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Origin and general ecology of the Marion Island ecosystem

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Introduction

The Marion and Prince Edward islands are situated in an ideal position for geological and biological research. Lying halfway between the continents of Africa and Antarctica, their oceanographic and climatic settings have moulded these islands into typical examples of the sub-Antarctic region. The surrounding ocean with its abundance of life and the stormy, wet and cool climate have made of these two small islands, with their millions of birds and thousands of seals, a rare, untouched and extremely interesting paradise which should be preserved for posterity.

Marion Island was annexed by the South African Government in 1948 and from that year onward continuous meteorological observations have been made on the island. The interesting bird and seal fauna immediately attracted attention and some studies of basic value have been published by Rand (1954, 1955) and La Grange (1962).

Organised biological–geological research, however, started in 1963 with a reconnaissance trip to the island by E.M. van Zinderen Bakker Sr. and Jr., which was followed by the first scientific expedition in 1965/66. The aims of this expedition were to study the following aspects of the island: the geological history and topography, the history of the vegetation and the systematics and biogeography of the biota. From the end of 1971, after the volume on the results of the 1965/66 expedition had been completed, the emphasis of the research approach changed. During this second phase of the programme investigations were primarily concerned with the study of the island ecosystem as a whole, with the flow of minerals and energy through the terrestrial communities and the interrelationship of the land ecology with the surrounding ocean. The annual expeditions organised since 1971 have had the good fortune that in 1972 the old field laboratory on the island was replaced by a new, well-equipped laboratory.

The biological–geological research on the island has, until 1978, been directed by the author, with the exception of the programmes dealing with ornithology and mammal research. Two independent programmes were established in 1972 for these activities. The ornithological programme has since then been directed by Professor W.R. Siegfried, director of the Percy FitzPatrick Institute for African Ornithology, while research on the mammals of the island falls under Professor J.D. Skinner, director of the Mammal Research Institute of the University of Pretoria.

The total research programme has from its initiation been organised and supervised by SASCAR (South African Scientific Committee for Antarctic Research of the CSIR) on behalf of the South African Department of Transport, which has generously sponsored the research. This Department has also provided all logistical facilities for the scientific teams on Marion Island and made the research ship *R.S.A.* available for the voyage to and from the island. The *R.S.A.* was replaced early in 1978 by the newly-built *S.A. Agulhas*.

Historic events

In the past the Marion and Prince Edward islands have often evaded and puzzled explorers and scientists. Not only was it difficult to find the tiny specks of land in the immense ocean but, once located, the elements prevented brave sailors and researchers from landing on their shores. It is three centuries ago, to be exact, in 1663, that the Dutch galleon *Maerseveen* on its way from the Cape to Batavia swerved far south and the islands were sighted for the first time. This first discovery can be disputed, as the geographical position was wrongly indicated by the sailors. This error can, however, be explained by the poor astronomical orientation as has also been the case with other southern islands. The real discoverer is generally accepted as being the Frenchman, Marion-Dufresne, who, in search of the mysterious southern continent, sailed with two ships and reached the islands roughly two centuries ago, in 1771. Soon afterwards, the famous Captain Cook rediscovered the islands in 1775. Important events seem to have occurred at intervals of a century because, again 100 years later, the first scientists from the well-known *Challenger* Expedition set foot on Marion Island in 1873. Another important landmark was the visit of the *Bougainville* Expedition 40 years ago. South Africa annexed the islands in 1948 and the first organised scientific research was initiated 15 years ago in 1963. For further information on historic events the reader is referred to the interesting account by Marsh (1948).

Geology

Marion is a volcanic island, situated at 46°54'S, 37°45'E, with an area of 290 square kilometres. It was formed in a very late stage of the evolution of the Southern Ocean. The distance from the island to the mid-ocean ridge is 370 km so that the island could not be expected to be very ancient. This was corroborated by the K/Ar age-determinations of the oldest exposed basalts of roughly 0,25 Myr (McDougall, 1971). However, the core of the island could well be twice as old (Verwoerd, 1971).

Rocks of the oldest exposed grey lava and specimens of the more recent or black lava had already been collected a century ago by the geologist of the *Challenger* Expedition in 1873 and were described by Lacroix (1940). The excellent volcanological map produced by Verwoerd and Langenegger (1971) after our first expedition shows how the black basaltic flows descended in a radial direction from the dome-shaped centre of Marion Island and poured out of many reddish coloured scoria cones. This second volcanic stage consisted of alternating explosive and effusive eruptions and covered most of the island surface, especially the western half.

Verwoerd (1971) has described the volcanic rocks and landforms in a very clear and comprehensive way. According to him, the black lava may be of three different types: pahoehoe with a flat or undulating surface, Aa flows covered with loose clinkers, or rough black lava streams. The last are very common and with their angular blocks and sharp edges are almost impassable.

Alternating with the volcanic events on the island were periods of glaciation. Hall (1978) has described three major episodes, each with stadials and interstadials. The thick tills, the moraines, fluvial deposits and glacial landforms provided material for detailed stratigraphic study. These glacial periods can be roughly dated with the aid of K/Ar age determinations of the intercalated lava flows. It is interesting to note that, according to Hall (1978), the glacial episodes were synchronous with the last three major glaciations of the Northern Hemisphere.

