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Climate Change and UV-B Impacts on Arctic Tundra and Polar Desert Ecosystems

Effects on the Structure of Arctic Ecosystems in the Short- and Long-term Perspectives

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Species individualistic responses to warming and increased UV-B radiation are moderated by the responses of neighbors within communities, and trophic interactions within ecosystems. All of these responses lead to changes in ecosystem structure. Experimental manipulation of environmental factors expected to change at high latitudes showed that summer warming of tundra vegetation has generally led to smaller changes than fertilizer addition. Some of the factors manipulated have strong effects on the structure of Arctic ecosystems but the effects vary regionally, with the greatest response of plant and invertebrate communities being observed at the coldest locations. Arctic invertebrate communities are very likely to respond rapidly to warming whereas microbial biomass and nutrient stocks are more stable. Experimentally enhanced UV-B radiation altered the community composition of gram-negative bacteria and fungi, but not that of plants. Increased plant productivity due to warmer summers may dominate food-web dynamics. Trophic interactions of tundra and sub-Arctic forest plant-based food webs are centered on a few dominant animal species which often have cyclic population fluctuations that lead to extremely high peak abundances in some years. Population cycles of small rodents and insect defoliators such as the autumn moth affect the structure and diversity of tundra and forest-tundra vegetation and the viability of a number of specialist predators and parasites. Ice crusting in warmer winters is likely to reduce the accessibility of plant food to lemmings, while deep snow may protect them from snow-surface predators. In Fennoscandia, there is evidence already for a pronounced shift in small rodent community structure and dynamics that have resulted in a decline of predators that specialize in feeding on small rodents. Climate is also likely to alter the role of insect pests in the birch forest system: warmer winters may increase survival of eggs and expand the range of the insects. Insects that harass reindeer in the summer are also likely to become more widespread, abundant and active during warmer summers while refuges for reindeer/caribou on glaciers and late snow patches will probably disappear.

INTRODUCTION

The impacts of changes in climate and UV-B radiation on species are both direct and indirect. Direct impacts act on behavior, physiology, growth, survival and reproduction (1, 2). However, species occur within ecosystems and link with other species through trophic interactions, that include predator-prey interactions, plant-herbivore interactions, decomposer organ-

ism interactions, pests and pathogens. In addition to these direct linkages between species, co-existence among species within communities and ecosystems controls the possibilities of species to access their resources, for example competition for light among plant species, while modifying the physical environment, for example provision of shade, shelter, moisture and insulation by various plant canopy dominants. Changes in climate in particular, and changes in UV-B radiation to some extent, have the potential to modify all of these many biological and physical interactions among species. In this paper, we assess the impacts of changes in climate and UV-B radiation on interactions among species aggregated into communities and ecosystems that lead to changes in ecosystem structure. We focus on responses of biomass, rather than organisms survival and numbers (1, 2).

We define ecosystem structure in terms of:

- spatial structure such as canopy structure, and habitat;
- trophic interactions;
- community composition in terms of biodiversity.

Although ecosystem structure and function are closely interconnected, we focus on the two aspects separately for clarity and limit the discussion here to plot (single m²) scale: Impacts of changes in climate and UV-B radiation on ecosystem function at the plot scale are assessed in a separate paper (3), while processes at the landscape and regional scales are discussed by Callaghan et al. (4, 5). This paper is part of an holistic approach within the Arctic Climate Impacts Assessment (ACIA) (6) to assess impacts of climate change on Arctic terrestrial ecosystems (7).

EFFECTS OF CHANGES IN CLIMATE AND UV-B ON ECOSYSTEM STRUCTURE

Local and Latitudinal Variation in Ecosystem Structure

The Arctic is characterized by ecosystems that lack trees. There is a broad diversity in ecosystem structure among these northern treeless ecosystems that follows a latitudinal gradient from the treeline to the polar deserts (Plates 1–4). Typical communities for a particular latitude are called “zonal” but local variation at the landscape level occurs and these “intrazonal communities” are frequently associated with variation in soil moisture and snow accumulation (8, 9).

According to Bliss and Matveyeva (10), zonal communities South of the Arctic boundary near the mean July isotherms of 10–12°C, consist of taiga, i.e. the northern edge of the boreal forest. This is characterized by closed canopy forest of northern coniferous trees with mires in poorly drained areas. To the north of this transition zone is the forest-tundra. It is



Plate 1. Forest tundra vegetation represented by the Fennoscandian mountain birch forest, Abisko, northern Sweden. Photo: T.V. Callaghan.



Plate 2. Zonal tussock tundra near Toolik Lake, Alaska, with large shrubs/small trees of *Salix* in moist sheltered depressions. Photo: T.V. Callaghan.

(Plate 3) in the south characterized by cryptogam-herb, cushion plant-cryptogam and, to a limited extent, mire communities. To the extreme north is the polar desert where only about 5% of the ground surface is covered by herb-cryptogam communities (Plate 4). In this zone, the mean July temperature is lower than 2°C and precipitation, which falls mainly as snow, is about 50 mm per year.

The tundra zone can be further subdivided into 3 sub-zones: the southern tundra with shrub-sedge, tussock-dwarf shrub and mire communities, the typical tundra with sedge-dwarf shrub and polygonal mire communities (Plate 5) and an Arctic tundra in the North consisting of dwarf shrub-herb communities. The end of the latitudinal gradient, mainly on islands and on the only mainland territory at Cape Chelyuskin (Taymyr), is occupied by polar deserts where woody plants are absent, and forbs and grasses with mosses and lichens are the main components of plant communities (12).

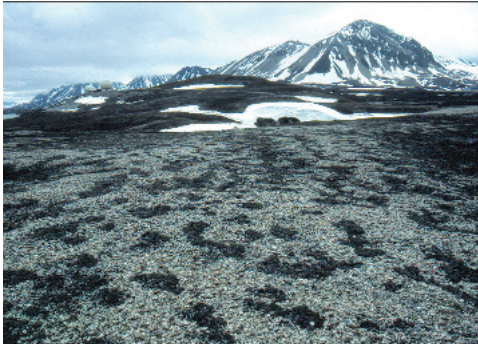


Plate 3. Polar semidesert dominated by *Dryas octopetala*, Ny Alesund, Svalbard. Photo: T.V. Callaghan.



Plate 4. Polar desert, Cornwallis Island, Northwest Territories, Canada. Photo: J. Svoboda.

characterized by white spruce *Picea glauca* in Alaska, birch in Fennoscandia (Plate 1), birch and Norway spruce *Picea abies* in the European Russian Arctic, by larch in central and eastern Siberia, and by evergreen coniferous trees in Canada (11). The vegetation is characterized by sparse, low-growing trees with thickets of shrubs. North of this zone is the Low Arctic which is characterized by tundra vegetation in the strict sense (Plate 2). This consists of communities of low, thicket-forming shrubs with sedges, tussock-forming sedges with dwarf shrubs and mires in poorly drained areas. To the north of this zone is the high Arctic which consists of polar semidesert communities

The classification of vegetation described above has geographical connotations and cannot be applied easily to reconstructions of past vegetation throughout the circumpolar North (13). A recent classification of tundra vegetation at the biome level (14) has been proposed by Kaplan et al. (13; Table 1; Fig. 2 in ref. 7).

