Oecologia (1990) 85:14–24

Oecologia

Climatic change and its ecological implications at a subantarctic island

V.R. Smith and Marianna Steenkamp

Department of Botany, University of the Orange Free State, Bloemfontein, South Africa, 9301

Received April 17, 1990 / Accepted in revised form July 5, 1990

Summary. Marion Island (47°S, 38°E) has one of the most oceanic climates on earth, with consistently low air temperatures, high precipitation, constantly high humidity, and low incident radiation. Since 1968 mean surface air temperature has increased significantly, by 0.025° C year^{-1}. This was strongly associated with corresponding changes in sea surface temperature but only weakly, or not at all, with variations in radiation and precipitation. We suggest that changing sealevel (atmospheric and oceanic) circulation patterns in the region underlie all of these changes. Sub-Antarctic terrestrial ecosystems are characterized by being species-poor and having a simple trophic structure. Marion Island is no exception and a scenario is presented of the implications of climatic change for the structure and functioning of its ecosystem. Primary production on the island is high and consequently the vegetation has a large annual requirement for nutrients. There are no macroherbivores and even the insects play only a small role as herbivores, so most of the energy and nutrients incorporated in primary production go through a detritus, rather than grazing, cycle. Ameliorating temperatures and increasing CO_2 levels are expected to increase productivity and nutrient demand even further. However, most of the plant communities occur on soils which have especially low available levels of nutrients and nutrient mineralization from organic reserves is the main bottleneck in nutrient cycling and primary production. Increasing temperatures will not significantly enhance microbially-mediated mineralization rates since soil microbiological processes on the island are strongly limited by waterlogging, rather than by temperature. The island supports large numbers of soil macro-arthropods, which are responsible for most of the nutrient release from peat and litter. The activities of these animals are strongly temperature dependent and increasing temperature will result in enhanced nutrient availability, allowing the potential for increased primary production due to elevated temperature and CO_2 levels to be realized. However, housemice occur on the island and have an important influence on the ecosystem, mainly by feeding on soil invertebrates. The mouse population is strongly temperature-limited and appears to be increasing, possibly as a result of ameliorating temperatures. We suggest that an increasing mouse population, through enhanced predation pressure on soil invertebrates, will decrease overall rates of nutrient cycling and cause imbalances between primary production and decomposition. This, along with more direct effects of mice (e.g. granivory) has important implications for vegetation succession and ecosystem structure and functioning on the island. Some of these are already apparent from comparisons with nearby Prince Edward Island where mice do not occur. Other implications of climatic change for the island are presented which emphasize the very marked influences that invasive organisms have on ecosystem structure and functioning. We suggest that changing sealevel circulation patterns, by allowing opportunities for colonization by new biota, may have an even more important influence on terrestrial sub-Antarctic ecosystems than is suggested merely on the basis of associated changes in temperature or precipitation.

Key words: Sub-Antarctic – Climate change – Alien biota – Primary production – Nutrient cycling

Arctic and sub-Arctic regions support substantial human populations and possess diverse vascular floras and large terrestrial bird, mammal, and invertebrate faunas. Their terrestrial ecosystems are complex and substantially utilized in subsistence and cash economies. Consequently, much effort is being devoted to understanding the socioeconomical, ecological, and agricultural implications of climatic change in these regions, in particular the warming they are expected to experience due to increasing atmospheric concentrations of radiatively-active gases (e.g. Miller 1981; French 1986; Jaeger 1988). In contrast, Antarctic and sub-Antarctic regions do not support indigenous human populations. So far their exploitation has overwhelmingly been of the marine eco-

---

Offprint requests to: V.R. Smith

system, as whaling, sealing, and fishing. Their terrestrial ecosystems are poorly developed with no indigenous land birds or mammals, an absence of most invertebrate orders and only a few score vascular plant species (almost wholly restricted to the sub-Antarctic islands; only two occur in the Antarctic). There is very little ice-free land and the regions have no agricultural potential. It is not surprising, therefore, that interest in the marked climatic change currently occurring there (e.g. Jacka et al. 1984; Raper et al. 1984; Adamson et al. 1988) has largely been restricted to considerations of the impact of increasing temperature on sea-levels (Polar Research Board 1985; Frei et al. 1988), glacier retreat (Hayward 1983; Allison and Keague 1986) and the possible relationship between climate and stratospheric ozone concentrations (Lal and Jain 1988). Little attention has been paid to the direct or indirect effects of climate change on biological processes or ecological phenomena despite the fact that, because of their isolation, impoverished biota, and harsh environments, terrestrial ecosystems of the Antarctic and sub-Antarctic are ecologically very sensitive (Smith and Lewis Smith 1987; Smith and French 1988).

The value of biological and ecological studies related to climatic change in Southern Hemisphere polar and subpolar regions is, in fact, increasingly being recognized. For example, the Fifth SCAR International Antarctic Biology Symposium held at Hobart in 1988 (Hempel and Kerry 1990) had as its theme *ecological change and ecosystem conservation*, although only a few papers dealt with changes in response to climate *per se*. In a recent formulation of an Antarctic science component of the International Geosphere – Biosphere Programme (IGBP), the Antarctic, southern ocean and sub-Antarctic islands were identified as critical areas for the global change studies of the IGBP (SCAR 1989). Lewis Smith (1990) has described environmental and biological changes at Signy Island in the maritime Antarctic in order to illustrate the diversity of changes which may affect the structure and function of Antarctic ecosystems in general. He pointed out that currently occurring climate-induced changes in the relatively simple ecosystems of the southern ocean islands offer ideal opportunities for studying ecological processes and ecosystem dynamics.

In this paper we describe climatic changes which have occurred at Marion Island (47°S, 38°E), which is (except perhaps for the Crozet Archipelago) the least climatically-extreme of all sub-Antarctic islands. We propose possible consequences of increasing temperature and changing amounts of precipitation on the structure and functioning of the island's ecosystem.

Materials and methods

A continuous series of daily surface air temperature, sea temperature, precipitation and radiation (hours of sunshine) records since 1951 is available for the island. Grass-minimum temperatures have been measured since 1960. The data bank is housed at the S.A. Weather Bureau, Pretoria, South Africa. From it, mean monthly values were extracted (up until October 1989) and annual means calculated. Mean daily surface air temperatures were estimated as the average of the daily maximum and minimum values and the monthly and annual means calculated from them. Time-series plots of the means were constructed and apparent trends tested by regression analysis.

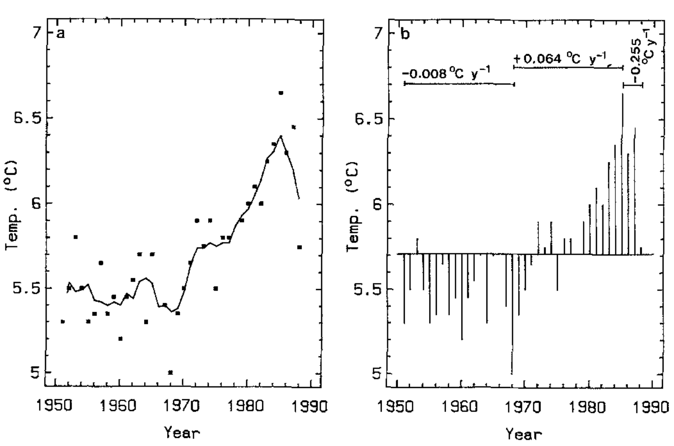

Fig. 1a, b. Mean surface air temperatures at Marion Island since 1951. Annual mean values (■) and their 5-year running averages (*line*). **b** Deviations of annual mean values from mean for 1951–1988. *Values above horizontal bars* are annual rates of change for the periods spanned by the bars, calculated by linear regression

Results

Overall, annual mean surface air temperature on the island increased during the period recorded (1951–1988) by 0.93 °C, or an average of 0.025 °C per year (Fig. 1a). In fact, most of the increase occurred over the second half of this period and 15 of the 17 years since 1972 have been warmer than the 1951–1988 mean (Fig. 1b). Regression analysis showed that between 1951 and 1968 surface air temperature was fairly constant, or at least did not change in a consistent direction. From 1968 to 1985 it increased, on average, by 0.064 °C year^{-1} ($P=0.0001$), a total calculated increase of 1.1 °C. The actual difference between the 1968 and 1985 means was 1.6 °C. Since 1985 values have declined markedly (0.255 °C year^{-1}); however, only four observations are included in this period and the decrease is not significant at $P \leq 0.1$.

