Chapter 6

Arctic Tundra and Polar Desert Ecosystems

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Summary

- The dominant response of current Arctic species to climate change, as in the past, is very likely to be relocation rather than adaptation. Relocation possibilities vary according to region and geographical barriers. Some changes are occurring now.
- Some groups such as mosses, lichens, some herbivores and their predators are at risk in some areas, but productivity and number of species is very likely to increase. Biodiversity is more at risk in some subregions than in others: Beringia has a higher number of threatened plant and animal species than any other ACIA sub region.
- Changes in populations are triggered by trends and extreme events, particularly winter processes.
- Forest is very likely to replace a significant proportion of the tundra and this will have a great effect on the composition of species. However, there are environmental and sociological processes that will probably prevent forest from advancing in some locations.
- Displacement of tundra by forest will lead to a decrease in albedo which increases the positive feedback to the climate system. This positive feedback will generally dominate over the negative feedback of increased carbon sequestration. Forest development will also ameliorate local climate.
- Warming and drying of tundra soils in parts of Alaska have already changed the carbon status of this area from sink to source. Although other areas still maintain their sink status, the number of source areas currently exceeds the sink areas. However, geographical representation of research sites is currently small. Future warming of tundra soils would probably lead to a pulse of trace gases into the atmosphere, particularly in disturbed areas and areas that are drying. It is not known if the circum-Arctic tundra will be a carbon source or sink in the long term, but current models suggest that the tundra will become a weak sink for carbon because of the northward movement of vegetation zones that are more productive than those they displace. Uncertainties are high.
- Rapid climate change that exceeds the ability of species to relocate will very probably lead to increased incidence of fires, disease and pest outbreaks.
- Enhanced CO\textsubscript{2} and UV-B affect plant tissue chemistry and thereby have subtle but long-term impacts on ecosystem processes that reduce nutrient cycling with the potential to decrease productivity and increase or decrease herbivory.

1. Introduction

The Arctic is generally recognized as a treeless wilderness with cold winters and cool summers. However, definitions of the southern boundary vary according to environmental, geographical or political biases. This chapter focuses on biota (plants, animals and microorganisms) and processes in the region beyond the northern limit of the closed forest (the taiga), but we also include processes South of this boundary that affect ecosystems in the Arctic. Examples are over-wintering periods of migratory animals spent in the South and the regulation of the latitudinal treeline. The geographical area we have defined as the current Arctic is the area we use for developing scenarios of future impacts: our geographical area of interest will not decrease under a scenario of replacement of current Arctic tundra by boreal forests.
1.1 Characteristics of Arctic tundra and polar desert ecosystems

The southern boundary of the circumpolar Arctic is the northern extent of the closed boreal forests (Chapter 11). There is not a clear boundary but a transition from South to North consisting of the sequence: closed forest _ forest with patches of tundra _ tundra with patches of forest _ tundra. The transition zone is relatively narrow (30-150 km) when compared with the forest and tundra zones in many, but not all areas. Super-imposed on the latitudinal zonation is an altitudinal zonation from forest to treeless areas to barren ground in some mountainous regions of the northern taiga. The transition zone from taiga to tundra stretches for more than 13,400 km around the lands of the northern Hemisphere and is one of the most important environmental transition zones on Earth (Callaghan et al., 2002a;b) as it represents a strong temperature threshold close to an area of low temperatures. The zone has been called forest tundra, sub-Arctic and the tundra-taiga boundary or ecotone. Vegetationally, it is characterized as an open landscape with patches of trees that have a low stature and dense thickets of shrubs that, together with the trees, totally cover the ground surface.

The environmental definition of the Arctic does not correspond with the geographical zone delimited by the Arctic Circle at 66.5 °N latitude, nor political definitions. Cold waters in ocean currents flowing southwards from the Arctic depress the temperatures in Greenland and the eastern Canadian Arctic whereas the northwards flowing Gulf Stream warms the northern landmasses of Europe (Chapter 2). Thus, at the extremes, polar bears and tundra are found at 51 °N in eastern Canada whereas agriculture is practiced beyond 69 °N in Norway. Arctic lands span some 20 ° of latitude reaching 84 °N in Greenland and locally, in eastern Canada, an extreme southern limit of 51 °N.

The climate of the Arctic is largely determined by the relatively low angles of the sun to the Earth. Differences in photoperiod between summer and winter become more extreme towards the North. Beyond the Arctic Circle (66.5 °N), the sun remains above the horizon at midnight on mid-summer’s day and remains below the horizon at midday on midwinter’s day.

Climatically (see Chapter 2), the Arctic is often defined as the area where the average temperature for the warmest month is lower than 10 °C (Köppen, 1931) but mean annual air temperatures vary greatly according to location, even at the same latitude. They vary from –12.2 °C at Point Barrow, Alaska (71.3 °N) to –28.1 °C at the summit of the Greenland ice sheet (about 71 °N) (Weller, 2000) and from 1.5°C at 52°N in sub-Arctic Canada to 8.9°C at 52°N in temperate Europe. The summer period progressively decreases from about 3.5 to 1.5 months from the southern boundary of the Arctic to the North, and mean July temperature decreases from 10-12 °C to 1.5 °C. In general, precipitation in the Arctic is low, decreasing from about 250 mm in the South to as low as 45 mm per year in the polar deserts of the North (Jonasson et al., 2000), with extreme precipitation amounts in maritime areas of the sub-Arctic, for example 1100 mm at 68°N in Norway. However, the Arctic cannot be considered to be arid because of low rates of evaporation: even in the polar deserts, air humidity is high and the soils are moist during the short growth period (Bovis and Barry, 1973). The word “desert” refers to extreme poverty of life.
The Arctic is characterized by the presence of continuous permafrost (Chapter 5), although there are exceptions such as the Kola Peninsula. Continuous, and deep (more than 200m) permafrost is also characteristic South of the treeline in large areas of Siberia that reach to Mongolia. The depth of the soil’s active layer during the growing season depends on summer temperatures and varies from about 80 cm close to the treeline to about 40 cm in polar deserts. However, active layer depth varies according to local conditions within landscapes according to topography: it can reach 120 cm on south-facing slopes and be as little as 30 cm in bogs even in the South of the tundra zone. In many areas of the Arctic, continuous permafrost becomes deeper and degrades into discontinuous permafrost in the South of the zone. Active layer depth, decreases in the extent of discontinuous permafrost and coastal permafrost will be particularly sensitive to climatic warming (Chapter 5). Permafrost and active layer dynamics lead to patterning such as polygons in the landscape. Topography plays an important role in defining habitats in terms of moisture and temperature as well as active layer dynamics (Brown et al., 1980; Webber et al., 1980) so that Arctic landscapes are a mosaic of microenvironments. Topographic differences of even a few tens of cm are important for determining habitats, for example poigron rims and centers, whereas greater topographical differences of metres to 10s of metres determines wind exposure and snow accumulation which in turn affect plant communities and animal distribution. Topographical differences become more important as latitude increases.

Disturbances of ecosystems are characteristic of the Arctic. Mechanical disturbances include thermokarst through permafrost thaw, freeze-thaw processes, wind, sand and ice-blasts, seasonal ice oscillations, slope processes, snow load, flooding during thaw, changes in river volume and coastal erosion and flooding. Biological disturbances include insect pest outbreaks, peaks of grazing animals that have cyclic populations, and fire. These disturbances operate at various geographical and time scales (Figure 6.1) and affect the colonization and survival of organisms and thus ecosystem development.

Figure 6.1 Schematic timescale of ecological processes in relation to disturbances in the Arctic. The schematic does not show responses expected due to anthropogenic climate change (based on Oechel and Billings, 1992; Shaver et al., 2000; Walker and Walker, 1991)

Arctic lands are extensive beyond the northern limit of the tundra taiga ecotone where, according to the classification of Bliss and Matveyeva (1992) they amount to about 7,567,000 km². They cover about 2,560,000 km² of the former Soviet Union and Scandinavia, 2,480,000 km² in Canada, 2,167,000 km² in Greenland and Iceland, and 360,000 km² in Alaska (Bliss and Matveyeva, 1992). Figure 6.2 based on a classification of Walker (2000) and mapped by Kaplan et al (2003) shows the distribution of Arctic and other vegetation types (this can be compared with a recent vegetation map; Circumpolar Arctic Vegetation Map Team, 2001; Chapter 1). The distribution of Arctic landmasses is often fragmented: seas separate large Arctic Islands (Svalbard, Novaya Zemlya, Severnaya Zemlya, New Siberian Islands, Wrangel Island) and the landmasses of the Canadian Archipelago and Greenland. Similarly, the Bering Strait separates the Arctic lands of the Old and New Worlds. Large mountains such as the East-West running Brooks Range in Alaska and the Putorana Plateau in Siberia separate tundra and taiga. Such areas of relief contain outposts of boreal species on their southern major slopes that could potentially expand northwards and areas that could act as refuges to arctic-alpine species at higher elevations. The Taymyr Peninsula is the only continuous landmass that stretches for 900 km from the northern tundra limit to taiga without
geographical barriers to the dispersal of animals and plants (Matveyeva and Chernov, 2000). The width of the tundra zone varies greatly in different parts of its circumpolar stretches. On average, it does not exceed 300 km, but in some regions (e.g. the lower reaches of the Kolyma River) the tundra zone extends only 60 km from treeline to coast. In such areas, the tundra zone is potentially highly vulnerable to climate warming.

Figure 6.2 Present day natural vegetation of the Arctic and neighboring regions from floristic surveys. Vegetation types 1-5 are classified as Arctic, whereas types 6-8 are classified as boreal forest (Kaplan et al., 2003).

The vegetation of the Arctic varies from forest tundra in the South where plant communities have all the plant life forms known for the Arctic, and have continuous canopies in several layers extending to more than 3 m high, to polar deserts in the North where vegetation colonizes 5% or less of the ground surface, is less than 10 cm high, and is dominated by herbs, mosses and lichens (Figure 6.3). Species richness in the Arctic is low and decreases towards the North: there are about 1800 species of vascular plants, 4000 species of cryptogams, 75 species of terrestrial mammals, 240 species of terrestrial birds, 3000 species of fungi, 3300 species of insects (Matveyeva and Chernov, 2000; Chernov, 2002) and thousands of prokaryotic species (bacteria and archaea) whose diversity in the tundra has only recently started to be estimated. However, the Arctic is an important global pool of some groups such as mosses, lichens and springtails (and insect parasitoids; H. Roininen, unpublished) because their abundance here is higher than in other biomes. Net primary production, net ecosystem production and decomposition rates are low. Food chains are often short and typically there are few representatives at each level of the chain. Arctic soils are generally shallow and underdeveloped with low productivity and immature humus of the moor-type (Brown et al., 1980). Substantial heterogeneity of the soil cover due to numerous spatial gradients has an important influence on the microtopographical distribution of the soil biota (invertebrates, fungi, bacteria) which can potentially amplify (exacerbate) any negative effects of climatic changes.

Figure 6.3 Growth forms of Arctic plants (modified from Webber et al., 1980).

The Arctic has a long history of human settlement and exploitation based initially on its rich aquatic biological resources and more recently on its minerals and fossil hydrocarbons. At the end of the last glacial stage, people migrated from the Old World to the New across the ice-free Bering land bridge and along its southern coast (ca. 14,000 – 13,500 years BP; Dixon, 2001). As early as ca. 12,200 years BP, areas North of the Fennoscandian ice sheet in northernmost Finnmark (Norway) had been settled (Thommessen, 1996). Even earlier palaeolithic settlements (ca. 40,000 years BP) have been recorded from the eastern European Arctic (Pavlov et al., 2001). The impacts these peoples had on terrestrial ecosystems are difficult to assess but were likely to be small given their ‘hunter–gatherer’ way of life and small populations. The prey species hunted by these peoples included the megafauna, such as the woolly mammoth, which became extinct. The extent to which hunting may have been principally responsible for these extinctions is a matter of continuing debate (Stuart et al., 2002) but this possibility cannot be excluded (Alroy, 2001). It is also uncertain to what extent the extinction of the megafauna may have contributed to, or been at least in part a result of, the accelerated northward movement of trees and shrubs, and consequent changes in vegetation structure (see section 2 and references therein). Although estimates of the
population density of megafaunal species have large uncertainties, it seems unlikely that they were sufficient to constrain the spread of woody taxa in response to favorable environmental change.

During the last 1,000 years, resources from terrestrial ecosystems have been central to the mixed economies of Arctic regions: many inland Indigenous communities still derive most of their protein from subsistence activities such as caribou hunting (Berkes and Fast, 1996). During this period, increasing trade between peoples of temperate latitudes and Arctic indigenous peoples is likely to have affected a few target animal species such as the reindeer that was domesticated in Fennoscandia and Russia, ermine hunted for fur, and birds of prey used for hunting as far away as the eastern Mediterranean lands. However, the most dramatic impacts occurred after World War II through exploitation of minerals and oil and fragmentation of the Arctic landscape by infrastructure (Nellemann et al., 2001). Vlassova (2002) suggests that industrial activities and forestry have displaced the Russian forest tundra southwards by deforesting 470,000 to 500,000 km² of lands that now superficially resemble the tundra. Although this estimate has been challenged as greatly exaggerated (because northern taiga areas have been included in forest tundra), such effects occur locally in the Yamal Peninsula and a need for a re-appraisal has been highlighted. We therefore have only a limited knowledge of possible past interactions between people and their environment that could have shaped the ecosystems we see today. This knowledge shows, however, that any future increases in population density and human activity could modify expected future responses of Arctic ecosystems to changes in climate and UV radiation.

1.2 Raison d’être for the chapter

The Arctic is experiencing dramatic environmental changes which are likely to have profound impacts on Arctic ecosystems for many reasons. The Arctic is outstanding amongst the biomes of the World in the dominance of climate change amongst the major factors affecting biodiversity (Sala and Chapin, 2000). Also, the Arctic biota of the present day are relatively restricted in range and population size compared with their Quaternary history. When the treeline advanced northwards during the warming of the early Holocene, a lowered sea level allowed a belt of tundra to persist around the Arctic basin whereas any future northwards migration of the treeline will further restrict the area of tundra because sea level is expected to rise. Arctic ecosystems are known to be vulnerable to current disturbances Crawford, 1997b; Walker and Walker, 1991; Forbes et al., 2001) and to have long recovery times: sub-Arctic birch forest defoliated by insects can take 70 years to recover (Tenow and Bylund, 2000). Current and predicted environmental changes are likely to add additional stresses and decrease the potential for ecosystem recovery from natural disturbances while providing thresholds for shifts to new states, for example when disturbance opens gaps for invasion of species new to the Arctic.

Changes in Arctic ecosystems and their biota are important to the peoples of the Arctic in terms of food, fuel and culture (Chapter 11) and potentially could have global impacts because of the many linkages between the Arctic region and those regions further South. Several hundreds of millions of birds migrate to the Arctic each year and their success in the Arctic determines their roles at lower latitudes (section 3.2.2.1). Physical and biogeochemical processes in the Arctic affect atmospheric circulation and the climate of regions beyond the Arctic (section 5). We know that ecosystems have responded to past environmental changes in the Arctic (section 2); we know that current environmental changes are occurring (Chapman and Walsh quoted in Weller, 2000; Dye,
2002; Fioletov et al., 1997; Chapters 2, 3,5). This understanding indicates that there will be future responses of Arctic ecosystems to expected future and ongoing changes in climate. We also know that current levels of UV-B radiation, as well as higher levels, can affect sub-Arctic plants (Phoenix et al., 2000; Johanson et al., 1995; Gwynn-Jones et al., 1997). Arctic plants may be particularly sensitive to increases in UV-B radiation because UV-B damage is not dependent on temperature whereas enzyme-mediated repair of DNA damage could be constrained by low temperatures (Li et al., 2002a;b; Björn, 2002; Paulsson et al., submitted).

For all these reasons, we need to understand the relationships between ecosystems and the Arctic environment. Although many aspects of the Arctic environment are changing concurrently, for example climate, pollution, atmospheric nitrogen deposition, atmospheric concentrations of carbon dioxide, UV-B radiation and land use, the specific mission of this chapter is to focus on impacts of changes in climate and UV-B radiation on Arctic terrestrial ecosystems and their species and processes.

1.3 Rationale for the structure of the chapter

The effects of climate are specific to species, age/developmental stages of individuals and processes from metabolism to evolution (Figure 6.1). Although there are many ways in which to organize an assessment of climate and UV-B impacts, we follow a logical hierarchy of increasing organizational biological complexity to assess impacts on species, the structure of ecosystems, the function of ecosystems, and landscape and regional processes. A basic understanding of biological processes related to climate and UV-B radiation is required before we can assess impacts of changes in climate and UV-B on terrestrial ecosystems (Smaglik, 2002). Consequently, our chapter structure progresses from a review of climate and UV controls on biological processes to an assessment of potential impacts of changes in climate and UV-B on processes at the species and regional levels. Some effects of climate change on ecosystems may be beneficial to people, while others maybe harmful.

The changes in climate and UV-B that we use to assess biological impacts are of two types: those already documented (Chapter 2) and those established from scenarios of UV-B (Chapter 3) and climate derived from GCMs (Global Climate Models) (Chapter 4). We know that mean annual and seasonal temperatures have varied considerably in the Arctic since 1965 (Chapman and Walsh quoted in Weller, 2000; Chapter 2). Western parts of North America and central Siberia have warmed by about 1.25 °C (mean annual temperature and up to 2 °C in winter) per decade while West Greenland and the eastern Canadian Arctic have cooled by the same extent.

Fennoscandia has seen little warming (about 1°C in the West to almost 0°C in the East (Lee et al., 2000)) over the past century. Precipitation has also changed. The duration of the snow-free period at high northern latitudes has increased by 5-6 days per decade and the week of the last observed snow cover in spring has become earlier by 3-5 days per decade over the period 1972-2000 (Dye, 2002). Stratospheric ozone has been depleted over recent decades, for example by a maximum of 45% below normal in the high Arctic in spring (Fioletov et al., 1997). This has probably led to an increase in UV-B radiation reaching the Arctic’s surface, although the measurement period is short (O. Engelsen and G. Hansen, unpublished). Scenarios of future changes suggest that mean annual temperatures could continue to increase in the Arctic by 2 to 5 °C (Källen et al., 2001) and that
UV-B radiation in spring could increase by 20-90% in April in much of the Arctic by 2010-2020 (Taalas et al., 2000). Our assessment of impacts on terrestrial ecosystems has been based on existing literature rather than new research or modeling activities within the ACIA assessment. Consequently, the scenarios of climate/UV-B changes that existing long term experimental manipulations of temperature and/or UV-B radiation were based on at their outset relied on earlier scenarios of change (IPCC I; Houghton et al., 1990). However, we use the most recent scenarios (Chapters 3, 4 and 5) to provide a context for our assessment, and to modify our predictions of ecosystem responses to earlier scenarios where appropriate. We also use the ACIA climate scenarios directly to illustrate the responses of some species to projected climate changes.

1.4 Approaches used for the assessment: strengths, limitations and uncertainties

We assess information on interactions between climate/UV-B radiation and ecosystems based on a wide range of sources derived experimental manipulations of ecosystems and environments in the field; laboratory experiments; monitoring and observation of biological processes in the field; conceptual modeling using past relationships between climate and biota (paleo analogs), and current relationships between climate and biota in different geographical areas (geographical analogs) to infer future relationships; and process-based mathematical modeling. Where possible, we include indigenous knowledge (limited to published sources) as an additional source of observational evidence.

We recognize that each method has uncertainties and strengths and we discuss these in a later section. By considering and comparing different types of information we hope to have achieved a more robust assessment. However, the only certainties of our assessment are that there are various levels of uncertainty with our predictions and that even if we try to estimate the magnitude of these, surprise responses of ecosystems and their species to changes in climate and UV-B radiation are certain to occur.
2. Past changes in Arctic terrestrial ecosystems, climate and UV radiation

2.1 Introduction

In order to understand the present biota and ecosystems of the Arctic, and to predict the likely nature of their responses to potential rapid future climate change, it is necessary to examine at least the last ca.121,000 yr of their history. This period, the late-Quaternary, extends from the present back to the last glacial maximum, encompassing the Holocene, or post-glacial, period that spans the last ca.11,400 yr. A review of this period of the history of the biota and ecosystems found in the Arctic today also must examine a spatial domain that is not restricted to the present Arctic regions. At the last glacial maximum many of these regions were submerged beneath vast ice sheets, whereas many of the biota comprising present Arctic ecosystems were found at lower latitudes.

2.2 Late-Quaternary environmental history in the Arctic

At the last glacial maximum vast ice sheets accumulated not only on many high latitude continental areas but also across some relatively shallower marine basins. The beds of relatively shallow seas such as the North Sea and Bering Sea were exposed as a result of the global fall of ca.120 m in sea level, the latter resulting in a broad land connection between eastern Siberia and Alaska and closure of the connection between the Pacific and Arctic Oceans. The reduction in sea level also exposed a broad strip of land extending northwards from the present coast of Siberia. Most, if not all, of the Arctic Ocean basin may have been covered by permanent sea ice.

Although details of the extent of some of the ice sheets continue to be a matter for controversy (see e.g. Astakhov, 1998; Grosswald, 1988; 1998; Lambeck, 1995; Siegert et al., 1999), it is certain that the majority of land areas North of 60°N were ice-covered. The principal exceptions were in eastern Siberia, Beringia and Alaska, although there is some geological evidence to suggest that smaller ice-free areas also persisted in the high Arctic, for example in the northernmost parts of the Canadian archipelago (Andrews, 1987) and perhaps even in northern and North-eastern Greenland (Funder et al., 1998). This evidence gains support from recent molecular genetic studies of Arctic species; for example, a study of the dwarf shrub Dryas integrifolia indicates glacial occurrences in the high Arctic (Tremblay and Schoen, 1999) as well as in Beringia, and a study of the collared lemming Dicrostonyx groenlandicus indicates separate glacial populations East and West of the Mackenzie River (Ehrich et al., 2000; Fedorov and Goropashnaya, 1999), the latter most probably in the Canadian archipelago. The latter conclusion is supported by the phylogeography (genetic and evolutionary relationships) of the Paranoplocephala arctica species complex, a cestode parasite of Dicrostonyx spp., indicating that two subclades probably survived the last glacial maximum with their host in the Canadian high Arctic (Wickström et al., 2003). More controversial are suggestions that elements of the Arctic flora and fauna may have survived the last glacial maximum on nunataks in glaciated areas of high relief such as parts of Greenland, Svalbard and Iceland (Rundgren and Ingolfsson, 1999). Although a recent molecular genetic study of the Alpine cushion plant Eriophorum vaginatum (Stehlik et al., 2001) provides strong evidence for survival of that species on nunataks within the
heart of the European Alps, similar studies of Arctic species have so far not supported the hypothesis of survival on nunataks in areas such as Svalbard (Abbott et al., 2000) which experienced extreme climatic severity as ice sheets extended to margins beyond the current coast in the last glacial maximum.

