 2002; le Roux 2008). A warmer, drier climate will directly influence ecological functioning at the island through its effect on changed rates of primary production, decomposition and nutrient cycling. Climate change will also have other, less direct effects, as discussed by Smith & Steenkamp (1990), Gremmen & Smith (2008) and Smith & Froneman (2008). For instance, altered atmospheric and oceanic circulation patterns underlie the climatic changes at the island (Rouault *et al.* 2005) and this might affect the trophic dynamics of the seal and seabird populations, by moving their feeding grounds, or making it harder/easier for them to reach the feeding grounds.

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This will result in a changed rate of transfer of nutrients from the ocean to the island, an important determinant of ecosystem function at the island. However, probably the most important effect of a warming climate is that it increases the ease with which invasive alien organisms can become established on the island (Bergstrom & Chown 1999). Like the example of the House Mouse, this can have far-reaching implications for ecological functioning at the island.

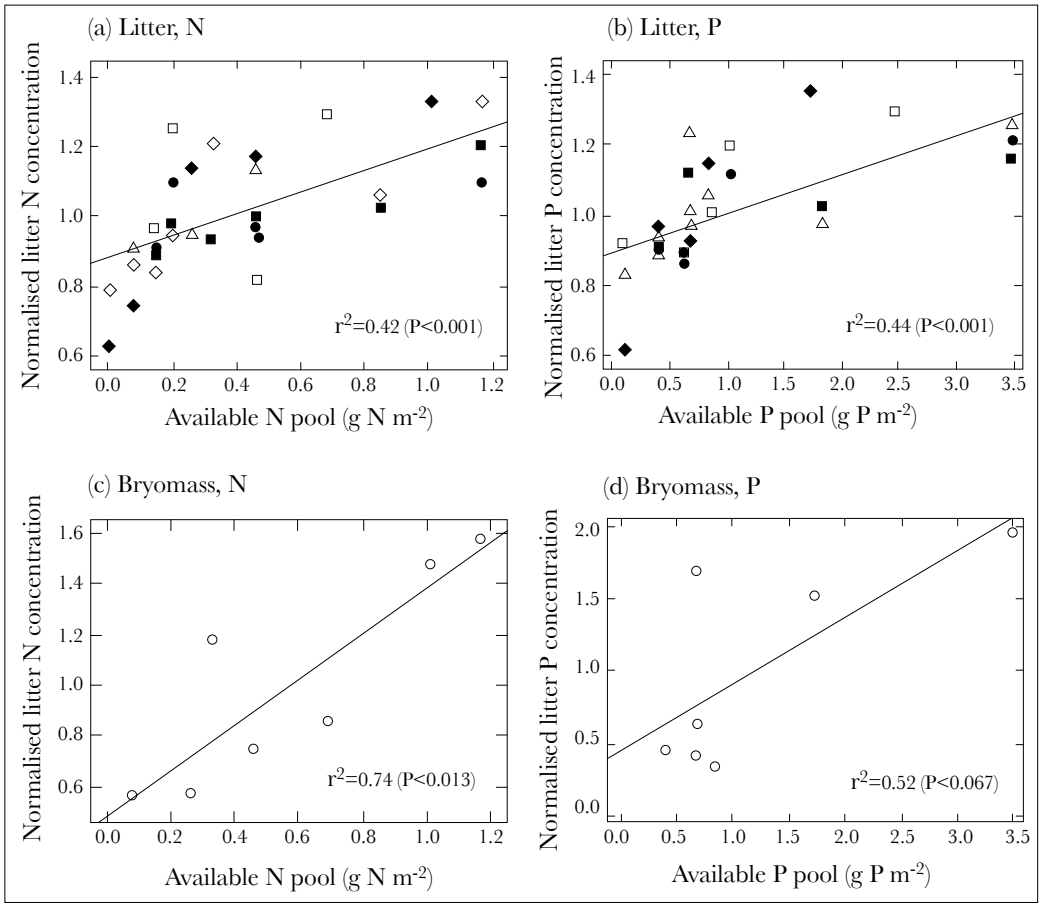

Figure 8.1 Relationship between N or P concentrations in plant litter or in bryomass and size of the available N or P soil pools. Each symbol represents the litter of a particular vascular plant species from three or more communities having different nutrient pool sizes. Within species, the concentrations were normalized by dividing by the mean concentration for that species. Based on data in Smith (1987b, d, e, 1988a, b) and unpublished data.

