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Responses of terrestrial plants and invertebrates to environmental change at high latitudes

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SUMMARY

Many invertebrates show flexibility in their life cycles and are likely to respond to changes in climate as they have in the past. However, changes in temperature and photoperiod may disturb the life cycles of some existing polar invertebrates while continuing to constrain the polewards migration of more temperate species. Higher plants are likely to have higher productivity as temperatures and atmospheric CO_2 levels increase but this productivity will be reduced by exposure to increasing UV-B radiation. Higher plants migrate more slowly than the rate at which climate is predicted to change and many species will be trapped in supra-optimal climates. Both mosses and lichens can migrate faster than higher plants, propagules of non-polar species already reaching the Antarctic, but they have fewer mechanisms of responding to changing environments.

Polar vegetation and ecosystems provide feedback to the climate system: positive feedbacks are associated with decreases in reflectivity and increased carbon emissions from warming soils. In the Antarctic, feedback and responses to environmental change will be smaller than in the Arctic because of the less responsive cryptogams which dominate the Antarctic, the paucity of Antarctic soils, and geographical barriers to plant and invertebrate migrations.

1. INTRODUCTION

General circulation models (GCMs) predict increases in rates of global mean temperatures of about 0.3° C per decade in response to increases in greenhouse gases and greater rates of warming at high latitudes (Houghton *et al.* 1990). As the earth's vegetation types are associated with particular climate zones which have changed their distributions during the earth's history (trees once grew at 80°N), we can expect a future redistribution of ecosystems. However, the rate of climate change is predicted to be much greater than that in the past and the migration rates of the biota may be insufficient to keep pace with the shift in climate zones (Melillo *et al.* 1990; Street & Semenov 1990).

Predicted responses of biota to climate change are generally based on species of economic importance: long-lived clonal perennials and cryptogams characteristic of high latitude ecosystems are under-represented while few experimental studies on the responses of whole ecosystems exist (but see Tissue & Oechel 1987). These factors confound our ability to predict how, and at what rate, our ecosystems will change but it is becoming obvious that changes in high latitude ecosystems will be particularly important (e.g. Chapin *et al.* 1992) because: (i) changes in climate are predicted to be greatest, and should be first identified, in polar regions; (ii) polar species are generally vulnerable to change because of slow growth, long generation times, infrequent reproduction and the inability to adapt quickly; (iii) species near the lower temperature limits of survival are more responsive to a given increase in temperature and should be early indicators of change; (iv) responses of polar biota to climate change are relatively independent of concomitant changes in land use or pollution; and (v) polar land surfaces provide feedback to climate change, mainly through albedo and increased emissions of CO_2 and CH_4 from organic soils.

This paper speculates on the relationships between the dominant terrestrial biota of high latitudes and climate change, drawing on basic principles often determined elsewhere. We also compare likely changes in terrestrial ecosystems of the Arctic with those of the Antarctic and, to some extent, use the Arctic as a long-term future analogue of the Antarctic.

2. RESPONSES OF BIOTA TO INCREASED CONCENTRATIONS OF ATMOSPHERIC CO_2

Levels of atmospheric CO_2 have increased as a result of man's activities from about 275 p.p.m. to about 350 p.p.m. and it is predicted that they will reach 470 p.p.m. by 2050 (Houghton *et al.* 1990). Concentrations of atmospheric CO_2 increase with increasing latitude and are lowest in the Antarctic and highest between 58° and 80°N. Locally, CO_2 concentrations may be high under snow and in the cryptogam layer above organic soils as a result of soil microbial respiration (Sonesson *et al.* 1993).

(*a*) *Responses of Invertebrates*

Soil invertebrates are likely to be little effected by increased atmospheric concentrations of CO_2 which are already an order of magnitude greater in the soil than in the atmosphere (Swift *et al.* 1979). Several invertebrates overwinter in the soil enclosed by ice, where they are exposed to even higher concentrations of CO_2 (Sømme & Block 1991).

(*b*) *Responses of Phanerogams*

The responses of higher plants to levels of atmospheric CO_2 above ambient (e.g. Bazzaz 1990, Oechel & Billings 1992) include: increased photosynthetic rates in C_3 plants (the CO_2 'fertilization' effect); increased productivity; damage to chloroplasts and leaves in some species; increased allocation of carbon to below ground tissues; reduction of period until sexual maturity is attained; increased tillering and branching; increased efficiencies of use of water, nutrients and light; increases in tissue carbon contents relative to nitrogen; changes in the timing of senescence; changes in seed output and modified architecture.