Direct evidence of the severity of the full glacial climate in the Arctic comes from studies of ice cores from the Greenland ice cap and other Arctic ice sheets (Chapter 2) which indicate full glacial conditions with mean annual temperatures 10–13°C colder than during the Holocene (Grootes et al., 1993). Palotemperature reconstructions based upon dinoflagellate cyst assemblages indicate strong seasonal temperature fluctuations, with markedly cold winter temperatures (de Vernal and Hillaire-Marcel, 2000; de Vernal et al., 2000).

The last glacial maximum was, however, relatively short-lived; within a few millennia of reaching their maximum extent many of the ice sheets were decaying rapidly and seasonal temperatures had increased in many parts of the Arctic. Deglaciation was not, however, a simple unidirectional change; instead a series of climatic fluctuations occurred during the period between about 18,000 and 11,400 years ago, these fluctuations varying in intensity, duration and perhaps also in geographical extent. The most marked and persistent of these fluctuations, the so-called Younger Dryas event (Peteet, 1993; 1995; Alley, 2000), was at least hemispheric in its extent, and is marked by the reglaciation of some regions and readvances of ice-sheet margins in others. Mean annual temperatures during this event fell substantially; although not as low as during the glacial maximum, they were nonetheless 4–6°C cooler than present over most of Europe (Walker, 1995a), and as much as 10–12°C colder than present in the northern North Atlantic and Norwegian Sea (Koç et al., 1996), as well as in much of northern Eurasia (Velichko, 1995). The end of the Younger Dryas was marked by a very rapid rise in temperatures. At some individual locations mean annual temperature rose by >5°C in less than 100 yr (Dansgaard et al., 1989). The most rapid changes most probably were spatially and temporally transgressive, with the global mean change thus occurring much less rapidly. Nonetheless; in many areas summer temperatures during the early Holocene rose to values higher than those of the present day. Winter conditions remained more severe than today in many higher latitude areas, however, because the influence of the decaying ice sheets persisted into the early millennia of the Holocene.

Despite higher summer temperatures in the early to mid-Holocene in most Arctic areas, Holocene climate has not differed qualitatively from that of the present. Following the general thermal maximum there has been a modest overall cooling trend throughout the second half of the Holocene. Superimposed upon these general longer-term patterns, however, have been a series of millennial and centennial fluctuations in climate (Huntley et al., 2001). The most marked of these, which occurred about 8200 years ago, appears to have been triggered by catastrophic discharge of freshwater into the northern North Atlantic from proglacial lakes in North America (Barber et al., 1999; Renssen et al., 2001). A reduction in strength, if not a partial shutdown, of the thermohaline circulation in the northern North Atlantic and Norwegian Sea was also associated with this event, as well as with the series of less severe climatic fluctuations that continued throughout the Holocene (Bianchi and McCave, 1999).
The most recent of these climatic fluctuations was that of the “Little Ice Age”, a generally cool interval spanning approximately the late 13th to early 19th centuries (Chapter 2). At its most extreme, mean annual temperatures in some Arctic areas fell by several degrees. Sea ice extended around Greenland and in some years filled the Denmark Strait between Greenland and Iceland (Lamb, 1982; Ogilvie, 1984; Ogilvie and Jonsdottir, 2000; Ogilvie and Jonsson, 2001); the Norse settlement of Greenland died out (Barlow et al., 1997; Buckland et al., 1996) and the population of Iceland was much reduced (Ogilvie, 1991; Sveinbjarnardóttir, 1992). Although there was great temporal variability of climate on decadal to centennial time scales within the overall period of the Little Ice Age, and there was also spatial variability in the magnitude of the impacts, it was apparently a period of generally more severe conditions in Arctic and boreal latitudes; the marked impacts upon farming and fisheries (Lamb, 1982) imply similarly marked impacts on other components of the Arctic ecosystem. Since the early 19th century, however, there has been an overall warming trend (Overpeck et al., 1997), although with clear evidence once again of both shorter-term temporal variability and of spatial variability (Maxwell, 1997). At least in those parts of the Arctic that have experienced the most rapid warming during the last 30 years or so, the magnitude of this recent warming is comparable to that during the warmest part of the Holocene.

The solar variability thought to be responsible for "The Little Ice Age", and for other similar centennial to millennial climatic fluctuations, probably also affected the ozone layer and UV-B radiation. UV-B irradiance at ground level relevant to absorption by DNA could have been between 9% and 27% higher during low-radiation (cool periods) than during high-radiation periods of the sun (Rozema et al., 2002).

2.3 Late-Quaternary history of Arctic biota

At the time of the last glacial maximum, when most land areas in the Arctic were ice covered, biomes able to support the elements of the Arctic biota, including some species that are now extinct, were extensive South of the Fennoscandian ice sheet in Europe (Huntley et al., 2003). Similar biomes apparently were extensive South of the Eurasian ice sheets of northern Russia, eastwards across Siberia and the exposed seabed to the North, and via Beringia into Alaska and adjacent northern Yukon (Ritchie, 1987), although they were much more restricted South of the Laurentide ice sheet in central and eastern North America (Lister and Bahn, 1995). The most extensive and important of these glacial biomes, the steppe–tundra, has been interpreted and referred to by various authors as “tundra–steppe” or “Mammoth steppe” (Walker et al., 2001; Yurtsev, 2001; Guthrie, 2001). The vegetation of this biome comprised a no-analog combination of light-demanding herbaceous and dwarf-shrub taxa that are found today either in Arctic tundra regions or in the steppe regions that characterize central parts of both North America and Eurasia (Yurtsev, 2001). The association with this biome of evidence of an abundance of grazing herbivores of large body mass, some extant (e.g. Rangifer tarandus – reindeer, caribou; Ovibos moschatus – musk oxen) and others extinct (e.g. Mealloceros giganteus – giant deer, ‘Irish elk’; Mammuthus primigenius – woolly mammoth; Coelodonta antiquitatis – woolly rhino), is interpreted as evidence that the biome was much more productive than is the contemporary tundra biome. This productive biome, dominated by non-tree taxa, corresponded to a no-analog environment that was relatively cold throughout the year, with a growing season short enough to exclude even cold-tolerant boreal trees from at least the majority of the landscape. The “light
climate”, however, was that of the relatively lower latitudes (as little as 45°N in Europe) at which this biome occurred, rather than that of the present Arctic latitudes; the greater solar angle and consequent higher insolation intensities during the summer months probably made an important contribution to the productivity of the biome.

The productive steppe–tundra and related biomes were much more spatially extensive during the last glacial stage than is the tundra biome today (Figure 6.4). The glacial was thus a time when many elements of the present Arctic biota thrived, almost certainly in greater numbers than today. Fossil remains of both Arctic plants (see e.g. West, 2000) and mammals (see e.g. FAUNMAP Working Group, 1996; Lundelius et al., 1983; Stuart, 1982) found at numerous locations attest to their widespread distribution and abundance. Similar conclusions have been reached on the basis of phylogeographic studies (studies of the relationships between genetic identity and geographical distribution) of Arctic breeding waders (Kraaijeveld and Nieboer, 2000). Species such as Calidris canutus (red knot) and Arenaria interpres (ruddy turnstone) are inferred to have had much larger populations and more extensive breeding areas during glacial stages, although others, such as C. alpina (dunlin), exhibit evidence of range fragmentation during glacial stages leading to evolution of distinct geographically restricted infra-specific taxa. Phylogeographic studies of other Arctic taxa reveal a picture of individualism of response of different species (see Weider and Hobæk, 2000 for a recent review). Some species, such as Salvelinus alpinus (Arctic char) (Brunner et al., 2001), and genera, such as Coregonus spp. (whitefish) (Bernatchez et al., 1999), exhibit evidence of sub-taxa whose origins are apparently related to recurrent periods of isolation of populations throughout the Pleistocene history of alternating glacial and interglacial stages. Dicrostonyx spp. (collared lemmings), however, apparently parallel C. alpinus in exhibiting genetic differentiation principally as a consequence of the relatively recent geographical isolation of populations during the last glacial stage (Fedorov et al., 1999b; Fedorov and Goropashnaya, 1999). Others, such as Ursus maritimus (polar bear) (Paetkau et al., 1999), exhibit little or no evidence of genetic differentiation that might indicate past population fragmentation, and Eurasian Lemmus spp. (true lemmings) (Fedorov et al., 1999a) are inferred to have experienced no effective reduction in population size during recent glacial–interglacial cycles.

Figure 6.4 Northern vegetation in the Mid- Holocene a) simulated by the IPSL-CM1 AOJCM model, b) simulated by the HADCM2 AOJCM model, c) observed vegetation reconstructed from pollen data (Bigelow et al. 2003; Kaplan et al., 2003).

In the context of their late-Quaternary history, the Arctic biota of the present day should be viewed as relatively restricted in range and population size. Although tundra areas were of even smaller extent at the time of the early Holocene period of greater northward extension of the Arctic treeline (Huntley, 1997; Huntley and Bradshaw, 1999; MacDonald et al., 2000), that reduction was marginal when compared to that suffered at the end of the last glacial stage. Similarly, whereas at the lower taxonomic levels, extant Arctic taxa often exhibit considerable diversity that can be related to their late-Quaternary history, the biota as a whole has suffered a recent reduction of overall diversity through the extinctions of many species, and some genera, that did not survive into the Holocene. Of at least 12 large herbivores and 6 large carnivores present in steppe-tundra areas at the last glacial maximum (Lister and Bahn, 1995; Stuart, 1982), only 4 and 3 respectively survive today and of those, only 2 herbivores (reindeer and musk ox)
and 2 carnivores (brown bear and wolf) occur today in the Arctic tundra biome. The present geography also imposes extreme migratory distances upon many tundra-breeding birds because of the wide separation of their breeding and wintering areas (Davidson et al., 1986; Wennerberg, 2001), in consequence rendering many of them, in common with much of the Arctic biota, extremely vulnerable to any further climatic warming (Evans, 1997).

2.4 Late-Quaternary ecological history in the Arctic

Although relatively few in overall number, paleoecological studies of the late-Quaternary have been made in many parts of the Arctic (see e.g. Anderson and Brubaker, 1993; 1994; Lamb and Edwards, 1988; MacDonald et al., 2000; Ritchie, 1987). In areas that were by then ice free, the transition to the Holocene was marked by evidence of rapid ecological response to the environmental changes at that time. Elsewhere, in proximity to the decaying ice sheets the ecological changes lagged the global environmental change because of the regional influence of the persisting ice. Although the precise nature of the ecological changes depends upon the location, the overall picture was one of widespread rapid replacement of the open, discontinuously vegetated tundra and polar desert that had characterized most ice-free areas during the late-glacial period, by closed tundra. This was in turn replaced by shrub tundra and subsequently by Arctic woodlands or northern boreal forest in lower Arctic areas. In areas such as Alaska, that were unglaciated at the last glacial maximum, the ecological transition began earlier, coinciding with the first rapid climatic warming recorded in Greenland at ca.14,700 years ago (Björck et al., 1998; Stuiver et al., 1995). In Alaska, tundra was replaced by shrub tundra during the late glacial and the first forest stands (of Populus balsamifera – balsam poplar) were present already before the transition to the Holocene (Anderson and Brubaker, 1994). South of the Arctic the extensive areas of steppe–tundra that were present at the last glacial maximum were rapidly replaced by expanding forests. Only in parts of northernmost Siberia may fragments of this biome have persisted into the Holocene, supporting the last population of woolly mammoths that persisted as recently as four thousand years ago (Vartanyan et al., 1993).

The early Holocene was characterized by enhanced summer insolation intensities in northern latitudes, compared to the present. The warmer summer months enabled trees to extend their ranges further northwards than at present; positive feedback resulting from the contrasting albedo of forest compared to tundra (see sections 4.2.4; 5.4.2) probably enhanced this extension of the forest (Foley et al., 1994). Boreal forest trees expanded their ranges at rates of between 0.2 and 2!km/yr⁻¹ (Huntley and Birks, 1983; Ritchie and McDonald, 1986). They exhibited individualistic responses with respect to their distributions and abundance patterns in response to climatic patterns that differed from those of today. Milder winters and more winter precipitation in western Siberia at that time, for example, allowed Picea abies (Norway spruce) to dominate in areas where Abies sibirica (Siberian fir) and Pinus sibirica (Siberian stone pine) subsequently have become important forest components during the later Holocene (Huntley, 1988; 1997; Huntley and Birks, 1983). Throughout northern Russia the Arctic treeline already had advanced more or less to the position of the present Arctic coastline by ca.110,200 years ago, although the lower sea level at that time meant that a narrow strip of tundra, up to 150!km wide at most, persisted to the North of this (MacDonald et al., 2000). Subsequently, as sea level continued to rise during the early Holocene, the extent of tundra reached a minimum that persisted for several millennia. For tundra species, including tundra-breeding birds, the early Holocene thus seems...
likely to have been a time of particular stress. This stress may, however, have been in part relieved by enhanced productivity in these areas, compared to modern tundra ecosystems, as a consequence of the warmer summers and their higher insolation intensity.

In glaciated areas of the Arctic, such as northern Fennoscandia and much of Arctic Canada, peat lands became extensive only after the mid-Holocene (see e.g. Lamb, 1980; Vardy et al., 1997) in response to the general pattern of climatic change towards cooler and regionally moister summer conditions. The same cooling trend led to the southward retreat of the Arctic treeline, which reached more or less its present location in most regions by ca. 4500 years ago (MacDonald et al., 2000). The consequent increase in extent of tundra probably relieved the stress experienced by tundra organisms during the early Holocene, although the cooler, less productive conditions, and the increasing extent of seasonally waterlogged tundra peat lands, may have offset this at least in part. Whereas at least in some regions the early Holocene was a time of permafrost decay and thermokarst development (Burn, 1997), the extent of permafrost has increased once again in many areas during the later Holocene (see e.g. Kienel et al., 1999; Vardy et al., 1997).

2.5 Late-Quaternary history of humans in the Arctic related to ecosystems

Recently discovered evidence (Pavlov et al., 2001) shows that Paleolithic “hunter–gatherers” were present ca. 40,000 years BP as far North as 66° 34’N in Russia, East of the Fennoscandian ice sheet and well-before the last glacial maximum. Although it seems likely that humans did not range so far North during the glacial maximum, it is clear that they expanded rapidly into the Arctic once again during the deglaciation.

Humans entered North America via the Beringian ‘land bridge’ and along its southern coast ca. 14,000-13,500 years BP (Dixon, 2001). These so-called Clovis hunters were hunter–gatherers who had developed sophisticated ways of working stone to produce very fine spear- and arrowheads. Over the next few millennia they expanded their range and population rapidly, occupying most of the North American continent. As they did so their prey apparently included many of the large vertebrate species that soon were to become extinct. The extent to which human hunting may have been principally responsible for these extinctions is a matter of continuing debate, but recent simulations for North America indicate that this possibility cannot be excluded there (Alroy, 2001). These extinctions coincide, however, with an environmental change that caused the area of the biome with which the large Arctic vertebrates were associated to be reduced to an extent that apparently was unprecedented during previous glacial–interglacial cycles (Sher, 1997). It thus is more probable that the hunting pressure exerted by humans was at most an additional contributory factor leading to the extinctions, rather than their primary cause.

In Eurasia, Paleolithic hunter–gatherers shifted their range northwards into the Arctic, as did their large vertebrate prey. To the South they were replaced by Mesolithic peoples who occupied the expanding forests. By the early Holocene these Mesolithic peoples had expanded well into the Arctic (Thommessen, 1996) where they probably gave rise to the indigenous peoples that in many cases continued to practice a nomadic hunter–gatherer way of life until the recent past or even up to the present day in some regions. The arrival of later immigrants has had major impacts upon the indigenous peoples and their way of life (Chapters 9, 10 and 11). In turn, land-use and natural resource exploitation by the immigrants, as well as the changes that they have brought
about in the way of life of the indigenous peoples, have had negative impacts upon many Arctic ecosystems. These impacts may in some cases have increased the vulnerability of these ecosystems to the pressures that they now face from climate change and increased exposure to UV-B.

### 2.6 Future change in the context of Late-Quaternary changes

The potential changes for the next century can be put into context by comparing their rates and magnitudes to those estimated for the changes documented by paleoecological and other evidence from the late-Quaternary (Table 6.1).

**Table 6.1. Summary comparison for key aspects of potential future environmental changes in the context of changes in the late-Quaternary.**

<table>
<thead>
<tr>
<th>Phenomenon</th>
<th>Late-Quaternary</th>
<th>Potential Future</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea-level</td>
<td>*ca.*120 m lower at last glacial maximum increased at maximum rate of *ca.*24 mm/yr (Fairbanks, 1989)</td>
<td>0.09–0.88 m higher in *ca.*100 yr (chapter 5); 3!–10 m higher in 1000 yr increase at rate of 1!–9 mm/yr (Houghton et al., 2001)</td>
</tr>
<tr>
<td>Climate</td>
<td><em>mean annual temperature:</em></td>
<td><em>mean annual temperature:</em></td>
</tr>
<tr>
<td></td>
<td>full glacial – global mean *ca.*5°C lower; regionally in the Arctic 10–13°C lower</td>
<td>2100 – global mean 1.5!–5.8°C higher; regionally in the Arctic 2.1!–8.1°C higher</td>
</tr>
<tr>
<td></td>
<td>Holocene – global mean &lt;1°C higher at maximum; regionally in the Arctic similar to present</td>
<td>(Houghton et al., 2001)</td>
</tr>
<tr>
<td></td>
<td><em>winter temperature:</em></td>
<td><em>winter temperature:</em></td>
</tr>
<tr>
<td></td>
<td>full glacial &gt;15°C cooler regionally</td>
<td>2100 – 4!–10°C higher regionally</td>
</tr>
<tr>
<td></td>
<td>Holocene *ca.*2–4°C warmer regionally at maximum</td>
<td>(Houghton et al., 2001)</td>
</tr>
<tr>
<td></td>
<td><em>rate of change:</em></td>
<td><em>rate of change:</em></td>
</tr>
<tr>
<td></td>
<td>mean annual temperature increase – globally ±1°C per millennium; regionally &gt;5°C in a century</td>
<td>mean annual temperature increase – globally 1.5!–5.8°C per century; regionally 2.1!–8.1°C in a century (Houghton et al., 2001)</td>
</tr>
<tr>
<td>Ecosystem responses</td>
<td><em>tree line displacement:</em></td>
<td><em>tree line displacement:</em></td>
</tr>
<tr>
<td></td>
<td>full glacial &gt;!1000/km southward</td>
<td>2100 – &gt;500/km northward</td>
</tr>
<tr>
<td></td>
<td>Holocene 50!–1200/km northward at maximum (Kaplan, 2001)</td>
<td>Anthropogenic disturbance, however, may result in an opposite response, see section 5.3.2.1</td>
</tr>
<tr>
<td></td>
<td><em>range margin displacement rates:</em></td>
<td><em>range margin displacement rates:</em></td>
</tr>
<tr>
<td></td>
<td>early Holocene rates of 0.2!–2 km/yr estimated for trees from pollen data (Huntley, 1988)</td>
<td>potential rates during 21st century of 5!–10 km/yr estimated from species–climate response models (Huntley et al., 1995)</td>
</tr>
<tr>
<td></td>
<td>Holocene 81% (ranging from 76 to 84%) of present</td>
<td>2100 – 51% of present (J. Kaplan, pers. Comm.; see Kaplan et al. (2003[BH1])</td>
</tr>
<tr>
<td>Area of tundra</td>
<td>full glacial 197% (ranging from 168 to 237%) of present</td>
<td></td>
</tr>
<tr>
<td>UV-B radiation</td>
<td>No long-term trend known. Due to solar variability, levels of DNA-active UV-B wavelengths may have varied by up to</td>
<td>In addition to the continuing internal cycles of the sun, anthropogenic cooling of the stratosphere may delay recovery of the ozone</td>
</tr>
</tbody>
</table>
It is apparent from table 6.1 that the potential future changes have several characteristics that pose a particular threat to the biota and ecosystems of the Arctic. Firstly, the climatic changes of the next century are likely to be comparable in magnitude to the changes seen between full glacial conditions and present conditions, and larger than the maximum changes seen during the Holocene. Secondly, the global increase in mean annual temperature is expected to occur at rates that are higher than the rate of global warming during the last deglaciation; even regionally the rate of warming is likely to match the most rapid regional warming of the late-Quaternary. Thirdly, as a consequence of this climate change, and the accompanying rise in sea level, tundra extent is likely to be less than at any time during the late-Quaternary. Fourthly, global mean temperatures and mean annual temperatures in the Arctic will reach levels unprecedented in the late-Quaternary; this will result in a further rapid reduction in the extent of permafrost, with associated thermokarst development in areas of permafrost decay leading to potentially severe erosion and degradation of many Arctic peatlands (Section 5.3.1). When climate projections are combined with human activities and their consequences (including enhanced levels of UV-B, deposition of nitrogen compounds from the atmosphere, heavy metal and acidic pollution, radioactive contamination, increased habitat fragmentation), the future will be without a past analogue and will pose unprecedented challenges to Arctic ecosystems and biota that evolved in response to global cooling throughout the last 5 million years or so (the late-Tertiary and Quaternary periods), a period similar to that during which our own species evolved.

**Summary: Late-Quaternary history of Arctic biota and environments and implications for future responses to rapid climate changes**

At the last glacial maximum, vast ice sheets covered many continental areas. The beds of some shallow seas were exposed thereby connecting previously separated landmasses. Although some areas were icefree and supported a flora and fauna, mean annual temperatures were 10 – 13 °C colder than during the Holocene. Within a few millennia of the glacial maximum, deglaciation started but this was not a simple unidirectional change; instead a series of climatic fluctuations occurred during the period between about 18,000 and 11,400 years ago. During the Younger Dryas event, mean annual temperatures fell substantially in some areas and reglaciation occurred. At the end of the event, mean annual temperatures rose by >5°C in less than 100 yr in at least some parts of the Arctic. Following the general thermal maximum in the Holocene, there has been a modest overall cooling trend. However, superimposed upon the general longer-term patterns have been a series of millennial and centennial fluctuations in climate, the most marked of which occurred about 8200 years ago. The most recent of these climatic fluctuations was that of the “Little Ice Age”, a generally cool interval spanning approximately the late 13th to early 19th centuries. At its most extreme, mean annual temperatures in some Arctic areas fell by several degrees and there were impacts on human settlements in the North.

In the context of at least the last 150,000 years, Arctic ecosystems and biota have been close to their minimum extent within the most recent 10,000 years. They suffered loss of diversity as a result of extinctions during the most recent large-magnitude rapid global warming at the end of the last glacial stage. Consequently, Arctic ecosystems and biota are already stressed; some are extremely vulnerable to the current and potential future global warming. For example, migratory Arctic breeding birds today face maximal migration distances between their wintering and breeding areas.

