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Potential responses of natural terrestrial ecosystems to Arctic climate change

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SUMMARY

The Arctic has been subject to major variations in climate in the past to which organisms have adapted in various ways. But now, warming of up to 9°C at high latitudes is forecast to occur this Century. Warming is associated with change in other environmental variables and with significant spatial variability. This paper summarises some expected responses in natural terrestrial ecosystems with the aim of sharing information with agricultural researchers.

Some of the main results are: (1) A complex of climate variables is expected to change, including frequency of extreme events, combined with enhanced CO_2, UVB and N deposition. Vegetation and soil microclimate will vary significantly from atmospheric climate. (2) Flora, fauna, microbial and community responses to winter climate, snow cover and soil climate are important. (3) Responses vary between processes, species and sites, often with compensatory effects and significant time-lags. Indirect, secondary and combined effects are as important as direct responses to climate change. (4) Species may be 'preadapted' to climate variability and show major intra-specific genetic variations. (5) Organism and community composition responses will be particularly apparent at the climatically determined edges of their range. (6) Soil microbial biomass shows little change following warming, but changes in soil community composition and process rates are significant. Decomposition rates are likely to change most in mesic soils. (7) Computer models at 3 spatial scales show how different microbial strategies respond to changing litter quality; how moisture and nutrient cycling determine the integrated response of a tundra ecosystem; and how expansion of forest may reduce tundra by 50% over 100 years and provide an important carbon sink.

Key words: Arctic, climate change, terrestrial ecosystem.

YFIRLIT

Hugsanleg viðbrögð náttúrulegra jarðvegsvistkerfa við breytingum á heimskautaloftslagi

Heimskautin hafa í fyrndinni orðið fyrir miklum veðurfarssveiflum sem lífverur hafa aðlagast á ýmsa vegu. Nú hefur verið spáð hlýnun um allt að 9°C á þessari öld á norðlægum breiddargráðum. Hlýnunin tengist breytingum í öðrum umhverfisþáttum víðs vegar um heiminn. Í ritgerðinni eru dregin saman væntanleg viðbrögð vistkerfa jarðvegsins með það að markmiði að deila upplýsingum með búvísindamönnum.

Meginniðurstöðurnar eru: (1) Margir veðurfarsþættir munu væntanlega breytast, þ.m.t. tíðni öfgakenndra viðburða, ásamt auknu CO_2-magni, útfjólublárri geislun og útfellingu köfnunarefnis. Nærveðurfar í jarðvegi og gróðri verður mjög frábrugðið veðurfari lofthjúpsins. (2) Viðbrögð flóru, fánu, örvera og samfélaga við vetrarveðráttu, snjóhulu og veðurfari jarðvegsins eru mikilvæg. (3) Viðbrögðin eru breytileg milli ferla, tegunda og staða, oft með töluverðum jöfnunar- og seinkunaráhrifum. Óbein, afleidd og samlegðaráhrif eru jafn mikilvæg og bein viðbrögð við veðurfarsbreytingum. (4) Tegundir geta verið aðlagaðar veðurfarsbreytingum fyrirfram og sýnt mikla erfðafræðilega sveiflu innan tegundar. (5) Viðbrögð lífvera og samfélaga verða augljósust á veðurfarslegum jöðrum þeirra. (6) Örverumassi jarðvegsins breytist lítið við hlýnun, en samsetning jarðvegssamfélagsins og ferlishraðar breytast verulega. Niðurbrotshraði mun líklega breytast mest í rökum jarðvegi. (7) Tölvulíkan byggt á þremur mismunandi forsendum sýnir viðbrögð ólíkra örveruhópa við breytingum á gæðum lífrænna leifa; hvernig rakastig og hringrás næringarefna hafa áhrif á samþætt viðbrögð vistkerfi freðmýra; og hvernig útþensla skóga getur eytt helmingi freðmýra á 100 árum og myndað mikilvægt kolefnisforðabúr.

INTRODUCTION

The paper summarises the current understanding of the potential impacts on natural ecosystems of the individual and combined climatic factors. It draws heavily on the results of a recent European Commission Concerted Action project, the Arctic-Alpine Terrestrial Ecosystems Research Initiative (ARTERI) (Heal *et al.*, 1998) but includes evidence from studies elsewhere in the circumpolar region. Emphasis is given to responses below-ground. This is because of three reasons: (1) Many of the important responses will occur in this hidden environment, with feedback to and from above-ground. (2) Much emphasis has been given to the climate in the atmosphere without recognition that the soil climate is markedly different. (3) The need to stimulate research on soil populations and processes which is currently very weak.

A detailed review of the responses to terrestrial ecosystems is not attempted. Rather, the main general conclusions are presented in summary form. These are extrapolated from the limited and often localised experimental research, combined with general ecological experience and theory.