The growth of tundra phanerogams is often limited by the infertility of polar soils (e.g. Chapin *et al.* 1992; Jonasson 1992). This limits the number of sinks which can utilize extra photosynthates acquired through the CO_2 fertilizer effect. Any initial increase in productivity in high CO_2 régimes may therefore, result in subsequent acclimation (Tissue & Oechel 1987; figure 1). Summer precipitation also often limits plant growth, particularly in the high Arctic, and any increased water use efficiency in high CO_2 environments could result in an increase in biomass and plant cover.

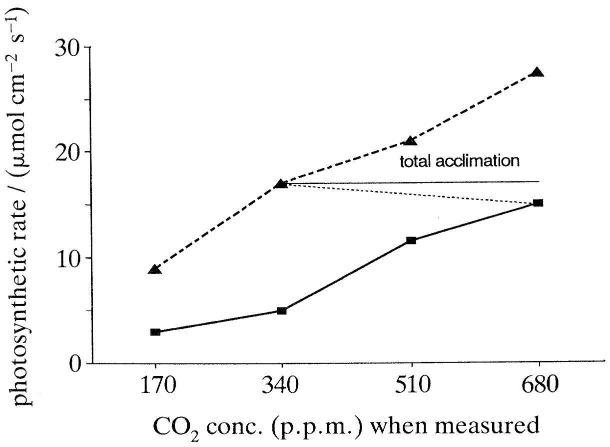

Figure 1. Acclimation of photosynthesis in *Eriophorum vaginatum* grown in two levels of atmospheric CO_2 for three weeks (from Tissue & Oechel 1987). Filled squares, grown in 680 p.p.m. CO_2; filled triangles, grown in 340 p.p.m. CO_2. The horizontal line denotes complete acclimation, the broken line actual acclimation.

Short growing seasons and low summer temperatures often limit seed set and the rate of vegetative spread of tundra phanerogams. However, their reproductive and demographic responses to higher CO_2 régimes should increase their chances of adapting to new environments, surviving disturbance, colonizing new climatically favourable areas, and spreading at faster rates (Callaghan & Carlsson 1993).

(*c*) *Responses of Cryptogams*

Physiological responses of photosynthesis in mosses and lichens to enhanced CO_2 régimes are essentially the same as in flowering plants (Proctor 1982; Kershaw 1985). Mosses and lichens of the sub-Arctic already experience concentrations of atmospheric CO_2 higher than ambient and they show no adverse effects until high levels, well above 1000 p.p.m., are experienced (Sonesson *et al.* 1993).

Mosses and lichens should not show increased water use efficiencies because these are achieved in phanerogams in which stomata, lacking in cryptogams, are partially closed in high CO_2, thus restricting water loss. However, an increased 'water content efficiency' of a moss at enhanced CO_2 levels partly compensates for drought (S. Dubé and M. Sonesson, unpublished results). Thus, doubling the CO_2 concentration at near optimal water content of the tissue will double CO_2 uptake without any change in rates of water loss.

(*d*) *Interactions between trophic levels*

Increased carbon fixed by plants in high CO_2 régimes favours an increased infection by parasitic and symbiotic organisms (e.g. mycorrhizae and symbiotic nitrogen fixing organisms) which depend upon their host for carbon (Melillo *et al.* 1990). This should enhance growth in nutrient poor soils. However, increases in carbon relative to nitrogen may inhibit herbivory. Grazing animals require 20–80% more biomass of plants grown under high CO_2 to gain a given amount of protein. Sometimes, grazers already satiated by bulk must find alternative plant species to gain sufficient protein. This puts them at risk while plant species grazed less become more productive and competitive. Similarly, any increase in the content of carbon to nitrogen in plant litter should reduce the rate of its subsequent decomposition (Couteaux *et al.* 1991; figure 2). This, in turn, may feedback to plant growth by reducing the supply of plant-available soil nutrients.

3. RESPONSES OF BIOTA TO INCREASED TEMPERATURES

The greatest temperature increases are predicted for polar regions during winter (up to 12° C) but smaller increases are more likely to occur (Maxwell 1992). However, the potential length of the growing season could still be increased by over 1 month. Overall, night-time temperatures could increase more than those during day-time (Karl *et al.* 1991).

