Oecologia (Berl.) 32, 239–253 (1978)

Oecologia

Animal-Plant-Soil Nutrient Relationships on Marion Island (Subantarctic)

V.R. Smith*

Institute for Environmental Sciences, University of the Orange Free State, Bloemfontein, Republic of South Africa

Summary. Manuring by the many seals and seabirds forms the major source of N and P to the Marion Island terrestrial ecosystem and plants at manured sites exhibit enhanced vitality and increased N and P contents in their leaf tissue and saps. A similar effect results from small applications of NPK fertilizer. Non-manured soils possess very low levels of available N but substantial quantities of organic N.

Introduction

Previous workers on southern subpolar vegetation have commented on the enhanced vitality, cover and production of plant communities associated with colonies of seals and seabirds (Moseley, 1892; Taylor, 1955; Wace, 1960, 1961; Gillham, 1962; Greene, 1964; Huntley, 1971; Smith and Walton, 1975; Smith, 1977a). These animals feed in the surrounding ocean and deposit their guano, dung and urine on the land and are generally considered to be important in maintaining the nutrient statuses of plants and soils of Subantarctic and maritime Antarctic islands. Data regarding the effects of manuring on the chemical composition of these plants and soils are, however, scant (Allen et al., 1967; Collins et al., 1975; Smith, 1976a; Walton and Smith, 1978).

Marion Island (46°54′S, 37°45′E) experiences a cool oceanic climate (annual mean temperature 5.1° C) with high rainfall (> 2500 mm per annum) and a high incidence of gale-force winds. The moderating influence of the ocean prevents the occurrence of any bitterly cold weather and the temperature difference between the coldest and warmest months is only 3.7° C. Because of the island's isolation (approx. 1600 km from the nearest continent, Africa) and geologically recent origin, only 38 vascular species (all low-growing graminoids or dwarf shrubs) occur in the flora. Seven of these account for more than 95% of the

* *Present address:* Merck Chemicals, Pty (Ltd), P.O. Box 1366, Johannesburg, Republic of South Africa

0029-8549/78/0032/0239/$03.00

vascular vegetation biomass. However, many bryophyte species occur which contribute approx. 25% of the total lowland vegetation biomass (Smith, 1977b) and 100% of that above 800 m (Huntley, 1970). Detailed descriptions of the island biome are provided in Van Zinderen Bakker, Sr., et al. (1971) and Smith (1977a).

Manuring influences of birds and seals on the island are vividly manifested by increased plant vitality and colour, a change in the relative proportions of the plant species present or, at heavily influenced sites, in the occurrence of the more nitrophilous or coprophilous plant species. The main animals responsible for these effects are the Wandering Albatross (*Diomedea exulans* L.), both species of Giant Petrel (*Macronectes giganteus* Gmelin and *M. halli* Mathews), King (*Aptenodytes patagonica* Miller) and Gentoo (*Pygoscelis papua* Forster) Penguins, burrowing petrel and prion species (family Procellariidae) and Elephant Seals (*Mirounga leonina* L.).

Smith (1976a) demonstrated that Marion Island soils in which petrel and prion species establish burrows exhibit enhanced N and P levels and that plants of these areas possess higher contents of N, P, K, Fe and, to a lesser extent, Na than do plants occurring in areas not inhabited by the birds. This paper presents the results of a similar investigation into the influence of other animal species on the chemical composition of the island plants and soils. The effect of small applications of NPK fertilizer on plant nutrient levels is also described.

Sites

All the above animals occur in substantial numbers on the island's eastern coastal plain, which formed the study site for the investigation. A detailed account of the chemistry of the non-manured soils of this area is provided in Smith (1976b). These soils possess low levels of inorganic N and P but because of their organic nature (up to 98% organic matter) contain substantial quantities of organic N and P. High soil acidities, high C:N ratios and low soil temperatures retard mineralization of these elements. In addition, most of the inorganic P occurs as unavailable Al and Fe complexes. Because of the marine influence (salt-spray) Na and Mg greatly predominate in the soil solution and Mg^{2+} is the most common exchangeable cation. There is evidence that Ca may be deficient in some soils of the coastal plain.

Several 4 m^2 plots were marked off in an open fernbrake community (Smith, 1976b), away from the direct influence of any animals. Four plots were each fertilized with four successive NPK applications between December 1973 and February 1974. A total of 70 kg ha^{-1} N (35 kg ha^{-1} each of NH_4^+-N and NO_3^--N), 45 kg ha^{-1} P and 57 kg ha^{-1} K was applied to each plot. Four additional plots in the community served as unfertilized control plots. The percentage aerial cover values of the major species in the community were 35% *Blechnum penna-marina* (Poir) Kuhn, 12% *Poa cookii* Hook. f., 11% *Acaena magellanica* (Lam) Vahl and 32% *Azorella selago* Hook. f. but these values varied by up to 80% between the various plots.