WHAT ARE THE EXPECTED ATMOSPHERIC CLIMATE CHANGES? HOW WILL THEY AFFECT PLANT AND SOIL CLIMATE?

Arctic climate has been severe and variable for thousands of years. Ecosystems and their components have been selected and adapted to the regime. However, the expected rate of climate change resulting from anthropogenic CO_2 is more extreme than previously experienced, with annual temperature increases of 6–8°C predicted by 2100 at the highest latitudes (White *et al.*, 2000). Further, it is a combination of factors that is changing and these are not uniformly distributed in time or space:

- Warming is expected to be greatest in winter, concentrated in western Canada and Alaska, and in Siberia, but cooling is expected in western Greenland and eastern Canada. Relatively rapid cooling may occur through changes in ocean circulation, e.g. in the North Atlantic.
- Precipitation is expected to increase or decrease by about 10%, probably in oceanic and continental areas respectively and related to mountainous topography.
- Cloud cover will increase where warmer air holds more moisture.
- Increased frequency and intensity of climatic events are expected.
- Atmospheric CO_2 concentrations will double by 2050.
- Independently, UV-B radiation will continue to increase, especially in spring, associated with stratospheric ozone depletion (there may be interaction with climate change through tropospheric cooling).
- Deposition of atmospheric nitrogen is expected to double over the century.

Natural and managed ecosystems will respond to the combination of changes in what might be described as the ‘climate envelope’, with additional responses to associated changes in land use, industrial development and pollution.

Temperatures within the vegetation canopy tend to be higher than air temperatures during the summer through radiation effects. In winter, snow cover provides a blanket that retains heat. It is the timing and depth of snow cover that causes significant variations in the general seasonal pattern. Early autumn snow retains more heat; early snow thaw allows radiation input and canopy warming, but with the chance of direct effects of late frosts. Soil warming, thawing and deepening of the active layer increases during the summer. Surface freezing of the active layer (and sometimes upwards from the permafrost) in autumn retains an unfrozen layer within the soil which might extend through to the following spring. Variations on this theme depend on soil moisture content and soil texture which affect thermal conductivity. In addition, topography causes variation – hummocks have warmer summer soil temperatures but shorter and shallower active layer seasons than adjacent hollows with greater water content.

These basic microclimate principles, well illustrated in the palsa mire at Stordalen in northern Sweden (Ryden and Kostov, 1980) (Figure 1), are critical in understanding the influence of climate change on ecosystems. In general:

- The response of canopy and soil temperatures tend to be 'damped' and lag behind air temperatures. The microclimate response is strongly influenced by radiation, snow and vegetation cover, soil texture, water content and permafrost, topography and aspect.
- Soil moisture conditions will also change with changes in evapotranspiration, precipitation, depth of active layer and permafrost.
- Extension of the period of soil thaw with increased air temperatures will be modified particularly by changes in snow depth, timing of fall, and quality.
- Zones where cryoturbation disturbs the soil surface will tend to move North with climate warming.
- Reduced snow cover will increase the influence of radiation through reduced albedo.

WHAT ARE THE PROBABLE CONSEQUENCES FOR ORGANISMS AND COMMUNITIES OF CLIMATE CHANGE; ESPECIALLY IN WINTER AND BELOWGROUND?

A key conclusion that has emerged from the various intensive experimental and historical studies is that species and growth forms have distinctive responses and that these responses vary under different conditions; responses tend to be individualistic and site specific. A consequence is that the composition of 'communities' is unstable and unlikely to be repeated over time.

The most detailed experimental studies of responses, mainly of plants, to climate change have been in moist tussock tundra and wet

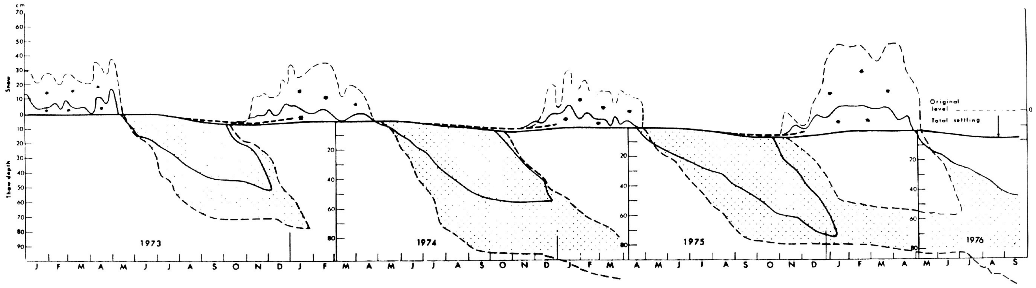

Figure 1. Duration of thaw period and refreezing at two subsites at the Stordalen mire at Abisko. A hummock (solid line), well drained after snow-melting, and a depression (dotted line), wet throughout the growing season. Note the heat flux downwards as mid-winter prevails above and that 1975 was a particularly cold year (from Ryden and Kostov, 1980).