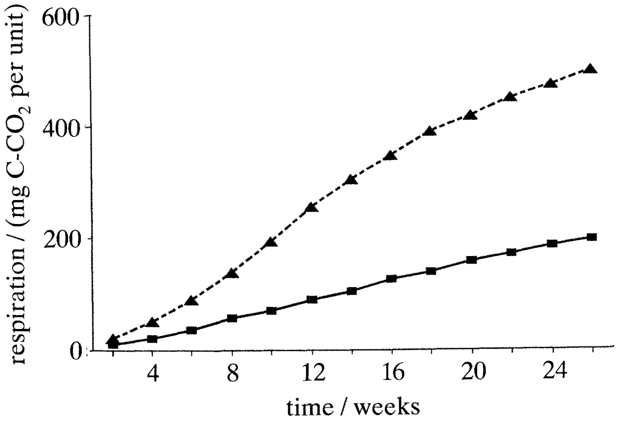

Figure 2. Effects of chestnut leaf litter quality (leaves grown in either ambient CO$_2$ (filled squares) or 700 p.p.m. CO$_2$ (filled triangles)) on initial decomposition by protozoa and microflora (more complex mixtures of decomposers change the relationship after several months). Decomposition rates measured as carbon efflux from litter in microcosms (from Couteaux *et al.* 1991).

(*a*) *Responses of Invertebrates*

Small increases in temperature may disturb the normal development of many species through its effect on diapause (the physiological suppression of growth in any developmental stage or in reproduction). It is triggered by environmental cues so that the animal enters the resting stage best adapted to withstand environmental stress (e.g. Zaslavski 1988). If the cue is delayed, for example by warmer temperatures, a sensitive life-cycle stage may be exposed to severe environmental conditions. At higher temperatures, diapause induction is shifted towards shorter photoperiods, and some species will not be able to enter their dormant state in long polar photoperiods.

Reactivation of development is a complex interaction between time, photoperiod and temperature. Its response to chilling varies in different species, and with time and temperature (e.g. Zaslavski 1988). In many species such as the codling moth (*Cydia pomonella*), chilling first increases reactivation and then decreases it as temperature is lowered. Thus the termination of diapause may be delayed or halted at high temperatures, thereby interfering with emergence in the spring.

The accumulation of low molecular weight cryoprotectant substances (e.g. glycerol) is important for invertebrate cold hardiness and winter survival. In several species, their accumulation is related to the photoperiodic induction of diapause, whereas in non-diapausing insects it is usually triggered by temperatures between 0 and 5° C. Levels of cryoprotectant substances are correlated with seasonal changes in climate in Antarctic springtails and mites such as *Alaskozetes antarcticus* (Block 1980, 1984). Temperature changes will affect the induction and regulation of cold hardiness in many such species, and could result in detrimental effects when warmer periods are followed by severe cold spells.

The short, cold summers of polar regions limit development in terrestrial arthropods. Prolonged life cycles are common in different kinds of insects, springtails, mites and spiders (Sømme & Block 1991) in which two or more stages must be adapted to survive winter conditions. This 'multistage' cold hardiness may represent a barrier for many potential immigrant species to hostile polar regions. Several stoneflies, caddis flies, chironomid midges and the Antarctic collembola *Cryptopygus antarcticus* (Burn 1984) and *C. sverdrupi* have flexible life cycles, and potential to adapt to new climatic conditions. The Antarctic mite *Alaskozetes antarcticus* may be even better prepared for changing climate as growth and development take place only when environmental conditions allow (Block 1980). In spite of unfavourable climatic conditions, several Arctic and alpine species complete their life cycle in one year (Sømme 1989). Such species appear to be closely tuned to their microhabitats and are particularly vulnerable to climatic changes.

The choice of overwintering sites is essential for the survival of insects and other terrestrial arthropods (Danks 1991) but we know little about how they are found. Low temperatures and decreasing photoperiod may trigger searching behaviour, which could easily be disturbed by a changing climate.

(*b*) *Responses of Phanerogams*

Increases in temperature can be expected to increase rates of photosynthesis, respiration, development, and flowering frequency. The balance between the rates of gross photosynthesis and respiration is particularly critical to plant productivity, photosynthesis being most responsive to small increases in temperature whereas respiration is more responsive at higher temperatures. As the temperature optimum of photosynthesis in polar plants is higher than the temperatures they usually experience (Semikhatova *et al.* 1992), small increases in temperature should stimulate the productivity of a particular species whereas larger increases are likely to decrease its productivity – particularly if it has a small shoot/root biomass ratio – because of disproportionate increases in respiration.

Asymmetric diurnal warming should stimulate 'night-time' net photosynthesis of polar plants during mid-summer (Semikhatova *et al.* 1992), but greater warming in winter relative to summer could, in contrast, stimulate respiration.