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8.2 Freshwater communities

8.2.1 The freshwater bodies

The island's freshwater bodies are lakes, lava-lakelets, crater lakes, wallows and streams (Grobbelaar 1978a). The term "lake" is a misnomer – none of the waterbodies are large enough, or deep enough, to be considered a lake in the usual sense. Rather, it designates a small number of larger ponds (over 1 000 m^2) on the island; the largest about 10 ha, the second largest about 3 ha and the rest < 1 ha. Since they mostly occur on flat, raised grey lava flows, they are exposed to the wind so strong wave action limits terrestrialization of the shore. Where terrestrialization does occur, this is generally on the northwest (windward) side, the rest of the shore being occupied by rocks or fine scoria. The bottoms consist of scoria or peat and are unvegetated or only sparsely vegetated by vascular species, all but two of which are much more common and abundant in the terrestrial habitats. Lake fringes not subjected to wave action are occupied by filamentous algae, mosses and vascular plants. Only two lakes possess a large submerged macrophyte (*Potamogeton nodosus*), which is very abundant throughout those lakes. None of the lakes are more than 2.5 m deep and most are shallower than 1.5 m. Lakes are less common on black lava flows, which are much more "blocky" and porous. However, because they are more protected, they are more terrestrialised than lakes on grey lava and their bottoms and sides commonly covered by epipelic algae, which often form a benthic felt-like layer.

In addition to this distinction between grey lava lakes and black lava lakes, the island's larger freshwater bodies are also classed according to whether they are, or are not, influenced by seal and seabird manuring; hence a subcategory "biotically-influenced lake" has been recognized (Grobbelaar 1978a).

Lava lakelets occur only on black lava and are the most common water body on the island. They are small (< 1 000 m^2 – most are only a few m^2 or tens of m^2) and mostly < 1 m deep. Several vascular plant species and mosses, often covered with filamentous algae, occur in them. Their bottoms and sides consist of peat and almost always support an epipelic algal layer.

Crater lakes occur in the craters of some of the island's numerous scoria cones. They are small (50 to 1 500 m^2), mostly shallow (< 2 m) and incessantly subjected to very strong winds, which results in strong wave action that moves the loose scoria that makes up their bottom and sides. Plants thus rarely root in crater lakes, but in some of them a peaty sediment does accumulate on the bottom and this contains epipelic algae.

In the coastal region, moulting elephant seals churn up the peat, forming depressions in which they wallow. Occupied wallows have no rooted vegetation, but their edges may have a cyanobacterial slime. When the wallows are abandoned, coprophilous vascular plants encroach from the sides and may eventually cover the wallow. In many instances the wallows fill with water

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that is highly nutrient-enriched by the seals and also by penguins and petrels which usually occur in the same area. The wallows take on the nature of small, highly eutrophic ponds. These water-filled wallows persist for many years and are common in shore regions.

In view of the high rainfall, there are surprisingly few streams on the island – most water flows underground. Those that do occur, are narrow (1 to 4 m wide), rarely > 1 m deep even in spate, and few flow persistently. The bottom is mainly rocky (small stones to large boulders), but it may be a layer of pebble-sized scoria. Where erosion is not severe, filamentous algae and mosses occur on the rocks. Where streams flow through peat areas there is generally a thick mat of fringing vegetation that extends over the stream.

Because they are shallow, and their waters regularly mixed by wind, all the island's water bodies are polymictic and thermal stratification is rare, although on sunny, calm days the bottom sediments absorb radiation and can become substantially warmer (4.5°C) than the overlying water (Grobbelaar 1975).

8.2.2 Nutrient composition

The chemical composition of the island's freshwaters is given in Table 8.5. They can be simply but accurately described as very dilute dilutions of seawater. The ionic composition order of the major ions is $Cl^{-}>Na^{+}>SO_4^{2-}>Mg^{2+}>Ca^{2+}>K^{+}>HCO_3^{-}$, identical to that in seawater. The same is true of rainwater at the island (Grobbelaar 1978b; Smith 1987e). This does not imply that the island's freshwater bodies are saline. In contrast, apart from some wallows, lava lakelets and west coast lakes that are close to the shore and heavily subjected to saltspray, they are very "fresh". Because of the dominance of Cl^{-} over HCO_3^{-} and the influence of the acidic peats and igneous rocks through which they percolate, they are also extremely soft. In the absence of limestone or any other calcareous rock, the waters are not enriched in Ca or HCO_3^{-} so they have a low alkalinity and buffering capacity. The island's freshwaters rarely contain detectable levels of N and P, unless they are influenced by seabirds or seals.