1. mynd. Lengd hláku og frystingar á tveimur stöðum á Stórdalsmýri við Abisko. Þúfa (heil lína), vel framræst eftir bráðnun snævar, og dæld (brotin lína), rök allan vaxtartímann. Athugið hitastreymið niður á við þegar líður á vetur og að 1975 var sérlega kalt ár (frá Ryden og Kostov, 1980).

sedge meadow in Alaska (Chapin *et al.*, 1997; McKane *et al.*, 1997ab), in dwarf shrub heath and fellfield in sub-Arctic Sweden and in polar semi-desert and heath in the high Arctic on Svalbard (Press *et al.*, 1998; Michelson *et al.*, 1996). These studies have included artificial warming, reduced light, and enhanced water, nutrients, carbon dioxide and UV-B. They have been complemented by standardised manipulation of temperature at 26 Arctic and alpine sites in the International Tundra Experiment (ITEX) (Arft *et al.*, 1999; Henry, 1997).

The experimental manipulations over periods of up to ten years have shown a wide variety of short- and long-term responses which are difficult to summarise or to generalise. However, Figure 2 is indicative of some of the responses, with a general reduction in plant biomass, but with marked changes in composition of the vegetation, notably the increase in deciduous shrubs with nutrient addition and the decrease in mosses mainly through shading. Further, in the control plots, the biomass of *Eriophorum vaginatum* at Toolik Lake in Alaska declined to 30% of its initial value during the 11-year study during the warmest decade on record (Chapin *et al.*, 1997). However, in later years, plant biomass has increased (Schmidt *et al.*, 2000).

Growth rates, phenology and reproduction were all influenced to varying degrees.

In relation to experimental warming, there are indications from the Alaskan, Scandinavian and ITEX studies that:

- Vegetative growth was greatest in warmed plots in the early years of experiments whereas reproductive effort and success increased in later years.
- Herbaceous forms had stronger and more consistent vegetative growth responses than did woody forms. Evergreen shrubs responded more strongly than deciduous species.
- Low Arctic sites produced strongest growth responses but colder sites produced a greater vegetative response and tended to invest more in seed production.
- Invading species played a more important role in vegetation change in the high Arctic than in the low Arctic, but increases in ground cover were very slow.
- Photosynthetic responses to temperature were generally smaller than the nutrient-driven vegetative and temperature-driven reproductive responses.
- Response to nutrient enrichment and temperature were greater than responses to elevated CO_2 and UV-B.
- Secondary effects of climate change mediated by vegetation change may be just as important as direct climate effects.

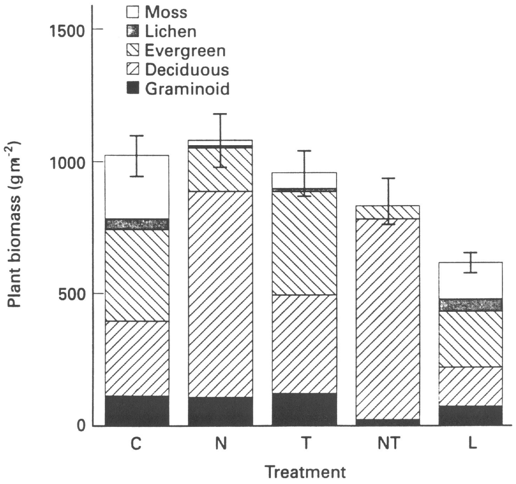

Figure 2. Total peak-season biomass (excluding roots) of Alaskan tussock tundra vegetation by growth form, in response to environmental manipulations after 9 years of treatments. Treatments are control (C), nutrient addition (10 g N m^{-2} and 5 g P m^{-2} annually) (N), temperature increase (summer air temperature raised by 3°C) (T), nutrient and temperature increase (NT) and light attenuation (light reduced by 50%) (L) (from Chapin *et al.*, 1997).

2. mynd. Viðbrögð heildarlífmassa ofanjarðar á hávaxtartíma í þýfðri freðmýri í Alaska flokkuð eftir gróðurflokkum að lokinni níu ára tilraunameðferð. Meðferðaliðir eru viðmið (C), áburðargjöf (10 g N m^{-2} og 5 g P m^{-2} árlega) (N), hitastigshækkun (sumarhiti hækkaður um 3°C) (T), áburðargjöf og hitastigshækkun (NT) og ljósdeyfing (ljósstyrkur minnkaður um 50%) (L) (frá Chapin et al.*, 1997).*