Short growing seasons may allow insufficient time for reproductive development (Callaghan & Carlsson 1992). Developmental processes such as flowering and leaf development in Arctic and some sub-Antarctic plants are, therefore, often extended over several years and they provide a buffering mechanism against shorter-term extremes in weather. Increases in temperature may, therefore, increase the rate of development and seed output but also increase the impact of short term weather extremes.

(*c*) *Responses of Cryptogams*

As in higher plants, the *in situ* temperature optima of photosynthesis of mosses (Rastorfer 1970) and lichens (Lange & Kappen 1972) are usually lower than their physiological optima and increases in photosynthesis with global warming can be expected if the water balance remains unchanged. Because mosses are largely undifferentiated (Longton, 1988; Sonesson & Callaghan 1991), the disproportionate increase in respiration of non-photosynthetic tissue will not apply and increases in temperature should be closely related to increases in productivity. However, lichens may more closely resemble higher plants as the ratio green:non-green biomass is often as low as 1:20 (Hawksworth & Hill 1984).

The interaction between increased temperatures and water availability is critical for the performance and abundance of cryptogams as they have fewer mechanisms to combat drought than higher plants. In warmer wetter polar areas, cryptogams will flourish whereas in warmer, drier polar areas, they will diminish in importance (Tenhunen *et al.* 1992). As in higher plants, the sexual reproductive cycle of cryptogams may be infrequent and the combination of warmer and longer growing seasons should lead to an increase in propagule production and dispersal with the potential for adaptation to a changing environment.

(*d*) *Interactions between trophic levels*

Decomposition of organic matter by the microflora is greatly accelerated by nematodes, annelid worms, mites, springtails and insects. If temperatures increase, enhanced decomposition of detritus by the action of both microflora and invertebrates should occur (Bouwman 1990). The balance between enhanced decomposition rates due to increased temperatures and reduced decomposition rates due to decreased nitrogen:lignin ratios in litter from plants grown in high CO_2 is critical both to the function of ecosystems and the size of biospheric feedback, yet we do not know where the balance will be.

Soil invertebrates may, sometimes, be adversely affected by higher temperatures. On sub-Antarctic Marion Island, soil macro-invertebrates such as slugs and larvae of the moth *Pringleophaga marioni* release most of the nutrients from peat and litter (Smith & Steenkamp 1990). However, an introduced house mouse population feeds on these and other soil invertebrates, annually 'preventing' the processing of at least 1000 kg of plant litter per ha. The mouse population appears to be increasing due to an increase in temperatures over the past 35 years and this will result in higher predation pressure on soil invertebrates and enhanced rates of peat accumulation. In the maritime Antarctic, a predator-prey relationship between collembola and a single species of predatory mite (Lister *et al.* 1988) represents another simple system which could be particularly vulnerable to climatic change.

4. PRECIPITATION

In high latitudes, winter precipitation as snow insulates biota in winter, controls the length of the potential growing season and provides a flush of free water at the beginning of the growing season. Warmer winters may initially result in increased precipitation as snow in some areas and shorter growing seasons but overall, the snow free period may be extended by over 1 month (Maxwell 1992).

Extensive areas of the Arctic receive little annual precipitation yet are waterlogged because permafrost prevents the drainage of water from seasonally thawing active soil layers and precipitation. In such situations, for example central Yakutia (Street & Melnikov 1990), a lowering of the permafrost in the soil profile due to increased temperatures could increase drainage and lead to a desertification process.

(*a*) *Responses of Invertebrates*

Excessive water losses during the hibernation period, which lasts for 8–9 months, are critical for most invertebrates but, at higher temperatures, desiccation rates of many species will be increased. At the other extreme, flooding will also disturb the development of many insects.

(*b*) *Responses of Phanerogams*

Some higher plants can withstand aridity and occur in arctic polar deserts extending up to almost 84°N, but are absent from Antarctic arid areas. Less than 5% of the surface of arid Arctic areas is covered by phanerogams which aggregate into small islands of vegetation where moisture sometimes accumulates. Any increase in aridity would result in a decrease in cover, performance and distribution of these species but the increase in water use efficiency characteristic of plants grown in a high CO_2 environment, would offset this effect of some extent. Any increases in precipitation would lead to an increase in cover and would facilitate establishment of any future immigrants to arid Antarctic areas and the spread of phanerogams now restricted to the maritime Antarctic (Hall & Walton, this Symposium).