Between 1951 and 1968 only the March temperature showed a consistent significant ($P=0.05$) change (Fig. 2a), a decrease which accounted for 42% of the slight (nonsignificant) lowering (0.008 °C year^{-1}) of annual mean temperature for this period (Fig. 1b). Warming during 1968–1985 occurred in all months (Fig. 2b), but the average annual increases for February, March, June, and July are not significant at $P \leq 0.1$. The greatest rate of increase (0.118 °C year^{-1}; $P=0.00001$) was for April but, overall, it was the late winter to midsummer period which accounted for most of the annual warming. Since 1985 all monthly temperatures, except March and July, have declined (Fig. 2c).

Changes in annual mean sea surface temperature between 1951 and 1988 corresponded closely, in time and

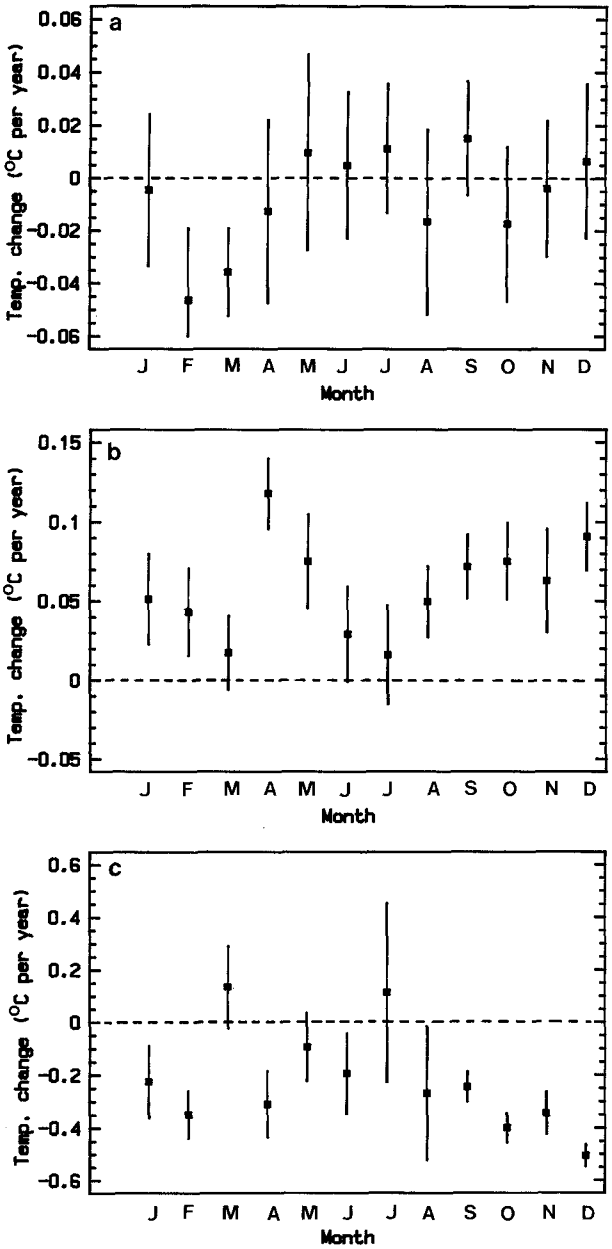

Fig. 2a–c. Annual changes in monthly mean air temperatures for the periods **a** 1951–1968, **b** 1968–1985, **c** 1985–1988/9

direction, to those in air temperature (Fig. 3a), with 1967 and 1985 being the coldest and warmest years respectively (missing sea temperature data for October and November prevented estimation of a mean value for 1968). Between 1951 and 1967 no consistent change in annual mean sea temperature occurred (Fig. 3b). From 1967 to 1985 there was an average increase of 0.048 °C year^{-1} ($P = 0.001$) and since 1985 a marked decline (0.18 °C year^{-1}; $P = 0.05$). Overall, the calculated increase between 1967 and 1985 was 0.9 °C and the actual difference between these years was 1.2 °C. All months exhibited this increase (Fig. 4b) but greatest warming was exhibited in summer and autumn (October to May). The decrease in annual values since 1985 was largely due to significant declines in temperature for April, June and the first half of summer (Fig. 4c).

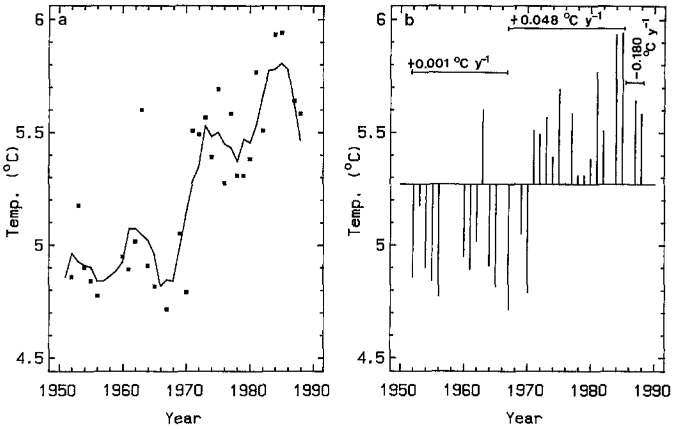

Fig. 3a, b. Mean sea surface temperature at Marion Island since 1951. **a** Annual mean values (■) and their 5-year running averages (*line*). **b** Deviations of annual mean values from the 1951–1988 mean. *Values above horizontal bars* are annual rates of change for the periods spanned by the bars, calculated by linear regression

Total annual radiation (measured as hours of sunshine) also showed a large degree of interannual variability between 1951 and 1988 (Fig. 5a). Overall, however, annual values increased significantly ($P = 0.002$) by about 4 h per year during the period. Only 3 of the 18 years prior to 1968, but 14 of the 20 years since then, were above the 1951–88 average (Fig. 5b). The five-year smoothed values suggest that the overall increase during 1951–1988 occurred in two stages, by 17 h year^{-1} between 1959 and 1968 ($P = 0.1$) and by 31.5 h year^{-1} from 1982 to 1988 ($P = 0.04$). These periods were separated by a period (1968–1982) when, overall, sunshine declined on average by about 11 h year^{-1} ($P = 0.06$). Changes in monthly totals of radiation during these periods (data not shown) were mostly insignificant at $P \leq 0.1$ and the changes in annual amounts could not be ascribed to any particular season.

Changes in annual totals of precipitation since 1951 are more marked than suggested by the 5-year running means in Fig. 6a. Between 1951 and 1967 precipitation increased by ca. 46 mm year^{-1}, a total of 831 mm (Fig. 6b). From 1967 to 1980 it decreased by ca. 43 mm year^{-1}. Since 1983 it has increased markedly, at an average rate of ca. 65 mm year^{-1}. All these changes are significant at $P < 0.05$. Therefore, during approximately the same periods that surface air and sea temperatures were increasing (late 1960s to mid 1980s) or decreasing (mid 1980s to present), opposite changes occurred in annual precipitation. However, prior to 1967, the marked increase in precipitation was not accompanied by significant or consistent changes in either sea or air temperature.