Within the biomes or zonal vegetation types, there are “intra-zonal habitats” which are frequently associated with variations in soil moisture and snow accumulation and which have a microclimate that deviates from the general macroclimate as-



Plate 5. Polygonal wet tundra near Prudhoe Bay, Alaska. Photo: T.V. Callaghan.



Plate 6. *Racomitrium/Empetrum* heath in Iceland (showing erosion). Photo: T.V. Callaghan.



Plate 7. Snow bank vegetation showing increasing vegetation development with increasing length of the growing season represented as distance from the snow patch, Disko Island, West Greenland. Photo: T.V. Callaghan.

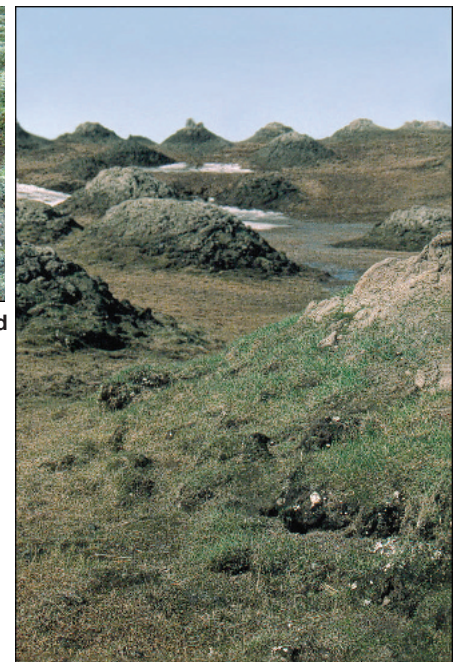


Plate 8. Thermokarst scenery in the Russian Tundra, New Siberian Islands. Photo: T.V. Callaghan.

Table 1. Circumpolar tundra biome classification from Walker (14) and Kaplan et al. (13).

Biome	Definition	Typical taxa
Low- and high-shrub tundra	Continuous shrubland, 50 cm to 2 m tall, deciduous or evergreen, sometimes with tussock-forming graminoids and true mosses ¹ , bog mosses and lichens	<i>Alnus</i> , <i>Betula</i> , <i>Salix</i> , <i>Pinus pumila</i> (in eastern Siberia), <i>Eriophorum</i> , <i>Sphagnum</i>
Erect dwarf-shrub tundra	Continuous shrubland 2 to 50 cm tall, deciduous or evergreen, with graminoids, true mosses, and lichens	<i>Betula</i> , <i>Cassiope</i> , <i>Empetrum</i> , <i>Salix</i> , <i>Vaccinium</i> , Poaceae, Cyperaceae
Prostrate dwarf-shrub tundra	Discontinuous "shrubbyland" of prostrate deciduous dwarf-shrubs 0 to 2 m tall; true mosses and lichens	<i>Salix</i> , <i>Dryas</i> , <i>Pedicularis</i> , Asteraceae, Caryophyllaceae, Poaceae, true mosses
Cushion forb, lichen, and moss tundra	Discontinuous cover of rosette plants or cushion forbs with lichens and true mosses	Saxifragaceae, Caryophyllaceae, <i>Papaver</i> , <i>Draba</i> , lichens, true mosses
Graminoid and forb tundra	Predominantly herbaceous vegetation dominated by forbs, graminoids, true mosses, and lichens	<i>Artemisia</i> , <i>Kobresia</i> , Brassicaceae, Asteraceae, Caryophyllaceae, Poaceae, true mosses

¹ "true" mosses exclude the genus *Sphagnum*

sociated with flat surfaces. The intrazonal habitats form a mosaic of communities. Each of these tend to have fewer species than the "plakor", or zonal, communities. For example, poorly drained areas are often dominated by sedges with an understory of mosses and liverworts but lack fruticose lichens (12). Although each intrazonal community is relatively poor, together they are more differentiated and diverse than zonal ones, and are responsible for about 80% of total species diversity in the regional flora and fauna. Disturbed areas also create landscape mosaics, particularly freeze-thaw cycles and thermokarst that form patterned ground (Plate 5). Diversity "focal points/hot spots" Walker (15) and "oases" (16, 17) enrich landscapes by possessing an increased number of species including those of more southern distribution. Examples are 2-m tall dense willow thickets in sheltered valleys at 75°N in Taymyr, stands of poplar trees (*Populus balsamifera*) north of the treeline in the northern foothills of the Brooks Range, Alaska that could respond rapidly to warming. There are numerous other types, such as the moss-dominated tundra of Iceland (Plate 6).

The vertical structure of Arctic ecosystems is as important as horizontal structure in explaining their current and future functioning. This structure is most pronounced in low-Arctic shrub communities, where there is a well developed shrub canopy and an understory of mosses, similar to the vertical structuring of boreal forests. Vertical structure is also pronounced below ground, with mosses and lichens lacking roots, some species rooted in the moss layer, others rooted just beneath the mosses, and a few species rooted more deeply.

The most striking latitudinal trend in plant functional types is the decrease in height of woody plants (from trees to tall shrubs, to low and prostrate shrubs, to dwarf shrubs, and eventually the loss of woody plants with increasing latitude). These functional types often occur in low abundance in zones north of their main areas of dominance, suggesting that they might rapidly expand in response to warming through vegetative reproduction (18, 19) and sexual reproduction (20), although range expansion will depend on geographical barriers such as mountains and seas (5). Recent warming in Alaska has caused a substantial increase in shrub density and size in moist tundra of northern Alaska (21). In areas where shrubs are absent, shrubs are likely to exhibit time lags in migration into new habitats (22). They colonize most effectively in association with disturbances such as flooding in riparian zones, thermokarst, frost boils, etc., throughout their latitudinal range, so migration may be strongly influenced by changes in climate- or human-induced changes in disturbance regime. Woody species affect ecosystem structure and function because of their potential to dominate the canopy and reduce light availability to understory species (19, 23) and to reduce overall litter quality (24) and rates of nutrient cycling.

A similar latitudinal decline in abundance occurs with sedges, which are absent from polar deserts, suggesting that this group might also expand northward with warming (12). *Carex stans* and *C. bigelowii* now mark the northernmost boundary of the tundra zone and might be a sensitive indicator of species responses to warming. Sedges have important effects on many ecosystem processes, including methane flux, because of their transport of oxygen to soils, transport of methane to the atmosphere, and inputs of labile carbon to the rhizosphere (25, 26). Prostrate and dwarf shrubs such as *Dryas* spp., *Salix arctica*, and *S. polaris* may decline in abundance

with warming in the low Arctic, due to competition with taller plants but may increase in abundance in the current polar deserts. These changes in distribution could substantially reduce the extent of polar desert ecosystems (4, 5), which are characterized by the absence of woody plants.