Examination of responses to changes in winter climate has been much more limited but there is evidence that ice-encasement resulting from thaw-freeze conditions during winter can cause plant death, despite the ability of at least some species to resist anoxia during encasement. Plant responses to extension of the growing season due to warming, particularly early snow melt, will also be influenced by the coincidence with early season maximum light. As usual, responses will be species and process specific as illustrated in a study along a snow-melt gradient in northern Sweden (Kudo *et al.*, 1999). Based on analysis of 5 deciduous and 5 evergreen species, they concluded that extension of season would decrease leaf nitrogen in both life forms and increase leaf turnover in evergreen plants. Although annual leaf production and shoot growth of boreal species may increase with season extension, they will remain unchanged in strictly arctic-alpine species. An additional variation is that in a warmer climate temperature-opportunistic species such as *Geum* spp. will profit in terms of biomass production and reproduction, while strongly photoperiod-controlled species, e.g. *Ranunculus glacialis,* will benefit little (Prock and Korner, 1996).

Arctic flora and fauna have been subject to a long history of climate variation. Major topographic variations in microclimate also provide conditions to which species have adapted. As a result, although species diversity may be small, considerable phenotypic and genotypic variation exists. In this respect, the present day flora of the Arctic has the necessary resilience to accommodate substantial and even rapid changes – a degree of 'pre-adaptation' to climate change (Crawford and Abbott, 1994).

Fauna and microflora responses

Direct and indirect responses of vertebrates and invertebrates to climate changes are reasonably well known. They include changes in composition and distribution of pasture vegetation for carribou (*Rangifer tarandus*); increased survival and fecundity of red deer (*Cervus elaphus*) 2–3 years after warm winters caused by the North Atlantic Oscillation NAO); reduced mortality of eggs of *Eperrita autumnalis* in warm winters causing defoliation of birch; changes in leaf palatability in response to CO_2 (see papers in Hofgaard *et al.*, 1999).

Changes in the composition of the vegetation affect the palatability for vertebrates and invertebrates, e.g. lichens for reindeer. Further, although the effects of enhanced CO_2 and UV-B may be less than other factors, they may have important consequences for leaf quality (e.g. increased lignin and reduced nutrient concentrations, increased cuticle thickness and tannin content) (Gehrke *et al.*, 1995; Chapin *et al.*, 1997; Gwynne-Jones, 1999). Such changes can affect leaf consumption, e.g. larvae of *Epperita autumnata* consumed three times greater leaf area of irradiated *Betula tortuosa* area than controls (Buck and Callaghan, 1999).

Most research on Arctic soil fauna and microflora has been descriptive. The limited field and laboratory experimental work has concentrated on physiological and life history adaptations to climate, particularly to low temperature, with a strong base in the International Biological Programme (IBP) in the 1970s (Bliss *et al.*, 1981; see more recent reviews by Nadelhoffer *et al.*, 1992; Robinson and Wookey, 1997; Bale *et al.*, 1997; Heal, 1997).

Evidence from such studies indicate a low biodiversity of species and, particularly amongst soil fauna, a restricted range of taxonomic and possibly functional groups, e.g. earthworms as 'soil engineers'. There are clear physiological and phenological adaptations to climate, particularly cold tolerance. It seems probable that soil communities have significant genotypic and phenotypic variation within species, related to past climate variability and to local habitat heterogeneity. These features, combined with short life-cycles and the potential for long-distance dispersal, indicate that soil organisms have the capacity to respond rapidly to climate change. There is no direct evidence that ecosystem functions are limited by low diversity. However, it has been argued that the response of some specific functions, e.g. mycorrhizal associations, methanogenesis and methanotrophy, and some nutrient transformations, may be limited by low diversity or by the combination of environmental factors including pollution stress (Schimel, 1995; Heal, 1997).

Key field experiments which have tested soil organism and process responses to long-term warming, combined with light, nutrient and other manipulations, are those at Abisko, Toolik Lake and Svalbard. Although no comprehensive organism studies have been undertaken and generalisations are tentative, some features emerge from the experiments:

- Microbial biomass contains as much or more labile nitrogen and phosphorus than the vegetation and there are major pools of dissolved organic nitrogen (Figure 3).
- Microbial biomass showed little or no response to warming and other treatments.
- Fungal biomass increased in response to combined warming and fertiliser in at least one site.
- Nematode populations doubled in response to warming and nutrient manipulations both individually and in combination (Figure 4), with positive responses of both bacterial and fungal feeders. Species number (29–60) and structure may be most affected by treatments (reduced) at sites already stressed by climate.
- Collembola were shown to be less able to survive heat stress (surface temperatures up to 30°C) than mites under conditions of low moisture, but neither collembola nor mite populations showed significant response to warming in the high Arctic.

In the intensive field experiments, processes of decomposition, nutrient and carbon flux have been given greater emphasis than the organisms involved. Results have been reviewed by Nadelhoffer *et al.* (1992), Robinson and Wookey (1997), Heal (1997) and Schmidt *et al.* (2000). In general, the results emphasise the basic principle that the rates of these processes are determined by the combination of physico-chemical environment and substrate quality factors acting on the soil organisms (Swift *et al.*, 1979).