Winter snow is important in insulating polar vegetation from extreme winter cold, desiccation and abrasion by wind-blown particles. Some species require a specific balance between the duration of snow cover and length of the growing season (Sonesson & Callaghan 1991): such species will obviously be sensitive to changes in winter snow duration.

(*c*) *Responses of Cryptogams*

Cryptogams generally lack roots and water-conducting tissues and have, therefore, relatively few mechanisms to combat drought. In dry conditions, mosses dehydrate and physiological activity is maintained at a minimum rate. In wet conditions, the mosses rehydrate and net photosynthesis is initiated again. An increase in the frequency of precipitation should increase growth in mosses and lichens, particularly in those lichens containing cyanobacteria since the photosynthetic process of the nitrogen-fixing 'blue-green lichens' needs liquid water for initiation. Free water is also essential for successful sexual reproduction in cryptogams which is an important factor in long-distance dispersal (Lewis Smith 1991). This provides genetic variability from which adaptations to a changing climate can be selected.

(*d*) *Interactions between trophic levels*

In well-drained soils with aerobic conditions, decomposer activity is more dependent on precipitation than on temperature. Microbial aerobic respiration is more efficient than anaerobic respiration in water-logged soils and releases CO_2 to the atmosphere and nutrients for potential uptake by plant roots. Any drying of wet soils will result in an efflux of CO_2 to the atmosphere (see § 7) and an increase in nutrient availability to possibly stimulate plant growth (Oechel & Billings 1992). In contrast, dry soils which become wet will release CO_2 and CH_4 to the atmosphere (see below) but reduced microbial activity will lower the rate of nutrient release to plants.

5. LIGHT

The quality of light is known to be changing in the Antarctic with increased fluxes of UV-B (Farman *et al.* 1985) and this is occurring in the Arctic too (Stolarski *et al.* 1992). The quantity of light could also change if cloudiness increased. Light quality, photoperiod and light 'quantity' may also be perceived by polar organisms to change if the onset of the growing season occurs earlier or is delayed.

(*a*) *Responses of Invertebrates*

Melanistic colours are common among polar and alpine insects, and most authors have attributed this to its importance in thermoregulation (Sømme 1989, Sømme & Block 1991). However, Mani (1990) has suggested that melanism in alpine insects has also evolved as a protection against intense UV-B radiation at high altitudes. In fresh water cladocerans internal body pigmentation by carotenoids probably acts as a more general protection against near UV-B and visible light (Hessen & Sörensen 1990). However, the sensitivity of terrestrial arthropods to increased UV-B flux at high latitudes is apparently unknown.

Photoperiod interacts with temperature to control diapause in some invertebrates. The percent of the population of the noctuid moth *Acronycta rumicis* that enters diapause under different photoperiods increases with decreasing temperatures (Zaslavski 1988) and this is genetically determined in populations from different latitudes. For example, the population from 43°N will not enter diapause at photoperiods above 15 h, while diapause at the same temperature in the population from 60°N is induced by photoperiods up to 20 h or longer. In this way, the northern population, which has only one generation per year, enters diapause early in the season in preparation for the early onset of winter. Southern populations may complete two or three generations before diapause is induced by shorter daylength but they may be unable to survive at higher latitudes as diapause would not be initiated before the onset of winter.

(*b*) *Responses of Phanerogams*

Higher plants are protected from UV-B radiation by having leaf waxes, hairs, pigments, cuticles and epidermis, and sensitive organs (e.g. pollen, seeds and growing points) are protected in buds etc. Plants in the low UV-B environment of the polar regions are likely to be more sensitive to increases than those from high UV-B environments, for example alpine areas, as they have less protection (Robberecht *et al.* 1980).

Impacts of UV-B which can be expected as levels increase in polar regions have been reviewed by Tevini *et al.* (1989) and include: increases in chlorosis and necrosis, decreases in chlorophyll, lipid and protein contents of leaves, increases in defense responses such as thicker cuticular wax, and flavonoid and anthocyanin pigmentation, morphogenetic aberrations such as leaf thickening and elongated palisade cells, decreases in photosynthesis, leaf area, plant height and fresh and dry mass, increases in stomatal resistance, changes in competitive balance between species, restricted seedling growth, and chromosome aberrations leading to long term damage in clonal plants when non-lethal. The negative effects of higher UV-B radiation on the growth, abundance and reproduction of some species will have a critical interaction with any increases in plant performance associated with other aspects of global change.