Response of Ecosystem Structure to Experimental Manipulations

Experimental manipulation of environmental factors expected to change at high latitudes (temperature, snow, nutrients, solar radiation, atmospheric CO₂ and UV-B) have strong effects on the structure of Arctic ecosystems, but the effects are regionally variable. Effects of these variables on individual species were discussed by Callaghan et al. (1, 2); here we emphasize overall community structure and species interactions.

Plant communities

Nutrient addition is the environmental manipulation that has strongest effect on the productivity, canopy height and community composition of Arctic plant communities (27–29; Fig. 1). Fertilization also increases biomass turnover rate, so actual biomass may or may not respond to nutrient addition. In northern Sweden, for example, nutrient addition to a mountain birch site (cf. the Paddus and Slåtta responses described below) caused an initial biomass increase. This biomass increase was not maintained over the long term, however, because expansion of the grass *Calamagrostis lapponica* negatively affected the growth of mosses and evergreen shrubs, leading to a negligible change in community biomass (30, 31). Similarly, in northern Alaska addition of nitrogen and phosphorus increased productivity and turnover within three years (18). There was, however, negligible change in biomass because the rapidly growing sedges, forbs, and deciduous shrubs responded most strongly, whereas evergreen shrubs and mosses declined in abundance (Fig. 2). After 9 and 15 years, competitive interactions altered the relative abundance of plant functional types, with the tallest species (the deciduous shrub *Betula nana*) responding most strongly (18, 19, 32). Litter and/or shade from this species reduced growth of lichens, mosses and evergreen shrubs. In vegetation types without any pronounced change in relative proportions of dominant species or life forms following fertilizer addition, as in Swedish treeline and high altitude heaths and in Alaskan wet sedge tundra, biomass of most dominant life forms increased. This resulted in up to a doubling of biomass after 5–9 years of treatment (33, 34). In polar semideserts, nutrient addition generally had a negative effect on vascular plants, due to enhanced winter kill, but stimulated the growth of mosses (35), an effect opposite to that in low Arctic tundra. This difference is probably due to

the immigration of N-demanding mosses from nearby bird cliff communities in the high Arctic compared with loss of existing moss species in the low Arctic.

fertilizer addition (28). A general long-term (10 years or more) response to environmental manipulations at sites in sub-Arctic Sweden and in Alaska was a decrease in total nonvascular plant biomass and particularly the biomass of lichens (29; Fig. 1).

Animal communities

Air warming experiments at Svalbard (79°N) had greater effects on the fauna above-ground than below-ground, probably because the soil is more buffered against fluctuations in temperature and moisture than the surface (41). Species with rapid life cycles (Aphids and Collembola) responded demographically more quickly than species (e.g. mites) with slow life cycles (42). Responses to warming differ among sites. Abundances of Collembola declined at barren sites where higher temperatures also caused drought and mortality due to desiccation, whereas the abundance of Collembola increased at moister sites. In summer, water availability is probably much more important to many invertebrates than is temperature. Mites are more resistant than Collembola to summer desiccation (41) and to anoxic conditions in winters due to ice crust formation following episodes with mild weather (43). Ice crust formation during the winter may increase over-winter mortality by 50% in Collembola (43). Also freezing-thawing events in spring may cause differential mortality among species, thus altering community composition (44).

In experiments conducted simultaneously at several sites and over several years, the natural spatio-temporal variability in community structure and population density of soil invertebrates was larger than the effects of the experimental manipulation within year and sites. This demonstrates that there is a large variability in the structure and function of high Arctic invertebrate communities due to current variation in abiotic conditions. It also indicates that Arctic invertebrate communities can respond rapidly to change.

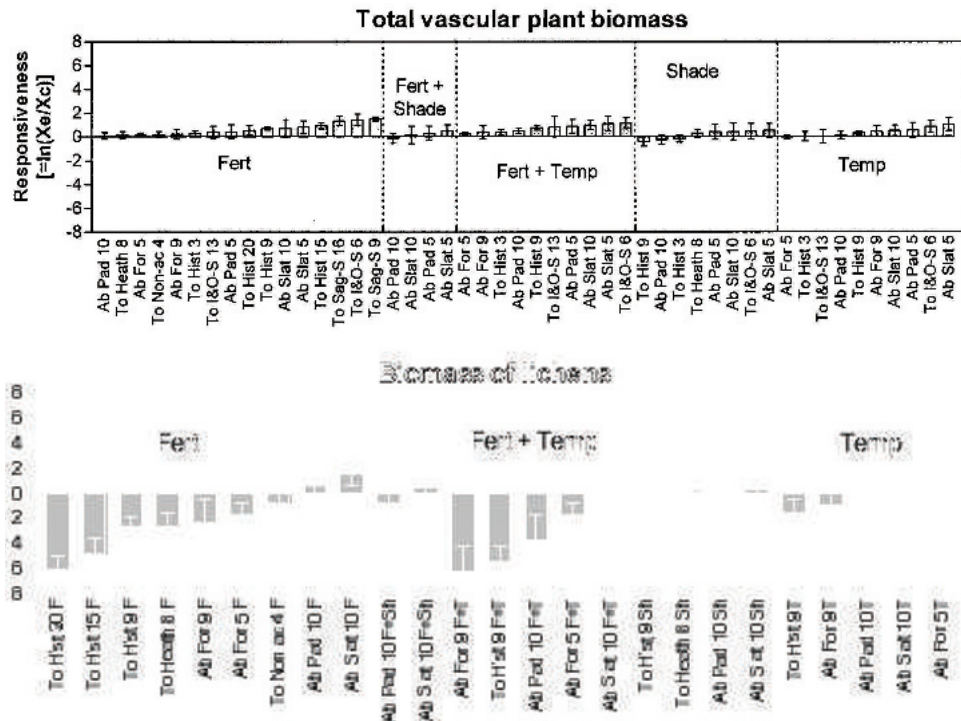


Figure 1. Results of long-term (generally 10 years or more) experiments in a range of habitats at Toolik Lake, Alaska and Abisko, Sweden. The figure shows the responsiveness of aboveground biomass ordered by treatment and size of responsiveness. Data are given for total vascular plant biomass and lichen biomass. Numbers in the graphs are the mean effect size (L^*) for each treatment and between parentheses the 90% confidence interval value. Codes relate to the geographical region (To=Toolik, Ab=Abisko), the site name and the duration of the experiment (29).

Water additions to simulate increased precipitation have generally had only minor effects on total biomass and production (27).