The Southern Ocean

Marion Island is a truly hyper-oceanic island, the nearest land being the small Île aux Cochons of the Crozet archipelago at a distance of 925 km, while the African coast is some 1 600 km to the NNW. The vast surrounding ocean developed gradually in the early Cretaceous when the southern continents started to drift apart. In early Eocene times this ocean was a warm sea (Shackleton & Kennett, 1975) and the few fossil floras which are known from Antarctica (Kemp *et al.* 1975; Cranwell, 1969) indicate that this continent had a temperate climate. It was not until the Middle Miocene that the present ice sheet started to develop as a consequence of the climatic deterioration in the early Tertiary (Drewry, 1975). Once the sea-ice formed round the coastal margins of Antarctica, the albedo effect accelerated the cooling of the Antarctic region. The Polar Front separating the sub-Antarctic and Antarctic Surface Waters gradually became an important oceanic boundary. The possible movements of this Front are very important for the explanation of the geological and climatological history of Marion Island. Seasonal meridional shifts of the Polar Front can amount to 80 km, but the position of this boundary is in general very stable. South-east of Africa its position is mainly determined by the bottom topography of the ocean (Bang *et al.* 1978). The

Atlantic–Indian Ocean Ridge in this area tends NNE and a very steep topography occurs along the western side of the Crozet Plateau, where the Marion and Prince Edward islands originated. In this region latitudinal movements of the Front were very restricted (Hays *et al.* 1976), but the southern part of the sub-Antarctic zone was strongly influenced by events in the Antarctic region. The changes in ocean temperature which have been registered in the sub-Antarctic zone in the southeastern Indian Ocean (Williams & Keany, 1978) were of a world-wide nature and are known from the oxygen isotope stratigraphy of the Caribbean Sea, and the Atlantic and the Pacific oceans. The last 13 stages of this stratigraphy, covering a period of 0,5 Myr, have been identified by Williams & Keany (1978). These will have affected Marion Island, which may well have a total age of this order. The provisional dating of the three major glaciations of Marion Island by Hall (1978) shows that the chronology of these events was synchronous with glaciations in the Northern Hemisphere.

Pollen analysis

The fossil pollen evidence which covers the last 16 000 years (Schalke & Van Zinderen Bakker, 1967, 1971; Van Zinderen Bakker, 1973) is in close agreement with the results obtained by the study of the glacial geology by Hall (1978). According to geological data, the temperature on the island dropped 3-4 °C during the last glacial maximum, 18 000 years ago, while fossil pollen spectra indicate a lowering of 3 °C at about 16 000 B.P. Hall (1978) has reconstructed the former extent of the glaciers on the island and shown that the site of the pollen study at Macaroni Bay was covered by the Albatross Lakes

Lithology	Pollen zones	Age BP	Pollen
Clay	Z	ca 2600	Samples could not be collected
			Gramineae, Cyperaceae, Ranunculaceae, *Lycopodium magellanicum* and other swamp plants
Clay		ca 12500	
	Y		*Acaena*, *Azorella* and fern spores dominate
		ca 14500	
Peat	X	15000-17000	*Azorella* dominant
Clay			
Bedrock			

Fig. 1. The pollen zones of the peat profile at Macaroni Bay.

Glacier during the last glacial maximum. After the glacier had waned and left its moraine No. 2 behind, the climate improved slightly and a pure *Azorella* stand occupied the surroundings from about 16 000 to 14 500 B.P. (Fig. 1). The *Azorella* dominance indicates a vegetation of high altitude (Fig. 2) (the highest present record is 765 m (Huntley, 1970)). From the occurrence of *Acaena* and ferns, it can be inferred that the climate improved further after 14 500 B.P. The final important climatic change was registered around 12 500 years ago when a mire vegetation developed, which has persisted up to the present.

Correlation of terrestrial and oceanographic evidence

At this stage it is possible to draw a close correlation between the oceanographic and terrestrial evidence for the last glacial maximum 18 000 years ago. The northward displacement of the Polar Front, which has already been alluded to, could, because of the ocean bottom topography, only have been of a minimal nature near Marion Island. The displacement was, however, approximately 7° of latitude in the western South Atlantic and somewhat less in the eastern South Atlantic and the western Indian Ocean (Hays *et al.* 1976). The consequence of this would have been that the wind system moved northward. Of much greater importance, however, was the fact that the sea-ice extended, even in summer, to almost 55°S latitude (*op. cit.*). This would have lowered the annual temperature considerably, as in winter sea-ice would have been close to the island. All these factors, viz. the slight northward displacement of the Polar Front, the northward shift of the wind system and the persistent pack-ice, would have lowered the temperature enough to change the heavy rainfall on the island into snow, with the consequence that glaciers started to descend from the top.

Using the palaeotemperatures inferred from the pollen evidence, the altitudinal positions of the 0 °C isotherm have been computed for the last 16 000 years (Van Zinderen Bakker, 1973). From these results it appears that, 16 000 years ago, even in the lowlands, the temperature was below freezing point during the months of July to September. These conditions must have been worse during the glacial maximum 18 000 years ago. It is certain that only a limited flora and fauna could have survived the rigours of the climate on certain nunataks on the E and NE sides of the island which were sheltered against the southerly polar winds (Van Zinderen Bakker, 1970). These conclusions were corroborated by recent meteorological observations covering many years.