Methods

Soil and plant samples were collected from manured and nonmanured sites in March 1973 and from fertilized and unfertilized plots in April 1974. Plants were clipped to soil level and the soils sampled from the surface using a core-borer. After removing the surface litter layer the top 10 cm of the intact cores were retained for chemical analysis.

Soil chemical analysis: Inorganic N was determined by MgO-Devarda alloy steam distillation of acidified KCl extracts of fresh, undried soils (Bremner, 1965a). Organic N was determined on air-dried, sieved (2 mm) samples according to the macro-Kjeldahl method of Bremner (1965b). All results are expressed per unit oven-dry weight of soil.

Leaf analysis: Oven-dried, ground (40 mesh) leaves were ashed at 450° C and the ash dissolved in conc. HNO_3. After dilution with 0.2% Sr solution the concentrations of Ca, Mg, Na, K and Fe in the extract were determined by atomic absorption spectrophotometry and the amount of P by the method of Kitson and Mellon (1944). N was measured according to Bremner (1965b).

Leaf sap analysis: Freshly collected leaves were rinsed briefly in distilled water, patted dry in tissue paper and placed in tightly stoppered glass tubes that were then immersed in boiling water for 1 hour. On cooling the cell sap was expressed and filtered using a hydraulic press. The concentrations of Ca, Mg, Na and K of Sr dilutions of the sap were determined on an atomic absorption spectrophotometer, that of P by the method of Murphy and Riley (1962) and those of NH_4^+-N and NO_3^--N by MgO-Devarda alloy steam distillation.

Results and Discussion

1. Description of Manured Sites

Gentoo Penguins are more agile and range further inland than do the other penguin species on the island. Breeding colonies are usually situated on the slopes of hills and ridges away from the sea (Van Zinderen Bakker, Jr., 1971). The vegetation of the upper reaches of these slopes is often badly trampled and covered in white guano 'stripes'. Lower down the plants exhibit enhanced stature and colour (Fig. 1). The mean *vitality index* (length × width) of leaves of *Cotula plumosa* Hook. f. at these sites is much greater than that of uninfluenced plants of this species (21.4 ± 10.7 versus 6.5 ± 6.4; $P = 0.001$). Soils and plants from lower slope areas were sampled during the investigation.

Complete plant annihilation occurs in the large rookeries of King Penguins (Fig. 2). Although these rookeries are vacant for approximately 6 months each year the density of the birds during spring and summer prevents any regeneration of the vegetation and surface drainage wears down the rookery surface to bedrock. On the periphery of rookeries breeding birds occur between stools of very fibrous peat, up to 1 m high and topped by dense tussocks of *Poa cookii* and rosettes of *Cotula plumosa*. Many channels containing a liquid mud heavily contaminated with guano are excavated between these peat stools. Plants rarely colonize these channels but *C. plumosa* and *Callitriche antarctica* Engelm ex Hegelmeyer usually occur anchored to the side of the peat stool and some of their roots and stems extend into the mud. At large rookeries non-breeding birds range further inland and the vegetation of several hectares is affected by trampling and manuring.

Fig. 1. Gentoo Penguin and chick on nest surrounded by luxuriant *Cotula plumosa*. Note splashes of guano on leaves to right of chick. Degree of manuring deleterious to *Poa cookii* grass tussocks at this site

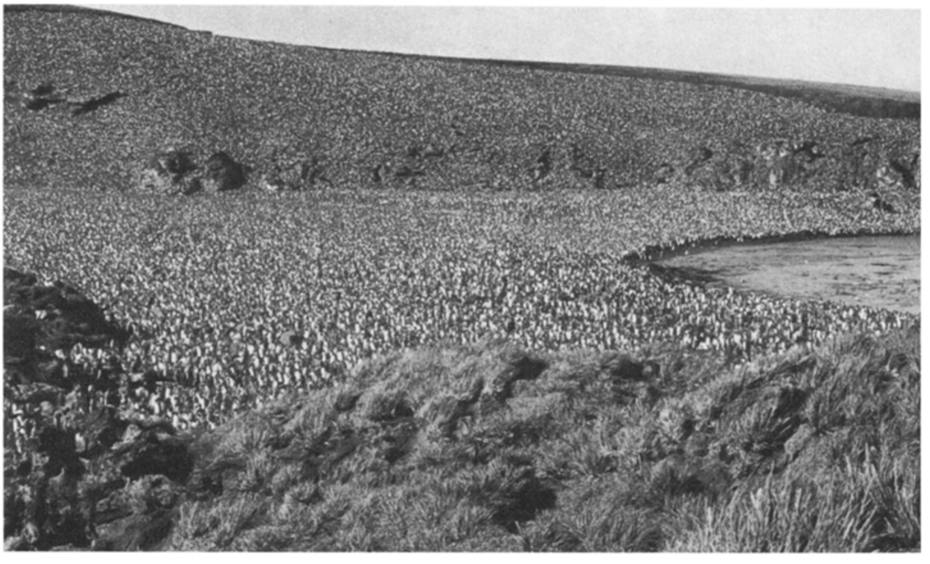

Fig. 2. Large rookery of King (flat beach) and Macaroni (slope in background) Penguins. Tussocks of *Poa cookii* codominant with *Cotula plumosa* in foreground