Summer warming of tundra vegetation within the range of expected temperature enhancement of 2–4°C for the next 100 years has generally led to smaller changes than fertilizer addition (28, 29, 36, 37) (Fig. 1). For instance, temperature enhancement in the high Arctic semi-desert increased plant cover within the growing seasons but the effect did not persist from year to year (35, 36). In the low Arctic, community biomass and nutrient mass changed little in response to warming in two Alaskan tussock sites (18, 38) and in two wet sedge tundra sites (33), coincident with relatively low changes in soil nutrient pools and net mineralization. Tussock tundra showed little warming response because some species increased in abundance and others decreased (18, 39, 40), similar to a pattern observed in the sub-Arctic Swedish forest-floor vegetation (31). The responses to warming were much stronger in the Swedish treeline heath and in the fellfield (34). The biomass in the low altitude heath increased by about 60% after air warming by about 2.5°C with little additional effect of a further warming by about 2°C. In contrast, the biomass approximately doubled after the low temperature enhancement and tripled in the higher temperature enhancement treatments at the colder fellfield. Hence, the growth response increased from the climatically, relatively mild forest understory through the treeline heath to the cold, high altitude fellfield where the response to warming was of the same magnitude as the response to

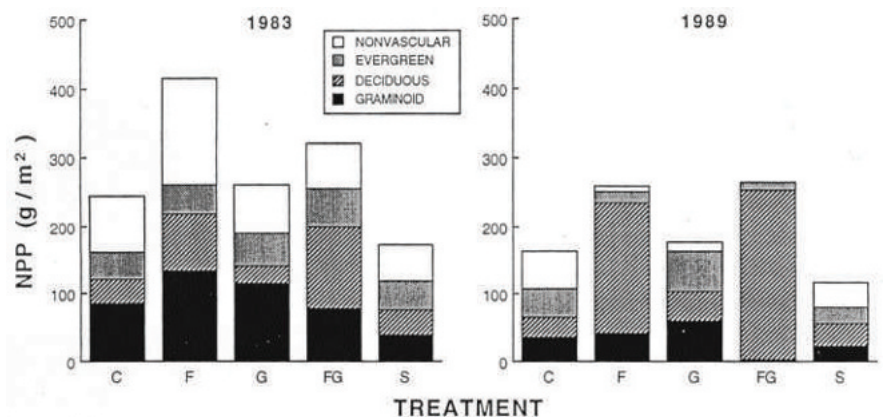


Figure 2. Effect of long-term fertilizer addition and experimental warming and shading during the growing season on aboveground net primary production (NPP) of different plant functional types at Toolik Lake, Alaska (18). The left-hand panel shows NPP by functional type and treatment in 1983, after three years of treatment, and the right-hand panel shows NPP by functional type and treatment in 1989, after nine years of treatment. C = control (unmanipulated) plots; F = annual N + P fertilizer addition; G = warming in a plastic greenhouse during the growing season; FG = fertilizer plus greenhouse treatment; S = 50% light reduction (by shading) during the growing season.

Compared to the high Arctic, sub-Arctic invertebrate communities at Abisko responded less to experimental warming (41). However, nematode population density increased strongly, and the dominance changed in favor of plant and fungal feeding species with elevated summer temperatures and NPK fertilization, indicating a shift in the decomposition pathway (45, 46).

Microbial communities

The sensitivity of microbial biomass, generally measured as biomass C, and nutrient content to changed environmental conditions in the Arctic is poorly examined. Long-term addition of easily processed C generally increases the microbial biomass, and addition of inorganic nutrients generally, but not always, increases its nutrient content without appreciable effects on the biomass (34, 47–49). In some cases, however, a combination of carbon and nutrient addition has led to a pronounced increase of both microbial biomass and nutrient content (49). This suggests a general C limitation to microbial biomass production and increased sink strength for soil nutrients if the amounts of both labile C and nutrients increase, but relatively low effect of increased nutrient availability alone. In the widespread drier ecosystem types in the Arctic, the soil microbial biomass is likely to be further limited by low water supply. Water addition to a high Arctic semidesert led to substantial increase in microbial biomass C and microbial activity (50).

Data on effects of growing-season ecosystem warming of 2–4°C over 5 (27, 38) and 10 (Jonasson and Michelsen, unpubl.) years have not shown appreciable long-term changes in microbial biomass and nutrient stocks. This suggests that increase of the growing season temperature alone is unlikely to have any strong impact on microbial C and nutrient sequestration, and that changes in the soil nutrient availability probably will lead to greater changes than the direct effect of increased temperature itself. The temperature effects on the ecosystem processes are likely, however, to be different from the observed relatively small effects on microbial biomass and nutrient stocks. This is because temperature changes may affect rates of decomposition and nutrient mineralization, rather than pool sizes, resulting in altered C balance and nutrient supply rates to the plants (3).

Appreciable seasonality in microbial bio- and nutrient mass have, however, been reported that seemingly are independent of ambient temperature. In general, the masses change little, or fluctuate, during summer (34, 51–53). In contrast, pronounced increases of both bio- and nutrient mass have been reported in autumn (54–56), probably as a function of increased input of labile C and nutrients from plants as they senesce, although these data are from mountain and alpine, rather than from Arctic soils. The increase seems to continue through winter, although with a slower rate (52, 57), despite soil temperatures below 0°C (1, 58). It is followed by a sharp biomass decline in the transition between winter and spring (56, 57, 59), which may (59) or may not (60, 57) coincide with a decrease also in microbial N and an increase of mineralized N, indicating a pronounced transformation of microbial N to soil inorganic N (51, 52). Indeed, this seasonal pattern suggests a temporal partitioning of resource uptake with low competition between plants and microbes for nutrients, as microbes absorb most nutrients in autumn and plants in spring, coincident with the nutrient release from declining microbial populations. However, it may also be an indication that plants compete well for nutrients during the growing season (61), and microbes access nutrients efficiently only when the sink strength for nutrients in plants is low (34).

Laboratory experiments have shown that the spring decline of microbial mass is a likely effect of repeated freeze-thaw cycles (62). Indeed, Larsen et al. (60) reported a microbial decline only in soils when subjected to repeated freezing and thawing but not in the same soil kept constantly at freezing before thawing.

The seasonal dynamics in microbial biomass, microbial and soil inorganic nutrients therefore suggests that “off growing-season” changes in climate during the transition between winter and spring with, e.g. changed frequency of freeze-thaw events and warmer winters may have greater impact on nutrient transformations between microbes, soils and plants than changes during the growing season.

Manipulations simulating enhanced UV-B radiation (a 15% reduction in stratospheric ozone) and a doubling of atmospheric CO₂ for 7 years altered the use of labile carbon substrates used by gram-negative bacteria (63). Although these rhizosphere bacteria are a relatively small component of the belowground microbial biomass, they are likely to be particularly responsive to environmentally induced changes in belowground plant carbon flow.

UV-B radiation also affects the structure of fungal communities. Microcosms of sub-Arctic birch forest floor litter exposed to enhanced UV-B radiation showed a reduction in fungal colonization of leaf veins and lamina (64). Fungal composition was also altered, with a reduction in *Mucor hiemalis* and a loss of *Truncatella truncata* in the UV-B treatments. Similar findings of fungal community change were obtained in the sub-Arctic (Abisko), in an ecosystem that was the source of the litter used by Gehrke et al. (64). In this field study of the decomposition rates of a standard litter type, there was also a change in the composition of the fungal community associated with litter resulting from elevated UV-B levels (65). So far, no change in plant community structure has been found in the Arctic in response to artificially enhanced or reduced UV-B and CO₂.