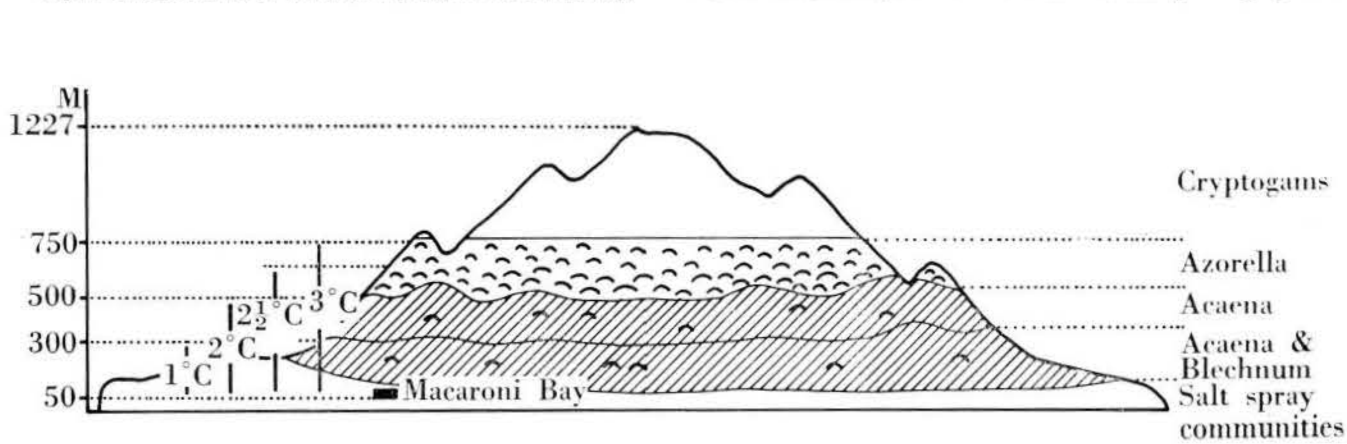


Fig. 2. The present vegetation belts on Marion Island and the average annual differences in temperature.

Hourly records of grass-minimum temperatures for the years 1969-1973 showed that on the NE side of the island near the weather station the temperature drops below zero on 116 days per year, with maximum frost from July to October (Van Zinderen Bakker, 1978).

It is reasonable to assume that the western side, which is exposed to the strong west winds and storms, would have accumulated much more ice than the eastern lee-side. After the warming up of the climate and the melting of the glaciers, radial faulting of the island occurred which was followed by the eruption of black lava lasting, according to isotopic dating, from > 20 000 to 13 000 years ago. This volcanic stage may, however, have been of much longer duration. A minimum age of the black lava flows can be inferred from the radiocarbon dates of 3000-4000 years of the superimposed peat deposits (Van Zinderen Bakker, 1973).

Ecesis and ecogenesis

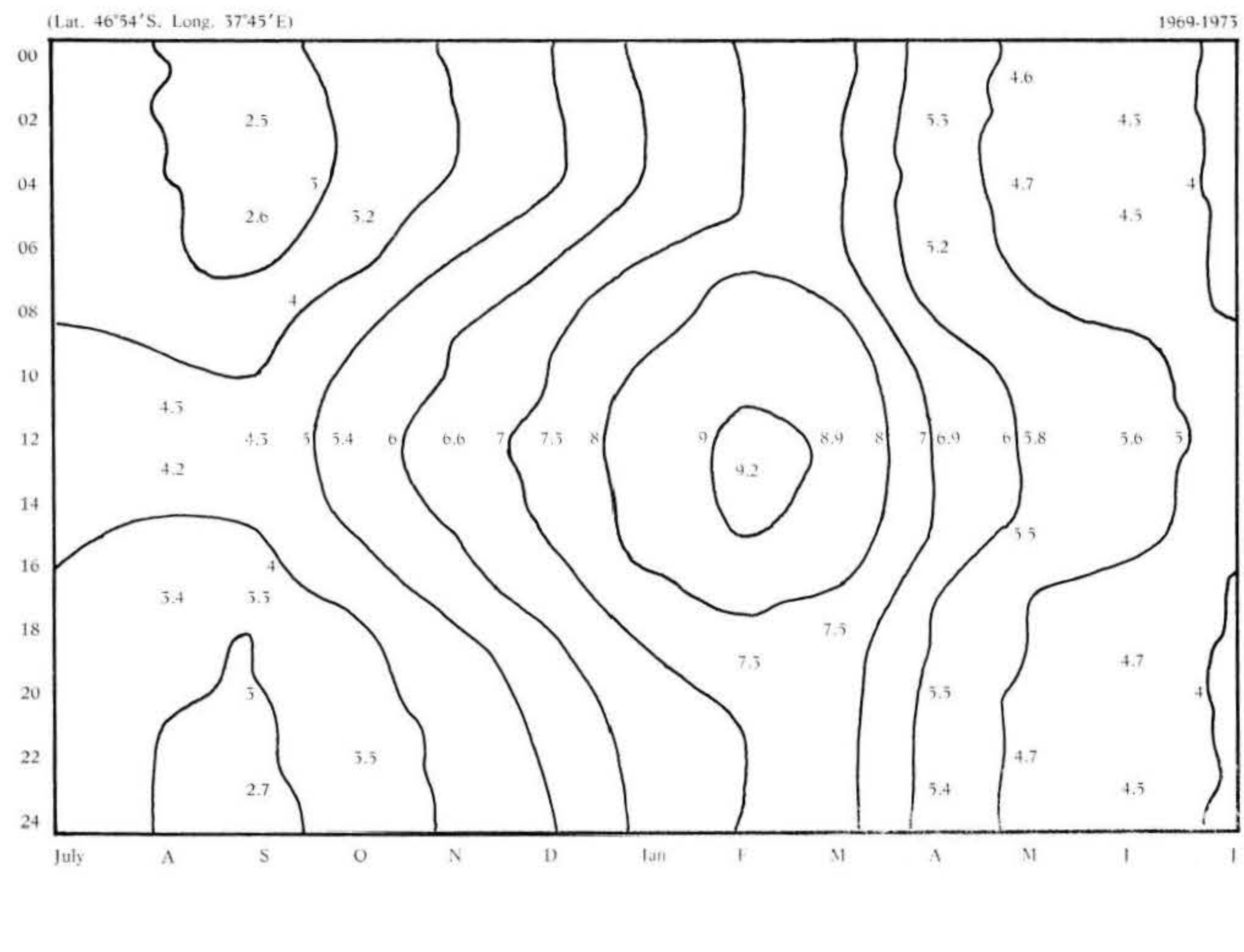
Once an oceanic island has originated by volcanic action and has survived the onslaughts of the elements, plants and animals migrate to this barren new piece of land and the process of ecesis, the settling of the new migrants, begins. The best known examples of these interesting events are the biological invasions on the tropical island Krakatau and, very recently, the ecogenesis on the polar island of Surtsey south of Iceland. A detailed study of this latter phenomenon (Fridriksson, 1975) has shown that the littoral and sublittoral zones were, shortly after the end of the volcanic activity in 1967, covered with a carpet of algae. On the island itself some 100 species of algae and also miniature moss cushions had established themselves by 1968 (Schwabe & Behre, 1971).