Discussion

Climatic change

Not surprisingly for such a small (290 km^2) island surrounded by the vast, thermally-stable Southern Ocean,

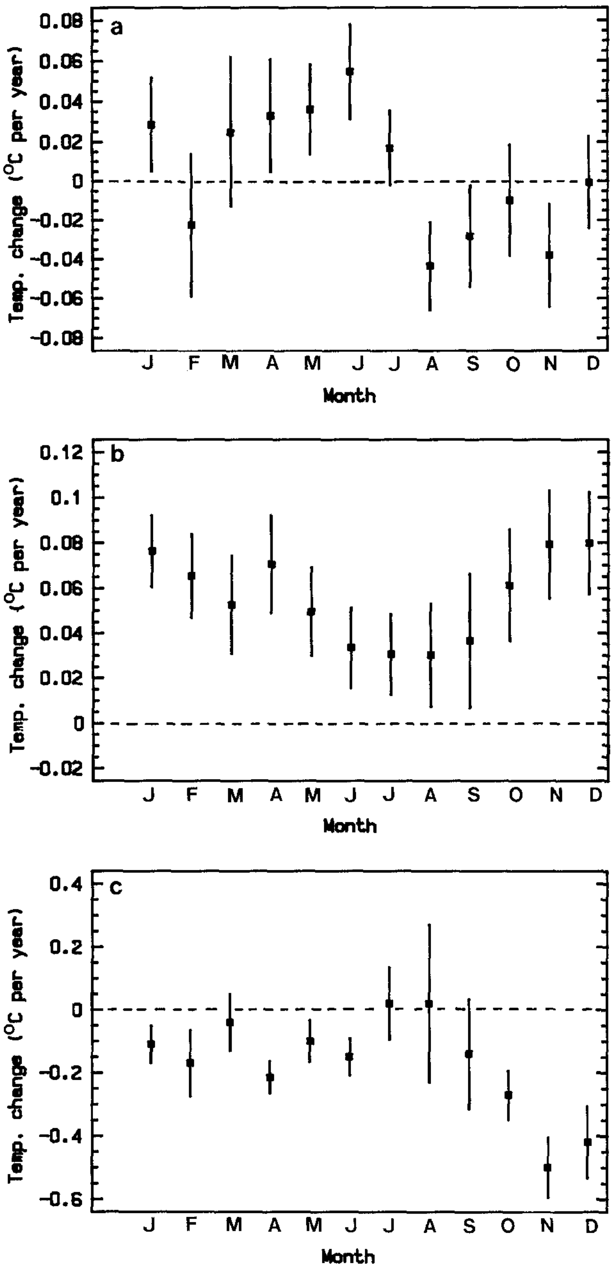

Fig. 4a–c. Annual changes in monthly mean sea surface temperatures for the periods **a** 1957–1967, **b** 1967–1985, **c** 1985–1988/9

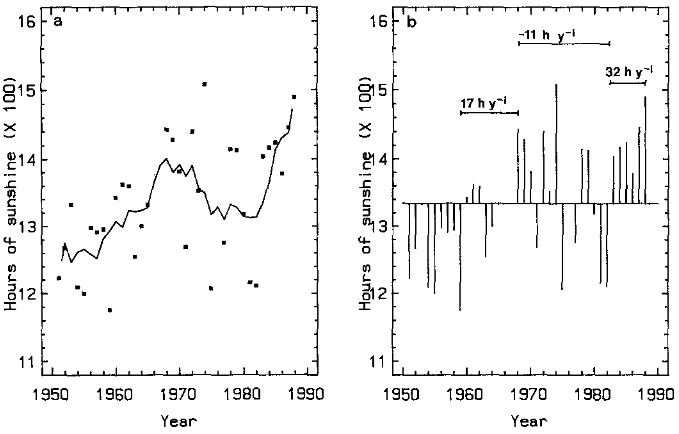

Fig. 5a, b. Annual total hours of sunshine at Marion Island since 1951. **a** Annual totals (■) and their 5-year running averages (*line*). **b** Deviations of annual totals from the 1951–1988 mean. *Values above horizontal bars* are annual rates of change for the periods spanned by the bars, calculated by linear regression

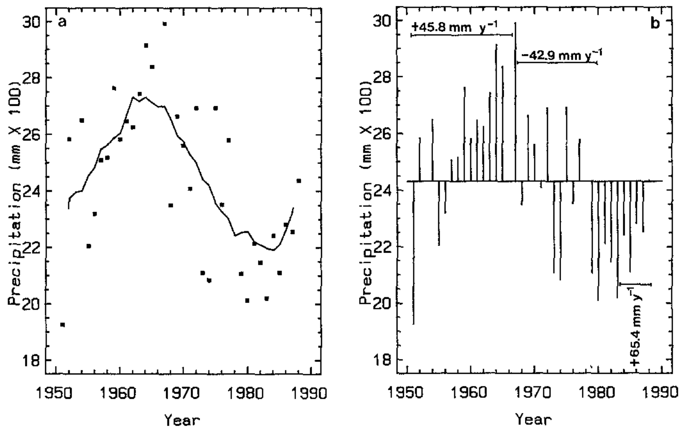

Fig. 6a, b. Total annual precipitation at Marion Island since 1951. **a** Annual totals (■) and their 5-year running averages (*line*). **b** Deviation of annual totals from the 1951–1988/9 mean. *Values above horizontal bars* are annual rates of change for the periods spanned by the bars, calculated by linear regression

Marion Island possesses one of the most oceanic climates on earth (Smith 1987a; Smith and French 1988). Surface air temperatures are consistently low, with an annual mean of 5.7 °C, total seasonal variation of 4.3 °C and maximum mean diurnal variations of <3 °C in summer and <2 °C in winter. Precipitation (ave. 2432 mm year^{-1}) is higher than for other sub-Antarctic islands, occurs mostly as rain and is fairly equally distributed throughout the year. Annual mean relative humidity is 83%, with a seasonal range of only 4%. Cloudiness is the rule and the island experiences only 25–30% of the astronomically-possible annual sunshine.

Against this background of hyperoceanicity the changes in air temperature, precipitation and, to a lesser extent, radiation that have occurred during the last three decades are remarkable. Similar changes have occurred at other sub-Antarctic islands, e.g. Adamson et al. (1988) reported that from 1949 to 1986 annual mean surface air temperature at Macquarie Island (55°S, 159°E) increased by 0.026 °C year^{-1}, very similar to the average increase of 0.025 °C year^{-1} at Marion Island between 1951 and 1985. Examination of the 5-year running means for Macquarie Island air temperatures (Fig. 1 in Adamson et al. 1988) indicates that, as at Marion Island, all of the increase actually occurred from the late 1960s to early 1980s. Most warming occurred during the late summer and autumn months at Macquarie Island, unlike at Marion island where increases in temperature were most marked during late winter and early summer. At Kerguelen Island (49°S, 69°E) annual mean air temperature increased by 1.5 °C between 1964 and 1986 and at Heard island (53°S, 74°S) mean monthly temperatures between April 1980 and February 1983 were also about 1.5 °C higher, on average, than they were in the early 1950s (Allison and Keague 1986). Overall, it appears

Table 1. Linear correlation coefficients for the deseasonalized monthly mean values of the climatic variables. ** $P=0.05$ *** $P=0.001$

	Sea temperature	Air temperature	Hours of sunshine	Precipit-action
Sea temperature	1			
Air temperature	0.538***	1		
Hours of sunshine	0.021	0.130**	1	
Precipitation	−0.132**	−0.136**	−0.135**	1

that Indian Ocean sub-Antarctic islands (Marion, Kerguelen, Heard) and cold temperate islands (Amsterdam) have experienced greater warming since the mid 1960s than have their counterparts in the Pacific Ocean (Macquarie, Campbell). At Signy Island (maritime Antarctic region, South Atlantic Ocean), summer (Dec to Feb) mean temperatures have increased significantly since the late 1960s (Lewis Smith 1990).