Because of their sedentary habits Macaroni (*Eudyptes chrysolophus* Brandt) and Rockhopper (*E. crestatus* Miller) Penguins do not influence the island's soils and vegetation to the same degree and were not considered during the investigation. Large rookeries of the former species occur (Fig. 2) but these are situated adjacent to, and sloping toward, the sea and the produced guano

Fig. 3. Abandoned nest of Wandering Albatross surrounded by luxuriant stand of *Poa cookii*. Nest had not been used for at least two previous breeding seasons

is quickly washed into the surrounding ocean by the high rainfall. Intensive volatilization of NH_3 from large penguin rookeries occurs, a proportion of which is deposited inland by wind (Allen et al., 1967; Jenkin, 1975).

Several hundred Wandering Albatrosses and Giant Petrels nest in the lowland island regions. The position of a nest is discernible from a considerable distance since the dark-green vegetation around it contrasts strikingly with the drab, yellowgreen surroundings (Fig. 3). The vegetation retains an enhanced colour for several years after desertion of the nest. Soil and plant samples were mostly collected from around disused rather than occupied albatross nests as it was difficult to obtain samples from occupied nests which were uncontaminated by fresh guano and also to avoid disturbing the nesting birds during the hatching period. Occupied Giant Petrel nesting sites only were sampled.

Prominent rocks are often the favourite perch of small, inland colonies of Dominican Gulls (*Larus dominicus* Lichtenstein). These rocks are sometimes covered with a bright-yellow lichen peculiar to the salt-spray zone of the island's rocky shores and it has been suggested (De Villiers, unpublished expedition report) that the gull guano may contain the critical mineral elements in comparable quantitities to those in salt-spray, thus allowing the occurrence of the lichen on these isolated, inland rocks. The vegetation around the rocks shows enhanced vitality and normally possesses a different species composition to that of the surrounding area (Fig. 4). *Gaimardia trapesina,* a pelecypod found on the laminae of *Macrocystis pyrifera* Turn. Ag., which forms an offshore kelp-belt surrounding the island, is a common food organism of the gulls and its pink shell often forms a layer on the soil surface where gulls congregate.

Elephant seals, although congregating on beaches, also proceed up to several hundred metres inland where they cause a flattening of the plants. As a result

Fig. 4. Stand of *Acaena magellanica* surrounding a rock perch of Dominican Gulls in an area otherwise dominated by bryophytes and *Agrostis magellanica*

Fig. 5. Recently occupied Elephant Seal wallow containing nitrogenous mud and surrounded by mounds supporting trampled *Cotula plumosa* and *Poa cookii*

of compression of the surface peat, pools are formed in depressions between mounds and tussocks. The appearance of sites habitually occupied by Elephant Seals is distinctive, comprising deeply-incised wallows of various sizes and confluent with other wallows, forming a pattern of mounds and hollows. The wallows contain a nitrogenous mud during their occupation by the seals (Fig. 5). This mud may contain *Callitriche antarctica* and the mounds and ridges between

Fig. 6. Abandoned Elephant Seal wallow. *Callitriche antarctica* (*centre*) and *Cotula plumosa* (*fringes*) colonizing the wallow mud. The absence of trampling by the seals and the influence of manuring allow luxuriant *Poa cookii* growth on the mounds

the wallows are generally covered with *Poa cookii* and *Cotula plumosa*. After the seals have left the area the mud is first colonized by blue-green algae and *C. antarctica*, followed by *Cotula plumosa* (Fig. 6). A comprehensive description of the vegetation succession in abandoned elephant seal wallows is provided in Huntley (1971).

2. *Influence of Manuring on Soil and Plant Chemistry*

Soils influenced by manuring are enriched in NH_4^+-N and NO_3^--N (Table 1). Organic N content varies considerably between sites experiencing similar intensities of manuring and depends largely on the soil organic matter level. Mud between peat stools surrounding King Penguin rookeries possesses especially high concentrations of organic and inorganic forms of N. Smith (1976c) found that manuring also increases soil inorganic P content by up to 25% at some sites. The variability and magnitude of the data indicated, however, that the extraction method employed (0.5 M HCO_3^-, pH 8.5) caused unavailable Al and Fe phosphate compounds in the soil to dissociate, yielding erroneously high available P estimates which tended to mask the effects of manuring. Muds from seal wallows and penguin rookeries on Signy Island have up to 40 times more extractable P than surrounding uncontaminated soils (Allen et al., 1967). Grobbelaar (1974) found high total dissolved PO_4 levels in waters of Elephant Seal wallows and biotically influenced lakes on Marion Island.