Decomposition of surface litter is closely related to temperature, moisture and litter quality (C:N or Lignocellulose index) as shown by the successful predictions resulting from IBP studies (Bunnell and Scoullar, 1981). The importance of moisture is emphasised in the consistent pattern of rates of litter decomposition from dry<wet<moist sites (Figure 5). Within the soil profile rates of decomposition decline not only because the more resistant fractions remain and move down the profile but, as shown by use of standard materials, temperatures decline with depth, and in wet sites anaerobic conditions impose a further constraint (Heal *et al.*, 1981). However, within

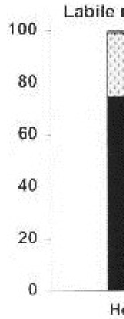

Figure 3. Partitioning of labile nitrogen between soil inorganic N, dissolved organic N and microbial N in the upper 10 cm or the entire soil organic layer (fellfield) in four tundra ecosystems in northern Sweden and Alaska. Data are means of pool sizes in June and August (from Schmidt *et al.*, 2000).

3. mynd. Skipting ólífræns N, uppleysts lífræns N og örverubundins N í efstu 10 cm eða öllu lífræna laginu (fellfield) í fjórum vistkerfum freðmýra í norður Svíþjóð og Alaska. Tölurnar eru meðaltöl í júní og ágúst (frá Schmidt et al.*, 2000).*

Figure 4. Nematode population density in soils from heath (0–3 cm) and fellfield (0–2 cm) in northern Sweden after 8 growing seasons with environmental manipulations. Control (C), enhanced temperature (T) and fertiliser (F) (from Ruess *et al.*, 1999).

4. mynd. Fjöldi þráðorma í heiðajarðvegi (0–3 cm) og fjallajörð (fellfield) í norður Svíþjóð eftir 8 vaxtarskeið með breyttum umhverfisþáttum. Viðmið (C), hitastigshækkun (T) og áburður (F) (frá Ruess et

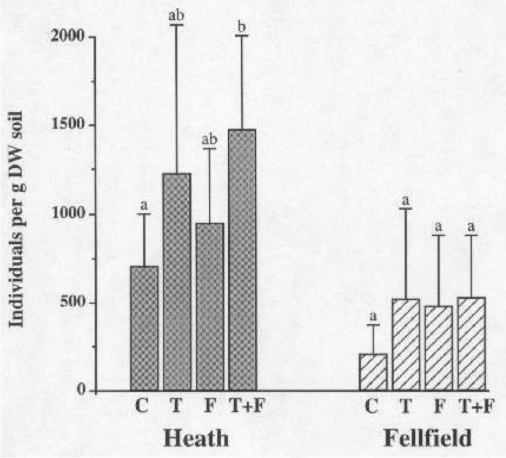

Figure 5. Litter weight loss in the first year in dry (solid line) mesic (dotted line) and wet (dashed line) IBP tundra sites. Data are from 12 sites and 74 litters (24 dry, 19 mesic, 31 wet) (from Heal *et al.*, 1981).

5. mynd. Þungi lífrænna efna á fyrsta ári í þurri (heil lína), rakri (brotin lína) og blautri (strikalína) IBP freðmýri. Tölur frá 12 stöðum og 74 sýnum (24 þurrum, 19 rökum, 31 votum) (frá Heal et al.*, 1981).*

the profile there are important inputs of organic matter from plant roots – a subject of little research. Input of root exudates provide a readily decomposed substrate in contrast to the more resistant root debris. Figure 6 illustrates the variability between soils of the various factors, including permafrost, and the organic accumulation which is the net result of the processes of primary production and decomposition.

The consequences of climate change, based on understanding of controls and on experiments are well summarised by Nadelhoffer *et al.* (1992) and indicate that:

- Changes in the quality of litter input through changes in plant communities will have important effects, particularly shifts from woody and evergreen shrubs to more deciduous shrubs and graminoids.
- Reductions in moss cover will reduce input of resistant organic fractions and will reduce moisture holding capacity.
- Warming will increase decomposition rates, especially where temperatures rise above about 10°C.
- Dry sites will be least affected because of moisture constraints. Moist sites are likely to be most responsive. Wet sites systems which remain saturated will show little change but where drainage is improved, e.g. by lowering or loss of per-

Figure 6. Schematic representation of dry, moist and wet tundra ecosystems (from Nadelhoffer *et al.*, 1992).

6. mynd. Teikning af þurru, röku og blautu vistkerfi freðmýrar (frá Nadelhoffer et al.*, 1992).*

mafrost, decomposition rates will increase and CH_4 production reduced.