Relationhips between the changes in air and sea temperatures, radiation and precipitation on Marion Island since 1951 were examined by simple regression analysis of their monthly mean values, which were first deseasonalized by subtracting the 1951–1988 means for each particular month. Except for hours of sunshine with sea temperature, they were all intercorrelated (Table 1). The highest correlation was between surface air and sea temperatures, hence the similarity in the variations of their annual mean values – compare Figs. 1 and 3). The other correlations were much weaker but still highly significant ($0.001 < P < 0.01$). Air temperature was positively associated with hours of sunshine and negatively with precipitation. Multiple regression showed that, in the presence of sunshine and rainfall, sea temperature accounted for 28% of the variation in mean monthly (deseasonalized) air temperature. Sunshine duration added another 1% ($P=0.01$) to the explained variation. In the presence of these two variables there was no correlation between precipitation and air temperature.

The strong positive correlation between air and sea temperature evidences the overwhelming influence of the ocean on the island's climate. The fact that over the whole recorded period deseasonalized monthly air temperatures are also positively associated with deseasonalized monthly sunshine totals (Table 1) and negatively with deseasonalized monthly precipitation totals appears rational, i.e. warm conditions might be expected to be sunny and dry, whereas cold ones are overcast and wet. However, the actual weather pattern at the island is exactly the opposite. Warmest temperatures occur just before the passing of cyclonic low-pressure centers (generally just to the southwest of the island; tracks *b* and *c* in Fig. 7). Then, cloud cover is complete and strong northwesterly wind and incessant rain occur. As the front passes, the wind shifts to southwesterly and, due to the advection of cold, relatively dry Antarctic air, temperatures drop sharply, there is less cloud and graupel (soft hail) showers occur. Some 100–130 cyclones pass the island each year so that, in effect, the island's weather is characterized largely by alternations of warm, overcast rainy periods with cold, clearer, drier ones. Hence the overall picture suggested by the regression of monthly mean values), that increasing temperatures are accompanied by sunnier periods, would seem anomalous and reflects the fact that, overall, both air temperature and sunshine totals increased from 1951 to 1988 (e.g. compare the overall trends shown by Figs. 1a and 5a). As noted above, however, during 1968–1982, approximately the same period during which air temperatures increased, sunshine totals actually decreased.

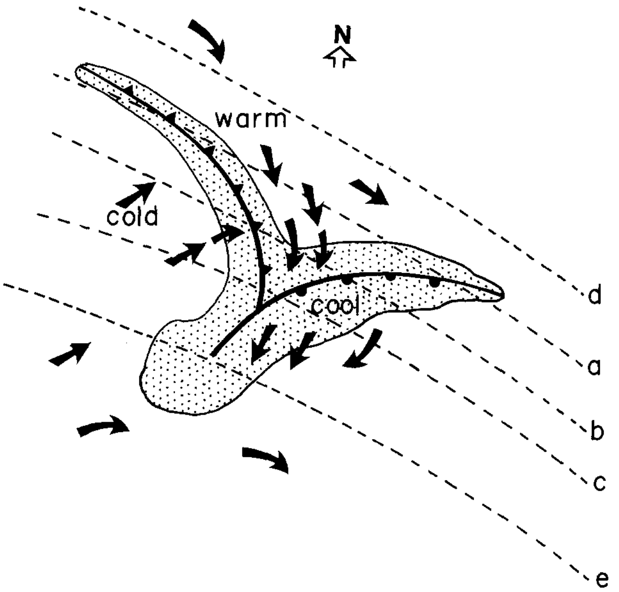

Fig. 7. Position of island relative to passing cyclonic centres. *Thick curved lines* are the fronts associated with the centre and the *dashed lines* indicate the island's position relative to its passing track. The centre passes either to the south (*a*, *b*, *c*, *d*) or north (*e*) of the island. The *dotted area* is the cloud cover associated with the passing fronts and the *arrows* indicate wind direction. Associated weather patterns for each track are discussed in the text

The actual causes of the air and sea temperature increases at the island are unknown but they may reflect changing atmospheric circulation patterns, associated with changes in oceanic circulation patterns. We suggest that in warmer years the cyclonic centers pass, on average, further to the south of the island (e.g. Fig. 7, track *a*) so that the island experiences longer periods of warm (but still cloudy) precyclonic conditions and less of the icy, post-cold front conditions. Because the island is then further from the low pressure centre, during the pre-cold front period winds will be less strong, more northerly (and probably warmer) and the rainfall intensity less, although cloud cover will still be high. In addition, the island will spend a longer time in the cloudy trailing arm of the cold front, so that total sunshine levels will be decreased even further. When the cyclonic centre passes far to the south (e.g. track *d*, Fig. 7) the island's weather is dominated by anticyclonic high pressure systems to the north and is clear and warm. However, should the centre pass far to the north (track *e*), the island will experience cold, clear weather for most of the time.

Biological and ecological implications

Because of its relatively recent origin, extreme isolation, and past glaciations the island's biota is very species poor. There are no indigenous land mammals or birds and only 17 indigenous insect species, 13 collembolans, 4 spiders, 3 earthworms, 19 mites, 1 snail and 1 slug species (Crafford et al. 1986). Only 38 vascular plant species (of which 14 are man-introduced aliens) occur, although 72 mosses, 35 liverworts, and approx. 100 lichens have been recorded. The vascular species, especially, have a wide ecological amplitude and most occur over much of the range of available habitats, e.g. seven occur in more than half of the 49 plant communities defined for the island by Gremmen (1981).

It is therefore unlikely that temperature changes *per se* will significantly influence species composition of the plant communities or cause any species to disappear from the island (except perhaps for the Kerguelen Cabbage, *Pringlea antiscorbutica*, which appears to be intolerant of warmth, especially when it is accompanied by low humidities). Distributions of particular communities will change; certainly, vascular plant-dominated ones will encroach to higher altitudes and they will become more important in the vegetation as a whole, at the expense of bryophyte communities. Any changes in precipitation and/or wind, however, will have a very marked influence on species composition and distribution of the plant communities, since the main factors influencing them (other than manuring and trampling by animals, where these occur) are hydrology and wind exposure (Gremmen 1981; Smith 1987a). Bryophyte communities, especially, are very sensitive to changes in the hydrological regime. However, we predict that the important implications of climatic change (and the associated changes described below) for the vegetation and ecosystem as a whole will be at a different level – i.e. by influencing primary and secondary production and nutrient cycling.