Evidence from the past indicates that Arctic species, especially larger vertebrates, are very likely to be vulnerable to extinction if climate warms. The treeline will very probably advance, perhaps rapidly, into tundra areas of northern Eurasia, Canada and Alaska, as it did during the early Holocene, reducing the extent of tundra and contributing to the pressure upon species that may result in their extinction. Species that today have more southerly distributions will
very probably extend their ranges northwards, displacing Arctic species as in the past. Permafrost will decay and thermokarst develop, leading to erosion and degradation of Arctic peat lands. Unlike the early Holocene, when lower relative sea level allowed a belt of tundra to persist around at least some parts of the Arctic basin when treelines advanced to the present coast, sea level is very likely to rise in future, further restricting the area of tundra and other treeless Arctic ecosystems.

The expected negative response of Arctic ecosystems in the face of a shift to global climatic conditions that are apparently without precedent during the Pleistocene is likely to be considerable, particularly as their exposure to co-occurring environmental changes (such as enhanced levels of UV-B, deposition of nitrogen compounds from the atmosphere, heavy metal and acidic pollution, radioactive contamination, increased habitat fragmentation) is also without precedent.
3. Species Responses to changes in climate and UV-B in the Arctic

3.1 Background

The individual of a species is the basic unit of ecosystems which responds to climate and UV-B changes. Individuals respond to environmental changes over a wide range of time scales from biochemical, physiological and behavioral processes occurring in less than a minute to the integrative responses of reproduction and death (Figure 6.1). Reproduction and death drive the dynamics of populations while mutation and environmental selection of particular traits in individuals within the population lead to changes in the genetic composition of the population and adaptation.

Current Arctic species have characteristics that have enabled them to pass various environmental filters associated with the Arctic’s environment (Körner, 1995; Walker, 1995), whereas species of more southern latitudes either cannot pass these filters or have not yet arrived in the Arctic. Changes in Arctic landscape processes and ecosystems in a future climatic and UV-B regime will depend upon the ability of Arctic species to withstand or adapt to new environments and upon their interactions with immigrant species that can pass through less severe environmental filters. This section focuses on the attributes of current Arctic species that constrain or facilitate their responses to a changing climate and UV-B regime.

3.2 Implications of current species distributions for future biotic change

3.2.1 Plants

3.2.1.1 Species diversity

About 3% (about 5,900) species of the global flora occurs in the Arctic as defined in this chapter (0.7% of the angiosperms (flowering plants), 1.6% of the gymnosperms (cone-bearing plants), 4% of the bryophytes and 11% of the lichens) (Table 6.2). There are more species of primitive taxa (cryptogams) i.e. mosses, liverworts, lichens and algae in the Arctic than of vascular plants (Matveyeva and Chernov, 2000). Less than half of the Arctic plant species are vascular plants (about 1,800 species). There are about 1,500 species common to both Eurasia (Sekretareva, 1999; Matveyeva and Chernov, 2000) and North America (Murray, 1995). A similar number of non-vascular plants probably occurs in the Arctic on both continents, although their diversity has been less thoroughly documented. In the Russian Arctic, for example, 735 bryophyte species (530 mosses and 205 liverworts) and 1,078 lichen species have been recorded (Afonina and Czernyadjeva, 1995; Andreev et al., 1996; Konstantinova and Potemkin, 1996). In general, the North American and Eurasian Arctic are similar to one another in their numbers of vascular and non-vascular plant species, of which a large proportion (about 80%) of vascular plants occurs on at least two continents. An even larger proportion (90%) of bryophytes occurs in both the North American and Eurasian Arctic.

About 40% of vascular plants (and a much higher percentage of mosses and lichens) are basically boreal species that now barely penetrate the Arctic (Table 6.3). They currently occur close to the treeline or along large rivers that connect the sub-Arctic with the Arctic. These boreal species

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within the Arctic will probably be the primary boreal colonizers of the Arctic in the event of continued warming. Polyzonal (distributed in several zones), arctoboreal (in taiga and tundra zones) and hypoarctic (in the northern taiga and southern part of the tundra zone) species have even greater potential to widen their distribution and increase their abundance in a changing climate. The majority of cryptogams have wide distributions all over the Holarctic. Such species may survive a changing climate, although their abundance can be reduced (Section 3.4.1.2; 4.1.2.1).

In contrast to the low diversity of the Arctic flora at the continental and regional scales, individual communities (100 m² plots) within the Arctic have a diversity similar to or higher than those of boreal and temperate zones. These diversities are highest in continental parts of the Arctic such as the Taymyr Peninsula of Russia, where there are about 150 species of plants (vascular plants, lichens and mosses) per 100 m² plot, 40-50 species per m² plot and up to 25 species per square decimeter (Matveyeva, 1998).

Table 6.2  Biodiversity estimates in terms of species richness (number of species) for the Arctic beyond the latitudinal treeline compared with world biota (Matveyeva and Chernov, 2000; Chernov, 2002).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Animals</th>
<th>% of world biota</th>
<th>Plants</th>
<th>% of world biota</th>
<th>Fungi</th>
<th>% of world biota</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group</td>
<td>Number of species</td>
<td></td>
<td>Group</td>
<td>Number of species</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammals</td>
<td>75</td>
<td>1.7</td>
<td>Angiosperms</td>
<td>1735</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>Birds</td>
<td>240</td>
<td>2.9</td>
<td>Monocotyledons</td>
<td>399</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>Insects</td>
<td>3300</td>
<td>0.4</td>
<td>Dicotyledons</td>
<td>1336</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>Diptera</td>
<td>1600</td>
<td>0.9</td>
<td>Gymnosperms</td>
<td>12</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
<td>Beetles</td>
<td>450</td>
<td>0.1</td>
<td>Pteridophytes</td>
<td>62</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>Butterflies</td>
<td>400</td>
<td>0.3</td>
<td>Mosses</td>
<td>600</td>
<td>4.1</td>
<td></td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>450</td>
<td>0.2</td>
<td>Liverworts</td>
<td>250</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td>Others</td>
<td>400</td>
<td>0.0</td>
<td>Lichens</td>
<td>2000</td>
<td>11.0</td>
<td></td>
</tr>
<tr>
<td>Springtails</td>
<td>400</td>
<td>6.0</td>
<td>Algae</td>
<td>1200</td>
<td>3.3</td>
<td></td>
</tr>
<tr>
<td>Spiders</td>
<td>300</td>
<td>1.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mites</td>
<td>700</td>
<td>1.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other Groups*</td>
<td>600</td>
<td>--</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Estimate</td>
<td>6000</td>
<td>--</td>
<td></td>
<td>5859</td>
<td>3</td>
<td></td>
</tr>
</tbody>
</table>

*Amphibians & reptiles (7 species), Centipedes (10 species), terrestrial Molluscs (3 species), Oligochaetes (earth worms and enchytraeids) (70 species), and Nematodes (~500 species).

3.2.1.2 Latitudinal gradients of species diversity

Latitudinal gradients suggest that Arctic plant diversity is sensitive to climate. The number of vascular plant species declines 5-fold from South to North in the Taymyr Peninsula in Russia (Matveyeva, 1998). Summer temperature is the environmental variable that best predicts plant
diversity in the Arctic (Young, 1971). Other factors are also important, however; regions of
different latitudes that have a similar maximum monthly temperature often differ in diversity.
Taymyr biodiversity values are intermediate between the higher values for Chukotka and Alaska,
which have a more complicated relief, geology, and floristic history, and the lower values in the
eastern Canadian Arctic with its impoverished flora resulting from relatively recent glaciation.
All diversity values on the Yamal Peninsula are even lower than in Canada because of a wide
distribution of sandy soils and perhaps its young age. Similar patterns are observed with
butterflies (Figure 6.5) and spiders (Chernov, 1995; Chernov, 1989). Therefore, latitudinal
gradients of species diversity are best described as several parallel gradients, each of which
depends on summer heat, but which may differ from one geographic region to another. This fact
has to be taken into consideration when predicting future changes in biodiversity.

Figure 6.5 Top: the relationship between the number of nesting bird species and July mean
temperature in western and middle Siberia. Middle: correlation between July mean temperature
and number of ground beetle species in local faunas of the Taymyr Peninsula. Bottom:
Correlation between July mean temperature and number of day butterflies in the middle Siberian
and Beringian sectors of the Arctic (Chernov, 1989; Chernov, 1995; Matveyeva and Chernov,
2000). The middle figure illustrates how current bioclimatic distributions are related to climate
change scenarios by plotting the likely changes in the number of ground beetles for three time
slices of mean July temperature derived from the mean of the five ACIA scenarios.

At the level of the local flora (the number of species present in a landscape of about 10 x 10 km),
there is either a linear or an “S”-shaped relationship between summer temperature and species
number (Figure 6.6). Species number is least sensitive to temperature near the southern margin of
the tundra and most sensitive to temperatures between 3-8°C. This suggests that the main
changes in species composition will occur in the northern part of the tundra zone and in the polar
desert, where species are now most restricted in their distribution by summer warmth and length
of growing season. July temperature, for example, accounts for 95% of the variance in number of
vascular plant species in the Canadian Arctic (Rannie, 1986) (although extreme winter
temperatures are also important – Section 3.4.1.3). In general, summer warmth, length of the
growing season and winter temperatures all affect the growth, reproduction and survival of Arctic
plants. The relative importance of each of these varies from species to species, site to site and
year to year.

Figure 6.6 The relationship between July mean temperature and the number of vascular plant
species in local floras of the Taymyr Peninsula and the Canadian Arctic Archipelago. 1. The
Matveyeva and Chernov, 2000).

The steep temperature gradient that has such a strong influence on species diversity occurs over
much shorter distances in the Arctic than in other biomes. North of the treeline in Siberia, mean
July temperature decreases from 12°C to 2°C over 900 km, whereas a 10°C decline in July
temperature is spread over 2,000 km in the boreal zone, and decreases by less than 10°C from
the southern boreal zone to the equator (Chernov, 1995). The temperature decrease of 10°C can
be compared with the expected mean 2.5°C (range of the two extremes of the five ACIA climate
scenarios – 1.1 to 4.2°C) increase in mean July temperature by 2080. Much of the region is very
likely therefore to remain still within the Arctic summer climate envelope (although the increase in winter temperature is expected to be higher).

Because of the steep temperature gradients with latitude in the Arctic, the distance that plants must migrate in response to a change in temperature is much less in the Arctic than in other biomes, particularly where topographic variations in microclimate enable plants to grow far beyond their climatic optima. The low sun angle and presence of permafrost make topographic variations in microclimate and associated plant community composition particularly pronounced in the Arctic. Thus, both the sensitivity of Arctic species diversity to temperature and the short distance over which this temperature gradient occurs suggest that Arctic diversity will very probably respond strongly and rapidly to high-latitude temperature change.

Latitudinal patterns of diversity differ strikingly among different groups of plants (Table 6.3). Many polyzonal, boreal and Hypoarctic species have ranges that extend into the Arctic. Some of these, e.g., the moss *Hylocomium splendens* and the sedges *Eriophorum angustifolium* and *E. vaginatum* are important dominants within the Arctic. Tussocks of *E. vaginatum* structure the microtopography of broad areas of tussock tundra (Bliss and Matveyeva, 1992), and *Hylocomium splendens* exerts a control over nutrient cycling (Hobbie, 1996). Tall willow (*Salix* spp.) and alder (*Alnus fruticosa*) shrubs as well as dwarf birch *Betula exilis*, *B. nana* form dense thickets in the southern part of the tundra zone and often have outlier populations that extend far to the North in favorable habitats (Matveyeva and Chernov, 2000). Those species that are important community dominants are likely to have a particularly rapid and strong effect on ecosystem processes where regional warming occurs. Hemiarctic species are those that occur throughout the entire range of the Arctic. Many of these species are common community dominants, including *Carex bigelowii/arctisibirica*, *C. stans*, *Dryas octopetala/punctata*, *Cassiope tetragona*, and the moss *Tomentypnum nitens*. Due to their widespread current distribution, their initial responses to climatic warming are likely to be increased productivity and abundance followed by probable later movement further to the North. The most vulnerable are likely to be Euarctic (*Salix polaris*) and Hyperarctic species that now have the largest abundance and widest ecological amplitude in the northernmost part of the tundra zone (the former) or in polar deserts (the latter). These groups of species are best adapted to the climate conditions of the high Arctic where they are distributed in a wide range of habitats where more competitive species of a general southerly distribution are absent. In the more southerly regions of the tundra zone, they are able to grow only (or mainly) in snow beds. It is probable that their ecological amplitude will narrow and abundance decrease during climate warming.

Thus, responses to climate changes will be different in various groups of plants. Some currently rare boreal species can move further North and the more common species increase in their relative abundance and in the range of habitats that they occupy. When southern species with current narrow niches penetrate into the poorer ecosystems at high latitudes, therefore, there can be a broadening of their ecological niches there. In contrast, some true Arctic species (endemics) that are widely spread in the high latitudes will probably become more restricted in their local distribution within and among ecosystems. They could possibly even disappear in the lower latitudes where the tundra territories are particularly narrow. Only few high Arctic plants of Greenland are expected to become extinct, for example *Ranunculus sabinei* that is limited to narrow outer coastal zone of North Greenland (Heide-Jørgensen and Johnsen, 1998). However,
temperature is not the only factor that currently prevents some species from being distributed in the North. Even in future warmer summer periods, the long period of daylight will support the existence of Arctic species but initially restrict the distribution of some boreal ones (see section 3.4.1.6). The actual latitudinal position is important, and life cycles depend not only on temperature but on the light regime as well. New communities with a peculiar species composition and structure are therefore, very likely to arise and these will not be the same as those existing now.

Table 6.3. Current diversity changes with latitude in the Arctic region, compiled and modified from information in Matveyeva and Chernov (2000) excluding limnic and marine animals. Note: general information on how species within the various categories are likely to respond to climate and UV change is presented in the text, but insufficient information is available for most of the species in the table.

<table>
<thead>
<tr>
<th>Category</th>
<th>Optimum of distribution</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zonal boreal</td>
<td>Not abundant and constrained to the South of the Arctic in benign habitats such as river valleys, South-facing slopes, and wet areas</td>
<td>Tree species of Larix; the orchid Corallorrhiza; the shrub Salix myrtylloides; the sedges Carex chordorrhiza; the herbs Allium schoenoprasum, Cortusa matthioli, Galium densiflorum, Sanguisorba officinalis; and forest mosses Cladoniaceae, Pleuroziaceae, Rhytidiadelphus triquetus</td>
</tr>
<tr>
<td>Zonal Arctic</td>
<td>Optima in the southern tundra subzone</td>
<td>This group characterizes the southern tundra subzone; the shrubs Betula nana/waliscils and sedges Eriophorum vaginatum</td>
</tr>
<tr>
<td>Hypoarctic</td>
<td>Optima in the southern tundra subzone</td>
<td>The ptarmigan Lagopus lagopus; the spotted redshank Tringa erythropus; the little bunting Emberiza pusilla, and the bar-tailed godwit Limosa lapponica</td>
</tr>
<tr>
<td>Hemiarctic</td>
<td>Throughout the tundra zone but most frequent in the middle</td>
<td>Most of the dominant species: the grasses Arctophila fulva, Dactylora fisheri; the sedges Carex bigelowii/arcticbaica and Carex stans; the shrub willow Salix reptans, the dwarf shrubs Dryas punctata/teaetapeta and Carex tetragon; the mosses Tomentypnum nives, Drepanocladus intermedius, and Cladoniaceae arctic; the herbs Lagoitys minor and Pedicularis hirsuta, the moss Polytrichum juniperinum</td>
</tr>
<tr>
<td>Euarctic</td>
<td>Northern part of the tundra zone, rare in the southern part</td>
<td>The dwarf shrubs Salix polaris and S. arctica (this group is relatively small, but it has an important value in the subdivision of the tundra zone into subzones)</td>
</tr>
<tr>
<td>Holarctic</td>
<td>Polar desert and in the northernmost part of the area</td>
<td>Almost no plants are restricted to these zones; the following have their highest Optimum of</td>
</tr>
</tbody>
</table>
3.2.2 Animals

3.2.2.1 Species diversity

The diversity of Arctic terrestrial animals beyond the latitudinal treeline (6,000 species) is nearly twice as great as that of vascular plants and bryophytes (Chernov, 1995; Chernov, 2002; Table 6.2). As with plants, the Arctic fauna accounts for about 2% of the global total, and, in general, primitive groups (e.g., springtails, 6% of the global total) are better represented in the Arctic than are advanced groups such as beetles (0.1%) (Chernov, 1995; Matveyeva and Chernov, 2000). There are about 315 species of vertebrates, of which about 75 species are mammals, 240 birds, 2 reptiles, and 5 amphibians. Insects are the most diverse group of Arctic animals (about 3,300 species), of which about 50% are diptera, and 10% each of beetles (Coleoptera), butterflies (Lepidoptera), and hymenoptera. The Arctic has about 300 species of spiders (Arachnida), 700 species of mites (Acarina), 400 species of springtails (Collembola), 500 species of nematodes, 70 species of Oligochaetes (of which most are Enchytraeidae), only a few molluscs, and an unknown number of protozoan species.

In the Arctic region as defined by CAFF, which includes forested areas, some 450 species of birds have been recorded breeding. Some of them extend breeding from the South only marginally into the Arctic region. Others are not migratory and stay in the Arctic region all year around. About 280 species have their main breeding distribution in the Arctic and migrate regularly (Scott, 1998). An estimation of the total number of individuals involved is not possible. Too little is known about the population size of most species or their Arctic proportion. But a rough first approximation accounts for at least several 100 million birds. Water birds are better known and the Arctic is of particular importance for most water birds, such as divers, geese and waders. Twelve goose species are breeding in the Arctic, eleven almost entirely and eight exclusively. These comprise about 8.3 million birds. The total number of Arctic breeding sandpipers (24 species) exceeds 17.5 million birds (Zöckler, 1998). The total number of water birds, including other wader species, divers, swans, ducks and gulls is estimated to be between 85 and 100 million birds.

3.2.2.2 Latitudinal gradients of species diversity

Latitudinal patterns of diversity in Arctic animals are similar to those described for Arctic plants. Species diversity declines in parallel with decreasing temperature in most animals groups (Figure 6.5), including birds, ground beetles, butterflies, etc. (Chernov, 1995). However, in some groups, for example, peat-land birds and sawflies in local sites of the European North, concentration per unit area both in species diversity and density can increase compared with more southern
territories, perhaps because the habitat types appropriate to these groups are more diverse in the tundra than in the boreal forest. In general, the decline in animal species is more pronounced (frequently greater than 2.5-fold) than in vascular plants. As with plants, there are more species in Beringia at a given temperature, with its complicated relief, geology, and biogeographic history than in the Taymyr Peninsula. Many animal species are restricted to the boreal zone because they depend on the crown, wood, roots, or litter of trees, which are absent in the tundra zone. These groups include wood-boring insects and wood-decaying fungi and their predators (Chernov and Matveyeva, 1997), as well as mammals and birds that specialize on tree-seeds and leaves. Other important animals, including the raven, wolf, red fox and ermine, are primarily boreal in distribution but remain an important component of many Arctic ecosystems. There are a few terrestrial animals restricted to the high Arctic such as the sanderling, i.e. the wader Calidris alba, and a common Collembolan, Vertagopus brevicaudis. Other Arctic species have their centers of distribution in the northern, mid or southern Arctic (Table 6.3). The more diverse patterns of animal than of plant distribution make it more difficult to project how animals will respond to climatic warming. Some herbivores have distributions that are more limited than those of their host plants (Strathdee and Bale, 1998), so warming may possibly allow these species to extend northward relatively rapidly.

As in the case of plants, latitudinal patterns of diversity differ strikingly among different groups of animals (Table 6.3). The common species tend to be more broadly distributed in the far North. In northern Taymyr there are only 12 species of springtails but 80% of these occur in all microsites and topographic locations investigated (Chernov and Matveyeva, 1997). Some boreal birds, such as the American thrush Turdus migratorius, penetrate only into the southern part of tundra while others can occur far from their climatic optimum (climatic region associated with the center of distribution): in the vicinity of Dickson (Taymyr), forest thrushes T. pilaris and T. iliacus form populations in the northernmost part of the tundra zone that is 400 km distant from the last outposts of the forests. At the southern limits of the tundra, there is greater specialization among microhabitats. Many more species occur in intrazonal habitats, occupying relatively small and isolated sites, than in zonal habitats that contain only a small proportion of the regional fauna. Warming is therefore likely to lead to more pronounced habitat and niche specialization.

An important consequence of the decline in numbers of species with increasing latitude is an increase in dominance. For example, one species of collembolan, Folsomia regularis, may constitute 60% of the total collembolan density in polar desert (Babenko and Bulavintsev, 1997). These “super-dominant" species are generally highly plastic, occupy a wide range of habitats, and generally have large effects on ecosystem processes. Lemmings (various Lemmus spp. and Dicrostonyx spp) are super-dominant species during peak years of their population cycles (Stenseth and Ims, 1993) and have large effects on ecosystem processes (Batzli et al., 1980; Laine and Henttonen, 1983; Stenseth and Ims, 1993).

3.2.3 Microorganisms

3.2.3.1 Species diversity

Microbial organisms are critically important for the functioning of ecosystems, but are difficult to study and are poorly known compared with other species. However, the International Biological
Program (IBP 1960-70), significantly advanced our understanding of Arctic microorganisms, compared with those of other biomes, when an inventory of microbial communities was undertaken in the tundra (Heal et al., 1981). Currently, at the start of 21st century, the knowledge on microbial diversity in tundra remains the same or a little better than 30-40 years ago, and recent outstanding progress in molecular microbial ecology has rarely been applied to Arctic terrestrial studies.

Presently there are 5000-6000 named bacterial species globally and about the same number of fungi (Holt et al., 1994) as compared with more than 1 million named plant and animal species (Mayr, 1998; Wilson, 1992). Some scientists have interpreted this difference to mean that the bacteria are not particularly diverse (Mayr, 1998). However, there are several reasons, listed in section 6.1.1, to believe that the apparent limited diversity of microbes is an artifact.

Recent progress in molecular biology and genetics has revolutionized bacterial classification and our understanding of microbial phylogeny (“family trees”) and biodiversity in general. The DNA sequencing technique has reorganized bacterial classification and brought order to microbial taxonomy (Wayne et al., 1987). Moreover, the microbial inventory can now be done without isolation and cultivation of the dominant microorganisms, because it is enough to extract from the soil the total community DNA, amplify, clone and sequence the individual genes. The described culture-independent approach has been applied occasionally for analysis of microbial communities in sub-Arctic and Arctic soils, most often to study relatively simple communities of hot springs, subsols and contaminated aquifers (see discussion in section 3.6.2). Analysis of Siberian subsurface permafrost samples (Tsapin et al., 1999; Gilichinsky, 2002) resulted in the formation of a clone library of 150 clones which has been separated into three main groups of Eu bacteria. From 150 clones so far analyzed, the authors have identified several known species (Arthrobacter, Clostridium, and Pseudomonas), while the most abundant phylotypes were represented by completely unknown species closely affiliated with Fe (iron)-oxidizing bacteria.