These processes will be studied under quite different climatic conditions on Marion Island. An extensive survey of the wind transport of diaspora has been started by erecting traps on two scoria cones near the base. This programme will be carried out for a period of 3 years and the results will be compared with similar surveys done simultaneously on several other southern lands (Tierra del Fuego, the Antarctic Peninsula, South Georgia, Signy Island, the Crozet and Kerguelen archipelagos and perhaps on Macquarie Island). Incidental surveys have already been undertaken on the role of birds (Kok, 1975).

After new migrants have arrived on an island their establishment depends on many factors, such as their ecological adaptability, the diversity of the available biota, competition, the size of the island and the climatic conditions. These processes cannot be separated from the historical aspect, as the number of species which inhabit an island is also determined by the geological age of that island.

In the biogeographical sense, the Marion and Prince Edward islands together with Heard Island and the Crozet and Kerguelen Archipelagos, belong to the Kerguelen Province. It is anomalous that the Marion and Prince Edward islands possess less diversity in their biota and fewer endemic taxa than the islands in this Province which are situated further to the east. The reason for this has not yet been established. The volcanic and glaciological history of the different islands and the means of transport of the biota have to be taken into account. The fact that Marion Island is certainly much younger than the Kerguelen islands, which are situated

Fig. 3. Thermoisopleth diagram of Marion Island (sub-Antarctic).



downwind, points to the possibility that transport by birds could be more important than transport by wind. In general, the islands of the Kerguelen Province have strong biogeographic connections with the temperate and cold-temperate South America and Tasmania–Southern Australia–New Zealand regions (Van Zinderen Bakker, 1971).

The climate and the biota

Meteorological observations have been made continuously on Marion Island since its annexation in 1948 and have provided invaluable data for ecological research on the island. The main characteristics of the climate are its isothermal low temperature, its hyperoceanic humidity (rainfall 2 400–2 700 mm per annum) and storminess.

The climatic system of Marion Island is dominated by the westerlies and by disturbances which originate over the southern Atlantic where sub-tropical and sub-Antarctic air meets between latitudes 30° and 40°S. The depressions which initiate here travel in a southeastward direction and pass over Marion Island up to twice a week, bringing much wind and rain (Schulze, 1971). Anticyclones, which follow, usually pass north of the island but can, especially in summer, bring dry weather to the island.

The temperature regime of the island depends primarily on the temperature of the surrounding cool sub-Antarctic Surface Water. The thermoisoplethdiagram based on hourly measurements during 1969-1973 shows that the seasonal and diurnal variations in temperature are very small (Fig. 3). The daily variations are only 0,9°-2,7 °C, which is slightly more than on Macquarie Island (Troll, 1966), where these fluctuations are 0,5°-2 °C. The latter island has the most isothermal climate on earth. A typical feature of these oceanic islands is the lag period in seasonal change of as much as two months. The coldest period is in mid-September and the warmest in mid-February. The surrounding water mass with its accumulating capacity is responsible for this delay in seasonal change.