Recent Decadal Changes in Ecosystem Structure Within Permanent Plots

Satellite measurements suggest a widespread increase in indices of vegetation greenness (e.g. NDVI) and biomass at high latitudes (66, 67; Fig. 3), although changes in satellites and sensor degradation may contribute to this trend (68). Aerial photographs show a general increase in shrubbiness in Arctic Alaska (21) and

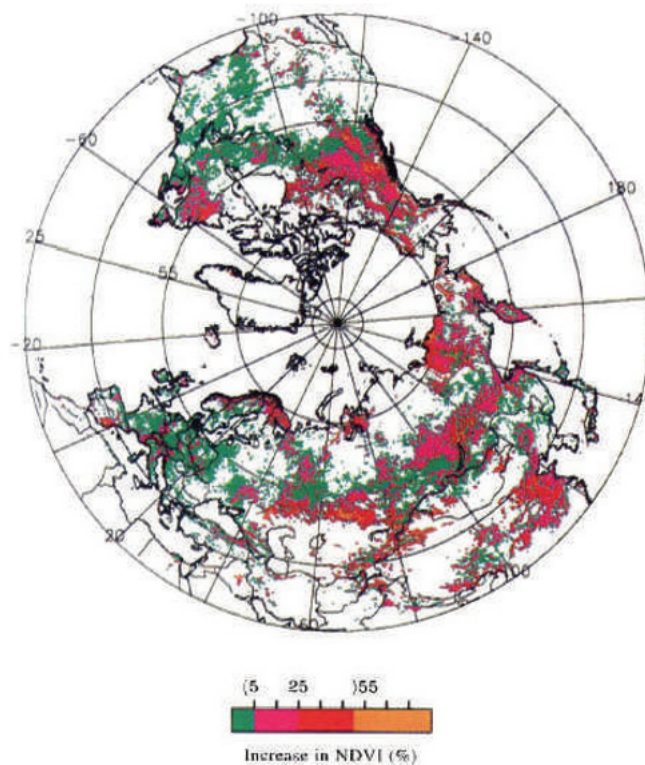


Figure 3. Changes in greenness (depicted by NDVI) of northern vegetation between 1981 to 1991 (66).

indigenous knowledge also reports an increase in shrubbiness in some areas. These observations are consistent with the satellite observations. However, it has been difficult to corroborate these studies from permanent plots, because of the paucity of long-term vegetation studies in the Arctic. In Arctic Alaska, for example, a trend toward reduced abundance of graminoids and deciduous shrubs during the 1980s was reversed in the 1990s (32). In Scandinavia, recent decadal changes in vegetation are affected more strongly by cyclic abundance of lemmings than by climatic trends (69).

Trophic Interactions

Trophic level structure is simpler in the Arctic than further south. In all taxonomic groups, the Arctic has an unusually high proportion of carnivorous species and a low proportion of herbivores (70). As herbivores are strongly dependent on responses of vegetation to climate variability, warming might therefore substantially alter the trophic structure and dynamics of Arctic ecosystems. The herbivore-based trophic system in most tundra habitats is dominated by one or two lemming species (71–73) while the abundance of phytophagous (plant-eating) insects relative to plant biomass is low on Arctic tundra (74). Large predators such as wolves, wolverines and bears are less numerous in the tundra than in the boreal forest (8) and predation impacts on tundra ungulates are usually low. Thus, the dynamics and assemblages of vertebrate predators in Arctic tundra are almost entirely based on lemmings and other small rodent species (*Microtus* spp. and *Clethrionomys* spp.) (75, 73) while lemmings and small rodents consume more plant biomass than other herbivores. Climate has direct and indirect impacts on the interactions among trophic levels, but there is greater uncertainty about the responses to climate change of animals at the higher trophic levels.

Plant-Herbivore Interactions

Changes in climate, UV-B, CO₂, plant tissue chemistry and herbivory

Arctic and boreal plant species often contain significant concentrations of secondary metabolites that are important to the regulation of herbivory and herbivore abundance (76, 77). These secondary metabolites are highly variable in their chemical composition and in their antiherbivore effects, both within and among species. One hypothesis about the regulation of these compounds that has received widespread discussion is the carbon-nutrient balance hypothesis of Bryant et al. (78, 79), which attempts to explain this variation in part on the basis of carbon versus nutrient limitation to plant growth. Although many other factors in addition to carbon-nutrient balance are probably important to the regulation of plant-herbivore interactions in the Arctic (e.g. 77, 80, 81) the abundance of secondary chemicals is often strongly responsive to changes in environment including temperature, light, and nutrient availability (e.g. 82–84). In a widespread Arctic shrub species, *Betula nana*, Graglia et al. (84) found that fertilization and shading generally led to decreased condensed and hydrolysable tannin concentrations in leaves, whereas warming in small field greenhouses increased condensed tannins and decreased hydrolysable tannins. There was also a large difference in both the average concentrations and the responsiveness of the concentrations of phenolics in plants from northern Alaska versus northern Sweden, with the plants from Sweden having generally higher concentrations but being less responsive to environmental changes. Such data suggest that the effects of climate change on plant-herbivore interactions will probably be highly variable and not only species-specific but also dependent on the nature of the change and on ecotypic or subspecific differences, perhaps related to local evolution in the presence or absence of herbivores.

Plant exposure to UV-B radiation has the ability to change the chemistry of leaf tissues which have the potential to affect the odor that herbivores such as reindeers use to detect food, and the quality of food in terms of palatability and digestibility (85). In general, enhanced UV-B can reduce soluble carbohydrates and increase phenolic compounds and flavonoids. Such changes are expected to reduce forage quality.

Plant exposure to increased CO₂ concentrations can also affect plant tissue quality and consequently herbivory (86). Enriched CO₂ may lead to the accumulation of carbohydrates and phenolic compounds while reducing nitrogen concentrations in leaves. However, these responses in phytochemistry can be significantly modified by the availability of other resources such as nutrients, water and light. Unfortunately, little information on CO₂ impacts on herbivory is available for the Arctic.