Enhanced CO_2 may increase root growth and exudation and reduce litter quality by increasing structural carbohydrates. Enhanced UV-B will tend to reduce litter quality through increased cuticle thickness, reduced cellulose and increased tannins (Gehrke *et al.*, 1995).

Although changes in nutrient content during decomposition give some indication of rates of nutrient release they provide little information on dynamics. More direct measurements of N and P changes have been made in field experiments but also show methodological limitations. The most detailed studies have been at Abisko and Toolik Lake and have been compared by Schmidt *et al.* (2000). The results again show the variability between and within sites but indicate some general features:

- Ammonium is the dominant product and nitrification is very limited. Warming is likely to increase nitrification.
- N mineralisation is very low (0.1–0.6 g N m^{-2} yr^{-1}) and the ratio of NPP:N mineralisation is much higher in the Arctic than in other systems.
- Net mineralisation varied 5-fold between dry, mesic and wet systems in Alaska and was lower in summer than in spring, possibly reflecting dominance of microbial immobilisation in summer and release in winter.
- Phosphorus is tightly conserved. Soluble and exchangeable pools are very small and turnover rapid. In mesic and wet soils with thick organic layers and thin active layers, P input is largely or entirely from precipitation.

Experimental warming tends to increase N and P mineralisation and immobilisation (Figure 7). The relatively large pools of dissolved organic N (Figure 2) decreased in some sites and increased in others in response to warming. The low rates of mineralisation must be placed in the context to other N sources. Thus N fixation is of the order of 0.02–0.26 g N m^{-2}

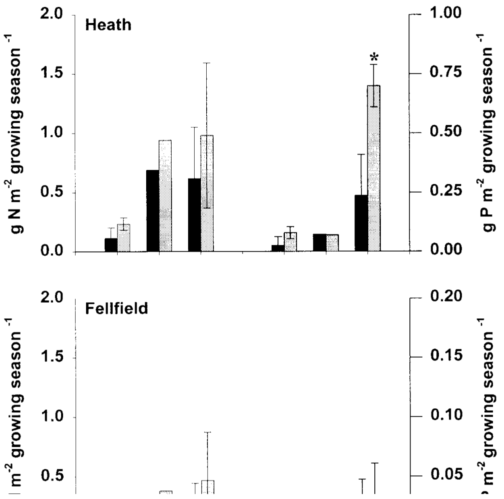

Figure 7. Net N and P mineralisation and microbial immobilisation in buried bags and estimated plant uptake during one growing season in control and greenhouse plots in northern Sweden (heath, fellfield) and Alaska (tussock and wet sedge) (from Schmidt *et al.*, 2000).

7. mynd. Nettó N- og P-binding og örverubinding í gröfnum netpokum og áætluð upptaka plantna á einu vaxtarskeiði í viðmiðunar- og gróðurhúsareitum í norður Svíþjóð (heiði, fjallshlíð) og Alaska (þýfi og blaut starmýri) (frá Schmidt et al.*, 2000).*

yr^{-1} (Chapin and Bledsoe, 1992). Deposition from atmospheric pollution contributes 0.1–0.5 (locally 1.0) g N m^{-2} yr^{-1} much of which may be released as a flush at snow melt (Woodin, 1997). Such sources of plant and microbial N will be affected by climate change through changing algal, lichen and moss cover, and through changing wind, precipitation and pollution sources. The levels of pollution input have been shown to influence plant growth and reduce mycorrhizal infection (Woodin, 1997).

A strength of the main experimental treatments considered above is that they have been maintained for up to a decade or more. They highlight:

- Variability in organism response both within and between sites.
- The importance of interaction between environmental factors.
- Methodological limitations, particularly in microbiology.

Basically, many of the techniques currently used in microbiological assay are not able to detect significant changes in microbial dynamics because of the habitat heterogeneity and lack of specificity to important functional groups. Greater use of isotopic tracers and molecular techniques has been advocated (e.g. McKane *et al.*, 1997a).

WHAT ARE THE EXPECTED NET RESPONSES TO THE COMBINATION OF CAUSES AND CONSEQUENCES?

Three modelling studies integrate information generated from individual laboratory and field experiments with basic ecological theory. They represent different scales of resolution (microbial; site; region) and explore the likely ecosystem consequences of climate change.

Microbial dynamics

A distinct approach to understanding the dynamics of Arctic microbial communities is provided by Panikov (1999), using simulation models based on microbial kinetics and driven by major independent variables (soil mineral resources, solar radiation, soil solid state). The approach provides a compromise between process and organism oriented models. It reflects the concept of coordinated microbial biosyntheses – a 'synthetic chemostat model'. Microbial diversity is represented as three types of life strategy:

- r-selected: synonymous with copiotrophic and zymogenic populations, characterised by *'Pseudomonas'*.
- K-selected: synonymous with autochthonous and oligotrophic bacteria and fungi, characterised by *'Arthrobacter'*.
- L-selected: representing organisms adapted to unfavourable environments, starvation stress or unfavourable substrates, characterised by *'Bacillus'*.