Another important meteorological factor is the limited sunshine received by the island's surface. In summer 33 per cent and in winter not more than 20-25 per cent of the possible quantity is received, as is shown by a 17-year record (Schulze, 1971). The dominant overcast condition limits the incoming radiation and provides a low energy budget for plant growth. The total radiation which reaches the island is approximately 210 cal. cm^{-2} day^{-1}, which is less than half the estimated world average of 700 cal. cm^{-2} day^{-1} (Smith, 1977c). However, short periods of bright sunshine can raise the temperature of certain habitats considerably, which must have important physio-ecological consequences. Cushion plants, moss carpets and algal mats in shallow water are very effective energy traps during short periods of sunshine. The limited day length of 7 hours in winter is also a very important factor in this connection. It would be interesting to study the physiological adaptations of different species to these conditions.

Of much importance is the storminess of the island climate. Winds of gale force, which prevail on 150 days per year, have a mechanical influence on plant growth and an aggravating cooling and drying effect. Certain growth forms like cushions of *Azorella* and mosses are well adapted to withstand the rigours of storms and gales. The brachypterous insects which occur on the islands are classical examples of adaptation to the stormy environment.

The wind-desert or *fjaeldmark* with its cushion plants and deflated 'hamada' pavement is a community which resists the force of the wind on the most exposed plateaux and ridges. At the other end of the ecological range we find the peculiar community which dodges the storms and lives protected under loose scoria blocks on the high volcanic cones. Here we find mosses, filmy ferns and a variety of small invertebrates living well sheltered against wind force, low temperature and desiccation. These communities and their biota are amongst the most typical of the islands and should receive much more attention in future.

The island's ecosystems

The rigour of the climate on Marion Island prevents the growth of trees and shrubs, so that the vegetation at low altitude has the appearance of tundra and is characterised by a dense moss carpet, extensive herb fields, tussock grasslands, swamps and hills covered with fernbrake and dwarf shrubs. Above the altitude of 300 m closed communities of vascular plants are replaced by open wind-desert vegetation (Huntley, 1971). This tundra-like vegetation of the island is exposed to such extreme influences as intensive salt spray along the shore, heavy manuring by birds in rookeries and also widespread enrichment of the soil by burrowing birds, concentrated excreta from seals, very high wind velocities and regular frost at higher altitudes. An extensive description of the vegetation has been given by Huntley (1971) and a phytosociological monograph is being prepared by N.J.M. Gremmen. (pers. comm.).

The following short description of a schematic transect of the different ecosystems could give an appreciation of the great variety of biomes which exist in close proximity and which are closely related to one another.

Beyond the kelp-zone lies the open ocean with its high productivity and enormous biomass. On sunny days thousands of birds, which breed on the island, can be seen foraging far away from the land. This is also the hunting ground of countless penguins, thousands of seals, occasional packs of killer whales and sometimes a rare whale.

Near the shore is the intertidal zone with its gigantic brown algae, filamentous green and foliose red algae full of epiphytes, the krill, phytoplankton, amphipods, polychaetes, limpets, fish and a host of other animals.

On land the salt spray zone forms a separate entity. *Tillaea moschata* is a typical halophyte which covers low areas exposed to spray and inundation with a reddish carpet.

Inland of this halophytic community *Cotula plumosa* occupies restricted areas which are still influenced by salt spray, but which are also enriched by excreta of birds or seals. Real coprophilous plant species such as *Montia fontana*, *Callitriche antarctica* and *Poa cookii* are found in great profusion where manuring by animals is pronounced, such as in old seal wallows and near nest sites of birds. The extreme of biotic influence on the vegetation is seen in the large king penguin rookeries where not only the vegetation but also the soft peaty soil have completely disappeared due to constant trampling. The air smells of ammonia, a product of the rich manuring which takes place.

Further inland, bogs, which are reminiscent of the raised bogs of the Northern Hemisphere, occur. In the trophic sense, these are the opposite of the rookeries. The dense moss carpets of these rare sites do not receive enriched water and survive mainly on the resources they receive from the atmosphere, viz. rainwater and carbon dioxide. Their unique oligotrophous nature is indicated by the occurrence of a variety of desmids and protozoa which are typical for these rare habitats.

The type of swamp which is, however, very common in the lowlands, is the mire with a mesotrophic nature. The surface of these large flat areas is covered with a mucilaginous mass of blue-green algae, hepatics and mosses in which grows a dense sward of the grass *Agrostis magellanica*. In the course of time thick deposits of peat may be laid down in these mires.

Still further inland, we find well-drained slopes covered with the fern *Blechnum penna-marina*, which yields to the dwarf shrub *Acaena adscendens* on wind exposed sites. These communities are typical examples of the dominance of one species on an island which numbers only 35 species of vascular plants, 13 of which are aliens.

As has already been mentioned, unique communities are found on the exposed sites at high elevation. The *fjaeldmark* is the community which covers the sites dominated by gales and intense frost at night. The widespread hard cushions of *Azorella selago*, the angiosperm which is the best adapted to the climatic extremes, grow here separated by a typical wind-desert 'hamada' pavement of stones. The cryptogam moss community of *Ditrichum* and *Bartramia* is found at still higher altitudes between 300 and 1 200 m. A very peculiar hypolithic community occurs hidden and sheltered beneath loose scoria blocks on the high volcanic cones (Huntley, 1971; Van Zinderen Bakker, 1978). Mosses, filmy ferns and a variety of small invertebrates live here protected against wind force, low temperatures and desiccation.