Another area of intensive application of molecular tools was northern wetlands (cold, oligotrophic (nutrient poor) and usually acidic type of habitats) as related to the methane cycle (see details in Sections 4 and 5). The most challenging and formidable tasks were to find out what particular microbial organisms are responsible for the generation and uptake of methane (so called methanogens and methanotrophs) in the northern ecosystems and what can be their reaction to warming of the Arctic’s soils. It was found that most of the boreal and sub-Arctic wetlands contain a wide diversity of methanogens (Hales et al., 1996; Galand et al, 2002) and methanotrophs (McDonald et al., 1999; Radajewsky et al., 2000), most of them being distantly related to known species. Only recently, some of these obscure microbes were obtained in pure culture or stable consortia (Dedysh et al., 1998; Sizova et al., 2003). The novel microbes of methane cycles are extreme oligotrophic species that evolved to function in media with very low concentrations of mineral nutrients. Taxonomically, the novel oligotrophic methanogens form new species, genera and even families within the Archaea domain (Sizova et al., 2003). The acidophilic methanotrophs form two new groups: Methylocapsa and Methylocella (Dedysh et al., 1998; 2000), the last one affiliating with heterotrophic Beijerinckia indica.

DNA-based techniques allow us to answer the question, “What is the upper limit for variation of microbial diversity in the Arctic as compared with other natural ecosystems?” How many species
(both cultured and unculturable) do soils contain? This technique is called DNA reassociation (how quickly the hybrid double helix is formed from denatured single-stranded DNA).

**Table 6.4. The microbial genome size in the Arctic as compared with other habitats (after Torsvik et al., 2002)**

<table>
<thead>
<tr>
<th>DNA source</th>
<th>Number of cells per cm²</th>
<th>Community genome complexity (bp)*</th>
<th>Genome equivalents**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctic desert (Svalbard)</td>
<td>7.5 $10^9$</td>
<td>0.5-1.0 $10^{10}$</td>
<td>1200-2500</td>
</tr>
<tr>
<td>Tundra soil (Norway)</td>
<td>3.7 $10^{10}$</td>
<td>0.5 $10^{10}$</td>
<td>1200</td>
</tr>
<tr>
<td>Boreal forest soil</td>
<td>4.8 $10^{9}$</td>
<td>2.5 $10^{10}$</td>
<td>6000</td>
</tr>
<tr>
<td>Forest soil, cultivated prokaryotes</td>
<td>1.4 $10^7$</td>
<td>1.4 $10^8$</td>
<td>35</td>
</tr>
<tr>
<td>Pasture soil</td>
<td>1.8 $10^{10}$</td>
<td>1.5 -3.5$10^{10}$</td>
<td>3500-8800</td>
</tr>
<tr>
<td>Arable soil</td>
<td>2.1 $10^{10}$</td>
<td>5.7-14 $10^8$</td>
<td>140-350</td>
</tr>
<tr>
<td>Salt-crystallizing pond, 22% salinity</td>
<td>6.0 $10^7$</td>
<td>2.9 $10^7$</td>
<td>7</td>
</tr>
</tbody>
</table>

*bp = base pair which is the number of nucleotides in each strand in the DNA molecule
** the number of genome equivalents is a measure of diversity specified at a molecular level

Arctic desert and tundra contain considerable microbial diversity comparable with boreal forest soil and much higher than arable soils. Although extreme environmental conditions restrain the metabolic activity of Arctic microbes, they preserve huge potential that is ready to display the same activity as boreal analogs immediately after climate warming.

There is a much higher degree of genomic diversity in prokaryotic communities (prokaryotes such as cyanobacteria have a simple arrangement of their genetic material whereas eukaryotes such as microalgae have genetic material arranged in a more advanced way in that the DNA is linear and forms a number of distinct chromosomes) of heterogeneous habitats (virgin soils, pristine sediments) as compared with more homogeneous samples: the DNA diversity seen in 30-100 cc of heterogeneous samples corresponds to about $10^4$ different genomes, while in pond water and arable soils the number of genomes decreases to $10^0$-$10^2$. Based on extrapolation and taking into account that listings of species can significantly overlap for microbial communities of different soils, a rough estimate is that there could be from $10^4$ to $10^7$ prokaryotic species globally (Staley and Gosink, 1999; Torsvik et al., 2002).

The conventional inventory approach based on cultivation suggests that, in the Arctic, at the present time, we are able to identify in any particular soil no more than 100 prokaryotic species from the potential of 1000-3000 ‘genome equivalents’ (see Table 6.4 above) and no more than 2000 species of eukaryotes. The 1750 named fungi species (not including yeast and soil fungi) are known for the Russian Arctic (in the broad sense) (Karatygin et al., 1999). About 350 of these are macromycetes. However, their number in the Arctic proper is 20–30% less, but these data are far from complete. The Arctic has fewer species of bacteria, fungi, and algae than other major biomes; actinomycetes are rare or absent in most tundra sites (Bunnell et al., 1980). While most major phyla of microfloras are represented in tundra ecosystems, many species and genera that are common elsewhere, even in sub-Arctic ecosystems, are rare or absent in tundra. Gram-positive bacteria including gram-positive spore forms are absent or rare in most tundra sites. *Arthrobacter* and *Bacillus* can rarely be isolated and then only from drier areas. *Azotobacter*, the free-living nitrogen fixing bacterium, is extremely rare in tundra, and the moderate rate of $N_2$
fixation observed in situ is mainly due to the activity of cyanobacteria. Sulfur-oxidizing bacteria are also reported to be rare or absent. Even using enrichment techniques, Bunnell et al. (1980) rarely found chemooautotrophic sulfur oxidizing bacteria. Photosynthetic sulfur bacteria have not been found in any IBP Tundra Biome Sites and have been reported from only one sub-Arctic site (Bunnell et al., 1980, Dunican and Rosswal, 1974), although they are common in coastal areas of the West and South coasts of Hudson Bay. Sulfur-reducing bacteria, while not abundant in tundra sites, have been reported from Arctic and Antarctic sites. Iron-oxidizing bacteria are very rare in tundra sites. Despite ample iron substrate in tundra ponds and soils, chemooautotrophic ferrous iron oxidizers were not found in IBP tundra sites (Dunican and Rosswal, 1974). In contrast, methanotrophic and methanogenic bacteria appear to be widely spread in tundra areas.

As with bacteria, many generally common fungi are conspicuous by their rare occurrence or absence in tundra areas. Aspergillus, Altenaria, Botrytis, Fusarium and Rhizopus, simply do not occur and even Penicillia are rare (Flanagan and Scarborough, 1974). Yeasts can be isolated readily but there is very low species diversity in culture media. Only three different species were reported for Pt. Barrow tundra (Bunnell et al., 1980). Aquatic fungi show high diversity, especially Chytridiales and Saprolegniales. However they may not be endemic and reflect the annual migration into the Arctic of many avian species especially water-fowl. The so-called higher fungi, Basidiomycetes and Ascomycetes, also have low diversity. They are reduced to seventeen families, thirty genera and about one hundred species. In comparison, sub-Arctic and temperate regions would contain at least fifty families, not less than three hundred genera and anywhere up to twelve hundred species (Miller and Farr, 1975). Mycorrhizal symbionts on tundra plants are common. Arbuscular, ecto-, ericoid, arbutoid and orchid mycorrhizal fungi are associated with plants in Arctic ecosystems (Michelsen et al., 1998). The ectomycorrhizal symbionts are important as they form mycorrhizal associations with Betula, Larix, Pinus, Salix, Dryas, Cassiope, Polygonum and Kobresia. Based on fungal fruitbodies, Borgen et al (in prep.) estimate 238 ectomycorrhizal fungal species in Greenland, which may increase to around 250 out of a total of 855 when some large fungal genera as Cortinarius and Inocybe have been revised. With the exception of Eriophorum spp. Flanagan (not published) found endotrophic Arbuscula-like mycorrhizae on all ten graminoid plants examined. The number of fungal species involved in other mycorrhizal symbioses is not clear.

Tundra algae exhibit the same degree of reduction in species diversity seen amongst the fungi and bacteria (Bunnell et al., 1980; Fogg, 1998; Elster, 2002), which document a diversity much reduced from that of the microflora of temperate regions. Cyanobacteria and microalgae are among the oldest, in evolutionary terms, and simplest forms of life on the planet that can photosynthesize. Mainly unicellular and filamentous photosynthetic cyanobacteria and microalgae are among the main primary colonizers adapted to conditions of the Arctic terrestrial environment. They are widespread in all terrestrial and shallow wetland habitats and frequently produce visible biomass. Terrestrial photosynthetic microorganisms colonize mainly the surface and subsurface of the soil and create the crust (Elster et al., 1999). Shallow flowing or static wetland algal communities produce mats or mucilaginous clusters that float in the water but are attached to rocks underneath (Elster et al 1997). Terrestrial and wetland habitats represent a unique mosaic of cyanobacteria and algal communities that occur up to the highest and lowest possible latitudes and altitudes as long as liquid or vapor water is available for some time in the year (Elster, 2002). The Arctic soil and wetland microflora is composed mainly of species from
Cyanobacteria, Chrysophyceae, Xanthophyceae, Bacillariophyceae, Chlorophyceae, Charophyceae, Ulvophyceae and Zygmenaphyceae. Species diversity reports from various sites range widely, between 53 to 150 – 160 species (Elster, 2002).

3.2.3.2 Latitudinal gradients of microbial species diversity

Arctic soils contain large reserves (standing crops) of microbial (mainly fungal) biomass, although the rate of microbial growth is generally lower than in the boreal zone. Surprisingly, under severe Arctic conditions, soil microbes fail to produce spores and other dormant structures (Figure 6.7). The species diversity of all groups of soil microorganisms is lower in the Arctic than further South, decreasing from about 90 in grassland in Ireland, through about 50 in Alaskan birch forest to about 30 in Alaskan tundra (Flanagan and Scarborough, 1974). As with plants and animals, there are large reductions in numbers of microbial species with increasing latitude, although these patterns are less well documented. A correlate of the decreasing number of species with increasing latitude is increasing dominance of the species that occur, as with plants and animals. One yeast, Cryptococcus laurentii, for example, constitutes a large proportion of yeast biomass across a range of community types in the northern Taymyr Peninsula (Chernov, 1985).

Figure 6.7 Latitudinal distribution of soil fungi (top) and bacilla (bottom). Recalculated from data in Mirchink (1988).

The hyphal length of fungi in the Arctic shows a latitudinal trend in which the abundance of fungi, as measured by hyphal length, decreases towards the North. Although it is not known if this trend also applies to the species diversity of fungal mycelia (the below ground network of fungal filaments or hyphae), it is clear that the amount of fungal hyphae is low in the Arctic (Robinson et al., 1996). In the high Arctic, fungal hyphal length was 23 ±1 mg\(^{-1}\) in a polar semi desert on Svalbard (78° 56’N), 39 mg\(^{-1}\) on a beach ridge, and 2228 in a mesic meadow on Devon Island (75° 33’N). At Barrow, Alaska hyphal length was 200 mg\(^{-1}\). In a sub-Arctic mire in Swedish Lapland, hyphal length was 3033 mg\(^{-1}\). These values can be compared with 6050-9000 for temperate uplands in the UK and 1900-4432 mg\(^{-1}\) for temperate woodland soils.

Summary: Implications of current species distributions for future biotic change

Species diversity appears to be low in the Arctic, and decreases from the boreal forests to the polar deserts of the extreme North. Only about 3% (about 5,900 species) of the world’s plant species (excluding algae) occur in the Arctic North of the treeline. However, primitive plant species of mosses and lichens are particularly abundant. Although the number of plant species in the Arctic is low in general, individual communities of small Arctic plants have a diversity similar to or higher than those of boreal and temperate zones: there can be 25 species per square decimeter. Latitudinal gradients suggest that Arctic plant diversity is sensitive to climate, and species number is least sensitive to temperature near the southern margin of the tundra. The temperature gradient that has such a strong influence on species diversity occurs over much shorter distances in the Arctic than in other biomes.

The diversity of Arctic animals beyond the latitudinal treeline (about 6,000 species) is nearly twice as great as that of vascular plants and bryophytes. As with plants, the Arctic fauna accounts for about 3% of the global total, and, in general, primitive groups (e.g., springtails,) are better represented in the Arctic than are advanced groups such as beetles. In general, the decline in animal species with increasing latitude is more pronounced than that of plants (frequently greater than 2.5-fold). An important consequence of the decline in numbers of species with increasing
latitude is an increase in dominance. “Super-dominant” plant and animal species (such as lemmings) occupy a wide range of habitats, and generally have large effects on ecosystem processes.

Microbial organisms are more difficult to enumerate. Arctic soils contain large reserves of microbial biomass, although diversity of all groups of soil microorganisms is lower in the Arctic than further South. Many common bacteria and fungi are rare or absent in tundra areas. As with plants and animals, there are large reductions in numbers of microbial species with increasing latitude, and increasing dominance of the species that occur.

The latitudinal temperature gradient within tundra is stronger than for any other biome, and outlier populations of more southerly species frequently exist in favorable microenvironments far North of their centers of distribution. Consequently, migration of southerly taxa is very likely to occur more rapidly in the Arctic than in other biomes. Temperature-induced biotic change will probably occur most strongly at the northern extreme of tundra, where species distributions are most temperature-sensitive.

The initial response of diversity to warming will likely be an increase in diversity of plants, animals, and microbes and reduced dominance of species that are currently widespread. Taxa most likely to expand into tundra are boreal taxa that currently exist in river valleys and could spread into the uplands or animal groups such as wood-boring beetles that are presently excluded due to lack of food resources. Although current extreme environmental conditions restrain the metabolic activity of Arctic microbes, they preserve huge potential that is ready to display the same activity as boreal analogs immediately after climate warming. Warming could cause extinction of some few Arctic plants that currently occur in narrow latitudinal strips of tundra adjacent to the sea. Some animals are Arctic specialists and could possibly face extinction. Those plant and animal species that have their centers of distribution in the high- or mid-Arctic are most likely to show reduced abundance in their current locations in the face of projected warming.

### 3.3 General characteristics of the Arctic’s species and their adaptations in the context of changes in climate and UV-B radiation

#### 3.3.1 Plants

For the past 60 years, Arctic plant ecologists have been concerned with the adaptations and traits of Arctic plants that enable them to survive in harsh climates (e.g. Sørensen, 1941; Russel, 1940; Billings and Mooney, 1968; Bliss, 1971; Porsild, 1951; Savile, 1972). It is now important to consider how plants that are adapted to harsh environments can respond to climatic warming and particularly how former adaptations might constrain their survival when they compete with more aggressive species immigrating from the South. Only in the past 20 years have ecologists considered Arctic plant adaptations to UV-B radiation (e.g. Robberecht et al., 1980; Björn, 2002).

Plant adaptations to the Arctic climate are relatively few compared with adaptations of plants to more southerly environments (Savile, 1972; Porsild, 1951) for several reasons (Jonasson et al., 2000): a) Arctic plants have inhabited Arctic regions (except for ice free refugia) for a relatively short period of time, particularly in Canada and Yamal, b) life spans and generation times are long with clonal reproduction predominating, c) flowering and seed set are relatively low and insecure from year to year, d) the complexity of the plant canopy is relatively small and the canopy is low so that climbing plants with tendrils, thorns etc. are not present. Annuals and ephemeral species are very few, e.g. *Euphrasia frigida* and *Koenigia islandica*. Many Arctic plants are pre-adapted to Arctic conditions (Crawford et al., 1994) and have migrated to the Arctic along mountain chains (Billings, 1992) or have migrated along upland mires and bogs.
Although specific adaptations to Arctic climate and UV-B are absent or rare, the Arctic’s climate and UV-B regime have selected for a range of plant characteristics (Table 6.5).

The first filter for plants that can grow in the Arctic is freezing tolerance, which excludes approximately 75% of the world’s vascular plants (Körner, 1995). However, many temperature effects on plants, particularly those with roots and in the long-term, are indirect (Chapin, 1983). Plant nutrients in Arctic soils, particularly nitrogen, are available to higher plants (with roots) at low rates (Russell, 1940) because of slow microbial decomposition and mineralization rates of organic matter constrained by low temperatures (Heal et al., 1981). Arctic plants use different strategies for nutrient uptake (Callaghan et al., 1991), and different sources of nitrogen, which reduces competition among plants and facilitates greater plant diversity (McKane et al., 2002).

Table 6.5 Summary of major current characteristics of Arctic plants related to climate and UV-B radiation

<table>
<thead>
<tr>
<th>Climatic factor</th>
<th>General effects on plants</th>
<th>Adaptations/characteristics of Arctic plants</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Above ground environment</td>
<td></td>
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<tr>
<td>Freezing temperatures</td>
<td>Plant death</td>
<td>Evergreen conifers tolerate temperatures between -40°C and -90°C; Arctic herbaceous plants between -30°C and -196°C</td>
<td>Larcher, 1995</td>
</tr>
<tr>
<td>Ice encapsulation</td>
<td>Death through lack of oxygen</td>
<td>Increased anoxia tolerance</td>
<td>Crawford et al., 1994</td>
</tr>
<tr>
<td>Low summer temperatures</td>
<td>Reduced growth</td>
<td>Increased root growth, nutrient uptake and respiration</td>
<td>Shaver and Billings, 1975; Chapin, 1974; Mooney and Billings, 1961; Mølgaard, 1982</td>
</tr>
<tr>
<td></td>
<td>Minimized coupling between the vegetation surface and the atmosphere: cushion plants can have temperature differentials of 25 °C</td>
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<td></td>
<td>Occupation of sheltered microhabitats and south-facing slopes</td>
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<tr>
<td>Short, late growing seasons</td>
<td>Constraint on available photosynthetically active radiation and time for developmental processes</td>
<td>Long life cycles</td>
<td>Callaghan and Emanuelsson, 1985</td>
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<tr>
<td></td>
<td></td>
<td>Slow growth and productivity</td>
<td>Wielgolaski et al., 1981</td>
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<tr>
<td></td>
<td></td>
<td>Dependence on stored resources</td>
<td>Jonasson and Chapin, 1985</td>
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<tr>
<td></td>
<td></td>
<td>Long flowering cycles with early flowering in some species</td>
<td>Sørensen, 1941</td>
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<tr>
<td></td>
<td></td>
<td>Increased importance of vegetative reproduction</td>
<td>Bell and Bliss, 1980</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Clonal growth: clones surviving for thousands of years</td>
<td>Jónsdóttir et al., 2000</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Long-lived leaves maximizing investment of carbon</td>
<td>Bell and Bliss, 1977</td>
</tr>
<tr>
<td>Inter-annual variability</td>
<td>Sporadic seed set and seedling recruitment</td>
<td>Dependence on stored resources</td>
<td>Jonasson and Chapin, 1985</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Long development processes buffer effects of any one year</td>
<td>Sørensen, 1941</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Clonal growth</td>
<td>Callaghan and Emanuelsson, 1985; see also Molau and Shaver, 1997; Brooker et al., 2001; Molau and Larsson, 2000</td>
</tr>
<tr>
<td>Snow depth and duration</td>
<td>Negative: constrains length and timing of growing season.</td>
<td>Where snow accumulates, snow beds form in which specialized plant communities occur</td>
<td>Gjerevoll, 1956</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Where snow is blown off exposed ridges (fell fields), plants are exposed to summer drought, winter herbivory and extreme temperatures</td>
<td>Billings and Bliss, 1959; Saville, 1972</td>
</tr>
<tr>
<td>Exerts mechanical pressure on plants</td>
<td>Responses and adaptations not measured</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Positive: Insulation in winter (it is seldom colder than -5°C under a 0.5 m layer).</td>
<td>Low plant stature</td>
<td>Crawford, 1989</td>
<td></td>
</tr>
<tr>
<td>Reduction of plant temperature extremes and freeze-thaw cycles</td>
<td>Low stature to remain below winter snow cover reduces the risk for premature dehardening</td>
<td>Ögren 1996; 1997</td>
<td></td>
</tr>
<tr>
<td>Protection from wind damage, abrasion by ice crystals and some herbivory.</td>
<td>Low stature to remain below winter snow cover: growth in sheltered locations</td>
<td>Sveinbjörnsson et al., 2002</td>
<td></td>
</tr>
<tr>
<td>Protection from winter desiccation when water loss exceeds water supply from frozen ground.</td>
<td>Low stature to remain below winter snow cover, deciduous growth</td>
<td>Barnes et al., 1996; Havas, 1985; Ögren, 1996; Taulavuori et al., 1997a; c</td>
<td></td>
</tr>
<tr>
<td>Protection from chlorophyll bleaching due to light damage in sunny habitats</td>
<td>Low stature to remain below winter snow cover; deciduous growth</td>
<td>Curl et al., 1972</td>
<td></td>
</tr>
<tr>
<td>Source of water and nutrients late into the growing season</td>
<td>Zonation of plants species related to snow depth and duration</td>
<td>Gjerevoll, 1956; Fahnestock et al. 2000</td>
<td></td>
</tr>
<tr>
<td>Increased UV-B radiation</td>
<td>Damage to DNA that can be lethal or mutagenic</td>
<td>Robberecht et al., 1980; Semerdjieva et al., 2003</td>
<td></td>
</tr>
<tr>
<td>Reflective/absorptive barriers such as thick cell walls and cuticles, waxes and hairs on leaves, and physiological responses such as the induction or presence of UV-B absorbing pigments (e.g. flavonoids) and an ability to repair some UV-B damage to DNA. Repair is mediated through the enzyme photolyase that is induced by UV-A. There is so far no indication of any specific adaptation of plants in the Arctic to UV-B radiation.</td>
<td>Li et al., 2002a;b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Variable CO₂ concentrations</td>
<td>Increased CO₂ concentrations usually stimulate photosynthesis and growth if other factors are non-limiting. Increased C:N in plant tissues</td>
<td>Tissue and Oechel, 1987</td>
<td></td>
</tr>
<tr>
<td>Photosynthesis of Alaskan graminoids acclimated to high CO₂ concentrations in 6 weeks with no long term gain</td>
<td>Beering and Rundgren, 2000</td>
<td></td>
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</tr>
<tr>
<td>The dwarf willow (<em>Salix herbacea</em>) has been able to change its carbon metabolism and morphology in relation to changing CO₂ concentrations throughout the last 9,000 years</td>
<td>Sonesson et al., 1992</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species such as the moss <em>Hylocomium splendens</em> are already adapted to high CO₂ concentrations; they frequently experience 400–450 ppm, and sometimes over 1,100 ppm, to compensate for low light intensities under mountain birch woodland</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2) Soil environment</td>
<td>Reduced growth and reproduction</td>
<td>Conservation of nutrients in nutrient poor tissues</td>
<td>Wielgolaski et al., 1975</td>
</tr>
<tr>
<td>Availability of nutrients, particularly nitrogen, at low rates</td>
<td>High nitrogen retention time resulting from considerable longevity of plant organs and resorption of nutrients from senescing tissues and retention of dead leaves within plant tufts and cushions</td>
<td>Berendse and Jonasson, 1992</td>
<td></td>
</tr>
<tr>
<td>Substantial rates of nutrient uptake at low temperatures.</td>
<td>Chapin and Bloom, 1976</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Increased surface area for nutrient uptake by increased biomass of roots relative to shoots (up to 95% of plant biomass can be below ground) associations with mycorrhizal fungi and uptake of N by rhizomes</td>
<td>Chapin, 1974; Shaver and Cutler, 1979</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Some Arctic plants can take up nutrients in organic forms, thereby by-passing some of the slow decomposition and mineralization processes Dependence on atmospheric nutrient deposition in mosses and lichens</td>
<td>Michelsen et al., 1998</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil movement at various spatial scales</td>
<td>Freeze-thaw cycles heave ill-adapted plants from the</td>
<td>Areas of active movement select for species with elastic and shallow roots or cryptogams without roots.</td>
<td>Perfect et al., 1988; Wager, 1938;</td>
</tr>
</tbody>
</table>
Many of the adaptations of Arctic species to their current environments, such as slow and low growth, are likely to limit their responses to climate warming and other environmental changes. If changes in climate and UV adversely affect species such as mosses, that play an important role in facilitation, then normal community development and recovery after disturbance could be constrained. Many Arctic plant characteristics are likely to cope with abiotic selective pressures (e.g. climate) more than biotic (e.g. inter-specific competition). This is likely to render Arctic organisms more susceptible to biological invasions at their southern distributional limits while populations at their northern range limit (e.g. boreal species in the tundra) will probably respond more than species at their southern limit to warming *per se*. Thus, as during past environmental changes, Arctic species are very likely to change their distributions rather than evolve significantly.