Soils surrounding occupied and disused Wandering Albatross nests have high concentrations of inorganic N. Croome (unpublished 1972 expedition report) found that the level of soil inorganic N increased rapidly following nest

Table 1. Effect of manuring on N status of Marion Island soils

Site	No.	Organic N (%)		NH_4^+-N (mg/100 g)		NO_3^--N (mg/100 g)	
		Mean ±S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range
Uninfluenced	10	2.6 ± 0.72	1.8–3.9	1.4 ± 1.26	0–3.5	0.2 ± 0.24	0–0.6
Wandering Albatross							
(i) Occupied nests	3	3.0 ± 0.32	2.8–3.3	54.5 ± 55.72	11.6–117.5	0.5 ± 0.11	tr.–0.6
(ii) Unoccupied nests	15	2.4 ± 0.64	1.7–3.7	10.2 ± 15.25	4.1–67.2	1.9 ± 2.55	0–4.8
Giant Petrel, occupied nests	3	2.8 ± 0.78	2.0–3.5	13.6 ± 12.46	2.0–26.8	3.5 ± 3.49	tr.–7.3
Gentoo Penguin	3	3.6 ± 0.29	3.4–3.9	42.5 ± 60.50	3.8–112.0	2.5 ± 3.99	0–7.1
King Penguin							
(i) Inland slope	3	2.9 ± 0.75	2.4–3.8	14.3 ± 2.54	11.9–16.8	3.5 ± 3.84	1.1–7.9
(ii) Top of peat stool	3	3.7 ± 0.18	3.5–3.9	34.4 ± 17.60	14.1–45.4	67.1 ± 18.54	52.1–87.8
(iii) Mud between peat stools	3	11.0 ± 1.07	10.0–12.1	1344.2 ± 97.02	1244.0–1437.7	260.3 ± 88.05	174.0–350.0
Elephant Seal							
(i) Mounds between wallows	3	N.D.	N.D.	6.1 ± 1.81	4.1–7.6	37.6 ± 14.1	23.3–51.5
(ii) Mud in wallows	3	N.D.	N.D.	190.2 ± 101.8	119.8–306.0	90.7 ± 38.52	47.9–122.6

No. = number of determinations; N.D. = not determined; tr. = trace (< 0.5 mg/100 g soil)

establishment (November to December) in a previously undisturbed area and that by the time the egg is laid (December to January) this level is up to 50% higher than in surrounding, uninfluenced soils. The most marked increase occurs after hatching (March) so that by late April a five-fold increase in the original soil organic N content is common and plant growth is strongly stimulated. The soil solution at this stage also possesses high concentrations of Ca and Cl^- but not of Mg, K or Na. Soils surrounding occupied nests which had also been used in previous seasons showed the highest levels of inorganic N and Croome proposes that it takes 5 to 6 years after the nest is abandoned before this N is depleted from the soil.

Manuring significantly increased leaf N and P contents of all plant species (Table 2). Affected *Poa cookii* plants also exhibit high Fe concentrations. Small increases in Na and K are noted in the leaves of some species but the variability of the data is high and these increases are generally not significant. Plants growing in seal wallows on South Georgia possess higher levels of all elements (except Ca) than plants from nonbiotically influenced stands (Walton and Smith, 1978).

Leaf saps of manured *Poa cookii* and *Cotula plumosa* plants exhibit higher N and P concentrations than those of uninfluenced plants (Table 3). This effect

Table 2. Concentrations (%) of ash elements plus N in leaves of plants from manured and non-manured sites