The hyperoceanic climate (no extremely cold or arid periods, hence a long growing season) allows for a high annual primary production (Smith 1987b). Vegetation production at the island (and other sub-Antarctic islands) is greater than for most tundra areas of the northern hemisphere (Fig. 8). In fact it is greater than for most temperate grasslands and the more productive communities in the sub-Antarctic are as productive as many forest ecosystems. Consequently, the island vegetation has a substantial annual requirement for nutrients; e.g. a fernbrake community (total production 1958 g m^{-2} year^{-1}) takes up 24.4 g N m^{-2} and 3.2 g P m^{-2} annually (Fig. 9). Inputs of N, P, and K through precipitation or biological fixation are negligible. Although seabird and seal manuring is an important source of nutrients at some (mainly shore zone) areas, most plant communities are not affected by this and pools of available nutrients are small, even by "tundra" stan-

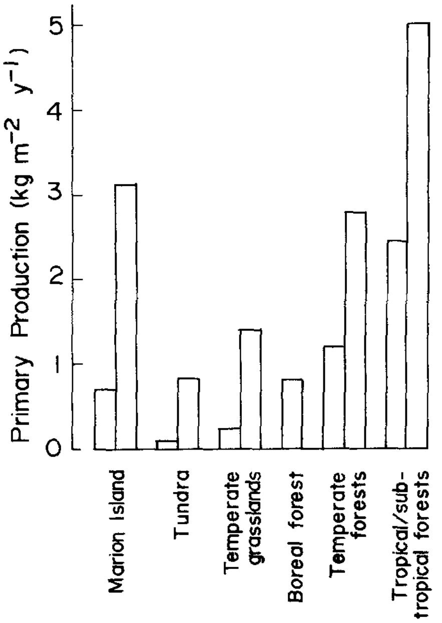

Fig. 8. Total (above- plus belowground) annual net primary production on Marion Island compared with that of other ecosystems. Where *two bars* are given this indicates minimum and maximum values reported for the particular ecosystem type. Marion Island: Smith (1987b) and unpublished data. Tundra (excluding Glenamoy and Moor House): various accounts in Rosswall and Heal (1975), Wielgolaski et al. (1981). Temperate grasslands: Sims and Singh (1978). Boreal and temperate forests: Art and Marks (1971). Tropical and sub-tropical forests: Kira et al. (1967), Art and Marks (1971)

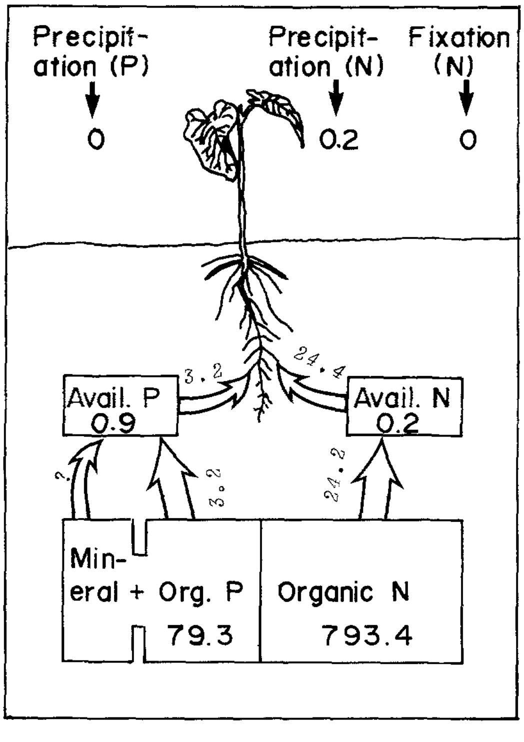

Fig. 9. Nitrogen and phosphorus budgets for a fernbrake community on Marion Island. Standing stocks (*boxes*) are in g m^{-2} and flows (*open arrows*) or inputs (*solid arrows*) are in g m^{-2} year^{-1}. From information provided by Smith (1988)

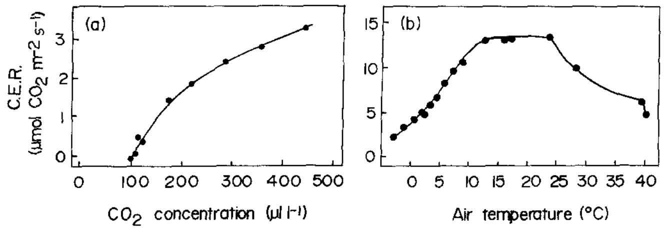

Fig. 10a, b. Response of photosynthesis (carbon dioxide exchange rate; C.E.R.) to **a** CO_2 concentration and **b** air temperature for the tussock grass *Poa cookii*. From Bate and Smith (1983)

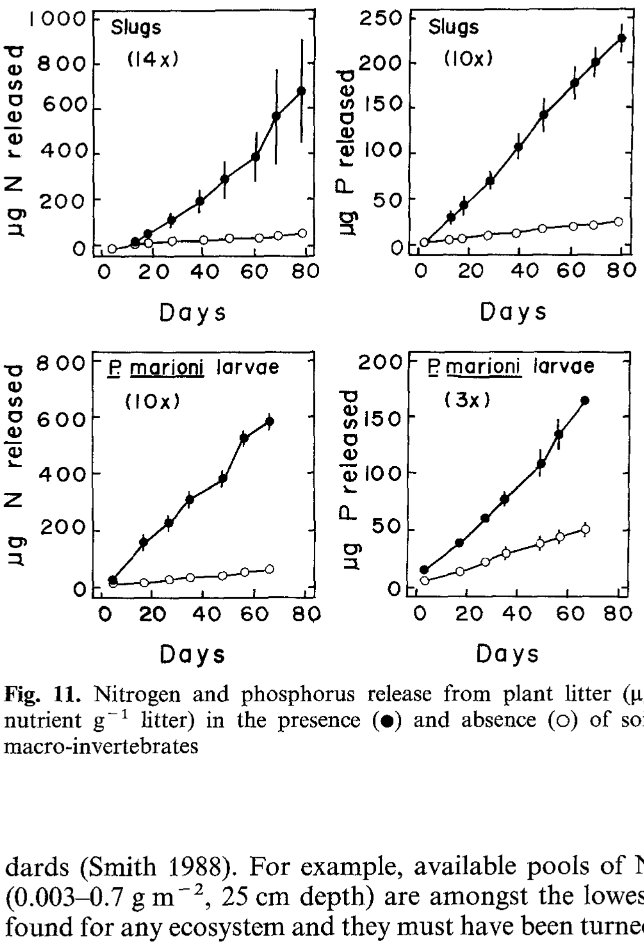

Fig. 11. Nitrogen and phosphorus release from plant litter (μg nutrient g^{-1} litter) in the presence (●) and absence (○) of soil macro-invertebrates

dards (Smith 1988). For example, available pools of N (0.003–0.7 g m^{-2}, 25 cm depth) are amongst the lowest found for any ecosystem and they must have been turned over rapidly (up to 2180 times) in the course of the growing season to supply the needs of the vegetation.

Atmospheric CO_2 concentrations at the island have increased by 16 vpm since 1976 and, in common with the rest of the world, are expected to double by some time in the first part of the next century (Pittock and Salinger 1982). The island plants are all "C_3" photosynthetic types and exhibit enhanced CO_2 assimilation rates in response to increasing atmospheric CO_2 levels (Fig. 10a). Ameliorating temperatures (possibly associated with increasing CO_2 levels through the greenhouse effect) will also lead to enhanced CO_2 assimilation rates since at present the plants are operating below their temperature optima (Fig. 10b and Pammenter et al. 1986). From studies on tundra and temperate C_3 species (Hilbert et al. 1987; Sage et al. 1988) we estimate that a doubling of atmospheric CO_2 concentrations coupled with a 2 °C rise in temperature will allow assimilation rates between 30% and 50% higher than at present. Potentially, this will lead to a higher primary production and concomitantly a greater requirement for nutrients.