Trophic cycles

In the course of time, the emphasis in the research programme has shifted from the descriptive to the quantitative and experimental approach. During the first expedition in 1965/66 we had to concentrate on taxonomical aspects and on the physiognomy of the biomes. Since the second expedition in 1971/72, priority has been given to much analytical and experimental work with the aim of explaining the geological and biological processes on the island. The well-equipped field laboratory has been of very great importance in this connection.

The cycling of minerals in the island's ecosystems has received much attention from Smith (1976a and b). Small oceanic islands like Marion depend for their mineral requirements on the island's own resources and on the atmosphere, but to a much greater extent on the surrounding ocean. A well-organised quantitative study of the interrelations which exist between the different ecological compartments is essential for the understanding of the overall ecology of the island.

The principal processes can be summarized as follows (Fig. 4):

- the basalts, pyroclasts and tuffs of the island decompose as a consequence of the high humidity and regular frost. The geochemical composition of these rocks has been studied (Kable *et al.* 1971). The contribution of this component to the soil and water chemistry will be limited.
- the salt spray of the ocean not only affects the coastal regions, but salt is deposited by rain all over the island with the consequence that the ionic dominance and chemical composition of all the water on the island is closely related to that of the surrounding ocean (Grobbelaar, 1975).
- millions of birds and thousands of seals regularly transport large quantities of organic and inorganic matter to the island. Bird manure has been chemically analysed by researchers such as Croome (unpublished 1971/72 expedition report), Burger, Lindeboom & Williams (1978). The bacteriological processes involved in the decomposition of the excreta leading to enrichment by NH_4- and NO_3- nitrogen has been investigated with much success by Lindeboom (1979). These processes take place in rookeries and seal wallows and, on a smaller scale, are widespread all over the island where millions of birds breed in open sites and in burrows (Smith, 1976a).
- in the extensive mires the gelatinous mass of *Cyanophyta* and probably also bacteria and lichens are responsible for the fixation of atmospheric nitrogen (Croome, 1973; Lindeboom, 1979). This process will probably be of great importance for the island's nitrogen budget and is particularly effective during short periods of sunshine when the mires act as energy traps.
- a great deal of the nutrients which, in the abovementioned processes, are added to the island's systems, are lost to the ocean by leaching and drainage as a consequence of the considerable rainfall (Grobbelaar, 1975).

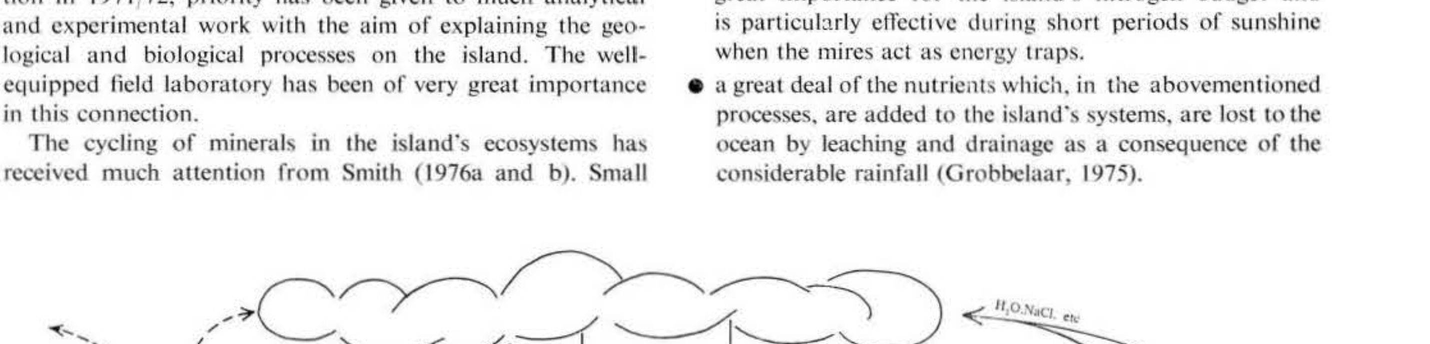


Fig. 4. General scheme of mineral cycling. Broken lines represent outflow of minerals. Pathways are (1) Kelp and pelagic community → birds and seals → excreta → organic and inorganic enrichment → vegetation → etc. (2) Evaporation of ocean water and salt spray → NaCl and other minerals → rain → etc. (3) Rock decomposition → minerals → mires → plankton and vegetation → soil → etc. (4) Decomposition of excreta → NH_3 → rain → oceanic plankton and island vegetation → etc. (5) N_2-fixation in mires → Cyanophyta and Bacteria → vegetation → etc. (6) Drainage to ocean.

The net result of these processes is that, except for some limited areas which are heavily manured, the island soil is poor in minerals especially inorganic N and P and perhaps also Ca (Smith, 1978). One of the aims of the research programme is to devise a quantitative model of the mineral cycling processes of the island's ecosystem.

Ecological energetics

The island is an ideal place to study the transfer of energy and organic matter through its living and abiotic systems. As in the case of the investigation of the mineral cycling, it is essential for the study of the bioenergetics to delineate the different compartments and to assess their qualitative and quantitative contribution to the overall system. As this study is far from complete only a few aspects will be mentioned here.

An energy flow diagram is presented in Fig. 5. In this representation it is shown that the primary production which is of importance to the island's energy flow takes place in the terrestrial vegetation, the freshwater bodies on the island and in the phytoplankton of the ocean.