Species and site	No.	Ca	Mg	Na	K	Fe	P	N
Poa cookii								
Uninfluenced	9	0.11 ± 0.04	0.07 ± 0.02	0.25 ± 0.04	0.97 ± 0.18	0.003 ± 0.001	0.15 ± 0.02	1.44 ± 0.17
Wandering albatross								
(i) Occupied nests	3	0.11 ± 0.03	0.06 ± 0.01	0.28 ± 0.02	1.09 ± 0.26	0.008 ± 0.002	0.22 ± 0.02	2.42 ± 0.11
(ii) Unoccupied nests	3	0.09 ± 0.05	0.10 ± 0.02	0.29 ± 0.03	0.99 ± 0.11	0.011 ± 0.003	0.24 ± 0.03	2.35 ± 0.05
Giant petrel	3	0.09 ± 0.01	0.11 ± 0.03	0.41 ± 0.04	1.12 ± 0.11	0.020 ± 0.004	0.30 ± 0.03	2.30 ± 0.28
Gentoo penguin	4	0.12 ± 0.01	0.09 ± 0.02	0.36 ± 0.05	1.36 ± 0.10	0.006 ± 0.002	0.29 ± 0.05	2.23 ± 0.39
Cotula plumosa								
Uninfluenced	9	0.50 ± 0.17	0.34 ± 0.07	1.79 ± 0.21	1.44 ± 0.73	0.006 ± 0.001	0.24 ± 0.05	1.56 ± 0.17
Wandering albatross								
(i) Occupied nests	3	0.45 ± 0.05	0.44 ± 0.06	1.38 ± 0.43	1.70 ± 0.17	0.006 ± 0.001	0.39 ± 0.02	2.52 ± 0.26
(ii) Unoccupied nests	3	0.48 ± 0.04	0.35 ± 0.08	1.21 ± 0.29	1.64 ± 0.10	0.007 ± 0.001	0.36 ± 0.02	2.36 ± 0.08
Gentoo penguin	3	0.61 ± 0.15	0.34 ± 0.03	2.04 ± 0.14	1.34 ± 0.21	0.007 ± 0.002	0.32 ± 0.08	2.42 ± 0.36
Dominican gull	4	0.93 ± 0.27	0.28 ± 0.03	2.26 ± 0.39	1.92 ± 0.12	0.007 ± 0.000	0.35 ± 0.01	2.58 ± 0.11
Agrostis magellanica								
Uninfluenced	3	0.12 ± 0.01	0.19 ± 0.01	0.40 ± 0.05	1.43 ± 0.22	0.009 ± 0.001	0.15 ± 0.01	1.81 ± 0.06
Wandering albatross								
(i) Occupied nests	3	0.11 ± 0.01	0.18 ± 0.01	0.37 ± 0.04	1.58 ± 0.07	0.008 ± 0.003	0.33 ± 0.05	2.73 ± 0.23
(ii) Unoccupied nests	3	0.11 ± 0.01	0.18 ± 0.01	0.33 ± 0.06	1.54 ± 0.15	0.007 ± 0.003	0.30 ± 0.01	2.45 ± 0.07
Callitriche antarctica								
King penguin and elephant seal colonies	6	0.45 ± 0.08	0.46 ± 0.05	1.57 ± 0.39	1.22 ± 0.29	0.007 ± 0.003	0.58 ± 0.04	4.20 ± 0.85
Acaena magellanica								
Uninfluenced	1	0.70	0.51	0.38	1.25	0.008	0.22	1.95
Wandering albatross								
Unoccupied nests	1	0.99	0.56	0.40	1.38	0.006	0.36	2.58
Tillaea moschata								
Uninfluenced	1	0.66	0.56	0.47	0.40	0.016	0.16	1.18
Dominican gull	1	1.42	0.25	1.38	1.36	0.016	0.37	2.55

No. = number of determinations. – Values expressed as means ± standard deviations

Table 3. Concentration of elements (p.p.m.) in the leaf saps of plants from manured and non-manured sites

Species and site	No.	Ca	Mg	Na	K	P	NH_4^+-N	NO_3^--N
Poa cookii								
Uninfluenced	15	191±59	395±61	1334±558	4363±424	518±260	69±31	2009±797
Wandering albatross								
Occupied and Unoccupied nests	12	196±23	450±58	1638±619	4423±1209	921±213	335±121	2524±945
Giant Petrel	3	183±40	464±148	1579±539	5617±547	922±100	274±70	4333±1100
Gentoo Penguin	3	138±64	483±65	1797±637	6050±800	986±36	248±57	2429±256
King Penguin								
(i) Top of peat stool	3	148±40	417±68	1786±301	4833±805	1077±178	621±194	3970±965
(ii) Inland, influenced by non-breeding birds	3	134±34	399±16	1743±210	4013±81	955±82	260±25	3920±585
Gull influenced	3	349±44	417±33	1057±98	4600±265	422±47	98±124	4903±910
Elephant Seal								
(i) Lower part of mounds between wallows	3	154±23	341±65	1920±95	4250±482	N.D.	269±33	3337±211
(ii) Top of mounds between wallows	3	172±61	313±32	1963±152	3267±710	N.D.	107±16	4067±416
Cotula plumosa								
Uninfluenced	10	446±101	488±182	2512±666	1690±595	116±20	59±29	953±217
Wandering albatross								
Occupied and Unoccupied nests	3	280±39	378±60	2563±67	1850±187	160±18	174±135	1697±397
Giant Petrel	3	315±117	362±24	2590±141	1575±35	190±29	249±3	1665±149
Gentoo Penguin	3	222±25	326±80	2507±31	1537±382	160±14	190±37	1597±345