There are no macroherbivores on the island and even the insects are insignificant herbivores; e.g. Crafford et al. (1986) estimate that insects consume only 3.5% of the aboveground net primary production. Thus virtually all of the plant productivity becomes dead organic matter and most of the energy flow and nutrient circulation occurs through the detritus, rather than grazing, subsystem of the island ecosystem (Smith 1977). Nutrient mineralization during decomposition is the main rate-limiting step in soil nutrient cycling and uptake of nutrients by the vegetation and rates of their release from organic matter are apparently closely coupled (Smith 1988). However, rates of nutrient release mediated by microorganisms alone are not sufficient to account for even a fraction of the vegetation's annual requirements and increasing temperature *per se* will not significantly enhance these rates, since microbial decomposition processes on the island, although temperature sensitive, are overwhelmingly limited by excessive soil moisture contents. For instance, a decrease in precipitation sufficient to halve the moisture contents of the mire peats would cause a 5 to 11-fold increase in decomposition rate, with concomitant increases in rates of nutrient release.

In any event, the effects of changing temperature and moisture levels on microbially-mediated nutrient cycling will be small compared with the influence of increased temperature on the activities of soil macroinvertebrates, which are the main mediators of nutrient mineralization on the island. For example, two larvae of a flightless moth (*Pringleophaga marioni*, the most abundant soil macroinvertebrate) added to microcosms containing plant litter or peat stimulate N mineralization 10-fold and P mineralization 3-fold (Fig. 11). These larvae annually process approximately 1500 kg litter ha^{-1} (Crafford 1990). Weevil larvae, earthworms, slugs and snails have also been shown to stimulate nutrient release from plant litter and/or peat (e.g. slugs cause up to a 14-fold enhancement of N-mineralization rates; Fig. 11) and in some communities these animals play an even more important role than the moth larvae.

Considering the current patterns of distributions of soil arthropods, it is unlikely that moderate changes in soil moisture content will significantly influence their population sizes or activities, except perhaps by decreasing earthworm populations in the drier communities. However, the activities of the soil macrofaunal species are strongly temperature-dependent. For the moth larvae, ingestion rates increase with temperature but assimilation efficiencies decrease (Jan Crafford, pers. comm.) so that, overall, the effect of elevated temperature will be to increase the amounts of litter and peat processed and of nutrients released. The enhanced nutrient availability will allow the potential for increased primary production due to elevated temperatures and CO_2 levels to be realized. Overall, decomposition rate will increase relative to primary production so peat accumulation

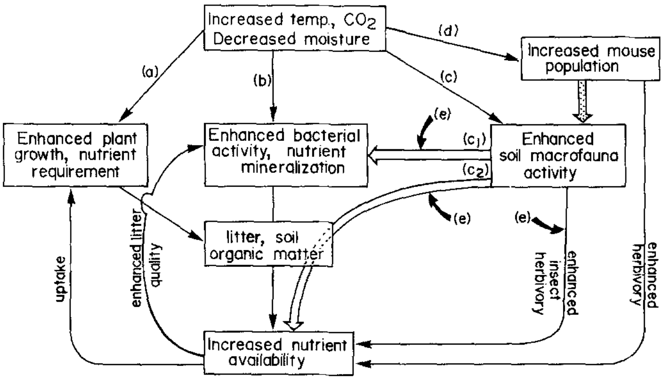

Fig. 12. Suggested implications of climatic change on primary production, decomposition and nutrient cycling at Marion and Prince Edward Islands. Increasing temperature and atmospheric CO_2 levels will result in enhanced production (*a*) and nutrient requirements by the vegetation. Q_{10} for soil microbial processes is very much greater than that for photosynthesis and a decrease in soil moisture contents from supra-optimal levels will markedly enhance decomposition and nutrient mineralization. Hence, $b > a$. However, the direct effect of temperature and moisture level changes on microbially-mediated nutrient mineralization is likely to be small in absolute terms.
Scenario A: The main effect of climatic warming is to enhance soil macrofaunal activities (*c*) i.e. change in c (and hence in c_1 and c_2) $>>>$ change in a (or b). Hence warming, through increased c, c_1 and c_2, will result in enhanced nutrient supply in relation to primary production, leading to better litter nutrient quality and even further stimulation of mineralization rates. This allows the full potential for increased primary roduction due to elevated temperature and CO_2 levels to be realized. Overall, decomposition will increase more than primary production and peat accumulation rates will decrease. This is thought to be the scenario for mouse-free Prince Edward Island.
Scenario B: Increased mouse activity caused by elevated temperature (*d*) negatively influences nutrient mineralization (c_1, c_2) through enhanced predation on the soil macrofauna. (*Heavy curved arrows* (*e*) indicate where the main influences of mouse predation will occur.) Enhanced plant growth and nutrient demand due to elevated temperature and CO_2 will therefore be accompanied by lower nutrient availability, a decline in litter quality and an even further depression of mineralization rates. This will ultimately result in a decline in primary production. However the decline will be less than that in decomposition so that rates of peat accumulation will increase. This is the suggested scenario for Marion Island

rates will decline. This is depicted as scenario A in Fig. 12). However, another factor which could change this scenario significantly needs to be considered.

Marion Island supports one of the southern-most populations of house mice (*Mus musculus*) in the world which, in the late 1970s and in terms of temperature, was thought to be existing at the limits of its ecological tolerance (Bonner 1984). The mice were introduced by sealers before 1818 (Watkins and Cooper 1986). There are strong indications that the mouse population has increased substantially over the past 20 years. For example, in April 1973 5 mice were trapped in a particular study site in 24 h; at the same site in April 1984, 17 were trapped in a similar period. They are now encountered far more often in the field than they were in the early 1970s and signs of their activity (pathways, burrows, breeding chambers, damaged inflorescences) are much more common. They now occur in habitats (e.g. albatross nests, *Azorella selago* cushions) where they were absent in the 1970s. Between 1975 and 1982 there was a very marked (ca. 3-fold) increase in the occurrence of mice in the stomach contents of feral cats on the island (Van Rensburg 1985), possibly reflecting an increased availability of mice.

The island mice are definitely temperature-stressed, keeping mainly to their burrows and carrying out most of their foraging and territorial and other behaviour during warmer periods. Mice trapped alive in the field soon die unless the traps are supplied with insulating material. The population also exhibits age-related genetic changes (Berry et al. 1978), interpreted by Bonner (1984) as affording strong presumptive evidence that cold stress is acting as an agent of natural selection. We suspect that the increase in the mouse population over the past 20 years or so has been due to ameliorating temperatures and/or a change in its genetic composition. Since 1986 there has been an intensive, ongoing effort to hunt out the island cats and cat numbers are now only a fraction of what they were then. Predation pressure on the mice has been reduced accordingly and this can also be expected to allow their numbers to increase.

Mice are the sole mammalian herbivore on the island although in 1979/80, considered throughout the year and across all habitats in which they occurred, only 17% of their diet on a dry mass basis consisted of plant material (Gleeson and Van Rensburg 1982). They eat negligible quantities of vegetative material but are having a significant effect on the vegetation through seed-gathering. In the late 1960s a sedge, *Uncinia compacta*, was abundant (in many cases, dominant) in mire vegetation (Huntley 1971), but it has now almost been eradicated due to seed harvesting by mice. On neighbouring, mouse-free, Prince Edward Island *Uncinia* is still the dominant or co-dominant vascular species in mires. Mice also consume seeds of other plants and gather large quantities of immature inflorescences to line their refuges and breeding chambers.