**Summary: General characteristics of Arctic plant species in relation to climate and implications for their responses to climate change**

Plant adaptations to the Arctic climate are absent or rare: many species are pre-adapted. The first filter for Arctic plants is freezing tolerance, which excludes approximately 75% of the world’s vascular plants. Short growing seasons and low solar angles select for long life cycles in which slow growth often uses stored resources while development cycles are often extended over multiple growing seasons. Some plant species occupy microhabitats, or exhibit behavior or growth forms that maximize plant temperatures compared with ambient. Low soil temperatures reduce microbial activity and the rates and magnitude of nutrient availability to higher plant roots. Mechanisms to compensate for low nutrient availability include the conservation of nutrients in nutrient poor tissues, resorption of nutrients from senescing tissues, enhanced rates of nutrient uptake at low temperatures, increased biomass of roots

<table>
<thead>
<tr>
<th>3) Biotic environment</th>
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</tr>
</thead>
<tbody>
<tr>
<td><strong>Herbivory</strong></td>
<td>Arctic plants do not have some morphological defenses e.g. thorns found elsewhere. Many plants have secondary metabolites that deter herbivores. Some substances are induced by vertebrate and invertebrate herbivores. Protected growing points, continuous leaf growth in summer, rapid modular growth in some graminoids, regeneration from torn fragments of grass leaves, mosses and lichens.</td>
</tr>
<tr>
<td></td>
<td>Removal of plant tissue sometimes leading to widespread defoliation and death</td>
</tr>
<tr>
<td><strong>Competition</strong></td>
<td>Secondary metabolites in some Arctic species inhibit the germination and growth of neighboring species.</td>
</tr>
<tr>
<td><strong>Facilitation</strong></td>
<td>Positive plant interactions are more important than plant competition in severe physical environments Nitrogen fixing species in expanding glacial forefields facilitate the colonization and growth of immigrant plants species Plant aggregation can confer advantages of shelter from wind Hemiparasites can stimulate nutrient cycling of potential benefit to the whole plant community</td>
</tr>
</tbody>
</table>
relative to shoots, associations with mycorrhizal fungi, uptake of nutrients in organic forms, and uptake of nitrogen by rhizomes. Temperature fluctuations around 0 °C cause frost-heave phenomena that can up-root ill-adapted plants.

Snow distribution determines the period over which plants can intercept solar radiation and can grow. A snow cover insulates plants against low air temperatures in winter, extremes of temperature in spring, protects plants from physical damage from abrasion by ice crystals and provides a source of water and often late into the growing season. Where snow cover is thin, for example in exposed ridge tops, growing seasons are usually long but water can become limiting: where snow accumulates in sheltered depressions, snow beds form in which specialized plant communities occur.

Many Arctic plants are pre-adapted to relatively high levels of UV-B radiation. They exhibit various mechanisms to protect DNA and sensitive tissues from UV-B and an ability to repair some UV-B damage to DNA. Thick cell walls and cuticles, waxes and hairs on leaves, and the presence or induction of UV-B absorbing chemical compounds in leaves, protect sensitive tissues. There appear to be no specific adaptations of Arctic plant species to high CO₂ concentrations.

Arctic plants do not show the often complex interactions with other organisms prevalent in southern latitudes. Arctic plants are adapted to grazing/browsing mainly by chemical defenses rather than the possession of spines and thorns. Facilitation increases in importance relative to competition at high latitudes and altitudes.

Thus, many of the characteristics of Arctic species to their current environments are likely to limit their responses to climate warming and other environmental changes. Many characteristics are likely to cope with abiotic selective pressures (e.g. climate) more than biotic (e.g. inter-specific competition). This is likely to render Arctic organisms more susceptible to biological invasions and they are very likely to change their distributions rather than evolve significantly in response to warming.

3.3.2 Animals

Classical Arctic zoology typically focused on morphological and physiological adaptations to a life under extremely low winter temperatures (Schmidt-Nielsen, 1986; Scholander et al., 1950). Physiological studies contribute to a mechanistic understanding of how Arctic animals cope with extreme environmental conditions (especially low temperatures), and what makes them different from their temperate counterparts. Ecological and evolutionary studies focus on how life history strategies of Arctic animals have evolved to tolerate environmental variation in the Arctic, how flexible life histories (both in terms of phenotypic plasticity and genetic variation) are adapted to environmental variation, and how adjustments in life history parameters such as survival and reproduction translate in to population dynamics patterns.

3.3.2.1 Animal adaptation to low temperatures

Arctic animals have evolved a set of adaptations that make them able to conserve energy at low winter temperatures. Warm-blooded animals that persist throughout the Arctic winter have thick coats of fur and feathers that often turn white (Scholander et al., 1950). The body shapes of high Arctic mammals such as reindeer, collared lemmings, Arctic hares and Arctic foxes are rounder and their extremities shorter than their temperate counterparts (Allen’s rule). The body size within some vertebrate taxa increase towards the North (Bergman’s rule), but there are several notable Arctic exceptions to this (e.g. reindeer; Klein, 1999; muskox; Smith et al., 2002) There are few physiological adaptations in homeotherms (i.e. warm blooded) that are unique to Arctic animals. However, several adaptations may be considered to be typically Arctic including fat storage (e.g. reindeer and Arctic fox; Prestrud and Nilssen, 1992) and lowered body core
temperature and reduced basal metabolism in the winter (e.g. Arctic fox; Fuglei and Øritsland, 1999). While hibernation during the winter is found in a few Arctic mammals such as the Arctic ground squirrel, most homeothermic animals are active year round. Small mammals such as shrews, voles and lemmings with relatively large heat losses due to a high surface-to-volume ratio stay in the subnivean space (a cavity below the snow) where they are protected from low temperatures during the winters. Even medium-sized birds and mammals such as ptarmigan and hares seek thermal refuges in snow caves when resting. In high Arctic areas, the normal diurnal activity patterns known from more southern latitude, are replaced by activity patterns that are independent of the time of the day (e.g. Svalbard ptarmigan; Reierth and Stokkan, 1998).

In heterothermic (i.e. cold-blooded) invertebrates hairiness and melanism (dark pigmentation) enable them to warm up in the summer season. Invertebrates survive low winter temperatures in dormancy mainly due to two strategies of cold hardiness; i.e. freeze tolerance and freeze avoidance (Strathdee and Bale, 1998). Typically, super-cooling points are lower in Arctic than in temperate invertebrates. Freeze tolerance, which appears to be an energetically less costly strategy than extended supercooling, is a common strategy in very cold regions. Wingless morphs occur frequently among Arctic insects, probably because limited energy during the short growth season is allocated to development and reproduction, rather than in an energetically costly flight apparatus. A short growth season also constrains insect body size and number of generations per year. Life cycles are often extended in time and/or simplified because invertebrates may need several seasons to complete their life cycles. Small body sizes in Arctic insects seem to be a strategy to shorten generation time (Strathdee and Bale, 1998). Moreover, individuals from Arctic populations are able to grow faster at a given temperature than southern conspecifics (e.g. Birkemoe and Leinaas, 2000). Thus Arctic invertebrates may be particularly efficient in utilizing relatively short warm periods to complete life cycle stages.

A short breeding season also underlies several life history adaptations in birds and mammals such as synchronized breeding, shortened breeding season, specific molting patterns and mating systems (Mehlum, 1999). Although adjustments to low temperatures and short growth seasons are widespread in Arctic animals, successful species cannot be generalized with respect to particular life history traits (Convey, 2000). Both flexible and programmed life cycles are common in polar arthropods (Danks, 1999).

While there are many examples that show that winter-temperatures lower than species-specific tolerance limits set the northern borders of the geographic distribution of animals, there are hardly any examples that demonstrate that high temperatures alone determine how far South terrestrial Arctic animals are found. Southern range borders are typically set by a combination of abiotic factors (e.g. temperature and moisture in soil invertebrates) or, probably most often, by biotic factors such as food resources, competitors and natural enemies.

3.3.2.2 Animal migrations and habitat selection

Many vertebrates escape unfavorable conditions through movements, either long-distance migrations or more short-range seasonal movements, between different habitats in the same landscape. Seasonal migration to over-wintering areas in the South is almost the rule in Arctic birds. Climate may in several ways interfere with migrating birds, such as mismatched timing of
migration, habitat loss at stopover sites and weather en route (Lindström and Agrell, 1999) and a mismatch in the timing of migration and the development of invertebrate food in Arctic ponds (Chapter 7). Many insects belonging to the boreal forest invade the low Arctic tundra in quite large quantities every summer (Chernov and Matveyeva, 1997), but few of these are likely to return in the fall. Year-round resident tundra birds are very few and include species such as Arctic red polls, willow grouse, ptarmigan, raven, gyr falcon and snowy owl. Like several other Arctic predators that specialize on feeding on lemmings and Arctic voles, the snowy owl emigrates when cyclic lemming populations crash to seek high-density prey populations elsewhere in Arctic and sub-Arctic areas. Such a nomadic life style is also found in small passerine seed-eating birds such as redpolls and crossbills in the forest tundra. These birds move between areas with asynchronous mast years in birch and conifers. Also a substantial fraction of Arctic foxes emigrates after lemming peaks and sometimes these emigrations may extend far into the taiga zone (Hersteinsson and Macdonald, 1992). Most reindeer and caribou populations perform seasonal migration from coastal tundra in summer to continental areas in forest tundra and taiga in the winter. Inuit ecological knowledge explains caribou migrations as triggered by seasonal “cues”, such as the length of the day, temperature or ice thickness (Thorpe et al., 2001). Reindeer on isolated Arctic islands are more sedentary without pronounced seasonal migrations (Tyler and Øritsland, 1989). Lemmings and ptarmigans shift habitat seasonally within the same landscapes (Kalela, 1961). In population peak years these seasonal habitat shifts may turn into more long distance mass movements in the Norwegian lemming (Henttonen and Kaikusalo, 1993). For small mobile animals, for example wingless soil invertebrates such as collembola and mites, habitat selection on a very small spatial scale (microhabitat selection) enables the individuals to find spatial refuges with temperature and moisture regimes adequate for survival (Hodkinson et al., 1994; Ims et al., 2004). The variability in microclimatic conditions may be extremely large in the high Arctic (Coulson et al., 1995).

3.3.2.3 Animal adaptations to the biotic environment

Generalists in terms of food and habitat selection seem to be more common among Arctic animals than in communities further South (e.g. Strathdee and Bale, 1998). This may be either due to fewer competitors and a less tightly packed niche-space in Arctic animal communities and/or because food resource availability is less predictable and the appropriate strategy is to opt for more flexible diets. Notable exceptions to food resource generalism are lemming predators (e.g. least weasels, several owls and raptors and skuas) and a number of host-specific phytophagous insects (e.g. aphids and saw flies). Many waterbirds, such as geese with 75%, and sandpipers (Calidrids) with 90% of the species breeding in the Arctic, are habitat specialists. Some species exhibit a large flexibility in their reproductive strategy based on food resources. Coastal populations of Arctic foxes with a relatively predictable food supply from the marine ecosystem (e.g. sea bird colonies) have smaller litter sizes than inland “lemming foxes” relying on a highly variable food supply (Tannerfeldt and Angerbjörn, 1998). Specialists on highly fluctuating food resources such as seeds from birch and conifers and lemmings/voles respond to temporary superabundant food supplies by having extraordinary high clutch/litter sizes.

High Arctic environments contain fewer natural enemy species (e.g. predators and parasites) and some animals seem to be less agile (e.g. Svalbard reindeer; Tyler and Øritsland, 1989) and are possibly less disease resistant (Piersma, 1997).
3.3.2.4 UV-B

Little is known about animal adaptations to UV-B radiation. Clearly, non-migrant species such as reindeer, Arctic foxes, hares and many birds have white feathers and fur that presumably reflect some UV-B radiation. There is some evidence, however, that feathers can be affected by high UV-B (Bergman, 1982) although this early research needs to be repeated. There is also a possibility that fur absorbs UV-B. Eyes of Arctic vertebrates experience extremes of UV-B from dark winter conditions to high UV-B environments in springtime. However, mechanisms of tolerance are unknown. Invertebrates in general have DNA that is robust to UV-B damage (Koval, 1988) and various adaptations to reduce UV-B absorbance. Some caterpillars of the sub-Arctic possess pigmented cuticles that absorb in the UV-B wavelengths while pre-exposure to UV-B can induce pigmentation (Buck and Callaghan, 1999). Collembolans and possibly other invertebrates have dark pigmentation that plays a role in both thermoregulation and UV-B protection (Leinaas, 2002).

3.3.2.5 Population dynamics patterns

In tundra habitats, population cycles in small to medium sized birds and mammals are the rule, with few exceptions. The periods of the cycle in lemmings and voles vary geographically and are between 3 and 5 years. Cyclicity such as spatial synchronicity and period between population peak years all seem to be associated with geographic climate gradients in Fennoscandia (coast-inland and South-North; Hansson and Henttonen, 1988; Strann et al., 2002), although the biotic mechanisms involved are still much debated (Hanski et al., 2001). Lemming populations may show geographic variation in the period of the cycle within the Arctic Siberia; also for example a long period of 5 years on Wrangel island and relatively short period of 3 years between peak years in Taymyr (Chernov and Matveyeva, 1997). Within regions (for example northern Fennoscandia) small rodent cycles may show distinct interspecific synchrony over large spatial scales (Myrberget, 1973). However, recent spatially extensive surveys in northern Canada (Predavec et al., 2001) and Siberia (Erlinge et al., 1999) have indicated that the spatial synchrony of lemming populations is not as large-scale as the snow-shoe hare cycles in boreal N-America (Elton and Nicholson, 1942). This is at least partly due to the geographically variable cycle period (see above).

Small and medium sized bird and mammal predators follow numerically the dynamics of their lemming and vole prey species (Wiklund et al., 1999). The signature of the lemming and vole dynamics can also be found in the reproductive success and demography of mammals and birds, for example waders and geese (e.g. Bety et al., 2002), that serve as alternative prey to the predators of lemmings. Among northern insects, population cycles are best known in geometrid moths, particularly *Epirrita autumnata*, a species exhibiting massive population outbreaks with approximately 10 year intervals that extend into the forest tundra (Tenow, 1972; 1996). On the tundra, no herbivorous insects are known to cycle (Chernov and Matveyeva, 1997). However, the population dynamics of tundra invertebrates is poorly known due to the lack of long-term time series data. It is clear, however, that soil invertebrates such as Collembola (Birkemoe and Sømme, 1998; Hertzberg et al., 2000) sometimes exhibit large inter-annual fluctuations in population density. Large fluctuations in numbers are also known in the Arctic ungulate...
populations (reindeer/caribou and musk oxen) and seem to be the outcome of several biotic factors in combination with climatic variation (Klein, 1996; 1999; Morneau and Payette, 2000).

Summary: General characteristics of Arctic animal species in relation to climate and implications for their responses to climate change

Terrestrial Arctic animals possess many adaptations that enable them to persist in the Arctic’s climate. Physiological and morphological traits in warm-blooded vertebrates (mammals and birds) include thick fur and feather plumages, short extremities, extensive fat storages before winter and metabolic seasonal adjustments, while cold blooded invertebrates have developed strategies of cold hardiness, high body growth rates together with pigmented and hairy bodies. Arctic animals can survive under an amazingly wide range of temperatures, including high temperatures. A short growing season represents a challenge for most Arctic animals and life history strategies have evolved to enable individuals to fulfill their life cycles under time constraints and high environmental unpredictability. The biotic environment (e.g. the ecosystem context) of Arctic species is relatively simple with few enemies, competitors and available food resources. For those reasons, Arctic animals have evolved fewer traits related to competition for resources, predator avoidance and resistance towards diseases and parasites than their southern counterparts. Specifically adjusted life cycles to seasonal and multi-annual fluctuations in resources are particularly important because such fluctuations are very pronounced in terrestrial Arctic environments. Many Arctic animals possess adaptations for escaping unfavorable weather, resource shortage or other unfavorable conditions by winter dormancy or by selection of spatial refuges at a wide range of spatial scales from microhabitat selection at any given site, through seasonal habitat shifts within landscapes, to long distance seasonal migrations within or across geographic regions.

Based on the above general characteristics, if climate changes, terrestrial Arctic animals are likely to be most vulnerable to following conditions: (1) warmer climate in summer that induces desiccation in invertebrates, (2) climatic changes that interfere with migration routes and staging sites en route for long distance migrants, (3) climatic events that alter snow conditions and freeze-thaw cycles in winter resulting in unfavorable conditions of temperature, O\textsubscript{2} and CO\textsubscript{2} for animals below the snow, and limited resource availability (e.g. vegetation or animal prey) for animals above the snow, (4) climate changes that disrupt behavior and life history adjustments to the timing of reproduction and development that are currently linked to seasonal and multi-annual peaks in food resource availability, (5) influx of new competitors, predators, parasites and diseases.

3.3.3 Microorganisms

As a group, microorganisms are highly mobile, can tolerate most environmental conditions and they have short generation times which can facilitate rapid adaptation to new environments associated with changes in climate and UV-B radiation.

3.3.3.1 Adaptation to cold

The development to resist freezing (and to restore activity after warming) and the ability to metabolize below the freezing point are fundamental microbial adaptations to cold climates prevailing at high latitudes.

Cell viability depends dramatically on the velocity of freezing, which defines the formation of intracellular water crystals (Kushner, 1981; Mazur, 1980). Cold-adapted microbial species are characterized by remarkably high resistance to freezing due to the presence of specific intracellular compounds (metabolic antifreeze), stable and flexible membranes and other adaptations. Lichens are extreme examples (Kappen, 1993): the moist thalli of such species as Xanthoria candelaria and Rhizoplaca melanophthalma fully tolerated gradual or rapid freezing.
to -196°C, and even after storage up to several years, almost immediately resumed normal photosynthetic rates when warmed and wetted. For 5-7 months of cold and continuous darkness, they remain green with intact photosynthetic pigments. However, freeze-resistance is not a unique feature of Arctic organisms.

Microorganisms’ ability to grow and metabolize in frozen soils, subsoils or water, is generally thought to be insignificant. However, microbial growth and activity below freezing point has been recorded in refrigerated food (Larkin and Stokes, 1968) as well as in Arctic and Antarctic habitats such as sea ice, frozen soil and permafrost (Kappen et al., 1996; Schroeter et al., 1994). Such activity has important implications for ecosystem function. The year-round field measurements of gas fluxes in Alaska and Northern Eurasia revealed that winter CO₂ emissions can account for up to half of the annual emissions of CO₂ (Sommerfeld et al., 1993; Zimov et al., 1993; Oechel et al., 1997; Panikov and Dedysh, 2000), implying a significant cold-season activity of psychrophilic (“cold-loving”) soil microbes. Soil fungi (including mycobionts in lichens) have been considered as the most probable candidates for the majority of the below-zero tundra soil respiration (Flanagan and Bunnell, 1980) because their live biomass was estimated to be ten times larger than that of co-habiting bacteria.

Winter CO₂ emissions have been also explained by other mechanisms, e.g. the physical release of summer-accumulated gases or abiotic CO₂ formation due to cryoturbation (Coyne and Kelley, 1971). Most recent studies (Finegold, 1996; Geiges, 1996; Russell, 1990; Mazur, 1980; Rivkina et al., 2000), agree that microbial growth is limited at about −12 °C and that occasional reports of microbial activity below -12°C (e.g. continuous photosynthesis in Arctic and Antarctic lichens down to -17°C (Kappen et al., 1996; Schroeter et al., 1994) and photosynthetic CO₂ fixation at -24°C (Lange and Metzner, 1965)) were not carefully recorded and confirmed. Under laboratory conditions, Rivkina et al. (2000) quantified microbial growth in permafrost samples at temperatures down to −20 °C. However the data points below −12 °C turned out to be close to the detection limits of the highly sensitive technique that they employed. The authors concluded that nutrient uptake at −20 °C could be measured, but only transiently ‘whereas in nature (i.e., under stable permafrost conditions)... the level of activity, if any, is not measurable …’ (Rivkina et al., 2000, p. 3232).

Recently, a new, precise, technique was applied to frozen soil samples collected from Barrow, Alaska, and incubated at a wide range of subzero temperatures under laboratory conditions (Panikov et al., 2001). The rate of CO₂ production declined exponentially with temperature and unfrozen water content when soil was cooled down below zero, but it remained surprisingly positive and measurable, e.g. 8 ng CO₂-C/day/kg, at −39 °C. A range of experimental results and treatments confirmed that this CO₂ production at very low temperatures was due to microbial respiration, rather than to abiotic processes.

Dark pigmentation causes higher heat absorption in lichens, being especially favorable in the cold polar environment (Lange, 1954; Kershaw, 1983).

3.3.3.2. Adaptations to drought

Freezing is always associated with deficiency of available water. Thus, true psychrophilic
organisms must also be *xerotolerant*, i.e. adapted to extremely dry environments. A number of plants and microorganisms in polar deserts, such as lichens (symbionts of algae and fungi) are termed *poikilohydrous*, meaning that they tend to be in moisture equilibrium with their surroundings (Blum, 1974). They have high-desiccation tolerance and are able to survive water loss of more than 95% and long periods of drought. Quick water loss inactivates the thallus and then in the inactive state, the lichen is safe from heat-induced respiratory loss and heat stress (Lange, 1953; Kappen, 1974). In unicellular microorganisms, drought-resistance can be also significant, although mycelial forms of microbial life (fungi and actinomycetes) seem to have a much higher capability due to their more efficient cytoplasm compartmentalization and spore formation.