King Penguin								
(i) Base of peat stool	2	217 ± 52	385 ± 21	3625 ± 530	1405 ± 50	308 ± 12	465 ± 35	4010 ± 127
(ii) Top of peat stool	3	295 ± 31	369 ± 22	2763 ± 475	1370 ± 56	261 ± 35	470 ± 105	2843 ± 595
(iii) Inland, influenced by non-breeding birds	3	278 ± 101	448 ± 158	2443 ± 75	1260 ± 167	209 ± 30	192 ± 59	1569 ± 14
Elephant Seal								
(i) Lower part of mounds between wallows	3	453 ± 116	353 ± 47	3003 ± 263	2127 ± 486	N.D.	201 ± 24	3813 ± 744
(ii) Top of mounds between wallows	3	250 ± 45	348 ± 37	2173 ± 500	2797 ± 684	N.D.	97 ± 11	3299 ± 436
Agrostis magellanica								
Uninfluenced	7	168 ± 35	661 ± 288	2314 ± 770	3333 ± 1522	555 ± 94	371 ± 168	2456 ± 476
Wandering albatross								
Occupied nests	4	195 ± 70	794 ± 206	2195 ± 432	3585 ± 382	758 ± 166	348 ± 136	2521 ± 988
Giant Petrel	2	91 ± 57	448 ± 37	2360 ± 424	3780 ± 156	604 ± 16	395 ± 35	3305 ± 134
Blechnum penna-marina								
Uninfluenced	3	392 ± 128	1287 ± 55	507 ± 79	4417 ± 506	N.D.	355 ± 46	2157 ± 122
Wandering albatross								
Unoccupied nests	7	437 ± 166	1274 ± 365	431 ± 126	4257 ± 396	N.D.	354 ± 142	1937 ± 229
Callitriche antarctica								
King Penguin								
(i) Base of peat stool	3	244 ± 53	582 ± 146	2663 ± 186	1783 ± 331	1783 ± 331	439 ± 88	7699 ± 763
(ii) Inland, influenced by non-breeding birds	3	285 ± 101	702 ± 88	2418 ± 132	484 ± 139	421 ± 120	213 ± 97	3417 ± 300
Elephant Seal								
(i) Organic mud in wallows	2	145 ± 35	303 ± 46	1775 ± 35	5025 ± 389	N.D.	714 ± 133	7820 ± 2800
(ii) Mound between wallows	3	217 ± 21	928 ± 46	1817 ± 25	3467 ± 1222	N.D.	300 ± 56	7740 ± 1340

No. = number of determinations; N.D. = not determined
Values expressed as means ± standard deviations

is less marked or absent in saps of *Agrostis magellanica* and *Blechnum penna-marina,* two species generally considered to be non-coprophilous (Huntley, 1971; Smith, 1976c). However, manuring markedly enhances total levels of N and P in *Agrostis magellanica* leaves (Table 2) and *Blechnum penna-marina* plants growing on slopes inhabited by burrowing bird species exhibit higher concentrations of N and K, but not of P, than plants from adjacent, non-disturbed sites (Smith, 1976a).

Sap K and Na concentrations vary greatly between plants experiencing similar kinds and degrees of manuring but manured *Poa cookii* plants tend to possess higher leaf-sap K levels than non-manured plants. *Cotula plumosa* from most manured sites has substantially lower sap Ca concentrations than uninfluenced plants. All species from sites influenced by Dominican Gulls exhibit especially high levels of Ca in their leaves and saps. Soils underlying the *Gaimardia* shell fragments deposited by the gulls have higher exchangeable Ca contents and are less acid than nearby, uninfluenced soils (Smith, 1976c). The Dominican Gull has been described as "the best Antarctic gardener" (discussion of paper by Holtom and Green, 1967, p. 344), as it surrounds its nest sites with limpet shells and several plant species survive and fruit most successfully at these sites. On Marion Island the increased soil pH associated with the shells results in a decreased C:N ratio and a more rapid breakdown of soil organic matter (Smith, 1976c), agreeing with similar observations on Skye and Mull Islands (Gillham, 1957) and Anglesey Island (Ranwell, 1959).

Callitriche antarctica, a highly coprophilous species, never occurs at non-manured sites on the island so that comparisons similar to those provided for the other plant species are not included in Tables 2 or 3. The highest levels of leaf N (4.8%), P (0.6%) and Na (2.0%) obtained for all island plants occurred in *C. antarctica,* agreeing with similar observations for this species on South Georgia (Smith and Walton, 1975).

3. *Influence of Fertilization on Soil and Plant Chemistry*

Soils fertilized with NPK possessed higher concentrations of inorganic N than did unfertilized soils (Table 4). The poor status of available N in the island soils is demonstrated by the fact that even the enhanced level of NH_4^+-N at fertilized sites (0.7 mg/100 g soil) is much lower than that in a surface

Table 4. Effect of NPK application on N status of the soils

Treatment	No.	Organic N (%)		NH_4^+-N (mg/100 g)		NO_3^--N (mg/100 g)	
		Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range
None	4	1.1 ± 0.08	0.9–1.1	tr.	0–tr.	tr.	0–tr.
Plus NPK	4	1.0 ± 0.10	0.9–1.1	0.7 ± 0.13	0.7–0.9	0.8 ± 0.38	0.4–1.2

No. = number of determinations; tr. = trace (< 0.5 mg/100 g soil)

Table 5. Effect of NPK application on plant chemical composition (%)