However, the dominant role of mice in the island ecosystem is that of carnivore (Gleeson and Van Rensburg 1982). In 1979/80 soil invertebrates constituted 83%, and in 1987 94%, of the diet of trapped mice (Rowe-Rowe et al. 1989). From mean mouse densities, their energy metabolism measured by a double-labelled H_2O technique, and the energy content of the main items in their diet, Rowe-Rowe et al. (1989) calculated that mice consume 39.4 kg ha^{-1} of soil invertebrates annually. Moth larvae, weevil larvae and adults, and spiders together accounted for 70% of their diet. Across habitats, the annual standing crop (dry mass basis) of these arthropods was 13.2 kg ha^{-1} $year^{-1}$ in 1976/77 (Burger 1978). The main daily impact by mice on them was 91 g ha^{-1}, or 0.7% of standing crop, per day. For the moth larvae (mean standing crop 6.2 kg ha^{-1}) alone, mean daily impact was 65 g ha^{-1} (1% of standing crop), or an annual total of 23.7 kg ha^{-1}. This consumption rate implies a production: biomass coefficient of at least 3.8 for the moth population. The exact duration of the moth's life-cycle is unknown but the larval stage lasts for at least 2 years (Crafford et al. 1986) and the larvae are slow growing. In addition, mouse predation is strongly size-selective and the most "ecologically-active" part of the population (semi-mature larvae) is depleted most.

From these considerations, Crafford (1990) estimated that currently (1989) mice annually "prevent" the processing of at least 1000 kg of plant litter per hectare, i.e. in the absence of mice the average annual turnover of litter by moth larvae alone would be 2500 kg ha^{-1}. Clearly then, by feeding on soil macroinvertebrates mice play an important role in decomposition and nutrient cycling on Marion Island. There are marked differences between Marion Island and Prince Edward Island in population size, structure and composition of their insect faunas (Crafford and Scholtz 1987), thought to be due to mouse predation on the one island. If ameliorating temperatures (or any other factor such as reduced cat numbers) allow the mouse population to increase, enhanced predation pressure on soil invertebrates will further exacerbate nutrient limitations on primary production. The overall effect will be to decrease rates of nutrient cycling, thus decreasing litter nutrient quality and causing further imbalances between primary production and decomposition (scenario B in Fig. 12). This will result in enhanced rates of peat accumulation which is one of the most important factors controlling vegetation succession on the island, mainly through its role in driving changes in the hydrological regime of a particular sere (Gremmen 1981; Smith 1987a). If this is superimposed on the more direct influences of mice (e.g. herbivory) and the effect of nutrient limitations on species composition and production of the plant communities, a changing climate might be expected to result in different patterns of vegetation change between Marion and Prince Edward Islands. There are signs that this is already occurring.

Lesser Sheathbills (*Chionis minor*) and Kelp Gulls (*Larus dominicanus*) together consume ca. 39 g ha^{-1} soil macroinvertebrates daily (Burger 1978). Sheathbills, especially, rely heavily on soil invertebrates to survive the winter, and increasing competition by mice will affect these birds. Already, there are differences between Marion and Prince Edward Islands in their foraging behavior and intensity (Crafford and Scholtz 1987). Since they are important agents transporting marine-derived nutrients to vegetated areas inland, in the form of kleptoparasitism on penguins and foraging for seaweed and intertidal invertebrates, this has implications for nutrient cycling.

In this account of possible ecological implications of climatic change on Marion Island we have focused mainly on the role of introduced house mice in ecological processes such as nutrient cycling, primary production, vegetation succession and peat accumulation. However, climatic variation will also influence other components of the biota and ecosystem, some of which might have as great, or even greater, effects on the same processes. For instance, approximately one million pairs of burrowing petrels and prions occur on the island (Williams et al. 1979) and they are an important source of marine-derived nutrients and energy at many inland areas and a major driving force in vegetation succession (Smith 1976). They use the atmospheric frontal systems passing the island to move between it and their feeding areas, which may be several hundred kilometers distant, in the surrounding ocean (Mendelsohn 1981). If the changes in temperature, precipitation, and radiation being experienced at the island are due to changing atmospheric circulation patterns then the birds may not be able to reach their usual feeding grounds; alternatively associated changes in oceanic circulation may move the feeding grounds to other localities. Thus, changing sea level circulation patterns may be expected to influence the breeding success and population densities of these animals, with obvious implication for nutrient cycling and vegetation succession on the island. Similar considerations possibly apply to the large populations of seals, penguins, and albatrosses.

Changes in atmospheric circulation patterns may also provide opportunities for new organisms to colonize the island and there are suggestions that this is already occurring. In palynological studies prior to 1965 very few (6 in a total of ca. 30000 counted) exotic pollen grains (i.e. belonging to taxa which do not occur there) were found on the island (Schalke and Van Zinderen Bakker 1971). In 1981, of 26632 pollen grains counted, 336 were exotic (mainly of African origin) and in some peat surface scrapings up to 40% of the pollen was exotic (Scott and Van Zinderen Bakker 1985). The greater proportion of exotic forms in the recent pollen rain might be due to changing atmospheric circulation patterns and similar considerations apply to recent records of some insects on the island. For example, *Vanessa cardui*, the cosmopolitan Painted Lady butterfly does not breed there but has been recorded sporadically since the 1950s as a wind-borne vagrant. Since the mid-1970s it has been increasingly frequently encountered. The Diamondback Moth *Plutella xylostella* recently (possibly in the early 1980s) colonized the island and infests the Kerguelen Cabbage, in some cases severely enough to kill off individual plants and substantially reduce the vigour of whole stands (Crafford and Chown 1987). Initially, this was suspected to be a man-mediated introduction caused by the importation of fresh vegetables but, on the basis of the moth's distribution on the island (and elsewhere), it is now thought that it reached there without man's aid (Crafford and Chown 1990). Chown (1990) has presented a model of insect colonization relying on airflow patterns at and around the island which supports this.

The moth population is currently limited by low winter temperatures. Obviously, as in the case of the mice, an ameliorating climate has important implications in this regard. However, both examples demonstrate the dramatic effects which invasive organisms may have on structure and functioning of the island ecosystem. Thus, through allowing opportunities for colonization by new biota, changing sealevel circulation patterns may have an even more important influence on terrestrial ecosystems of the sub-Antarctic than might be suggested only on the basis of associated changes in temperature or precipitation.

References

Adamson DA, Whetton P, Selkirk PM (1988) An analysis of air temperature records for Macquarie Island: decadal warming, ENSO cooling and Southern Hemisphere circulation patterns. Pap Proc R Soc Tasm 122:107–112

Allison F, Keague PL (1986) Recent changes in the glaciers of Heard Island. Polar Record 23:255–271

Art HW, Marks PL (1971) A summary of biomass and net annual primary production in forest ecosystems of the world. In: Forest biomass studies, Sec. 25: Growth and yield. 15th Internat Union Res Organ Congr, pp 3–32

Bate GC, Smith VR (1983) Photosynthesis and respiration in the sub-Antarctic tussock grass *Poa cookii*. New Phytol 95:533–543

Berry RJ, Peters J, Van Aarde RJ (1978) Sub-Antarctic house mice: colonization, survival and selection. J Zool (Lond) 184:127–141

Bonner WN (1984) Introduced mammals. In: Laws RM (ed) Antarctic ecology, Vol 1. Academic Press, London, pp 237–278

Burger AE (1978) Terrestrial invertebrates: a food resource for birds at Marion island. S Afr J Antarct Res 8:87–99

Chown SL (1990) A physical model of insect colonization of islands in the sub-Antarctic. S Afr J Sci (in press)

Crafford JE (1990) The role of feral house mice in ecosystem functioning on Marion Island. In: Hempel G, Kerry KR (eds) Ecological change and the conservation of Antarctic ecosystems. Proc 5th SCAR Biology Symposium, Hobart 1988, Springer-Verlag, Heidelberg (in press)

Crafford JE, Chown SL (1987) *Plutella xylostella* L. (Lepidoptera: Plutellidae) on Marion Island, J Entomol Soc South Afr 50:259–260