Changes in photoperiod, if growing seasons begin on different dates, would interact with higher temperatures and could affect the initiation of flowering (Heide 1980) and even the productivity of existing plants (Heide *et al.* 1985) in which long days stimulate the early development of a leaf canopy at the beginning of season. In addition, the consequences for growth and reproduction of immigrating species without adaptations to polar photoperiods are obvious.

Reduced productivity due to low light intensities is common in tundra areas. If cloudiness increases, higher plants are likely to show decreased photosynthetic rates and hence, decreased productivity. Increased light-use efficiency resulting from high CO_2 concentrations (see above) may compensate for this to some extent.

(*c*) *Responses of Cryptogams*

UV-B sensitivity in polar mosses should be particularly high as these plants, like the polar phanerogams, have become acclimated or adapted to a low UV-B régime, and they often grow in shade. Although it has been shown that an Antarctic moss can produce pigments for protection against UV-B (figure 3; Markham *et al.* 1990), tissue protection is generally less than in phanerogams and lichens.

Even in open canopies at high latitudes, the photosynthesis of cryptogams, like that of lichens, is limited by light during a substantial part of the growing season (Sonesson *et al.*, 1992, 1993). Consequently, any further reduction in irradiance due to

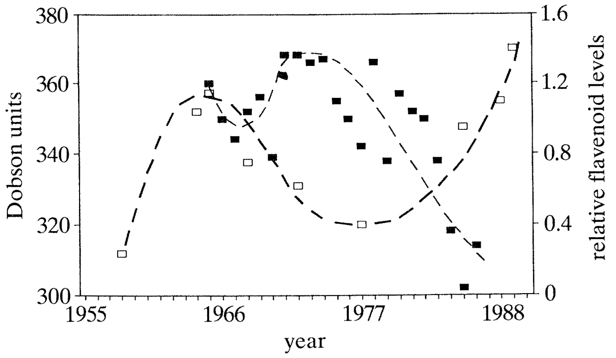

Figure 3. Relationship between levels of UV-B protecting flavonoid pigments (open squares) in the moss *Bryum argenteum*, determined by HPLC from herbarium specimens, and mean December ozone levels (closed squares) at the South Pole (from Markham *et al.* 1990).

increased cloudiness or shading by competitors is likely to further reduce productivity. Shading will be more important in the Arctic than in the Antarctic where only two indigenous higher plant competitors exist. Photoperiodic effects on cryptogams may be similar to those on higher plants and they prevent some mosses from migrating to high latitudes (Kallio & Valanne 1975).

(*d*) *Interactions between trophic levels*

Few light-induced interactions between trophic levels are apparent although high UV-B fluxes can stimulate the rate of litter decomposition purely by photo-chemical oxidation (J. M. Melillo, personal communication). The higher UV-B fluxes in the Antarctic and greater exposure of plant litter may enhance decomposition rates there.

6. MIGRATION AND ECOSYSTEM CHANGE

(*a*) *Invertebrates*

The terrestrial arthropod faunas of the maritime and continental Antarctic zones (142 species) are more impoverished than those of the Arctic due to their extreme climatic conditions and geographical isolation. The fauna of the sub-Antarctic islands is also much poorer than anticipated from climatic conditions and plant diversity (Sømme & Block 1991). The present Arctic fauna also has a lower diversity than might be expected (more than 2200 species of terrestrial arthropods in Arctic North America but only 553 from the Queen Elizabeth Islands further north) but present immigration from the south may be incomplete (Danks 1981). The Arctic fauna has experienced many climatic changes through geological times, with corresponding fluctuations in number of species at high latitudes. Arctic invertebrate faunas are, therefore, flexible and large changes in the composition of invertebrate communities must be expected with increasing temperatures and changes in vegetation. However, present anthropogenic changes in climate may be faster than changes in the past and natural selection may not operate fast enough to generate adaptive responses to new conditions. Geographically isolated areas such as the Antarctic and sub-Antarctic islands are likely to show the greatest mis-match between their faunas and climate régimes.

(*b*) *Phanerogams and cryptogams*

Populations at their lower latitudinal or altitudinal limits of distribution will be at a competitive disadvantage in closed vegetation where temperatures rise (Havström *et al.*, 1993) and may be killed directly by high temperatures (Gauslaa 1984). Conversely, populations growing at their upper limits in sub-optimal temperatures should extend their ranges as temperatures increase. In both polar areas with open vegetation, competitive interactions are likely to be less important and non-replacement vegetation succession will occur as existing species expand onto bare ground (Bliss & Peterson 1992).