3.3.3.3. Adaptations to mechanical disturbance

Wind, sand and ice-blasts, and seasonal ice oscillations are characteristic features of Arctic environments that affect colonization and survival of organisms. Most lichens are adapted to such effects by forming a mechanically solid thallus firmly attached to the substrate. Windswept habitats such as hillsides can be favorable if they provide suitable rough substrate and receive sufficient moisture from the air. In contrast, shallow depressions or small valleys, although more sheltered, are bare of lichens because snow recedes from them only for very brief periods each season or persists over several years. This phenomenon is one reason for the so-called trimline effect (Smith, 1972; Corner and Smith, 1973; Koerner, 1980). The abrasive forces of the ice at the bottoms of glaciers may destroy all epilithic (rock-attached) lichen vegetation, but lichens once established are able to survive long periods of snow cover, even glacial periods (Kappen, 1993).

3.3.3.4. Adaptation to irradiance

Strong pigmentation is typical for numerous microorganisms of tundra and polar deserts, especially for those which are frequently or permanently exposed to sun on the soil surface (lichens and epiphytic bacteria). Pigments (melanin, melanoids, carotenoids, etc) are usually interpreted as a protection against strong irradiation. Pigmentation may be constitutive for particular species or appear as a plastic response to irradiance, e.g. originally colorless *Cladonia* and *Cladina* lichens quickly develop dark-pigmented thalli after exposure to stronger sun radiation (Ahmadjian, 1970). Buffoni Hall *et al.* (2002) demonstrated that in *Cladonia arbuscula ssp. mitis* an increase in phenolic substances is specifically induced by UV-B radiation, and that this increase leads to attenuation of the UV-B radiation penetrating into the thallus. Also the accumulation of the protective pigment parietin in *Xanthoria parietina* is induced specifically by UV-B radiation (Gauslaa and Ustvedt, 2003), while in *Cladina uncialis* and *Cladina rangiferina* only UV-A radiation had a stimulating effect on the accumulation of usnic acid and atranorin, respectively. Photorepair of radiation-damaged DNA in *Cladonia* requires not only light, but also high temperature and that the thallus is hydrated (Buffoni Hall *et al.*, 2003). As in higher plants, carotenoids protect against excessive photosynthetically active light (MacKenzie *et al.*, 2002) and perhaps also have a role in protection from ultraviolet radiation. In contrast to higher plants, flavonoids do not act as screening compounds in algae, fungi, and lichens.
Braga et al. (2001a;b) survey the UV sensitivity of conidia (spore-forming bodies) of thirty strains of the fungus *Metarhizium* (belonging to four species). This fungus is an important agent of insect disease. Exposure to UV-B within an ecologically relevant range, showed great differences between the strains: strains from low latitudes were generally more tolerant than those from high latitudes.

### 3.3.4 Algae

Seven inter-related stress factors (temperature, water, nutrient status, light availability and/or UV radiation, freeze/thaw events, length of growing season and unpredictability) are important for life in Arctic terrestrial and shallow wetlands (Convey, 2000). Cyanobacteria and algae have developed a wide range of adaptive strategies that allow them to avoid, or at least minimize injury. Three main strategies for coping with living in the Arctic terrestrial and wetland habitats are avoidance, protection and the formation of partnerships with other organisms (Elster and Benson, 2004). Poikilohydricity (tolerance of desiccation) and shelter strategies are frequently interconnected, and when combined with cell mobility and development of complex life cycles, afford considerable potential for avoidance. The extracellular production of protective compounds and structures such a multi-layered cell walls, sheets of mucilage that together with intracellular control of cell solute composition and viscosity (changes in the cell’s carbohydrate and polyols composition) is also a very common phenomenon. The association of cyanobacteria/algae with fungi in lichens gives a benefit of physical protection.

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**Summary: General characteristics of Arctic microorganisms in relation to climate and implications for their responses to climate change**

Arctic microorganisms are not only resistant to freezing, but some can metabolise at temperatures down to −39 °C. This process could be responsible for up to 50% of annual CO₂ emissions during winter from tundra soils. Cold-tolerant microorganisms are usually also drought-tolerant. Microorganisms are tolerant of mechanical disturbance and high irradiance. Pigmentation protects organisms such as lichens from high irradiance including UV radiation and pigments can be present in considerable concentrations. Cyanobacteria and algae have developed a wide range of adaptive strategies that allow them to avoid, or at least minimize UV injury. However, in contrast to higher plants, flavonoids do not act as screening compounds in algae, fungi, and lichens.

As a group, microorganisms are highly adaptive, can tolerate most environmental conditions and they have short generation times which can facilitate rapid adaptation to new environments associated with changes in climate and UV-B radiation.

### 3.4 Phenotypic responses of Arctic species to changes in climate and UV-B radiation

Species responses to climate change are complex. They respond individualistically to environmental variables such as temperature (Chapin and Shaver, 1985a) and even various processes within one species (e.g. reproductive development, photosynthesis, respiration, leaf phenology in plants) respond individualistically to any one environmental change. Knowledge on how species respond to changes in temperature come from many sources including indigenous...
knowledge (IK), current species distributions related to climate, and experimental manipulations of temperature in the laboratory and field.

3.4.1 Specific responses of plants to changes in climate and UV-B radiation

The information presented below relates to individual plant species and how they have been found to respond to changes in various aspects of climate and UV. This information is taken mainly from experiments in which some climate variables or UV have been modified and the responses of the individual species have been determined while they are growing in natural communities.

3.4.1.1 Plant responses to current changes in climate

IK studies in Canada describe poor vegetation growth in eastern regions associated with warmer summers and less rain (Fox, 2002) while those in western regions describe increased plant biomass and growth, particularly in riparian areas and with moisture tolerant species such as shrubs (Thorpe et al., 2001; Riedlinger, 2001) due to lengthening of the active growing season, marked springtime warming and increased rainfall.

Inuit within the Tuktu Nogak project in the Kitikmeot region of Nunavut (Thorpe, 2000; Thorpe et al., 2001) observed that vegetation is more lush, plentiful and diverse in the 1990s compared to earlier decades. Willows and alders are described as taller, with thicker stem diameter and producing more branches, particularly along shorelines. Other indigenous communities are also reporting increases in vegetation, particularly grasses and shrubs. They say there is grass growing in places where there used to be only gravel. On Banks Island, in the Canadian western Arctic, Inuvialuit use the fact the umingmak (musk oxen) are staying in one place for longer periods of time as additional evidence that vegetation is richer (Riedlinger, 2001). In addition, Riedlinger (2001) has documented Inuvialuit observations of an increase in forbs such as qungalik (Arctic sorrel, Oxyria digyna), which is described as coming out earlier in the spring, and noticeably “bigger, fresher and greener”.

Monitoring of the annual quality and quantity of salmonberries locally called akpiks (=cloudberry=Rubus chamaemorus) by the Arctic Borderlands Ecological Knowledge Co-op, (Kofinas et al., 2002) documented recent observations of high temperatures early in the year that ‘burn’ berry plant flowers, early spring melt that results in inadequate moisture for the plants later in the year and intense summer sun that ‘cooks’ the berries before they can be picked. On Banks Island in the Western Canadian Arctic, local residents report years where the grass remained green right into autumn, leaving it vulnerable to freezing (Riedlinger, 2001). This corresponds to experiments that show the same effect on Svalbard (Robinson et al., 1998).

In northern Finland, marshy areas are said to be drying up. Sami reindeer herders from Kaldoaivi in Utsjoki have observed that berries such as bog whortleberry (Vaccinium uliginosum) have almost disappeared in some areas. Other berries such as cloudberrries (Rubus chamaemorus) and lingon berries (V. vitis-idaea) are said to have declined in the last 30 years (Helander, 2002). The indigenous peoples’ observations on declining berry production from Rubus chamaemorus are supported by experiments which postulate declines in growth in warm winters (Marks and
Taylor, 1978) and provide detailed mechanisms for fruit production (Lapinte, 2001; Wallenius, 1999; Korpelainen, 1994).

IK also records changes in species distribution: some existing species are becoming more widespread and new species are being seen. In addition to increased shrub abundance, Thorpe et al. (2001; 2002) documented reports of new types of lichens and flowering plants on Victoria Island in Nunavut and more individual plants of the same species (Thorpe, 2000). The increases in shrubs in this area correspond to aerial photographic evidence of increases in shrub abundance in Alaska (Sturm et al., 2001b). However, the reports of new types of plants, and lichens in particular, contrast with experimental evidence that shows a decrease in lichens and some mosses when flowering plant biomass increases (Cornelissen et al., 2001; Potter et al., 1995). A possible reason for this is that results from warming experiments cannot be extrapolated throughout the Arctic because of variations in recent and projected climate from cooling and warming (Chapters 2 and 4): warming experiments in continuous vegetation show declines of lichens whereas lichens can expand their distribution during warming in the high Arctic where vascular plant competitors are sparse (Heide-Jørgensen and Johnsen, 1998).

In contrast to observed responses of plants to recent warming, remote sensing by satellites has shown that the start dates of birch pollen seasons have been delayed at high altitudes and in the northern boreal regions of Fennoscandia (Høgda et al., 2002). Also, in the Faroe Islands, there has been a lowering of the alpine zone in response to a 0.25 °C cooling in the past 50 years (Fossa, 2003).

### 3.4.1.2 Predicted responses of plants to future changes in temperature

Warming per se is very likely to be favorable to the growth, development and reproduction of most Arctic plant species, particularly those with high phenotypic plasticity (flexible/responsive growth and development). However, other limiting factors such as nutrients and moisture or competition from immigrant species are likely to modify response to warming. In some cases, direct and indirect effects of warming are expected to generate negative responses.

- Increased respiration relative to photosynthesis, particularly in clonal plants that accumulate old tissues, can result in negative carbon balances (e.g. the cushion form ecotype (Figure 6.3) of Saxifraga oppositifolia (Crawford, 1997a) and some species of the herb Ranunculus (Cooper, 1996)).
- Cushion forms of Arctic plants including mosses, that have low atmospheric coupling and experience high temperatures could experience thermal death during warming, particularly when combined with reduced cooling by evapotranspiration under drought conditions.
- Exposure to high radiation and increases in temperature could possibly cause damage and death to some species, particularly those of shady and wet habitats, that have low thermo tolerances (as low as 42 °C in the herb Oxyria digyna; Gauslaa, 1984).
- During warming, Arctic species with conservative nutrient use strategies, slow growth and particularly strongly determined morphologies of plants such as those of cushion and mat plants, are likely to be at a competitive disadvantage with more responsive, faster growing, taller species immigrating from southern latitudes. After 6 years of shading (simulating competition), warming and fertilizing a heath and a fellfield community in
Swedish Lapland, shading was found to have the greatest effect on above ground growth (Graglia et al., 1997). In another experiment, flowering of the dwarf heather-like shrub Cassiope tetragona stopped when it was shaded (Havström et al., 1995a). In contrast, in a meta analysis by Dormann and Woodin (2002), no significant effect of shading was found on biomass.

Populations at the most environmentally extreme boundary of their distributions (in terms of latitude, altitude and habitat mosaics within landscapes) tend to be responsive to amelioration of physical environmental factors such as temperature that limit their distributions and have the potential to expand their distribution. In contrast, populations at the most environmentally benign boundary of their distribution tend to be constrained by competition with more responsive species of more benign environments (Wijk, 1986) and tend to be displaced by environmental amelioration.

An ITEX (International Tundra Experiment – Henry and Molau, 1997) meta-analysis of Arctic vascular plant species responses to simulated summer warming (1.2°C- 1.8 °C mean daily near surface and soil temperature increase) using standard open top chambers compared key species from 13 sites over a period of one to four years (Arft et al., 1999). This increase can be compared with the expected increase in mean summer air temperature for the Arctic of 1.8°C by 2050 (Mean of the five ACIA scenarios). Phenology in terms of bud burst and flowering in ITEX and earlier experiments (Wookey et al., 1993; 1995) was advanced in warming treatments at some sites. In Swedish Lapland, growth accelerated and the period between thawing and anther appearance advanced by 2 weeks (Welker et al., 1997). In contrast, there was little change in growth cessation at the end of the season in response to warming. Nutrient addition, however, prolonged the period of growth of polar semi desert species in autumn on Svalbard but reduced frost hardening leading to dramatic loss of above ground biomass during the extreme warm, wet, November of 1993 (Robinson et al., 1998). This corresponds to indigenous observations noted above.

ITEX experiments showed that initial increases in vegetative growth were generally, but not always, reduced in later years probably because warming stimulated the use of stored resources more than the uptake of new resources. Similarly, responses of sub-Arctic dwarf shrubs to soil warming increased initially but soon returned to former levels. This response followed an initial increase in nitrogen mineralization in response to soil warming that did not persist (Hartley et al., 1999). In contrast, reproductive success improved in later years in the ITEX experiments (Arft et al., 1999) due to the extended period of flower bud initiation to seed set in Arctic flowering plants. Similarly, flowering of the widespread sedge Carex bigelowii was strongly correlated with July temperature over an 18 year period, but in the year before flowers are seen (Brooker et al., 2001). Eriophorum species exhibit even more dramatic variation in flowering among years than Carex species, but there is no simple correlation with current or previous year’s weather (Shaver et al. 1986).

The ITEX experiment showed that responses of growth and reproduction varied among vascular plant life forms. Herbaceous species responded more strongly and consistently to warming than did woody forms over a four year period (Arft et al., 1999). Over longer time periods, the growth form, number and position of meristems in some woody plants such as Betula nana allows a
much greater response that completely changes the height and structure of the whole canopy (Bret-Harte et al., 2001; but see Graglia et al. (2001a) for a different response). In the sub-Arctic, Graglia et al. (2001a) showed that initial plant responses (abundance) to warming and other treatments persisted throughout a ten year period. Graminoids were particularly responsive to fertilizer additions in the sub-Arctic and their increased growth and litter production suppressed the growth of mosses and lichens (Potter et al., 1995; Molau and Alatalo, 1998; Graglia et al., 2001a; Cornelissen et al., 2001). Evergreens were more responsive to nutrient addition and warming than deciduous species (Arft et al., 1999).

Mosses and lichens appear to be particularly vulnerable to climate warming, at least in areas of continuous vegetation cover. A meta-analysis of lichen responses to warming experiments across the Arctic showed that lichen biomass decreased as vascular plant biomass increased following warming (Cornelissen et al., 2001). This group of plants is particularly important as a large proportion of global lichen diversity is found in the Arctic, because some species are important winter forage for reindeer, and because some are important nitrogen fixers in strongly nitrogen limited systems. A 22-year study of the lichen flora of the Netherlands similarly showed changes that are suggested to be related to an increase in temperature, although the subtropical species might be more sensitive to nitrogen (Palmqvist et al., 2002). 50% of the Arctic-alpine/boreal-montane lichen species were declining while sub tropical species were invading (van Herk et al., 2002). The widespread moss Hylocomium splendens shows a complex response to warming (Callaghan et al., 1999). Growth in warming experiments is reduced (Potter et al., 1995; Graglia et al., 2001a) whereas growth increases in relation to mean annual temperature increases throughout its Arctic distribution range (see Section 3.6.2.1; Figure 6.14; Callaghan et al., 1997). This suggests some limitation in the simulation of natural warming. If, however, moss growth and abundance are reduced by warming, then soil thermal regimes, biogeochemical cycling and energy and heat exchange between the biosphere and atmosphere will be significantly impacted (Hobbie, 1996).

Plant species respond differently to warming according to previous temperature history related to latitude, altitude, interannual temperature variations and interactions among species. Phenological responses to warming are greatest at cold, high Arctic sites (Wookey et al., 1993; Arft et al., 1999), whereas growth responses to warming are greatest at low Arctic sites. Growth responses of Cassiope tetragona to warming were greatest at a high Arctic and a high altitude-low Arctic site when compared with the warmest low latitude, low Arctic site (Havström et al., 1993). Over a period of 5 years, shoot elongation responses to warming were greatest in cold summers (Molau, 2001; Richardson, 2000). Laine (1988) showed that the reproduction of Vaccinium myrtillus depended to some extent on the climate in the previous years (see chapter 13 for examples from trees) whereas Shetsova et al. (1995; 1997) showed no such response for co-occurring V. vitis-idaea and Empetrum nigrum.

Most information on plant responses to climate warming is limited to the short term and small plot – even if the short term is 2 decades. Because of the great longevity of Arctic plants and clonal growth, it is difficult to extrapolate plant responses from the individual plant to the population. However, climate change (temperature, nutrients, CO₂) impacts on demographic parameters and population growth statistics were determined for the sedge Carex bigelowii by Carlsson and Callaghan (1994) and Callaghan and Carlsson (1997) and showed that climate
change increased tiller size, vegetative production of young tiller generations, survival of young tillers and flowering while reducing the age of a tiller at flowering and tiller life span. Two mathematical models showed that the changes in demographic parameters led to an increase in population growth rate, with young tillers dominating this increase. The rate of vegetative spread more than doubled while cyclical trends in flowering and population growth decreased substantially.

3.4.1.3 Responses of plants to precipitation changes

Precipitation in the Arctic is extremely variable among seasons and from place to place but amount of snow is difficult to measure (Chapter 2). Precipitation varies from over 1000 mm in coastal areas e.g. Norway, Iceland, to less than 45 mm in the polar deserts where most of the annual precipitation occurs as snow. The interaction between precipitation and temperature is extremely important for plant growth and ecosystem processes and it is difficult to separate their effects.

Observations show that precipitation has increased by up to 15% in northern latitudes within the last 40 years (Groisman and Legates, 1995) although the spring hemisphere snow cover has retreated by 10% in the last 20 years (Chapter 2). The most recent climate scenarios!for the North Atlantic Region suggest increased mean annual temperatures and precipitation for the entire region (Houghton et al., 2001; Chapter 4).

Effects of changes in snow depth, duration and timing of the snow-free period

The interaction between snow amount and temperature will determine the start and duration of the snow-free period. The duration of the snow-free period at high northern latitudes has increased by 5-6 days per decade and the week of the last observed snow cover in spring has become earlier by 3-5 days per decade over the period 1972-2000 (Dye, 2002). Increased precipitation can therefore be associated with shorter duration of snow and less snow cover (Groisman and Legates, 1995; ACIA Chapter 4). (In contrast, the start of the growing season has been delayed by up to one week over the last 20 years in the high altitude and northern boreal regions of Fennoscandia (Høgda et al., 2001)). Hydrological models applied to the Tana River Basin of northernmost Finland predict increases in the length of growing seasons from 30 days in the mountains to 70 days near the coast of the Barents Sea by 2100 (Dankers, 2002). This change is associated with an earlier start of the growing season of about 3 weeks and a delayed end of 2 to 3 weeks.

The timing of the start of the snow free period is of critical importance, and more important than the timing of autumn snow fall, because solar angles are already high when plants currently start growth and each extra snow-free day at the beginning of the growing season will enable plants to access high levels of PAR (Figure 6.8; see also Section 5). In an Alpine area, productivity decreased by about 3% per day delay in snow release date (Ostler et al., 1982). The timing of snowmelt has also been found to have considerable effects on plant phenology (more so than temperature in some cases: Hollister and Webber, 2000), with a contracting of development time that is associated with a decrease in productivity and reproductive output (Callaghan, 1974). Some plant species such as the Arctic deciduous shrub species, Salix pulchra and Betula nana,
can respond to changes in timing of the growing season (Pop et al., 2000), but others, particularly evergreen and early flowering species appear to be particularly vulnerable (Kudo, 1991; 1993).

Figure 6.8 Schematic showing relationship between timing of the growing season and the seasonal pattern of irradiance together with an indication of where transient switches from carbon sink to carbon source could occur (modified from Chapin and Shaver, 1985b).

An experiment that manipulated snow conditions by using snow fences at Toolik Lake, Alaska, showed that drifts increased winter time temperatures and CO₂ flux (Walker et al., 1999; Jones et al. 1998, Welker et al. 2000). Under the drifts, temperatures were more constant than in control plots. Plant growth increased despite a shorter growing season, although this was thought to be a transitory response and contrasts with the reduced growth of late snow bed plants (Plate 6.7).

**Frost resistance and avoidance**

Changes in snow depth and duration are likely to cause hazardous impacts on the frost resistance and avoidance of many plants at high latitudes. Damage to foliage and apical meristems occur when they are "triggered" to premature bud burst and development by an earlier onset of the growing season, resulting from early snowmelt, when the annual hardening/dehardening is at its most sensitive phase, and when there is a risk of short periods of cold weather. Bilberry is a species whose requirements for cool temperatures to enable it to break dormancy (i.e. chilling requirement) are fulfilled early (Havas, 1971). Accelerated dehardening of bilberry was found as a consequence of a minor (2-3°C) elevation in temperature (Taulavuori et al., 1997c) suggesting that climatic warming is very likely to entail a real risk of early dehardening and subsequent shoot frost damage. The explanation for this may be the higher but fluctuating temperature, which increase the cryoprotectant-consuming freeze-thaw cycles (Ögren 1996; 1997; Ögren et al., 1997). In addition to frost resistance, frost avoidance may also be disturbed by a thin or lacking snow cover. The risk is likely to be highest at high latitudes, where plants that are genetically adapted to the presence of snow may have lost some potential for frost resistance during their evolution. Provenances of bilberry from the sub-Arctic, for example, have shown reduced frost resistance compared to provenances from southern Finland (Havas, 1971).

Other global change factors might affect frost resistance but few, and sometimes conflicting, reports have been published of studies performed at high latitudes. Nitrogen pollutant (or fertilizer) can impair the frost resistance of plants. Such an effect was demonstrated for Dryas octopetala on Svalbard during a warm period in early winter (see Section 3.4.1.2; Robinson et al., 1998). However, recent studies with Calluna vulgaris (Caporn et al., 1994), Vaccinium myrtillus (Taulavuori et al., 1997a) and V. vitis-idaea (Taulavuori et al., 2001) have demonstrated improved frost resistance caused by extra N. Probably, this is because these ericaceous species are plants adapted to low-nutrient habitats, such as those at high latitudes.

Snow depth and duration vary greatly with topography at the landscape level. High summer temperatures will decrease the abundance and sizes of snow beds. Current changes in snow patches recorded by IK are already causing concern in Baker Lake, Clyde River and Iqualuit. Fox (2002) describes anuuvak (permanent snow patches) that are melting in the hills around the communities there. Aniuvak are good areas for caching meat and provide a sanctuary for reindeer
against flying insects. Indigenous peoples’ explanations for the melting are related more to changes in precipitation and mean relative humidity, rather than temperature increases. The specialized plants characteristic of late snow beds (Gjærevoll, 1956) will be at particular risk.