These three types of heterotrophs compete for common organic substrates from root exudates and plant litter in a varying physical environment. Grazing by protozoa above a threshold microbial biomass represents a population control mechanism.

The general model was used to simulate community dynamics under global warming at Point Barrow, Alaska, based on information from the IBP studies at that site (Brown *et al.*, 1980).

- Simulation of the earlier cold conditions over two years showed a community dominated by organisms with *'Arthrobacter'* and *'Pseudomonas'* strategies. *'Bacillus'* showed only sporadic short-term activation in spring. Dynamics of *'Arthrobacter'* were stable throughout the year but *'Pseudomonas'* populations varied widely with peaks in late spring and autumn. These results are consistent with general observations in Arctic microbiology and were generated on the basis of competition for substrates.
- Simulated climate warming by 2, 5 and 10°C generated only modest community change – some increase in *'Arthrobacter'* biomass, a slight decrease in *'Pseudomonas'* populations (mainly through predation), but accelerated growth of *'Bacillus'* in spring.

- The main effect of warming was increased decomposition due to higher production of hydrolytic enzymes by L-strategists. After 20–30 years accumulated litter was reduced to 50% of its original value despite increased plant production.
- Separate simulations explored competition between psychrophilic and mesophilic sub-populations of *'Pseudomonas'*. Warming by 5°C slightly increased total populations with a small rise in psychrophiles. Only with a 10°C rise did mesophiles dominate and the balance remained due to seasonal temperature fluctuations.
- The simulations displayed a high degree of stability within the microbial community in response to warming, with significant changes only after a large rise in temperature, but with significant increases in decomposition.

The simulations indicate that the principal driving forces controlling microbial dynamics are substrate quality and quantity, combined with predator control. These features, plus the relative stability of the community despite changes in process rates, indicate why other observations of microbial biomass show little response to manipulated climate change yet decomposition and nutrient flux change significantly. Thus, the use of life strategies or functional groups provides a useful compromise between the oversimplification of process models and the complexity of organism population models.

Tundra ecosystem model

McKane *et al.* (1997ab) used a process-based General Ecosystem Model (GEM) to simulate historical (1829–1990) C and N dynamics and to integrate and analyse results from a variety of experiments on moist tussock tundra at Toolik Lake. The model simulates stand-level photosynthesis and N uptake by plants, allocation of C and N to foliage, stems and fine roots, respiration of these tissues, turnover of biomass through litter fall, and decomposition of litter and soil organic matter.

The results of historical analysis showed that:

- Historical increases in temperature and CO_2 resulted in increased system C storage, as rising respiration losses were more than compensated by increased photosynthesis through enhanced soil to plant N transfer with increased mineralisation and uptake.
- At hypothesised constant soil moisture (425%) decomposition was inhibited. In contrast, when a decline in moisture was simulated, decomposition increased as the effect of rising temperature was amplified by more favourable moisture conditions, resulting in increased transfer of N from soil to plants.
- The model predicted a small increase in ecosystem C over the historical period, but also predicted relatively large transient C losses, including a large loss between 1988 and 1990 which corresponding to measured changes.

Integration of data from the experimental manipulation of CO_2 temperature, light and soil nutrients revealed:

- Widely different patterns between treatments in C-N interactions and constraints on storage of C.
- Enhanced CO_2 gave small increases in C storage, as did fertiliser application but by different mechanisms. In contrast, warming (with some light reduction) and reduced shade gave small reductions in C store.
- Simulated warming without change in light resulted in a short-term decline in C store due to increased decomposition, followed by a gradual long-term rise in soil C associated with a delayed shift of N from soil to plant giving increased photosynthesis.

The results from the simulations indicate that changes in the C sink-source balance will not be as great as earlier estimated. They also show the critical role in C flux played by soil-plant N transfers, possibly more important because the system is considered to be strongly N limited. Interactions and competition between micro-organisms and plant roots for nutrients are clearly key processes within the system but ones which are difficult to detect at a sufficiently sensitive level.

Regional changes in ecosystem distribution

One consequence of climate change will be shifts in the distribution and composition of vegetation and ecosystems. One of the recent regional models has examined the potential long-term and large-scale changes for areas north of 50°N (White *et al.*, 2000). A dynamic, global vegetation model was driven by transient climate predictions and scenarios of increasing CO_2, suplhate aerosols and atmospheric N deposition. The model combined coupled plant-soil C, N and water cycles (biogeochemistry), atmosphere-vegetation energy and mass fluxes (biophysics) and dynamic shifts in vegetation types and properties (biogeography). Changes in vegetation types and carbon storage were predicted from 1860 to 2100.