Crafford JE, Chown SL (1990) The introduction and establishment of the diamondback moth, *Plutella xylostella*, on Marion Island. In: Hempel G, Kerry KR (eds) Ecological change and the conservation of Antarctic ecosystems. Proc 5th SCAR Biology Symposium, Hobart 1988, Springer-Verlag, Heidelberg (in press)

Crafford JE, Scholtz CH (1987) Quantitative differences between the insect faunas of sub-Antarctic Marion and Prince Edward Islands: a result of human intervention? Biol Conserv 40:255–262

Crafford JE, Scholtz CH, Chown SL (1986) The insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of entomology of the Kerguelen Biogeographical Province. S Afr J Antarct Res 16:42–84

Frei A, MacCracken MC, Hoffert MI (1988) Eustatic sea level and CO_2. Northeast Environ Sci 7:91–96

French HM (ed) (1986) Impact of climatic change on the Canadian Arctic. Proceedings of the Canadian Climate Programme Workshop, Orillia, Ontario, March 3–5, 1986. Atmospheric Environment Service, Downsview, Ontario, pp 171

Gleeson JP, van Rensburg PJJ (1982) Feeding ecology of the house mouse *Mus musculus* Linnaeus, on Marion Island. S Afr J Antarct Res 12:34–39

Gremmen NJM (1981) The vegetation of the Subantarctic islands Marion and Prince Edward. Geobotany 3:149 pp

Hayward RJC (1983) Glacier fluctuations in South Georgia, 1883–1974. B Antarct Surv Bull 52:47–61

Hempel G, Kerry KR (eds) (1990) Ecological change and the conservation of Antarctic ecosystems. Proc 5th SCAR Biology Symposium, Hobart 1988, Springer-Verlag, Heidelberg (in press)

Hilbert DW, Prudhomme TI, Oechel WC (1987) Response of tussock tundra to elevated carbon dioxide regimes: analysis of ecosystem CO_2 flux through nonlinear modelling. Oecologia 72:466–472

Huntley BJ (1971) Vegetation. In: Van Zinderen Bakker EM, Winterbottom JM, Dyer RA (eds) Marion and Prince Edward Islands. AA Balkema, Cape Town, pp 98–160

Jacka TH, Christou L, Cook BJ (1984) Data bank of mean monthly and annual surface temperatures for Antarctica, the southern ocean and South Pacific Ocean. ANARE Research Notes no. 22:1–97

Jaeger J (1988) Developing policies for responding to climatic change. WMO/TD no. 225. World Climatic Programme, Impact Studies, World Meteorological Organization, Geneva, pp 53

Kira T, Ogawa H, Yoda K, Ogino K (1967) Comparative ecological studies on three main types of forest vegetation in Thailand IV. Dry matter production, with special reference to the Chong Rain forest. In: Kira T, Iwata K (eds) Nature and life in Southeast Asia vol. 5, Kyoto Fauna and Flora Research Society, pp 149–174

Lal M, Jain AK (1988) Climatic effect of observed changes in atmospheric trace gases at Antarctica. Atmospheric Environment 22:2047–2048

Lewis Smith RI (1990) Signy Island as a paradigm of biological and environmental change in Antarctic terrestrial ecosystems. In: Hempel G, Kerry KR (eds) Ecological change and the conservation of Antarctic ecosystems. Proc. 5th SCAR Biology Symposium, Hobart, 1988. Springer-Verlag, Heidelberg (in press)

Mendelsohn J (1981) Movements of prions *Pachyptila* spp. and low pressure systems at Marion Island. In: Copper J (ed) Proceedings of the Symposium on birds of the sea and shore, 1979. African Seabird Group, Cape Town, pp 223–231

Miller PC (ed) (1981) Carbon balance in northern ecosystem and the potential effect of carbon dioxide induced climatic change. Carbon dioxide effects research and assessment programme workshop, San Diego, March 7–9, 1980. United States Department of Energy, Washington D.C. 20565, pp 109

Pammenter NW, Drennan PM, Smith VR (1986) Physiological and anatomical aspects of photosynthesis of two *Agrostis* species at a sub-antarctic island. New Phytol 102:143–160

Pittock AB, Salinger MJ (1982) Towards regional scenarios for a CO_2-warmed earth. Climatic Change 4:23–40

Polar Research Board (1985) Glaciers, ice sheets and sea level: effects of a CO_2-induced climatic change. US Dept. of Energy, Office of Energy Research Publication DOE/ER/60235-1, Washington DC, pp 348

Raper SCB, Wigley TML, Mayes PR, Jones PD, Salinger MJ (1984) Variations in surface air temperatures, Part 3: The Antarctic, 1957–82. Mon Wea Rev 112:1341–1353

Rosswall T, Heal OW (eds) (1975) Structure and function of tundra ecosystems. Ecol Bull 20, p 450

Rowe-Rowe DT, Green B, Crafford JE (1989) Estimated impact of feral house mice on sub-Antarctic invertebrates at Marion Island. Polar Biol 9:457–460

Sage RF, Sharkey TD, Seemann JR (1988) Acclimation of photosynthesis to elevated CO_2 in five C_3 species. Plant Physiol 89:590–596

SCAR (1989) The role of Antarctica in global change. Scientific priorities for the IGBP. ICSU Press, Miami, U.S.A., p 26

Schalke HJWE, Van Zinderen Bakker EM (1971) History of the vegetation. In: Van Zinderen Bakker EM, Winterbottom JM, Dyer RA (eds) Marion and Prince Edward Islands. AA Balkema, Cape Town, pp 89–97

Scott L, Van Zinderen Bakker (1985) Exotic pollen and long distance wind dispersal at a sub-Antarctic Island. Grana 24:45–54

Sims PL, Singh JS (1978) The structure and function of ten western North American grasslands. 3. Net primary production, turnover and efficiencies of energy capture and water use. J Ecol 66:573–597

Smith VR (1976) The effect of burrowing species of Procellariidae on the nutrient status of inland tussock grasslands on Marion Island. J S Afr Bot 42:265–272

Smith VR (1977) A qualitative description of energy flow and nutrient cycling in the Marion Island terrestrial ecosystem. Polar Rec 18:361–370

Smith VR (1987a) The environment and biota of Marion Island. S Afr J Sci 83:211–220

Smith VR (1987b) Production and nutrient dynamics of plant communities on a sub-Antarctic island. 2. Standing crop and primary production of fjaeldmark and fernbrakes. Polar Biol 7:125–144

Smith VR (1988) Production and nutrient dynamics of plant communities on a sub-Antarctic island. 5. Nutrient budgets and turnover times for mire-grasslands, fjaeldmark and fernbrakes. Polar Biol 8:255–269

Smith VR, French DD (1988) Patterns of variation in the climates, soils and vegetation of some subantarctic and antarctic islands. S Afr J Bot 54:35–46

Smith VR, Lewis Smith RI (1987) The biota and conservation status of sub-Antarctic islands. Environment International 13:95–104

Van Rensburg PJJ (1985) The feeding ecology of a decreasing feral house cat, *Felis catus*, population at Marion Island. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin Heidelberg

Watkins BP, Cooper J (1986) Introduction, present status and control of alien species at the Prince Edward islands. S Afr J Antarct Res 16:86–94

Wielgolaski FE, Bliss LC, Svoboda J, Doyle G (1981) primary production of tundra. In: Bliss LC, Heal OW, Moore JJ (eds) Tundra ecosystem: a comparative analysis. International Biological Programme, vol 25. Cambridge University Press, Cambridge, pp 187–225

Williams AJ, Siegfried WR, Burger AE, Berruti A (1979) The Prince Edward Islands: a sanctuary for seabirds in the Southern Ocean. Biol Conserv 15:59–71