Species most likely to migrate rapidly have long distance dispersal and high reproductive output. Propagules of some ‘exotic’ species are already found in the Antarctic (Lewis Smith 1990; Walton 1990) but only become established now in warm microsites such as areas of volcanic activity (Lewis Smith 1984). Some ‘weedy’ higher plants already have restricted distributions in polar areas such as South Georgia (Walton 1975), probably as a result of anthropogenic introductions.

Floras of the Antarctic are impoverished mainly because of geographical isolation and lack of suitably adapted species such as those characteristic of extreme Arctic environments. The vascular flora of northeast Greenland (reaching almost 84°N) has 117 vascular plants species (Bay & Fredskild pers. comm.) whereas that of sub-Antarctic South Georgia (54°S) contains only 24 (Greene 1964). Thus, constraints on distribution and rates of migration in the two polar areas must be very different (Callaghan 1974) and anthropogenic introductions of alien species are likely to dominate initial immigration into the Antarctic.

(*c*) *Interactions between trophic levels*

Species separated from potential pests, pathogens or herbivores might be threatened if their migration rate is slower than those of the invading threatening species. During a period of ecological stress and imbalance, many unexpected situations may appear through differential migration rates of interacting species.

7. FEEDBACK FROM THE BIOTA

The impact of vegetation and soils on the climate system is often poorly represented in general circulation models. Geophysical feedbacks are the most important (an amplification of about +0.64), but biogeochemical feedbacks are also significant (+0.16: Lashof 1989), particularly in high latitudes.

(*a*) *Changes in albedo*

Radiation reaching the earth is either absorbed, thereby warming its surface, or reflected. Currently, there is a net loss of energy from high latitudes (Roots 1989), but the extent of snow and ice is likely to decrease, thereby increasing the absorption of radiation and, in the Arctic, taller shrubs and trees will probably replace sparse dwarf vegetation and further decrease albedo. The northward movement of the tundra-boreal forest boundary will give the greatest positive feedback from albedo at a global level (Lashof 1989).

(*b*) ***CO_2 and CH_4 exchange between biosphere and atmosphere***

Any increased productivity of plants resulting from climate change will act as a negative feedback because of the sequestration of CO_2 but the effect would probably be small as the CO_2 fertilizer effect may be only temporary, while changes in litter quality due to high CO_2 and UV-B will retard decomposition rates and reduce subsequent nutrient availability. Also, the greatest increases in productivity, particularly in the Antarctic, would depend on plant species migrations rather than increased growth of existing species, and the potential for this is probably low.

Positive feedback is provided by the emission of CO_2 from microbial respiration in dry soils and CO_2 plus CH_4 from wet soils. Any climatic change which affects soil temperature, soil moisture or plant litter quality will affect decomposition rates and the magnitude of the positive feedback. A 4°C temperature increase could increase loss of carbon by 60–80 g m^{-2} from tundra soils if the water table is 5 cm below the surface (Billings *et al.* 1982) and it has been claimed that soils in Alaska may have already changed from carbon sink to carbon status (Oechel & Billings 1992). This feedback from the Arctic would have global significance because of the vast store of soil carbon in the Arctic (Oechel & Billings 1992) but soil development is rudimentary in the Antarctic and the potential for feedback from there is low.

(*c*) ***Evaporative cooling***

Radiation is absorbed by photosynthesising vegetation as the latent heat of vaporisation and this drives the transfer for water between the leaf canopy and the lower atmosphere providing a negative feedback to the climate system. The loss of water vapour from the leaf surface is less from smooth vegetation (e.g. high latitude dwarf and cushion vegetation and grass) than from rough vegetation (e.g. trees) which increases the eddying of air flows, the mixing of air layers and the size of the negative feedback mechanism. If polar vegetation becomes more extensive and taller, roughness lengths and transpiration rates will increase, and the magnitude of the negative feedback from this source will increase.

8. CONCLUSIONS

Predictions of plant responses to climate change are confounded by the complexity of the numerous interactions between the many environmental factors which control plant growth. Predicted changes in some environmental factors have opposite effects on plant growth (e.g. increased CO_2 and UV-B radiation) and research aimed at determining the points of balance between such opposing responses must receive a high priority. Many invertebrates appear to have flexible survival strategies and are likely to be less affected than plants by climate change. Biotic feedback processes are dynamic and adaptive and loops occurring in one direction may change direction completely if an organism's environment changes or invading species replace existing species. Because of this complexity, the net effects of the numerous feedbacks occurring in different directions at the same time are unknown yet critical to our understanding of ecosystem function and subsequent climate change.