Climate and UV-B change, herbivore abundance, and vegetation production: *Invertebrates.* Population outbreaks of insects seldom extend into the tundra. However, in the forest near the treeline, insect defoliators can have devastating impacts on the ecosystem. Climate change may modify the population dynamics of such insects in several ways (87, 88). In *Epirrita autumnata*, eggs laid on birch twigs in autumn cannot tolerate winter temperatures lower than -36°C . For this reason *Epirrita* is destroyed in portions of the terrain (e.g. depressions) where winter temperatures can get lower than this critical minimum (89, 90). Warmer winters will probably reduce winter mortality and possibly increase outbreak intensity. Moreover, lower minimum temperatures are likely to allow *E. autumnata* and the related, less cold tolerant *Operophtera brumata* to extend their geographic distributions into continental areas with cold winters (91). However, the effect of a changing climate is not straightforward to predict because moth responses are season-specific. For instance, increasing spring temperatures may cause a mismatch between the phenology of birch leaves and hatching of larvae that are currently synchronized (92). Moreover, natural enemies such as parasitoid wasps and ants are likely to increase their abundances and activity rates if summer temperature rises. Currently, there is cyclicality in the populations and outbreak proportions occur approximately every 10 to 11 years (93, 91). The forests defoliated require about 70 years to attain their former leaf area although insect outbreaks in sub-Arctic Finland followed by heavy reindeer browsing of regenerating birch shoots have led to more or less permanent tundra (94, 95). There are no population outbreaks in *E. autumnata* further south in Fennoscandia, most likely due to high abundance of generalist parasitoids that keep the moth populations below outbreak levels (96). However, the border between outbreaking and non-outbreaking populations of geometrid moths is likely to move northwards if climate changes.

Enhanced UV-B radiation applied to birch leaves alters the chemistry or structure of the leaves such that caterpillars eat three times as much leaf biomass to maintain body development (97–99). There is also a trend that enhanced UV-B radiation could increase the immunocompetence of the caterpillars, which would make them more tolerant to the wasp parasitoid (100). Although the effect of winter warming on eggs, UV-B on leaves, and immunocompetence on caterpillars may point to future increased damage to sub-Arctic birch forests, it is not known to what extent other processes susceptible to spring and summer climate variability may alleviate these effects.

Vertebrates. The herbivore-based trophic system in most tundra habitats is dominated by one or two lemming species (71–73). Lemming abundance is the highest in coastal tundra, especially in moist sedge meadows which are the optimum habitat for *Lemmus. Dicrostonyx* (collared lemming) usually does not reach as high densities in their preferred habitats on drier ridges

where herbs and dwarf shrubs dominate. Voles (*Microtus* and *Clethrionomys* spp.) may become more abundant than lemmings in some low Arctic tundra habitats and forest tundra (8). At the landscape scale, lemmings and voles are very patchily distributed according to the abundance of their preferred food plants, as well as the distribution of snow (1, 75). Lemming peak densities exceed 200 individuals per ha in the most productive *Lemmus* habitats both in Siberia and North America (101) and the standing crop of lemmings may approach 2.6 kg d.w. ha⁻¹. The population builds up during the winter (due to winter breeding) and peak densities may be reached in late winter/early spring when the standing crop of food plants is minimal. The diet of *Lemmus* consists mainly of mosses and graminoids, while *Dicrostonyx* prefers herbs and dwarf shrubs (102). Lemmings have a high metabolic rate and *Lemmus* in particular has low digestive efficiency (about 30%, compared to 50% in other small rodents). Consequently, their consumption rate and impact on the vegetation exceeds that of all other herbivores combined (with the exception of local effects of geese near breeding colonies). Moreover, lemmings destroy much more vegetation than they ingest and after population peaks typically 50% of the aboveground biomass has been removed at snow melt (103). In unproductive snow beds, which are favored winter habitats of *Lemmus lemmus* (104), up to 90–100% of the moss and graminoid present during the winter may be removed (105). If winters become so unfavorable for lemmings so they are not able to build up cyclic peak densities, the species rich predator community relying on lemmings is likely to collapse (see below). Moreover, their important, pulsed impact on vegetation by grazing and nutrient recycling will probably cease. Changes in snow conditions, relative abundances of preferred food plants and climate impacts on primary production will all affect lemming populations, and might result in a northwards displacement of the climatically determined geographic borders between cyclic and noncyclic populations of small herbivores (small rodents and moths), as well as the species distributions *per se*.

Wild populations of other herbivorous mammal species on the tundra, such as hares, squirrels, musk ox and reindeers/caribou never reach population densities or biomass that can compare with peak lemming populations (8). Moving herds of caribou/reindeers represent only patchy and temporary excursions in numbers, biomass and impacts on the vegetation, but averaged over space and time some of the largest herds only approach 0.01 individuals and 0.5 kg d.w. ha⁻¹ (101) on their summer pastures and usually < 10% of the vegetation is taken (77). The only cases where reindeers have been shown to have large impacts on the vegetation seem to be in unusual circumstances (stranding on islands; 106) or under human intervention (e.g. removing top predators or introductions to islands) where overshooting reindeer populations have led to destruction of the vegetation, degradation of habitats and subsequent population crashes.

Although the cooling since the mid-1970s in the Hudson Bay region has affected the reproduction of snow geese, the mid-continental population is currently growing at 5% per year (107). This, in combination with the staging of snow geese in La Pérouse Bay, Manitoba, because of bad weather further north, leads to increasing foraging for roots and rhizomes of the graminoids *Puccinellia phryganoides* and *Carex subspathacea* (108). The rate of removal of below-ground organs on the salt marshes combined with intense grazing of swards during summer time exceeds the rate of recovery of the vegetation. It is estimated that geese have destroyed 50% of the salt marsh graminoid swards of La Pérouse Bay since 1985. This loss of the vegetation cover exposes the sediments of the salt marshes, which have become hypersaline (salinities exceeding 3.2‰) as a result of increased

evapotranspiration. This further reduces plant growth and forage availability to the geese. In turn, this is reducing goose size, survivorship and fecundity. Other factors that are affected by the trophic cascades initiated by the geese include reduced nitrogen mineralization rates, and declines in the populations of soil invertebrates, waders and some species of duck such as widgeon (*Anas americana*).

Cyclical populations and climate change: Herbivore-plant interactions have been proposed to produce population cycles in Arctic herbivores by several mechanisms such as nutrient recycling (109), production cycles inherent in food plants (110), induced chemical defense in plants (111) and recurrent overgrazing (112). The empirical evidence is mixed. There is at least partly supporting evidence for induced chemical defense in the *Epirrita*-birch system (113) and for overgrazing in the *Lemmus*-plant system in unproductive tundra habitats (114). There is little evidence, however, for mechanisms involving nutrient cycling and chemical defense in the case of lemmings and voles (115, 80). Climate is somehow involved in all the hypotheses of population cycles related to plant-herbivore interactions. For example allocation strategies in plants and the amount of secondary compounds (induced chemical defense hypothesis) depend on temperature and growing season length (see above). Of course, plant production and biomass are also controlled by temperature (overgrazing hypothesis). Climate change may thus modify the population dynamics patterns and roles of key herbivores such as lemming and moths because the dynamics of herbivore-plant interactions will change. As early as 1924, Elton (116) pointed out the potentially decisive role of climate in determining the generation of cycles in northern animal populations.