Notwithstanding the low incoming radiation of only 304 cal. cm^{-2} day^{-1}, it appears that the primary production processes on the island are very efficient. The standing crop of the lowland vegetation has been assessed by V.R. Smith (1976b, 1977a) who came to the conclusion that the value was extremely high compared with circum-arctic vegetation types.

In this connection it should be noted that, as a consequence of the paucity of species on the island, many niches of the ecosystems are not filled. Consumers are very rare, herbivores in the terrestrial environment are the introduced mice, some beetles (Smith, 1977b) and the larvae of beetles and flightless butterflies. Similarly, the food chain in the aquatic system is very short as no fish occur (except for the trout introduced in the Van den Boogaard River). Consequently the produced plant material is, under favourable conditions of high humidity and low pH, transformed into thick peat deposits. These peat beds reach an average thickness of 3-4 m and can attain a depth of up to 6 m. A number of ^{14}C age-determinations show that the annual increase in thickness of the deposits varies from 0,2 to 0,9 mm (compression included). Work on the possible influence of penguin rookeries on peat deposition by Lindeboom (1979) indicates that under such conditions an annual growth of as much as 0,9 mm can be inferred.

The decomposition of organic matter in the soil has so far received scant attention and the soil micro-flora and fauna have still to be studied in detail. During my second stay on the island in 1964, I noticed the great activity of southern black backed gulls, *Larus dominicus*, and the lesser sheathbills, *Chionis minor*, foraging on peatlands. These birds fed on the incredibly rich fauna of earthworms and caterpillars and in so doing, turned the peat surface over so that it afterwards looked like barren ploughed land. Detailed results of a study of this phenomenon have been prepared by Burger (1978). This soil fauna may live on detritus and algae. The only predators exploiting the herbivores on land are spiders and mites (Smith, 1977c). The top of the food pyramid is occupied by the introduced cat, the skua (*Stercorarius skua*) and the two species of giant petrel (*Macronectes giganteus* and *M. halli*).

The primary production in the many small freshwater bodies on the island is low and ranges from *c*.4 to 100 mg C m^{-2} day^{-1}. In biotically enriched water much higher values have been assessed. In seal wallows the productivity even reached 6 000 mg C m^{-2} day^{-1} (Grobbelaar, 1974). The freshwater zooplankton biomass, which consists mainly of Entomostraca, is correlated with the primary production (Kok & Grobbelaar, 1978).

This short summary shows that the structure of the overall ecosystem of the island is not complicated. The study of the unusual communities which occur on the island and the island's dependence on the surrounding ocean will result in the construction of a unique energy transfer model.

Conservation

The Marion and Prince Edward islands have, since their annexation by the South African Government, been declared

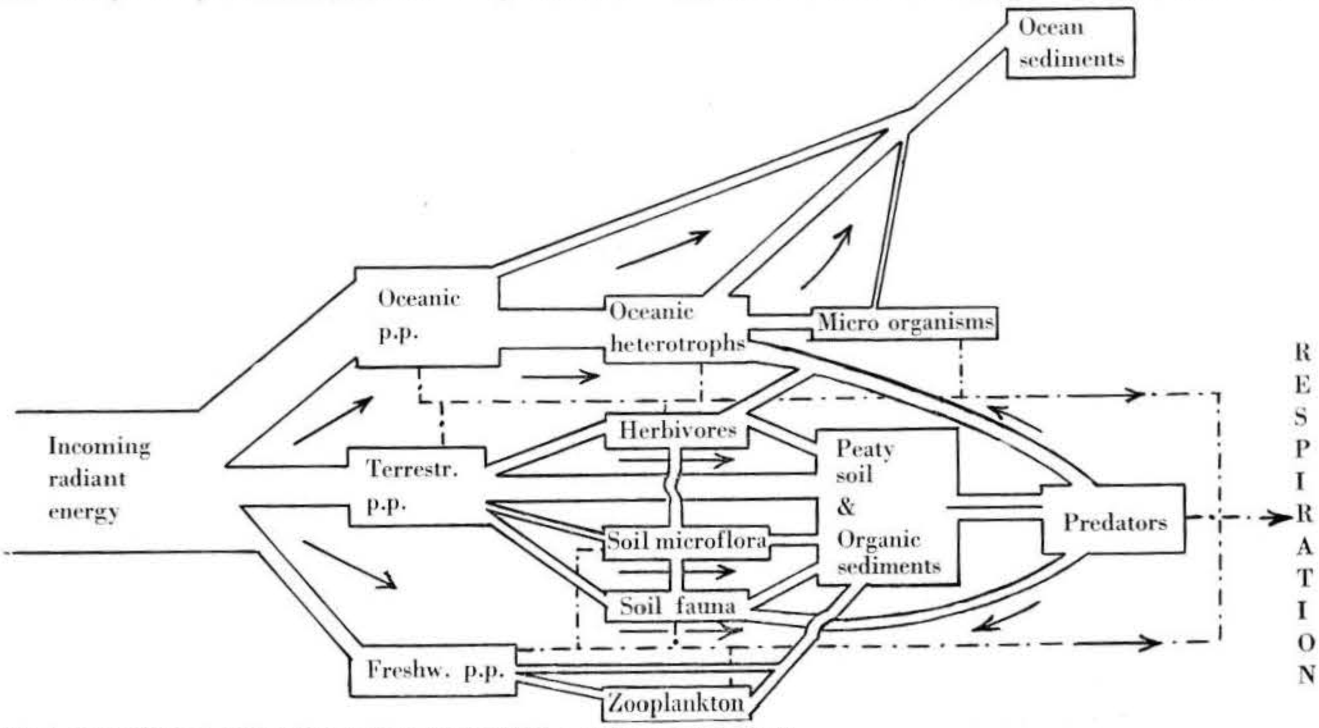


Fig. 5. Compartments and pathways of energy flow (p.p. = primary production).

nature reserves in the widest sense. The protection of the islands is regulated by the Acts No. 43 of 1948 and No. 46 of 1973.