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Discussion

D. W. H. Walton (*British Antarctic Survey, Cambridge, U.K.*). I note the value of plastic cloches for experimental use has been recognized in both Arctic and Antarctic terrestrial sites. I want to underline the importance of immigration to the Antarctic. As yet we know little about the range, frequency and viability of propagules arriving in Antarctica: a problem which is being addressed by the international BIOTAS programme. It is possible there already is a range of immigrant species unable to establish under existing conditions which will be able to find acceptable niches under a warming environment. The fumarolic vegetation suggests that this already happens.

T. V. Callaghan. I agree that environmental conditions limit the colonization of some species; it is also likely that ocean barriers to dispersal prevent the immigration of others. Fewer species of invertebrates and plants occur in the Antarctic than at high latitudes in the Arctic. Also, the bipolar plant species which occur in the sub-Antarctic are characteristic of low Arctic latitudes whereas high Arctic plant species are lacking from the south. This must be a dispersal problem.

T. Christensen (*Scott Polar Research Institute, Cambridge, U.K.*). From our work on methane emissions from tundra soils it is evident that vascular plant communities have significantly higher methane emission rates than non-vascular plant communities. This is probably due to the root systems of the vascular plants helping to bypass the aerobic zone in the upper soils where microbial oxidation of methane occurs. It might therefore have consequences for future emissions of methane how the ratio of vascular to non-vascular plants might change under a global warming scenario. Could Dr Callaghan speculate on how this ratio would respond to different global warming scenarios?

T. V. Callaghan. Under warmer drier climates, the bryophyte component of moss-dominated communities would be expected to be replaced by higher plants. Such environmental conditions would lead to a drying of the soils and a reduction in methane emissions. In relatively dry areas, soils may act as a sink – rather than source – of methane. Under a warmer but wetter climate, mosses would thrive and methane emissions would increase. As far as I am aware, the relative contributions of life form and soil moisture to methane efflux have not been assessed.

W. C. Block (*British Antarctic Survey, Cambridge, U.K.*). There may well be very different responses shown by polar plants and polar invertebrates in the face of climate change in terrestrial habitats. In the Arctic, there are arthropods with circumpolar distributions, relatively short generation times, life cycles that are largely temperature dependent, and species which have a high level of phenological (life cycle) synchrony with their host plants. These features are likely to be very sensitive indicators of environmental changes. Responses of plant species will be slower in time, taking perhaps decades rather than a few years, especially in the Arctic as most plants there are long-lived perennials adapted to wide interannual climate variation. The Antarctic flora, dominated by lichens and mosses, pose similar problems.

Long-term studies of selected arthropods, including both herbivores and carnivores, above ground and below ground forms, with both univoltine (single generation per year) and free-running life cycles will be vital to such research. Field studies over two or three years will not provide the database required to develop predictive models of such populations. It is necessary to understand the ecological constraints influencing the life cycles of such invertebrates and their performance in the polar environment through studies of their ecophysiology. Temperature may not be the over-riding factor in all cases, water may be more important particularly in Antarctic ecosystems. Only then will we be in a position to identify the likely consequences of climate change of different magnitudes and timescales, which might have general applicability throughout the polar regions, but perhaps not in a global context.

T. V. Callaghan. Dr Block's comments are appropriate and his emphasis on ecophysiological studies of invertebrates is important. Polar invertebrates may well be better indicators of climate change than polar plants. However, I disagree that polar plants may not respond to climate change for decades. In the Arctic, the breakdown of cyclical flowering and the regular recruitment of young plants to populations in areas of bare ground are likely to be good indicators of a changing climate. Also, many arctic plants contain records of past climate-related growth which provide a good base-line for identifying future changes: such records are absent in invertebrates where prolonged monitoring is required.

W. C. Block. Dr Callaghan's talk contained information on flowering plants and higher insects in the Arctic. Both these groups are of low incidence in the Antarctic, and we must extrapolate with considerable caution from the Arctic to the Antarctic with such data. With respect to invertebrates, the Antarctic species have generally free-running life cycles, whereas several Arctic insects are herbivores with life cycles highly synchronized to their host plants. Such differences will be crucial in any prediction on the possible effects of climate change in the south polar region.

T. V. Callaghan. I agree that we must extrapolate with caution from responses to climate of arctic biota to likely responses of antarctic biota. However, in many cases, such as responses to high CO_2 and enhanced UV-B, data are lacking from the Antarctic and such extrapolations are required. Many similarities exist between the two regions and we believe that a comparative approach is most useful.