Mathematical modeling shows that specialist resident predators such as small mustelids and the Arctic fox can also impose prey population cycles due to sufficiently strong numerical and adequate functional responses (117, 118). Moreover, nomadic specialists such as birds of prey can dampen lemming cycles and decrease the degree of regional asynchrony given their predation rates are sufficiently high (119, 120). The impacts of bird predators have a strong seasonal component since most migrate south for the winter (119). Reliable estimates of predation rates on cyclic lemming populations are rare. Indirect estimates based on the energy requirements of predators at Point Barrow in Alaska indicated that avian predators could account for 88% of the early summer mortality, but it was concluded that neither this nor winter predation by weasels could stop lemming population growth under otherwise favorable winter conditions (101). In the Karup Valley in Greenland, the combined impact of different predators both limited population growth and caused population crashes in collared lemmings (118). In a declining lemming population in an alpine area in Norway, almost 50% predation could be demonstrated by following the fates of radio-tagged individuals (121). Using the same methodology, Reid et al. (122), Wilson et al. (123) and Gilg (124) showed that predation was the predominant mortality factor in populations of collared lemmings at various localities in northern Canada and eastern Greenland.

Predator-Prey Interactions

The dynamics and assemblages of vertebrate predators in Arctic tundra are almost entirely based on lemmings and other small rodent species (*Microtus* spp. and *Clethrionomys* spp.) (73, 75). Birds of prey such as snowy owls, short-eared owls, jaegers (skuas) and roughlegged buzzards are lemming and vole specialists that are only able to breed at peak lemming densities and they aggregate in areas with high lemming densities. Since lemming cycles are not synchronized over large distances (125, 126), the highly mobile avian predators can track lemming population peaks in space. Mammal lemming and vole special-

ists in the Arctic, such as the weasel and the ermine, are less mobile than birds but both have high pregnancy rates and produce large litters in lemming peak years (127). In lemming low years weasel and ermine reproduction frequently fails and mortality rate increases (128, 118). On coastal and inland tundra habitats where bird colonies are lacking, the Arctic fox also exhibits the population dynamics typical of a lemming specialist (129). The lemming cycles also impose cyclic dynamics in other animals such as geese and waders because they serve as alternative prey for predators in lemming crash years (130, 131). Recently observed increased predation pressure on waterbirds in various Arctic regions might reflect a change of the lemming cycle in response to climate change with secondary effects on predators and waterbirds as an alternative prey (132, 133). Thus, a large part of the tundra vertebrate community cycle is in a rhythm dictated by the lemming populations (134).

This rhythm is likely to be disrupted by future variation in snow properties (e.g. snow season length, snow density and snow cover thickness) (135). For small mammals living in the subnivean space, snow represents insulation from low temperatures as well as protection from most predators such as foxes and raptors (136). The effect on large mammal prey species (ungulates) will be the opposite as deeper snow makes caribou and moose more vulnerable to predators such as wolves (137), but more extensive snow patches give relief from insect pests (2). If climate change results in more frequent freeze-thaw events leading to a more shallow and icy snow pack, this will probably act to expose small mammals to predators, disrupt population increases and thereby prevent cyclic peak abundances of lemmings and voles. For nomadic predators whose life history tactic is based on asynchronous lemming populations at a continental scale, an increased frequency of large-scale climatic anomalies that induces continental-wide synchrony (the "Moran effect"; 138), is very likely to have devastating effects.

Long-term monitoring (> 50 years) of small rodents near the treeline at Kilpisjärvi in sub-Arctic Finland has shown a pronounced shift in small rodent community structure and dynamics since the early-1990s (139) (see Fig. 5 in ref. 2). In particular, the previously numerically dominant and cyclically fluctuating grey-sided vole (*Clethrionomys rufocanus*) has become both less abundant and variable in abundance. Also the Norwegian lemming (*Lemmus lemmus*) and *Microtus* voles have lower peak abundances, and the small rodent community is currently dominated by the relatively more stable red-backed vole (*C. rutilus*). Similar changes took place earlier (in the mid-1980s) in the northern taiga (140–142), and still prevail. For predators that specialize in feeding on small rodents, the lack of cyclic peak abundance of small rodents, especially in the spring (72), is likely to have detrimental consequences as they need to breed successfully at least every 3–4 years to sustain viable populations. At Kilpisjärvi the least weasel (*Mustela nivalis*) has become rare. Moreover, the severe decline of the Arctic fox and the snowy owl in Fennoscandia, both of which prey on *Microtus* voles and lemmings in mountain and tundra habitats, may be due to lower peak abundances of small mammal prey species in their habitats (143). In Alaska a similar decrease in cyclicity of lemmings occurred in the 1970s (71).

Large predators such as wolves, wolverines and bears are less numerous in the tundra than in the boreal forest (8). Consequently, predation impacts on tundra ungulates are usually low. While 79% of the production in small herbivores (voles, lemming, ptarmigan and Arctic hares) was consumed by predators averaged across a number of sites in Arctic Canada, the corresponding number was only 9% for large herbivores (reindeer and musk ox) (144).

Insect Pests, Parasites and Pathogens

Plants: Disease in plants is likely to increase in those parts of species distribution ranges where a mismatch between the rate of relocation of the species and the northward/upward shift of climatic zones results in populations remaining in supra-optimal conditions. Here, species can experience thermal injury particularly plants of wet and shady habitats (145), drought and other stresses that make plants more susceptible to disease.

Very little is known about the incidence and impacts of plant diseases in Arctic ecosystems. However, recent work has shown that a fungal pathogen (*Exobasidium*) of *Cassiope tetragona* and *Andromeda polifolia* reduces host plant growth, reproductive investment and survival (146). As the incidence of disease increases with an increase in temperature downwards along an altitudinal gradient, climate warming is likely to increase the incidence of at least this naturally occurring disease in the Arctic. The incidence of new diseases from increasing mobility of pathogens with a southern distribution is a possibility.

Animals: UV-B can reduce the impact of viral and fungal pathogens on insects. The nuclear polyhydrosis virus (NPV) is a major cause of death of the defoliating insect pest *Epirrita autumnata*. However, this virus is killed by UV-B (147). Species and strains of the fungus *Metarhizium* are important agents of insect disease but some, particularly high latitude strains, are sensitive to UV-B (148, 149).

Parasitism is perhaps the most successful form of life, but until recently certainly underestimated, especially in the Arctic regions (150, 151). Parasitism in Arctic areas has been poorly studied both in respect of taxonomy and biodiversity as well as the ecological impact parasites may have on the animal species and communities.

Recent research on the evolution and phylogeography of typical Arctic animals like lemmings has revealed how greatly the alternating glacial and interglacial periods have influenced their distribution and genetic diversity (151, 152). The impact seems to be at least as profound on the helminth parasites of Arctic rodents (153, 154). Such impacts of past climatic fluctuations can be used to predict some possible consequences of the present warming. If the Arctic host populations become fragmented due to the northward expansion of southern biogeographic elements, extinction of parasites in small host populations can follow and/or cryptic speciation in refugia. Phylogeographic structure (often cryptic speciation) can be seen in rodent cestodes in the Arctic even if there is no such structure in the host. This is true also for ruminant parasites.

Phylogenetic studies have shown that host switches have occurred in many clades of rodent cestodes. It is tempting to speculate on the factors promoting host switches of parasites, i.e. does reduced parasite population size in fragmented host populations, due to climatic fluctuations, promote host switching.