Species and treatment	No.	Ca	Mg	Na	K	Fe	P	N
Poa cookii								
None	4	0.21 ± 0.00	0.06 ± 0.01	0.16 ± 0.03	0.93 ± 0.06	0.007 ± 0.001	0.15 ± 0.01	1.50 ± 0.03
Plus NPK	4	0.22 ± 0.00	0.08 ± 0.02	0.16 ± 0.05	0.86 ± 0.06	0.006 ± 0.002	0.20 ± 0.01	2.05 ± 0.10
Blechnum penna-marina								
None	4	0.76 ± 0.02	0.68 ± 0.01	0.35 ± 0.03	1.63 ± 0.19	0.020 ± 0.005	0.25 ± 0.02	1.65 ± 0.14
Plus NPK	4	0.80 ± 0.02	0.68 ± 0.01	0.35 ± 0.06	1.67 ± 0.09	0.018 ± 0.004	0.27 ± 0.04	1.67 ± 0.11
Acaena magellanica								
None	4	1.63 ± 0.13	0.48 ± 0.00	0.44 ± 0.09	1.27 ± 0.10	0.003 ± 0.001	0.17 ± 0.02	1.62 ± 0.11
Plus NPK	4	1.73 ± 0.11	0.48 ± 0.01	0.45 ± 0.10	1.13 ± 0.08	0.005 ± 0.002	0.24 ± 0.03	1.95 ± 0.06

No. = number of determinations
Values expressed as means ± standard deviations

peat of similar bulk density from a wet tundra meadow at Barrow, Alaska (14.1 mg/100 g soil; Flint and Gersper, 1974).

Leaves of fertilized *Poa cookii* and *Acaena magellanica* plants possessed higher N and P concentrations than did those of unfertilized plants, whereas no such increases were observed for *Blechnum penna-marina* (Table 5). Plant levels of all other elements were unaffected by NPK fertilization. Fertilized plants did not exhibit obvious signs of enhanced vitality or colour by April but the standing crop of green *B. penna-marina* fronds at this time was 31% greater ($P = 0.001$) at fertilized than at unfertilized plots (determined by clipping 50 cm^2 circular areas from sites supporting 100% *Blechnum* cover within each plot). Before NPK application no such difference between the plots was noted. The standing crops of *Azorella selago, Acaena magellanica* and *Poa cookii* leaf material were not determined. However, the specific leaf area of larger (> 16 cm) *P. cookii* leaves was significantly lower at fertilized than at unfertilized plots, indicating thickening of the leaves, a known response of grass species to enhanced N concentration.

Conclusion

Although Russell (1940) found enhanced plant production associated with animal droppings in Arctic vegetation and Wilson (1957, 1959) noted increased plant cover under similar conditions in Arctic and Alpine areas, the activities of birds and mammals have not usually been associated with plant nutrient availability in northern hemisphere polar and tundra soils. All investigations to date in southern subpolar regions, however, demonstrate the importance of manuring in maintaining the soil N and P status at levels compatible with plant growth. On Marion Island high soil acidity and low temperatures retard organic matter decomposition and nitrification so that the level of available N is especially low. This is aggravated by intensive leaching caused by the high rainfall. Physical and chemical weathering seem to play a minor role as mechanisms supplying nutrients to the soil (Smith, 1977a). Atmospheric industrial pollution is negligible and the major sources of supply are directly (Na, Mg and K in salt-spray) or indirectly (N and P via excretion of sea-going animals) marine. Greatest enhancement of soil N and P levels occurs at isolated, heavily contaminated sites but the acid surface peats of the island probably form effective "traps" for the NH_3 volatilized from these contaminated areas.

Acknowledgements. The investigation was sponsored by the South African Department of Transport and formed part of a programme directed by Professor E.M. van Zinderen Bakker who provided valuable support and advice throughout.

References

Allen, S.E., Grimshaw, H.M., Holdgate, M.W.: Factors affecting the availability of plant nutrients on an Antarctic island. J. Ecol. **55**, 381–396 (1976)

Bremner, J.M.: Inorganic forms of nitrogen. In: Methods of soil analysis, Vol. 2 (C.A. Black, ed.), pp. 1178–1237. Wisconsin, USA: American Society of Agronomy 1965a

Bremner, J.M.: Total nitrogen. In: Methods of soil analysis, Vol. 2 (C.A. Black, ed.), pp. 1149–1178. Wisconsin, USA: American Society of Agronomy 1965b

Collins, N.J., Baker, J.H., Tillbrook, P.J.: Signy Island, maritime Antarctic. In: Structure and function of tundra ecosystem (T. Rosswall, O.W. Heal, eds.). Ecol. Bull. (Stockh.) **20**, 345–374 (1975)