PCA ordination of the chemistry data for 257 waterbody and 71 precipitation samples listed in the appendix of Grobbelaar (1974a) has shown that freshwater chemical composition at the island is characterised by two components. The major component comprises Na, Mg, Ca, K, Cl, SO_4 and conductivity. It accounts for 49% of the total variance in the data and represents the oceanic influence on freshwater chemical composition. The other component comprises NH_4-N, NO_3-N and PO_4-P, accounts for 27% of the total variance, and shows the influence of animal manuring. Grobbelaar (1975, 1978a), also from PCA, found a third component (Fe, pH and alkalinity) and argued that this represented the influence of inflowing humic-rich groundwater, on the basis that humic acids would lower pH and alkalinity and increase Fe concentration. However, Fe, pH and alkalinity are significantly positively

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Table 8.5 Chemical composition and primary productivity of the freshwater bodies on Marion Island. Mean values are given, with the range in brackets. Chemical concentrations are in mg l^{-1}, except where indicated otherwise. Primary productivity was measured as net ^{14}C uptake and expressed as mg C m^{-2} d^{-1}. Brackets in column headings indicate the number of water samples used for chemical analysis. Water chemistry from Grobbelaar (1978b) and primary productivity from Grobbelaar (1974b). Where a value of zero is given it means the concentration of the nutrient was below the limit of detection by the particular method used for the analysis.

Water chemistry	Lakes (130)	Lava lakelets (31)	Crater lakes (12)	Streams (26)	Biotic Lakes (12)	Wallows (45)
pH	6.0 (5.2-7.3)	5.8 (5.2-6.8)	6.1 (5.8-7.0)	6.6 (6.1-7.3)	5.3 (4.5-6.7)	5.9 (4.5-8.3)
Conductivity (µS cm-1)	139 (40-3180)	52 (30-107)	63 (36-196)	63 (40-160)	138 (74-257)	228 (58-1630)
Alkalinity (µequiv. l-1)	24 (0-220)	20 (0-178)	14 (0-54)	117 (37-210)	42 (0-193)	460 (0-3370)
Na	19.7 (5.6-420)	7.2 (4.4-16.2)	10.0 (5.1-43.5)	9.2 (5.6-33.0)	16.1 (9.0-27.2)	38.4 (7.0-312.0)
K	0.8 (0.1-17.5)	0.4 (0.1-1.4)	0.4 (0.1-1.7)	0.5 (0.1-1.5)	1.5 (0.6-2.5)	3.4 (0.1-16.3)
Ca	0.9 (0.2-12.0)	0.5 (0.2-3.6)	0.5 (0.3-1.3)	0.6 (0.3-1.5)	0.8 (0.3-1.1)	1.8 (0.2-11.0)
Mg	2.6 (0.8-50.3)	1.0 (0.5-2.6)	1.3 (0.7-5.1)	1.4 (0.5-5.2)	2.2 (1.5-3.2)	5.4 (0.7-35.0)
Fe	0.1 (0-1.2)	0.02 (0-0.3)	0	0.01 (0-0.1)	0.9 (0-7.0)	1.3 (0-11.3)
Cl	46 (7-1100)	17 (10-62)	21 (12-82)	17 (10-72)	32 (15-59)	142 (25-930)
SO4	4.5 (0-106.0)	0.3 (0-4.0)	1.6 (0-16.5)	1.9 (0-17.5)	3.8 (0-11.3)	7.3 (0-67.2)
NO3-N	0.04 (0-0.6)	0.02 (0-0.5)	0	0	9.4 (4.5-14.8)	3.7 (0-21.4)
NH4-N	0.01 (0-0.5)	0	0	0	2.9 (1.0-9.5)	8.8 (0-55.2)
PO4-P	0(0-0.04)	0	0	0	0.4 (0-2.1)	0.2 (0-4.3)
Primary productivity	**Lakes (130)**	**Lava lakelets (31)**	**Crater lakes (12)**	**Streams (26)**	**Biotic Lakes (12)**	**Wallows (45)**
Phytoplankton	19 (1-102)	32 (20-41)	-	-	270 (46-793)	4985 (3494-6004)
Benthic algae	258 (91-556)	44 (17-61)	-	-	-	-
Macrophytes and epiphytic algae	833 (446-1270)	-	-	-	-	-

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intercorrelated and occurred on the same side of the principal component, so it is difficult to accept Grobbelaar's interpretation. This is not to deny that groundwater influences the chemical composition of the island's freshwaters (many of which are coloured by humic acids), simply that the degree and nature of the influence cannot be established from the available data.