Macroparasites, such as intestinal worms, often have complicated life cycles. In the main host, in which the parasite reproduces, parasites are controlled by the host immunity. On the other hand, the free-living intermediate stages, eggs and larvae, and those in intermediate hosts, are subject to extrinsic environmental conditions like temperature and humidity. Temperature strongly affects the development speed of parasite larvae. For example, a small increase in temperature has a clear effect on the development of the musk ox lungworm *Umingmakstrongylus pallikuukensis* in their gastropod intermediate hosts (155). Therefore, a slight increase in temperature and in the length of growing season is very likely to profoundly affect the abundance and geographic distribution of potentially harmful parasites such as lungworms. Lungworm infections have become conspicuous in recent years when summer temperatures in the Arctic have

been increasing.

The free-living stages of parasites are prone to desiccation. In addition to temperature effects on their development, the survival and abundance of free-living intermediate stages depend greatly on humidity. In addition, the same factors affect drastically the abundance, survival and distribution of the intermediate hosts of parasites, like insects, gastropods and soil mites. Haukisalmi and Henttonen (156) found that the precipitation in early summer was the most important factor affecting the prevalence of common nematodes and cestodes in *Clethrionomys voles* in Finnish Lapland. Temperature and humidity also affect the primary production and development of the free-living stages of abomasal nematodes of reindeers (157). Recently Albon et al. (158) have shown that abomasal nematodes affect the dynamics of Svalbard reindeer through fecundity. Consequently, even slight climatic changes are likely to have surprising effects on the large ungulates, and possibly on humans exploiting them, through enhanced parasite development (6).

The complicated life cycles of parasites cause intrinsic lags in their capacity to track the changes in the population density of their hosts, and these lags are further retarded by unfavorable Arctic conditions. Any climatic factor promoting the development of a parasite, so that it can respond in a density-dependent way to host dynamics, is likely to alter the interaction between parasite and host, and their dynamics.

There is considerable uncertainty about the possibilities for invasion of pathogens and parasites in to the Arctic during climate warming. However, increased tourism combined with warmer climate may increase the risk of such invasions.

Climate change is likely to affect the important interaction between parasitic insects and reindeer/caribou. Insect harassment is already a significant factor affecting the condition of reindeer in the summer (2). These insects are likely to become more widespread, abundant and active during warmer summers while refuges for reindeer/caribou on glaciers and late snow patches will probably disappear.

Microbe-Plant and Microbe-Microbivore Interactions

Although data on the dynamics and processes in Arctic microbial communities and on processes in the soil-microbial-plant interface are accumulating rapidly, it is yet not possible to reach firm conclusions on how the dynamics and processes will change in a changing climate. However, the following can be stated. First, short-term (seasonal) changes in microbial processes may not have major influences on longer term (annual to multi-annual) processes. Second, microbes and plants share common nutrient resources, although they do not need to be limited by the same resource. For instance, while nutrient supply rates generally control plant productivity, microbial productivity may be constantly or periodically controlled by the abundance of labile C. Third, the nutrient supply rate to the plant available pool may not be controlled principally by continuous nutrient mineralization, but rather by pulses of supply and sequestration of nutrients linked to microbial population dynamics and abiotic change, such as freeze-thaw cycles.

Jonasson et al. (34) showed that despite no appreciable effect on the microbial bio- and nutrient mass, warming increased plant productivity. Because plant productivity was limited principally by low supply rate of N, it appears that the mineralization of litter or SOM, or microbial solubilization of organic N increased, and that the plants rather than the microbes sequestered the "extra" N in inorganic or organic form. However, microbes increased the nutrient content in cases when the sink strength for nutrients in the plants decreased, e.g. after shading, at the same time as soil inorganic N also increased. This suggests either that

plants compete successfully with microbes for nutrients, or that the microbial requirement for nutrients was satisfied, and they absorbed a "surplus" of nutrients, which is likely if they were C rather than nutrient limited. This does not fully preclude nutrient competition, however, because it is possible that the plants accessed the nutrients from pulse-releases from microbes during periods of population dieback. If so, seasonal changes in the frequency of such pulses, indeed, are of importance for predicting changes in ecosystem function and need further investigations. This is particularly obvious, considering that the microbial N and P content typically exceeds the annually sequestered amounts by plants severalfold and should constitute an important plant nutrient source (28, 159).

The plant-microbe interaction may also be mutualistic through the mycorrhiza by which the fungal partner supplies nutrients to the plant in exchange for carbon supplied by the plant. A large part of the plant species in shrubby vegetation, common in the Arctic, associate with ecto- or ericaceous mycorrhizal fungi. These mycorrhiza types have enzyme systems able to break down complex nitrogen-holding organic molecules and thereby supply the plant partner with nitrogen (160), the most common production-limiting element for plant production. Changes in plant species composition as a consequence of climatic changes are very likely to strongly affect the microbial community composition, including that of mycorrhizal fungi. Unfortunately, studies on effects of expected climate change on mycorrhizal associations in the Arctic are virtually nonexistent. However, unpublished data by Clemmensen and Michelsen from a decade of warming of a fellfield led to a strong increase in willow biomass, but few changes in the community of the associated ecto-mycorrhizal fungi.

The effects of microbivores on the microbial community are yet poorly explored and can only be listed as potentially important for predicting effects of global change. It appears, however, that the populations of nematodes increase strongly with warming. Because nematodes are main predators on fungi and bacteria, it may be that increased biomass production of microbes is masked in a warmer environment because of predation by strongly responding microbivores (45, 46). If so, the release rate of plant available nutrients is likely to increase (e.g. 161), which may explain the enhanced nutrient sequestration by plants in warmer soils rather than pulse sequestration after microbial dieback.

CONCLUSIONS

The impacts of changes in climate and UV-B radiation on species (1, 2) will be modified by numerous and complex interactions among species. The spatial structure of vegetation, such as height of the canopy, trophic interactions and community composition in terms of biodiversity will all be affected. Some groups of species, such as mosses, lichens, some herbivores and their predators are at risk in some areas and some changes are already evident. Rapid climate change that exceeds the ability of species to relocate together with a likely influx of pests and pathogens will very probably lead to increased incidence of disease and pest outbreaks. In some cases, the reduction in the abundance of a keystone species such as lemmings, can result in reduction or even loss of many species that depend on it, for example arctic foxes, skuas and snowy owls. In other cases, such as the snow goose in Manitoba, climate impacts can result in denudation of vegetation and habitat.

Such impacts of changes in climate and UV-B radiation on the structure of Arctic ecosystems will also have consequences for the functioning of Arctic ecosystems in terms of flows of nutrients and carbon (3) and exchanges of water, energy and carbon

between biosphere and atmosphere (3, 4). The changes in ecosystem function, initiated by impacts at the species level, have the potential to affect regional and global atmospheric chemistry and circulation (4, 5). Consequently, it is important to relate the changes in ecosystem structure discussed above to changes in ecosystem function (3).

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