The region covered includes temperate grasslands, mixed forests, coniferous forests and tundra. The model can be visualised as a series of 200 m^2 plots within large (2.5–3.75° latitude-longitude) grid squares. In each plot, the vegetation option is determined by ecological responses to the prevailing environment, with no dispersal constraints. When run with historical climate patterns from 1860, the current area of tundra was calculated to be 7.9×10^{12} m^{-2}, with 230 Pg and 17 Pg of soil and vegetation C respectively. These estimates are similar to other, independent estimates.

When the model was run through from the current situation to 2100:

- Predicted ‘potential’ tundra vegetation cover was almost halved. Reduction was largely through extension of boreal forest in response to warming, which increased N mineralisation and the depth and period of thawing.
- The rate of forest extension was over 1 km per year in some areas. This is high, and although it is at the upper end of postglacial forest migration rates, it should be regarded as an upper extimate.
- Where tundra remained as tundra or changed to forest, NPP increased by 122 or 600–700% from present. NEP showed a small decrease (C source) where tundra remained but approximately doubled where tundra changed to forest, mainly through enhanced plant biomass (C sink).

Whilst many other factors could alter these predictions, e.g. lower rates of forest movement or changes in land use, the estimates are in broad agreement with comparable recent modelling studies. Such changes will also have feedback effects to climate through C flux and change in surface albedo.

CONCLUSIONS

Despite the limitations in evidence some general features of terrestrial responses are emerging. These should be regarded as ‘working hypotheses’ and can help to guide further research.

- Plant, animal and microbial responses to climate change are individualistic and strongly related to site conditions.
- Climate variability and change has been a feature of the Arctic environment and organisms are adapted or selected to such changes. Genotypic and phenotypic variability will tend to buffer responses.
- Responses may be most obvious at the (climatically determined) edges of the range of individual species and systems. Observations at these positions are likely to be particularly effective in detecting redistribution of species and systems.
- Within the range of species and systems, changes in community composition as species or functional groups are likely to be more obvious than changes in biomass or production and will affect other biotic and abiotic features.
- Changes in soil temperature will be less than and lag behind air temperatures (‘damping’), especially in soils with high

water content and with permafrost/shallow active layer. Many processes are strongly affected by soil moisture and changes in soil moisture will be as important as temperature.
- Changes in depth (and quality) of snow cover will be inversely related to season length and have important effects on selected species.
- Increased decomposition and mineralisation may be mainly through extension of soil (decomposition) season when plant uptake is minimal. Changes in soil processes will probably be greatest in moist and in wet soils where soil moisture is reduced.
- The composition of the soil organism community will change but there is no evidence that this will significantly affect soil processes. A more important effect is likely to be 'outbreaks' of individual species populations, e.g. epidemics of pest and diseases, which may be short-term but could have long-term consequences, e.g. *Eperitta* changing birch tundra to treeless tundra.
- More important than individual species responses to individual factors is the combination of factors (temperature + moisture + light + nutrients + CO_2 + UVB) and indirect effects (herbivores + vegetation change).
- The frequency and intensity of climatic events (e.g. winter thaw-freeze events, storms) and local long-term changes in permafrost (e.g. soil subsidence) are likely to cause major disruptions to general patterns of change.

Despite its importance, our understanding of climate change effects on soil populations and processes is particularly weak. It is based on a very few experiments and observations at a very small number of sites.

- Individual experiments on individual species under specific conditions provide an important basis for understanding potential responses. These need to be balanced by examination of the effects of combinations of factors over decadal time scales.
- Integration of soil observations into intensive plant experiments (and vice versa), plus observations over a much wider range of sites and conditions are now high priorities.
- Models at differing scales of resolution remain an important tool to integrate information and explore potential responses to combinations of factors and conditions.

Finally, regional variations in changing climate, with some areas warming and others cooling, provide major opportunities for comparative research. They represent a circumpolar experiment, including control areas with little change. Exploiting this opportunity, especially in the North where climate change is most rapid, is a challenge to the international research community and their national and international sponsors.

Some international actions are being taken: International Geosphere-Biosphere Programme through their High Latitude Terrestrial Transect initiative (Koch *et al.*, 1995); ITEX (Henry, 1997); the various International Arctic Science Committee projects (IASC, 1999); the European Commission through ARTERI (Turunen *et al.*, 1999) and various projects. The planned Arctic Climate Impact Assessment, initiated through the Arctic Council and implemented through IASC, CAFF (Conservation of Arctic Flora and Fauna) and AMAP (Arctic Monitoring and Assessment Programme), should provide a clearer and integrated focus. Yet, as evidenced by this review, the practical research effort remains small, localised, short-term, fragmented, and inadequate to address the magnitude of the problem – and little emphasis is given to the potential effects of climate cooling in parts of the region!

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