8.2.3 Primary production

Phytoplankton productivities in the non-biotically influenced lakes (1 to 102 mg C m^{-2} d^{-1}) and lava lakelets (20 to 41 mg C m^{-2} d^{-1}; Table 8.5) are low and typical of cold, oligotrophic waters of shallow lakes in temperate and sub-polar areas. For instance, similar phytoplankton productivities (3 to 85 mg C m^{-2} d^{-1}) are found in Northern Hemisphere tundra ponds (Kalff 1970; Alexander *et al.* 1980). Benthic (epipelic) algal productivity in the island's lakes (mean, 258 mg C m^{-2} d^{-1}) and lava lakelets (44 mg C m^{-2} d^{-1}) are also similar to those in tundra ponds (53 to 131 mg C m^{-2} d^{-1}; calculated from total season production values and growing season duration given in Alexander *et al.* 1980). Mostly, benthic production far outweighs phytoplankton production. Highest production of all the components of the island's non-manured freshwater bodies was for *P. nodosus* and the epiphytic filametous algae that occur on it; between 446 and 1 270 mg C m^{-2} d^{-1}, considerably more than the maximum reported for submerged macrophytes in tundra ponds (250 mg C m^{-2} d^{-1}; Alexander *et al.* 1980).

Phytoplankton productivity in biotic lakes (46 to 793 mg C m^{-2} d^{-1}) and wallows (3 500 to 6 000 mg C m^{-2} d^{-1}) is high, in keeping with their high N and P status. Enrichment studies (Grobbelaar 1978c) showed that it is the combination of N and P that stimulates algal production at the island; neither element has any effect if added alone. No other macro- or micronutrients, alone or in combination, enhanced algal production.

In the absence of aquatic insects, decapod crustaceans, fish or amphibians, the top of the trophic chain in the island's freshwaters is occupied by zooplankton. Nine species have been recorded, but by far the most abundant ones are the calanoid copepod *Boeckella vallentini* (previously *Pseudoboeckella volucris*, see Pugh *et al.* 2002) and the water flea *Daphniopsis studeri* (Kok & Grobbelaar 1978). A detailed investigation of primary and secondary production in the pelagic zone of a lava lakelet (Grobbelaar *et al.* 1987) revealed that grazing by these two zooplankton species, together with their respiration and phytoplankton photosynthesis, dominated carbon flow, with only a small contribution by bacteria. Phytoplankton fixed, on average, 24.3 mg C m^{-2} d^{-1}. Of this, 15.3 mg C was grazed by zooplankton, which also grazed 2.7 mg bacterial C and respired 24.1 mg C. The heavy rates of zooplankton grazing, coupled with low phytoplankton and bacteria biomasses, result in fast C turnover in the lava lakelet. The basic structure and rates of C flow in the lava lakelet's pelagic zone are thus essentially similar to those in a typical tundra pond (Hobbie 1980). The contribution of the benthic system to C flow has not been measured.

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8.3 The trophic dynamics disparity between the island's terrestrial and aquatic systems – how real is it?

The presence of an active herbivore level results in the island's freshwater bodies having a very different trophic dynamic to that of the terrestrial ecosystem. In the freshwaters most of the carbon (and hence energy and nutrients) go through a grazing chain rather than a detritus chain, whereas the opposite is true for the terrestrial system. However, this distinction, held since the early days of ecological research at the island (Smith 1977; Kok & Grobbelaar 1978) might not be that definite. Certainly, a grazing chain dominates in the pelagic zone of the freshwater bodies, but nothing is known about the fate of the very substantial inputs of energy and nutrients by benthic algae, or by submerged macrophytes and their algal epiphytes. It is possible that a detritus chain predominates in the benthic mats. Similarly, in terrestrial communities the grazing chain might be more important than currently thought, since there might be appreciable levels of meso- and/or microherbivory. Our current concept of terrestrial ecosystem functioning at the island is almost entirely based on information on large organisms; animals the size of insect larvae and upward, plants as large as mosses and upwards. Recent studies of the larvae of small insects such as the midge *Limnophyes minimus* (Hänel & Chown 1998), and of springtails and mites (Chown *et al.*, unpublished data), are making it increasingly clear that smaller organisms are cardinal to the spatial and temporal dynamics of the island's terrestrial communities. Likely, they also play an important role in the functional dynamics of the communities.

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