Summer precipitation

Altered timing and speed of snowmelt may differentially alter the availability of water in different facies of the tundra landscape mosaic which, in turn, impact greatly upon the predominant vegetation type and its growth dynamic through the active season (Molau, 1996). Artificial increases in summer precipitation produced few responses in Arctic plants compared with manipulations of other environmental variables (Dormann and Woodin, 2002). However, mosses benefited from moderate summer watering (Potter et al., 1995; Phoenix et al., 2001; Sonesson et al., 2002) and nitrogen fixation rates by blue green algae associated with the moss Hylocomium splendens were increased (Solheim et al. 2002). Addition of water in summer time to a polar semi desert community produced surprisingly few responses (Press et al., 1998a). In the high Arctic, comparisons were made of sites with high and low plant densities. Although there was little difference in soil moisture and plant water relations, and water availability did not constrain the adult vascular plants, surface water flow in snow flush areas allowed greater development of cyanobacterial soil crusts, prolonged their nitrogen fixing activity and resulted in greater soil nitrogen concentrations (Gold and Bliss, 1995). Because of their importance in facilitating vascular plant community development, Gold and Bliss (1995) predict that the affects of climate change on non-vascular species are very likely to be of great consequence for high Arctic ecosystems.

3.4.1.4 Responses of plants to increased atmospheric CO₂

There are very few manipulation experiments of atmospheric CO₂ concentrations in the field in the Arctic (Tissue and Oechel, 1987; Gwynn-Jones et al., 1996; 1999) but there are more laboratory experiments on Arctic vascular plants (Oberauer et al., 1986) and mosses and lichens (Schipperges and Gehrke, 1996; Sonesson et al., 1992; 1995; 1996).

The first experiment that manipulated CO₂ in the Arctic concluded that elevated CO₂ had no long term effects because photosynthetic acclimation (i.e. down-regulation) of Eriophorum vaginatum was apparent within 6 weeks and biomass did not increase, although there was prolonged photosynthetic activity in autumn and more biomass was allocated to roots (Tissue and Oechel, 1987). The lack of responses and enhanced root biomass were attributed to nutrient limitation (Oechel et al., 1997). Increases in tiller production of Eriophorum vaginatum were not considered to be an important response but can lead to long term increases in population growth (Carlsson and Callaghan, 1994).

Longer term CO₂ enrichment experiments in the sub-Arctic also show that growth responses are dominated by early, transient responses (Gwynn-Jones et al., 1997). Four dwarf shrubs were studied over the first 3 years of the experiment; one, the deciduous Vaccinium myrtillus showed increased annual stem growth (length) in the first year whereas two other evergreen dwarf shrubs (Empetrum hermaphroditum and Vaccinium vitis-idaea) showed reduced growth. In year 7, increased CO₂ significantly increased the leaf ice nucleation temperature (i.e. reduced the frost
resistance which can be harmful during the growing season) of 3 of 4 dwarf shrub species tested (Beerling et al., 2001). *Vaccinium uliginosum, V. vitis idaea* and *Empetrum hemaphroditum* showed increases of leaf ice nucleation temperature exceeding 2.5 °C whereas *V. myrtillus* showed no significant effect as in another study, (Taulavuori et al., 1997a). Increased CO₂ interacted with a high UV-B treatment to give an increase in leaf ice nucleation temperature of 5 °C in *V. uliginosum*. This affect coincides with indigenous knowledge and other experiments that show increased frost sensitivity of some Arctic plants to changes in climate and UV-B radiation (see sections 3.4.1.6).

An expected response to increased CO₂ was a change in leaf chemistry, e.g. an increase in C:N ratio, that would affect herbivory (Fajer et al., 1989) and decomposition (Robinson et al., 1997). Surprisingly, herbivory was not affected. However, increased CO₂ was found to play a role in nutrient cycling by altering the composition of microbial communities after 5 years (Johnson et al., 2002) (see section 3.4.1.6). This suggests that chemical changes are occurring in plants exposed to high CO₂ but these have not yet been identified.

In laboratory studies, the moss *Hylocomium splendens* that naturally experiences high CO₂ levels in the birch woodlands of the Swedish sub-Arctic, was shown to have photosynthetic rates that were limited by light, temperature and water for most of the growing season (Sonesson et al., 1992). Enhanced CO₂ for 5 months decreased photosynthetic efficiency, light compensation point and maximum net photosynthesis and, surprisingly, growth (Sonesson et al., 1996). Similar experiments on 3 lichen species, *Cladonia arbuscula, Cetraria islandica* and *Stereocaulon paschale* failed to show any response of fluorescence yield to enhanced CO₂ (1,000 ppm) although there was an interaction between CO₂ and UV-B levels (Sonesson et al. 1995). Perhaps the lack of responses of the moss and lichens reflects their adaptation to the currently high levels of CO₂ that they experience close to the ground surface (Sonesson et al., 1992) via the process of down-regulation.

In contrast to some views that responses of plants (mainly growth) to increased CO₂ concentrations are relatively small and by inference insignificant (Dormann and Woodin, 2002), recent results show that increased CO₂ concentrations can have the wide ranging and important effects discussed above in the long term (Beerling et al., 2001; Johnson et al., 2002).

3.4.1.5 Responses of plants to increased UV-B

One common method for simulating the effects of ozone depletion has been to irradiate organisms and ecosystems with artificial UV-B radiation. Results are often repeated in relation to the % equivalent ozone depletion. It should be noted, however, that the radiation spectrum from the lamps used differs from the spectrum of the radiation increase that would ensue from real ozone depletion. Therefore the degree of simulated ozone depletion depends on the "weighting function" applied in the calculations, and the knowledge of the appropriate weighting function is very incomplete and is species-specific. A certain amount of artificial radiation applied does not correspond to the same ozone depletion for, e.g., a plant and a tadpole. The information in the following sections should be read with this in mind.
Relatively little is known about plant responses to changes in UV-B radiation. Field experiments on sub-Arctic and high Arctic ecosystems (Table 6.6) show species-specific responses to ambient UV-B and to enhanced UV-B simulating a 15% decrease in stratospheric ozone (1990 levels). (The 15% decrease is equivalent to losses of ozone expected to occur throughout much of the Arctic. However, the values do not apply to Beringia for April and October 2015; Taalas et al., 2000.) On the whole, the effects of UV-B are relatively few compared with effects of increased temperature and nitrogen (Dormann and Woodin, 2002).

A meta analysis of plant responses to increased UV-B radiation globally, showed that there was a small but significant reduction in biomass and plant height (Searles et al., 2001). In the sub-Arctic, measurements of stem length, branching, leaf thickness, flowering, berry production, phenology and total UV-B absorbing compounds were affected significantly by ambient UV-B in only two of three dwarf shrubs i.e. Vaccinium uliginosum and V. vitis-idaea (Phoenix, 2000). Empetrum hermaphroditum and Vaccinium vitis-idaea showed no responses to enhanced UV-B after 7 years of exposure whereas V. uliginosum and V. myrtillus showed few responses (Table 6.6). Enhanced UV-B radiation has been shown to reduce the height growth, but not biomass, of the mosses Sphagnum fuscum and Hylocomium splendens in the sub-Arctic (Gehrke et al., 1995).

The UV-B studies (Table 6.6) showed that Arctic species were more tolerant of enhanced UV-B than previously thought, and that the production of UV-B absorbing compounds showed no simple relationship with UV-B dose as expected from laboratory studies. Another surprise effect was the responsiveness of frost hardiness in some Arctic dwarf shrubs to increased UV-B. Dunning et al. (1994) made pioneering work to investigate the relationship between UV-B and frost resistance in a Rhododendron species and concluded that exposure to UV-B increases (although only marginally) cold resistance. In contrast, K. Taulavuori, E. Taulavuori and K. Laine (unpubl.) found decreased frost resistance in bilberry in response to elevated UV-B and Beerling et al., (2001) showed decreased frost resistance in the ericaceous dwarf shrubs Vaccinium uliginosum, V. vitis idaea and Empetrum hermaphroditum. A combination of elevated CO₂ and UV-B reduced late season frost sensitivity of leaves of V. uliginosum from –11.5 °C to –6 °C. Increased frost sensitivity at the beginning and/or end of the short Arctic growing season is likely to curtail the season even further. As some models of vegetation redistribution related to temperature change use the critical freezing temperatures for leaf damage in temperate trees and shrubs (Prentice et al., 1992), modeled past and future northwards migration of temperate vegetation should be reconsidered in relation to changing CO₂ and UV-B levels.

**Table 6.6. Summary of UV-B effects on sub-Arctic dwarf shrubs based on Phoenix (2000) and other sources referred to in the text (↑= increase, ↓= decrease, 0=no effect compared to control, -= no information).**

<table>
<thead>
<tr>
<th></th>
<th>V. myrtillus</th>
<th>V. uliginosum</th>
<th>V. vitis-idaea</th>
<th>E. hermaphroditum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Response</td>
<td>Zero to ambient UV</td>
<td>Ambient to enhanced UV-B</td>
<td>Zero to ambient UV</td>
<td>Ambient to enhanced UV-B</td>
</tr>
<tr>
<td>Stem length</td>
<td>-</td>
<td>↓</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Branching</td>
<td>-</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Leaf thickness</td>
<td>-</td>
<td>↑</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
The resilience of the sub-Arctic dwarf shrubs to enhanced UV-B radiation probably reflects pre-adaptation to higher levels than currently experienced in the Arctic (Phoenix, 2000). The species currently extend southwards to about 40 °N and they probably existed even further South in a higher UV-B regime during the early Holocene. The increased UV-B radiation currently applied in experiments is equivalent to the difference in ambient UV-B between the site of the experiment (68 °N) and Helsinki (59 °N) (Figure 6.9). In addition, many Arctic plants have thick leaves that might attenuate UV-B entering leaf tissues. However, one particular climate-UV interaction that could increase the damage experienced by plants is the combination of possible earlier snow free periods ( Dankers, 2002) with higher spring UV-B radiation at the earth’s surface (Taalas et al., 2000). Such a combination of effects would expose young, potentially sensitive, plant shoots and flower buds to particularly high UV irradiation (Zepp et al., 2002).

**Figure 6.9 Dwarf shrub distributions (labeled boxes) in relation to latitude and solar UV-B radiation incident at the Earth’s surface (Hultén, 1962; Gwynn-Jones et al., 1999; Phoenix, 2000).**

3.4.1.6 Plant responses to changes in cloudiness and photoperiod

A major characteristic of Arctic environment is the daily and seasonal patterns of the light period or photoperiod. Intermediate latitudes (40-50°N) exhibit about 8-hour day length at mid-winter, whereas a polar night without sunrise prevails North of the Arctic Circle (66.5 °N). Consequently, day length change during spring and autumn occurs much faster at high latitudes.

Frost resistance patterns change seasonally and are environmentally controlled, mainly by temperature and day length, the predominance of which depends on the seasonal growth cycle (Fuchigami et al., 1982). The development of frost resistance by almost all woody plants at high latitudes is characterized by strong dependency on the photoperiod for growth cessation and cold hardening. Scots pine (Pinus sylvestris) seedlings from the northern boreal forest develop a high degree of frost resistance during the late summer as a consequence of the shortening days (Taulavuori et al., 1997b). The frost hardening process is initiated even at high temperatures (+20°C) in experimental conditions which mimic the ambient photoperiod (Taulavuori et al., 2000). Due to the marked photoperiodic control of the frost hardening process of woody species at high latitudes, it is understandable that they harden more extensively compared to populations at lower latitudes under similar temperatures. For example, the lowest survival temperature of bilberry (Vaccinium myrtillus L.) in the Central Alps (ca. 50°N) at mid-winter is around –35 °C.
(Sakai and Larcher, 1987 and references therein), while the same level of frost resistance is already achieved at the end September in northern Finland (65°C) (Taulavuori et al., 1997a).

Photoperiod will not change, but species that are migrating will experience changes in photoperiod. It is unlikely however, that this will constrain species initially as many northern boreal species, for example, experienced Arctic photoperiods earlier in the Holocene before they were displaced southwards by climate cooling (see Section 2). If and when species with a more southern distribution migrate into the Arctic, constraints of photoperiod might affect growth and flowering but this is largely unknown. However transplant experiments of herbs between the Austrian Alps, Abisko and Svalbard showed that allocation of biomass in some species such as Rannunculus glacialis was effected by photoperiod and this constrains any potential increases of vigor that might have occurred due to climate warming (Prock and Körner, 1996). In contrast herbs, such as Geum (Prock and Körner, 1996) and some grasses (Heide et al., 1995) not sensitive to photoperiod could benefit from climate warming.

It has been suggested that increased UV-B radiation effects might be small in the future because of increased cloudiness that would counteract to some extent decreasing ozone (Dormann and Woodin, 2002). However, predictions of increased cloudiness and particularly future cloud types are uncertain. Instead, UV-B effects will be reduced by decreases in albedo as snow and ice distribution and seasonal duration decline, and as the boreal forest displaces part of the current tundra.

Arctic plants differ in the degree to which they gain or loose carbon in photosynthesis at “night time.” In conditions of cloudy nights, those species that have carbon gain at nighttime (e.g. Dryas integrifolia, Alopecurus alpinus, Salix glauca and Salix arctica (25-30% of diurnal carbon gain (Semikhhatova et al., 1992)) are likely to have a reduced competitive ability compared with species that do not. In contrast, increased cloudiness in daytime probably favors those species that have a carbon gain at night. Those species that loose carbon at nighttime (e.g. Eriophorum angustifolium, Semikhhatova et al, 1992) would be disadvantaged by warming.

3.4.1.7 Plant responses to potential changes in pollinator abundance and activity

The rapid phenological changes that have been observed in response to simulated climate change have the potential to disrupt the relationships that plants have with animal, fungal, and bacterial species that act as pollinators, seed dispersers, herbivores, seed predators and pathogens (Dunne et al., 2003). These disruptions are likely to have the strongest impact if the interacting species are influenced by different abiotic factors or if their relative responses to the same factors (e.g. elevated temperatures) are different. However, wind and self-pollination are more widespread among Arctic flowering plants so any mismatch between pollinator activity and flowering phenology would probably be of greater significance to any plants moving in to the Arctic during warming. Little appears to be known about these processes.

Summary: Responses at the plant species level to changes in climate and UV-B radiation

Species responses to changes in temperature and other environmental variables are complex. Species respond individualistically to each environmental variable. Also, plant species respond differently to warming according to previous temperature history related to latitude, altitude, interannual temperature variations and interactions among
species. Some species are already responding to recent environmental changes. Indigenous knowledge, air photographs and satellite images show that some Arctic vegetation is becoming more shrubby and more productive.

Summer warming experiments showed that initial increases in the growth of vascular species were generally reduced with time whereas reproductive success improved in later years. Over short periods (4 years), herbaceous plants responded more than woody plants but over longer periods, woody plant responses were dominant and could change the canopy height and structure. Mosses and lichens were generally disadvantaged by higher plant responses to warming.

Responses to warming are critically controlled by moisture availability and snow cover. Already, indigenous observations from North America and Lapland show a drying trend with reduced growth of economically important berries. However, experimental increases in summer precipitation produced few responses in Arctic plants, except for mosses which showed increased growth. An experiment that manipulated snow conditions showed that drifts increased winter-time temperatures and CO₂ flux and, surprisingly, that plant growth increased despite a shorter growing season. In general however, any earlier onset of the snow free period is likely to stimulate increased plant growth because of high solar angles whereas an increase in the snow-free period in autumn, when solar angles are low, will probably have little impact.

CO₂ enrichment experiments show that plant growth responses are dominated by early, transient responses. Surprisingly, enhanced CO₂ did not affect levels of herbivory but it significantly increased the leaf ice nucleation temperature (i.e. increased frost sensitivity) of 3 of 4 dwarf shrub species and altered the composition of microbial communities after 5 years. A general lack of responses of mosses and lichens reflects their adaptation to the currently high levels of CO₂ that they experience close to the ground surface.

Ambient and supplemental UV-B produced complex, individualistic and somewhat small responses in species. Overall, Arctic species were far more tolerant of enhanced UV-B than previously thought, and the production of UV-B absorbing compounds showed no simple relationship with UV-B dose as expected from laboratory studies. There was increased frost sensitivity in some Arctic dwarf shrubs with increased UV-B. The Arctic photoperiod is not seen as a general constraint to species migrations from the South as trees and southern species previously occurred further North than at present.

### 3.4.2 Specific responses of animals

In contrast to plants, there are relatively few experiments that have addressed how animal populations respond to simulated climatic change and UV-B levels in the Arctic. The few experiments have focused on invertebrates (e.g. insects and soil animals) for which the microclimate can be manipulated on small experimental plots. Experiments on free-ranging vertebrate populations may not be feasible for logistical reasons. On the other hand, time series of population data are available to a greater extent for conspicuous vertebrates such as reindeer and lemmings than, for example, soil invertebrates. Time series can be analyzed with respect to the influence of current climate variability (including recent changes).

#### 3.4.2.1 Responses of animals to current changes in climate and UV

Ice crust formation on the tundra as a result as freeze-thaw events during the winters affects most terrestrial Arctic animals. Dense snow and ice severely limit forage availability for large ungulates such as reindeer and musk ox (Klein, 1999). Dramatic population crashes in reindeer resulting from periodic ice-crusting have been reported from the western, coastal part of the Russian Arctic, Svalbard and Fennoscandia, (Reimers, 1982; Syroechovski and Kuprionov, 1994; Aanes et al., 2000; Putkonen and Roe, 2003). Similar events have been reported for musk ox in the southern parts of their range in Greenland (Forchhammer and Boertmann, 1993). Inuit in
Nunavut report that caribou numbers decrease in years when there are many freeze-thaw cycles (Thorpe et al., 2001) and the probability of such freeze-thaw events is said to have increased as a result of more short-term fluctuations in temperature. In central Siberia, where winter climate is colder and more stable, reindeer population dynamics are less climate driven (Syroechovski and Kuprionov, 1994). Swedish Saami note that over the last decade, autumn snow lies on unfrozen ground rather than on frozen ground in the summer grazing areas and this results in poor quality spring vegetation that has rotted (E. Nutti pers comm.). Certain microfungi seem to be responsible for such instances (Kumpula et al., 2000).

Long and accurate time series data on population sizes for the Svalbard reindeer (Solberg et al., 2000, Aanes et al., 2000) show that the amount of precipitation during the winter, which is highly variable and is well described by the Arctic Oscillation (AO) index (Aanes et al., 2002), provides the most important check on reindeer population growth rate in concert with population density. Winters with freezing rain were associated with severe population crashes both in one population of the reindeer (although the natural dynamics of an introduced herd may have contributed to this) and an introduced population of Microtus voles (Figure 6.10).

Figure 6.10 Population dynamics of Svalbard reindeer (solid line) at Brøggerhalvøya and sibling voles (broken line) at Fuglefjella on Svalbard (Aanes et al., 2000; Yoccoz and Ims, 1999). Also included are data from Robinson et al. (1998) and Callaghan et al. (1999) showing observed (circles) and projected (squares) changes in vegetation.

Episodes with mild weather and wet snow lead to a collapse of the subnivean space and subsequent frost encapsulates food plants in ice making them unavailable to small mammal herbivores, and even killing plants in some cases (Robinson et al., 1998; Callaghan et al., 1999). Accordingly, the survival rate of tundra voles decreases dramatically in winters with many alternating periods of melting and frost (Aars and Ims, 2002, Figure 6.11). For example, the last two lemming increases at Kilpisjärvi (NW Finnish Lapland) in 1997 and 2001 were probably curtailed by warm spells and rain in January resulting in freezing of the ground layer (Henttonen unpubl.). Inuit residents of the western Canadian Arctic are also concerned with the impacts of thaw slumping on lemming populations and their predators (owls). Thaw slumps at lake edges are occurring more extensively and at a faster rate in recent years, linked to warmer temperatures and an increase in wind activity and rain while melting ice-bound soil destroys burrows of lemmings (IISD and the community of Sachs Harbour, 2001).

Figure 6.11 Yearly winter survival rate (with 95% confidence intervals) of experimental tundra vole Microtus oeconomus populations plotted against the number of days with temperatures above 0 °C during mid winter (December-February). Mean winter temperature and the year are denoted above the survival rate estimates (Aars and Ims, 2002).

It has been speculated whether the recent dampened amplitude of population cycles and more spatially asynchronous dynamics of voles and lemmings in northern Fennoscandia (Figure 6.12) could result from occasionally unfavorable winters disrupting the normal population dynamics (Yoccoz and Ims, 1999). In long qualitative time series (up to 100 yrs), periods with loss of cyclicity and synchrony (Steen et al., 1990; Stenseth and Ims, 1993; Angerbjörn et al., 2001) are evident, but is unclear whether this is related to periods with fluctuations in climate. There is a
correlation between sunspot activity and snow-shoe hare cycles in N-America (Sinclair et al., 1993), but no such relation for the mountain hare in northern Finland (Ranta et al. 1997). There are no relationships between sunspot activity and outbreak years in the autumnal moth in Fennoscandia (Ruohomäki et al., 2000), although the role of climatic variability in Arctic insects and soil arthropods has been hardly studied because of lack of long quantitative time series.

Figure 6.12 Evidence from the beginning of the 1990s for change in the population dynamics in the formerly cyclic and numerically dominant grey-sided vole and other vole species (combined) at Kilpisjärvi, N-Finland (Henitonen and Wallgren, 2001).

The native people of the Arctic are rich sources of information about recent changes in animal health and behavior, in particular concerning the caribou/reindeer. Increases in vegetation (longer grass, thicker riparian areas) are linked to increased forage availability and more mosquitoes and flies, resulting in increased insect harassment of caribou (Riedlinger, 2001). Changes in “the warmth of the sun”, length of daylight and the timing of the season may trigger caribou to cross a frozen lake or river when the ice is no longer thick enough to support their weight (Thorpe et al., 2001). However, some of the environmental changes may be beneficial. Stronger and more frequent winds are said to provide caribou with relief from insect harassment, meaning they can spend more time inland and not in coastal areas (Riedlinger, 2001). Qitirmiut in Nunavut know that caribou adapt to the heat by staying near coastal areas and shorelines, lying on patches of snow, drinking water, standing in the water, eating moist plants, and sucking mushrooms (Thorpe et al., 2001). However, increases to the number of extremely hot days combined with changing water levels and vegetation patterns may impact the ability of caribou to respond in these ways.