The South African Department of Transport, which is responsible for the islands and sponsors the expeditions thither, takes extreme precautions to prevent interference with animal and plant life and the introduction of alien species. The former practice of bringing sheep and hay, chickens and their feed and even plants to the island has been discontinued with the result that these islands are an example of wise conservation. The 13 alien plant species which have found their way to the island still cause some problems, especially *Cerastium fontanum*, *Poa annua*, *Sagina apetala* and *Stellaria media* which are widespread (Gremmen, 1975). Island biota poor in species are very sensitive to the introduction of hardy competitive aliens as can be seen in the case of the introduction of cats to combat the unintentionally introduced mice. These cats, which take a heavy toll of the defenceless young birds, are difficult to control.

An ideal nature reserve is the smaller of the two islands, Prince Edward, where cats and mice do not disturb the balance and where only one alien plant species, the grass *Poa annua*, has been found. Both islands have in the past been the site of reckless exploitation of seals and penguins, but they have recovered remarkably well from this human influence and abound again in animal life, which makes them havens of natural beauty with great aesthetic and scientific value.

Acknowledgements

I wish to thank the South African Scientific Committee for Antarctic Research for the opportunity given me to direct research on Marion Island during a period of 15 years. The valuable assistance given by the Department of Transport, which was of very great importance for the success of the expeditions, is gratefully acknowledged. The University of the Orange Free State, which made it possible for me to give my time to this fascinating research, deserves my deep gratitude.

Last, but certainly not least, I wish to thank the members of the expeditions for their unfailing enthusiasm, their valuable work and their great personal sacrifices, without which this programme could never have succeeded.

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Plant ecology of Marion Island: a review

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Introduction

Geographically, geologically and climatologically, Marion Island is truly oceanic (Van Zinderen Bakker, 1978a). Situated in the sub-Antarctic region, it is subject to cold temperatures (annual mean air temperature 5,1 °C), a high rainfall (> 2 500 mm per annum) and a high incidence of gale-force winds. The moderating influence of the ocean, however, prevents the bitterly cold weather which characterizes continental winters of most northern hemisphere subpolar sites, and permafrost does not occur.

The island consists of two distinct lava types, a grey pre-glacial and a black post-glacial eruption. As expected of a young volcanic island, the morphology of any particular area is strongly dependent upon the geological structure and most of the island surface is of a primary construction with no subsequent modification of landforms through fluvial erosion. There is, therefore, a striking contrast between the formerly glaciated areas and those which have subsequently been covered by younger, black lava flows. These latter generally form a hummocky, well-vegetated mosaic of slope herbfields, mire, bog and *fjaeldmark*, while the smooth topography of the glaciated areas offers little protection from wind erosion and supports mainly *fjaeldmark* on the ridges and mire vegetation in the ill-drained basins.

The coastal plain on the northern, eastern and south-eastern portions of the island forms an area 4-5 km wide, rising gently from sea-level to the foot of the mountainous interior at about 300 m a.s.l. In contrast, the western and southern coastal areas consist of a narrow, discontinuous plain of less than 100 m altitude and occupied largely by halophytic plant communities capable of withstanding the large amounts of sea-spray deposited onto the surface by the strong, predominantly westerly winds.

The history of research on the island is well documented in Van Zinderen Bakker (1971, 1978a). This paper reviews the results and observations gained from botanical and plant ecological investigations carried out by various workers since 1965. The extensive limnological and phycological data are presented elsewhere in this volume and are therefore not considered in this account.

The vegetation

Description of the plant communities

Because of the rigorous terrestrial environment, the island's geographical isolation and its geologically recent origin, only 38 vascular species occur in the island flora, of which only six contribute significantly to the aerial cover and standing crop of the vegetation (Smith, 1977a). An overall, offshore view of the island presents a bleak, barren appearance owing to the absence of trees or tall shrubs in the vegetation. However, 80 species of mosses (Van Zanten, 1971) and 36 species of liverworts (Grolle, 1971) occur and these form an important component of the vegetation of some areas.

Huntley (1967, 1968, 1971) groups the island's plant communities into five complexes; slope, swamp, salt-spray, biotic and wind-desert. He recognises 13 'noda' in these complexes, depending upon the dominant species present. The paucity of the vascular flora and the wide ecological amplitude of many of the species prevent the classification of the noda into narrower categories. However, these groups provide a clear general picture of the physiognomy and ecology of the vegetation and they are described in detail, including their floristics, distribution, edaphic, and microclimatic conditions.

N.J.M. Gremmen (unpublished) conducted a detailed phytosociological survey of the island during 1973-75 and approximately 600 relevés were made. At each relevé a number of habitat factors were recorded, including altitude,