Flint, P.S., Gersper, P.L.: Nitrogen nutrient levels in Arctic tundra soils. In: Soil organisms and decomposition in tundra (A.J. Holding, O.W. Heal, J.F. MacLean, Jr., P.W. Flanagan, eds.), pp. 375–387. Stockholm: International Biological Programme Tundra Biome Steering Committee 1974

Gillham, M.E.: Coastal vegetation of Mull and Iona in relation to salinity and soil aeration. J. Ecol. **45**, 757–778 (1957)

Gillham, M.E.: Modifications of Subantarctic flora on Macquarie Island by seabirds and sea elephants. Proc. R. Soc. Victoria **74**, 1–12 (1962)

Greene, S.W.: The vascular flora of South Georgia. British Antarctic Survey Scientific Reports **45** (1964)

Grobbelaar, J.U.: A contribution to the limnology of the Subantarctic island Marion. D.Sc. Thesis, Bloemfontein, Republic of South Africa, University of the Orange Free State (1974)

Holtom, A., Greene, S.W.: The growth and reproduction of Antarctic flowering plants. Phil. Trans. R. Soc. London **B252**, 323–337 (1967)

Huntley, B.J.: Altitudinal distribution and phenology of Marion Island vascular plants. Tydskr. Natuurwet. **10**, 255–262 (1970)

Huntley, B.J.: Vegetation. In: Marion and Prince Edward Islands (E.M. van Zinderen Bakker, Sr., J.M. Winterbottom, R.A. Dyer, eds.), pp. 98–160. Cape Town: Balkema 1971

Jenkin, J.F.: Macquarie Island, Subantarctic. In: Structure and function of tundra ecosystems (T. Rosswall, O.W. Heal, eds.). Ecol. Bull. (Stockh.) **20**, 375–397 (1975)

Kitson, R.E., Mellon, M.G.: Colorimetric determination of phosphorus as molybdovanado-phosphoric acid. Ind. Eng. Chem. Anal. Ed. **16**, 379–383 (1944)

Moseley, H.N.: Notes by a naturalist. In: H.M.S. Challenger, pp. 163–181. London: Murray Press 1892

Murphy, J., Riley, J.P.: A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta **27**, 31–36 (1962)

Ranwell, D.: Newborough Warren, Anglesey. I. The dune system and dune slack habitat. J. Ecol. **47**, 571–601 (1959)

Russell, R.S.: Physiological and ecological studies on an Arctic vegetation. II. The development of vegetation in relation to nitrogen supply and soil microorganisms. J. Ecol. **28**, 289–309 (1940)

Smith, R.I.L., Walton, D.W.H.: South Georgia, Subantarctic. In: Structure and function of tundra ecosystems (T. Rosswall, O.W. Heal, eds.). Ecol. Bull. (Stockh.) **20**, 399–423 (1975)

Smith, V.R.: The effect of burrowing species of *Procellariidae* on the nutrient status of inland tussock grasslands on Marion Island. Jl. S. Afr. Bot. **42**, 265–272 (1976a)

Smith, V.R.: Standing crop and nutrient status of Marion Island (Subantarctic) vegetation. Jl. S. Afr. Bot. **42**, 231–263 (1976b)

Smith, V.R.: The nutrient statuses of Marion Island plants and soils. M.Sc. Thesis, Bloemfontein, Republic of South Africa, University of the Orange Free State (1976c)

Smith, V.R.: A qualitative description of energy flow and nutrient cycling in the Marion Island terrestrial ecosystem. Polar Record **18**, No 115, 361–370 (1977a)

Smith, V.R.: Vegetation standing crop of the grey lava flows and of the eastern coastal plain on Marion Island. Jl. S. Afr. Bot. **43**, 105–114 (1977b)

Taylor, B.W.: The flora, vegetation and soils of Macquarie Island. A.N.A.R.E. Reports, Series B **2**, (1955)

Van Zinderen Bakker, E.M., Jr.: Comparative avian ecology. In: Marion and Prince Edward Islands (E.M. van Zinderen Bakker, Sr., J.M. Winterbottom, R.A. Dyer, eds.), pp. 161–172. Cape Town: Balkema 1971

Van Zinderen Bakker, E.M., Sr., Winterbottom, J.M., Dyer, R.A.: Marion and Prince Edward Islands. A Report on the South African Biological and Geological Expedition, 1965–1966. Cape Town: Balkema 1971

Wace, N.M.: The botany of southern oceanic islands. Proc. R. Soc. London B **152**, 475–490 (1960)

Wace, N.M.: The vegetation of Gough Island. Ecol. Monogr. **31**, 337–367 (1961)

Walton, D.W.H., Smith, R.I.L.: The chemical composition of South Georgian vegetation. Br. Antarct. Surv. Bull. (in press, 1978)

Wilson, J.W.: Arctic plant growth. Advan. Sci. **13**, 383–388 (1957)

Wilson, J.W.: Notes on wind and its effects in arctic and alpine vegetation. J. Ecol. **47**, 415–425 (1959)

Received July 29, 1977