Climatic cooling is to some extent involved in the degradation of habitat in some coastal habitats as a result of grubbing by snow geese on their staging ground. The lesser snow goose (Anser caerulescens caerulescens) breeds in coastal areas of the Hudson Bay region which has experienced climatic cooling since the mid 1970’s. This has delayed migration of the breeding populations (Hansell et al., 1998). Huge aggregation of staging and local geese in the coastal marshes has led to intense grubbing and degradation of salt-mash swarms (Srivastava and Jefferies, 1996). Long term observations and modeling have shown that goose reproductive variables are both directly and indirectly dependent on selected climatic variables, and particularly those relating to the early season (Skinner et al. 1998). Nest initiation date, hatching date, and clutch size were associated with date of last snow on the ground, and mean daily temperature between 6 and 20 May. Early snowmelt allows geese to forage and for females to build up nutrient stores before nest initiation. Also, goslings that hatch earlier in the spring have a higher probability of survival than those hatching later. Inclement weather, such as cumulative snowfall, freezing rain and northerly and easterly winds can result in nest abandonment by females and even adult starvation while on nest incubating eggs.

3.4.2.2 Responses of animals to possible changes in climate

Despite adaptations to low temperatures, warming experiments have shown that temperatures higher than normal do not present any physiological problem for Arctic arthropods given that water is available (Hodkinson et al., 1998). Arctic aphids were more successful in terms of number of completed generations through the summer when temperature was experimentally
elevated (Strathdee et al., 1993). The effects of experimental warming were more pronounced in the high Arctic at Svalbard than in the sub-Arctic at Abisko (Strathdee et al., 1995a). However, the combination of high temperatures and drought seem to be very problematic for terrestrial invertebrates (Strathdee and Bale, 1998) but the hydrological aspect of climate change in tundra habitats is an important issue that has rarely been addressed in studies on Arctic animals (Hodkinson et al., 1999).

Some of the most important effects of higher summer temperatures in Arctic terrestrial animals are likely to be mediated through intensified inter-specific interactions (parasitism, predation and competition). Higher temperatures in the Arctic will lead to invasions of more southerly-distributed species. Such range expansions are expected to be particularly rapid in those species for which food resources (e.g. host plants) are already present (Hodkinson and Bird, 1998). For instance, the mountain birch, the main food plant of the autumnal moth Epirrita autumnata, occurs in the continental parts of the Fennoscandian forest tundra where winter temperatures are occasionally lower than the tolerance limit for over-wintering eggs (Tenow, 1972) but warmer winters could lead to the exploitation of this existing food source. Already, many insects belonging to the boreal forest invade the low Arctic tundra in quite large quantities every summer (Chernov and Matveyeva, 1997) and the Arctic region is subject to a “steady rain” of wind-dispersed small invertebrates (Elton, 1925) that may rapidly establish when the environmental conditions are adequate. Due to the lack of long-term monitoring programs, there are presently no Arctic equivalents of the detailed and quantitative documentation of the northward spread of insects in Europe (e.g. Parmesan et al., 1999). Several generalist predators yet not present in the Arctic are likely to spread northwards with increased ecosystem productivity due to warming. The red fox has already expanded into the Arctic, probably at the expense of the Arctic fox (Hersteinsson and MacDonald, 1992).

Winter warming will alter snow cover, texture and thickness. A deeper snow cover is likely to restrict access to winter pastures by reindeer/caribou, their ability to flee from predators and energy expenditure traveling across snow. Changes in snow depth and texture will also determine whether warm-blooded small vertebrates may find thermal refuges when resting in snow dens (ptarmigan and hares) or by being active in the subnivean space (Pruitt, 1957). Ice crust formation reduces the insulating properties of the snow pack (Aitchinson, 2001) and makes the vegetation inaccessible for herbivores. There is ample observational evidence that the current incidence of rate of winter ice crusting clearly affects the population dynamics patterns of both large and small mammal herbivore species (see section 3.4.2.1). Moreover, there is experimental evidence that population densities of numerically dominating tundra Collembola (springtail) species such as Folsomia quadrioculata and Hypogastrura tullbergi may be halved following an episode of freezing rain on Spitzbergen (Coulson et al., 2000). The expected winter temperature increase of 6.3 °C for 2080 (mean of 5 ACIA scenarios) is very likely to result in an increase of alternating periods of melting and freezing: Putkonen and Roe (2003) found that such episodes with rain-on- snow in the winter presently covered an area of 8.4 x 10⁶ km² in the Arctic and they predicted a 40% increase by 2080-89. This expected increasing frequency of such climatic events is very likely to severely suppress population densities, distort the cyclic dynamics degree of geographic synchrony in lemming, voles and geometrid moths and in some cases even lead to population extinctions.
3.4.2.3 Response of animals to possible increases in UV-B

The extent to which animals are adapted to UV-B must be inferred in most cases. Hairs and feathers necessary for insulation against low temperatures also presumably protect the skins of mammals and birds from UV-B while white winter hair and feathers will reflect UV-B radiation to some extent. Eyes of non-migratory animals must be extremely well-adapted to UV-B in order to be effective in the dark Arctic winter yet also cope with high UV-B in the bright, snowy spring. Invertebrates have coloring that might serve many functions. Melanic forms of invertebrates might have advantages in thermoregulation and UV-B protection (Leinaas, 2002).

Four species of collembola on Svalbard were investigated by Leinaas (2002) with respect to UV-B tolerance: Hypogastrura viatica, Folsomia sexoculata, Onychiurus groenlandicus and O. arcticus. The first-mentioned three species coexist in wet shore habitats, with the very heavily pigmented H. viatica on the surface and F. sexoculata, which is as adult also very heavily pigmented lower down. O. groenlandicus is a soil-living, unpigmented species. O. arcticus is most commonly found under small stones and in rock crevices, and thus living rather unexposed, but has some pigmentation. In an experiment with UV-B radiation (0.5 W m\(^{-2}\) in the 300-320 nm band for 12-14 h day\(^{-1}\), approximately equivalent to clear sky summer conditions in southern Norway) the unpigmented O. groenlandicus had 100% mortality within 1 week, while the heavily pigmented H. viatica was not affected.

Caterpillars of sub-Arctic moths have skins that absorb UV-B to varying extents and the degree of absorption can respond to preconditioning in high UV-B (Buck and Callaghan, 1999). However, UV-B affects animals indirectly via the quality and quantity of food that is available to them as a result of UV-B impacts on plant growth and secondary metabolite production (see below).

It is possible to infer some responses of animals to future increases in UV-B by comparing relationships of animals to natural UV-B along latitudinal gradients. Along these gradients, ambient UV-B radiation reduced hatching size of frogs at sites up to 66° N and no latitudinal gradient in UV-B tolerance existed (Pahkala et al., in press). Surprisingly, for a given time of the year, although the UV-B decreases with increasing latitudes, they are in fact exposed to more UV-B during their sensitive stages at high as compared to low latitude (Merilä et al., 2000). These studies suggest that an increase in UV-B radiation due to anthropogenic causes is likely to reduce the populations of those amphibians that have distribution ranges extending into the Arctic.

Enhanced UV-B is thought to improve the immune system of the autumn moth in the sub-Arctic and to destroy the polyhydrosis virus. As this virus, together with the parasitoid wasp Cotesia jucunda are both important controllers of the survival of moth caterpillars, increased UV-B radiation could potentially lead to increased population sizes and birch forest defoliation. However, no direct effects of enhanced UV-B were detected on fecundity or survival of the moth (Buck and Callaghan, 1999).

Summary: Responses of animal species to changes in climate and UV-B radiation
Evidence for responses of animals to changes in climate are fewer than for plants because field experiments are less feasible for mobile animals, especially vertebrates. In many case inferences are made based on time-series analyses of data on population abundance of a few conspicuous species such as ungulates, and lemmings.

Winter climate impacts, especially those events that affect properties of snow and ice, are particularly important. Freeze-thaw cycles leading to ice-crust formation have been shown to severely reduce winter survival rate of a variety of species ranging from soil dwelling spring-tails (Collembola), through small mammals (lemmings and voles) to ungulates (in particular reindeer/caribou). Such icing induces conditions of anoxia that affect invertebrates, unfavorable thermal conditions for animals under the snow, and renders vegetation unavailable for herbivores. A deeper snow cover is likely to restrict access to winter pastures by reindeer/caribou and their ability to flee from predators. An expected increased frequency of freeze-thaw cycles is very likely to disrupt the population dynamics of many terrestrial animals, and indications that this is already happening to some extent are apparent in the recent loss of the typical 3-4 year population cycles of voles and lemmings in sub-Arctic Europe.

Experimental elevation of summer temperature has shown that many invertebrates respond positively to higher temperatures in terms of population growth, as long as desiccation is not induced. Many invertebrates, such as insects, are very likely to quickly expand their ranges northwards into the Arctic if climate warming occurs because they have vast capacities to become passively or actively dispersed and host species (both plants and animals) are already present North of their present range borders.

Little is known about the responses in Arctic animals to expected increases in UV-B. However, there are some indications that Arctic animals are likely to be more exposed and susceptible to such changes than their southern counterparts. The effects of UV-B on animals are likely to be subtle and indirect such as reduced food quality for herbivores and increased disease resistance in insect pest species.

### 3.4.3 Specific responses of microorganisms to changes in climate and UV-B radiation

Recent experiments that manipulate the environment e.g. soil heating, changing water table, CO₂ enrichment, UV-B supplementation and attenuation, etc. have added new information on the effect of environmental change on the soil microbial community at the species level. In general, climate change is likely to alter microbial community composition and substrate utilization (Lipson et al., 2002). Tundra soil heating, CO₂ enrichment and amendment with mineral nutrients generally accelerate microbial activity (higher growth rate). Enriched CO₂ tends to intensify root exudation, which is the main source of available C for soil and rhizosphere bacteria. Much less is known about the transient changes in the species composition of soil microorganisms induced by manipulation, although supplementation of UV-B in the field resulted in changes in the composition of microbial communities (Johnson et al. 2002). However, laboratory incubation of tundra soils (Barrow, Alaska) at different temperatures had strong effects on community composition assessed from the molecular biology approach called SSU 16S rRNA sequence and fatty acid profiling, but only after a temperature shift of more than 10 °C (Panikov and Perlin, in press).

A mathematical simulation of the changes in microbial community structure in the tundra (Panikov, 1994; 1997) showed, surprisingly, that the effects of many factors on the soil microbial community were essentially less significant compared with effects on the plant community. This is probably indicative of stronger stabilizing forces within microbial communities regulated by negative feedbacks.

The model generates realistic patterns of mass and energy flow (primary productivity, decomposition rates, soil respiration) under present-day conditions and in response to warming,
pollution, fertilization, drying-rewetting of soil, etc. (Figure 6.13). Soil warming results in acceleration of both primary productivity and organic matter decomposition, but the latter was more affected. The total C-balance of soil turned out to be negative: respiration exceeded photosynthesis leading to decline of accumulated organic C (Figure 6.13, right panel) under conditions of soil warming (this topic is addressed in detail in sections 4.2.1.5; 4.2.2; 5.1.1 and 5.4). L-selected microbial species exemplified by *Bacillus* which, under normally cold conditions displayed only weak growth in spring, showed considerable stimulation of bacilli growth and a better competitive advantage under soil warming.

*Figure 6.13 Simulation of changes in a tundra microbial community (Barrow, Alaska) induced by climate warming. Left: population dynamics of dominant soil bacteria; note that L-selected species (Bacillus) display only sporadic occurrence under normally cold conditions of the tundra, which is in agreement with observations, and attains high population density after soil warming. Right: carbon budget including net primary production (NPP), soil respiration and litter dynamics. It was assumed that average air temperature was instantly (see y-axes break) shifted by 10 °C (Panikov, 1994).*

Conidia (spores) of the fungus *Metarhizium* are sensitive to UV-B. There are great differences between strains but strains from high latitudes are less tolerant than those from lower latitudes (Braga *et al.*, 2001a;b). In one species (*M. anisopliae*) it was shown that UV-A also had a negative effect and when comparing strains the sensitivity to UV-A did not correlate with that of UV-B (Braga *et al.*, 2001c). Several groups have studied effects of UV-B on phylloplane (leaf surface-dwelling) fungi and litter decomposing fungi. Moody *et al.* (1999) found that five of the investigated species were sensitive and seven relatively insensitive. The spore production in the litter decomposers was generally inhibited by UV-B (except for one species), while that in phylloplane species was unaffected. However, the sensitivity of spores is not equivalent to sensitivity of metabolic machinery of the vegetative body of a fungus (i.e. the thallium or mycelium), which produces the spores.

In the sub-Arctic (Abisko), a study of the decomposition rates of a standard litter type showed that there was a change in the composition of fungal species resulting from elevated UV-B levels (Moody *et al.*, 2001). These results to some extent resemble those from an earlier experiment on decomposition of dwarf shrub litter from the same site (Gehrke *et al.*, 1995).

The Arctic periglacial environment represents a unique mosaic of unstable habitats (graduation between terrestrial and shallow wetland environments) where large variations in cyanobacteria and algal diversity, productivity and life strategy exist (Elster and Svoboda, 1995; 1996; Elster *et al.*, 1997; 2002; Kubeckova *et al.*, 2001). Prokaryotic cyanobacteria and eukaryotic algae have different life strategies with respect to their susceptibility to severe unstable conditions (Elster, 2002). Cyanobacteria are well adapted to changeable conditions involving low and high radiation (including UV-B), cycles of desiccation, rehydration, salinity and freeze-thaw episodes. This gives them a great ecological advantage and allows them to be perennial. Eukaryotic algae, in contrast, have higher rates of photosynthesis and lower resistances to changes in irradiation, desiccation, rehydration and freeze-thaw cycles. This pre determines their annual behavior. It can be expected that with increasing severity of the Arctic terrestrial environment, the cyanobacteria will probably become the dominant community. In contrast, if
the conditions become milder, the eukaryotic algae will probably start to predominate. In addition, the ongoing temperature rise in the Arctic may also influence cyanobacteria and algal production, as well as the balance between cyanobacteria and algae and invertebrate herbivore activity. Invertebrate grazing pressure is likely to increase and much of the visible cyanobacteria and algae biomass could possibly disappear from Arctic localities (Elster et al., 2001).

Summary: Responses of microorganisms to changes in climate and UV-B radiation

Tundra soil heating, CO₂ enrichment and amendment with mineral nutrients generally accelerate microbial activity. Enriched CO₂ tends to intensify root exudation, which is the main source of available C for soil and rhizosphere bacteria. Supplementation of UV-B in the field resulted in changes in the composition of microbial communities. Laboratory incubation of tundra soils had strong effects on community composition after a temperature shift of more than 10 °C. Surprisingly, the effects of many factors on the soil microbial community were essentially less significant as compared with effects on the plant community. However, a mathematical simulation of the changes in microbial community structure in the tundra showed that soil warming resulted in stimulation of bacilli growth.

Effects of increased UV-B radiation on microorganisms include damage to high latitude strains of fungal spores, and damage to some species of leaf-dwelling fungi as well as soil-dwelling decomposer fungi that result in a change in the composition of the fungal communities.

Cyanobacteria are better adapted to changeable and harsh conditions than algae and in milder climates are likely to be dominated by algae. However, herbivory of both cyanobacteria and algal biomass would increase in a warmer climate.

3.5 Genetic responses of species to changes in climate and UV-B radiation

Many widely distributed Arctic species show large ecological amplitude (broad niches), are taxonomically complex, often representing many subspecies, while species of narrower distribution range often show more restricted amplitude. It is necessary to know the extent of genetic variation in Arctic species and the underlying causes of differentiation/homogenization (biogeography, historical bottle necks, reproductive biology and demography) in order to assess responses of species to climate change.

3.5.1 Plants

In spite of a fast development in recent years of different molecular techniques suited for population genetic studies, there are still rather few studies on Arctic plants. Most have focused on biogeographical and phylogeographical questions related to vascular plant species. Such studies may reveal the migratory potential of the species in response to climate change. During the Pleistocene glaciations, Arctic plants were restricted to refugia, either within or South of present day Arctic regions, from where they could re-colonize areas as conditions improved during interglacial periods (Tremblay and Schoen, 1999; Abbott et al., 2000). The rate of colonization by different species during the Holocene probably depended on where their closest refugia were situated, their dispersal biology and genetic makeup. Genetic phylogeographical studies provide evidence for relatively fast migration rates in most vascular species (Bennike, 1999; Abbott and Brochmann, 2003; Brochmann et al., 2003) and possibly bryophytes as well (Derda and Wyatt, 1999). However, in the modern context of fast climate change, migration rates need to be considered on somewhat shorter time scales than thousands of years.
The level of genetic variation within and between populations indicates the potential for local adaptation to environmental change and hence population resilience to environmental change. Based on the relatively young age of populations and low recruitment of sexually reproduced offspring it was long believed that genetic variation in Arctic plants would be low. However, the number of genetic studies is limited and no such general pattern of genetic variation has been identified. Arctic plants show the same range of genetic variation as temperate plants, ranging from comparatively high levels (Jeffries and Gottlieb, 1983; Bauert, 1996; Jonsson et al., 1996; Philipp, 1997; Gabrielsen and Brochmann, 1998; Stenström et al., 2001) to very low levels of variation (Bayer, 1991; Odasz and Savolinen, 1996; Philipp, 1998; Max et al., 1999; Stenström et al., 2001). However, genetic variation among Arctic plants may be of greater value in terms of biodiversity due to much lower species diversity than in other biomes. Furthermore, high levels of polyploidy in many Arctic vascular plant species may promote the proportion of the genetic variation partitioned within individuals which may be important when passing through evolutionary bottlenecks (Brochmann and Steen, 1999).

By comparing 19 different populations of three rhizomatous Carex taxa, distributed among 16 sites along a major circumpolar sector in Eurasia, ranging from northern Scandinavia in the West to Wrangel Island in the East, Stenström et al. (2001) showed that the levels of genetic variation were not related to climate, but were to a large extent explained by differences in glaciation history at the sampling sites: populations in areas deglaciated ca 10 000 years ago had significantly lower genetic variation than populations in areas deglaciated 60 000 years ago or those in areas not glaciated at all during the Weichselian. Relatively young population age may also be responsible for a low genetic variation in some other populations (e.g. Bayer, 1991; Max et al., 1999), while in yet others, breeding systems apparently play a large role (e.g. Odasz and Savolinen, 1996; Philipp, 1998). In general, populations of insect pollinated or self pollinated plant species have lower genetic variation than populations of wind pollinated species (Hamrick and Godt, 1990) and this seems to apply to Arctic plants as well.

Those plant species representing populations with relatively high levels of genetic variation usually have a large geographic distribution, as for example Saxifraga oppositifolia (Abbott et al., 1995), Saxifraga cernua (Gabrielsen and Brochmann, 1998), Silene acaulis (Abbott et al., 1995; Philipp, 1997), Carex bigelowii sensu lato (Jonsson et al., 1996; Stenström et al., 2001) and Carex stans (Stenström et al., 2001). In these species, the genetic variation among populations (Gst) is a relatively small proportion of the total genetic variation, i.e. they show low degrees of population differentiation. Large variation within populations, however, increases possibilities for ecotypic differentiation. In the Arctic, extremely steep environmental gradients are frequent on a microtopographical scale and ecotypic differentiation has been demonstrated over such short distances for Phleum alpinum (Callaghan, 1974), Carex aquatilis (Shaver et al., 1979), Dryas octopetala (McGraw and Antonovics, 1983) and Saxifraga oppositifolia (Crawford and Smith, 1997), all widely distributed plant species in the Arctic. Ecotypic differentiation to this small-scale heterogeneity may preserve genetic variation and in that way contribute to resilience to change at the species, rather than the population level. Thus, an initial response to climate change in such species is likely to be a change in the distribution and abundance of ecotypes within a species distribution (Crawford and Smith, 1997). In addition, many Arctic
plants show large phenotypic plasticity, which would further increase their resilience (Stenström et al., 2002; Table 6.5).

If the degree of genetic variation can be used as an indication of resilience of populations to change, we would expect this resilience to be greatest among plants in old populations of widely distributed, wind pollinated vascular species as for example rhizomatous Carex populations in eastern Siberia. However, generation time and seedling recruitment may affect the adaptation rate. Many of the dominating Arctic plants like the rhizomatous Carex species are clonal, i.e. they do not rely on seed production through sexual reproduction for short term population maintenance. The genetic individual of these plant species may become thousands of years old (Jónsdóttir et al., 2000) which may slow down the adaptation rate. However, experiments with plants from outside the Arctic have shown that UV-B may speed up genetic change. High UV-B exposure can activate mutator transposons that amplify the mutation effect beyond the immediate UV-B damage (Walbot, 1999), and increased UV-B may lead to increased tendency for mutations in future generations (Ries et al., 2000).

For plants with long-lived seed, further genetic variation is preserved in the seed banks. Dormant seed populations may be genetically different from the above ground populations (McGraw, 1995) and potentially able to better exploit a new climate.

Genetic variation has been studied in fewer moss and lichen species than in vascular plants. However, boreal and Antarctic bryophytes usually show high levels of variation (Cronberg et al., 1996; Derda and Wyatt, 1999; Skotnicki et al., 1998; 1999) but the partitioning of genetic variation among and within populations depends on species. Scandinavian populations of the widely distributed moss Hylocomium splendens, including two sub-Arctic-alpine populations showed high genetic variation within populations, low G_{st} and a similar pattern as in widely distributed, wind pollinated vascular species (Cronberg et al., 1996). In contrast, North American and European populations of Polytrichum commune have low within population variation and high G_{st} (0.51) (Derda and Wyatt, 1999).

3.5.2 Animals

The genetics of Arctic terrestrial animals have been studied thoroughly mainly for a few well-known mammal species such as reindeer (Flagstad and Røed, 2003), lemmings (Fedorov et al., 1999a;b; Ehrich et al., 2000) and Arctic fox (Dalén et al., 2003). These studies have focused on phylogeographical patterns and the relative roles of present gene flow and historic processes (especially concerning glacial-interglacial cycles; see Section 2) based on neutral genetic markers (especially mtDNA). The present genetic differentiation reflects to a large extent historic processes and the presence of current migration barriers. For mammals with relatively restricted mobility such as lemmings, even small scale barriers (e.g. large rivers) can form the borders between sub-species (Fedorov et al., 1999a;b), while a very mobile animal such as the Arctic fox, which readily moves among continents and islands on sea ice, appears to be relatively panmictic (i.e. shows little genetic structuring) at the circumpolar scale (Dalén et al., 2003).

Current gene flow (an indication of mobility) and population history (origin and differentiation) indicate a species’ ability to track the location of their habitats through time. A mobile species
will have better prospects than a relatively sedentary species. Moreover, a species with high genetic/racial diversity has proved an ability to adapt to different environmental conditions in the past and is likely to do so also in the future. It should be noted, however, that markers of genetic variation/differentiation currently used (e.g. mtDNA) may have little bearing on the genetic variation in morphology and life history traits (see Flagstad and Rød, 2003). It is these latter traits that decide whether a species or a morph will be able to adapt to future changes. Currently, there is a paucity of studies on Arctic animals using a quantitative genetics approach (Roff, 1997) that have addressed the potential for rapid adaptations to climatic change. Elsewhere, using a quantitative genetic research protocol, Réale et al. (2003) recently showed that northern boreal red squirrels were able to respond genetically within a decade to increased spring temperatures.

3.5.3 Microorganisms

Assessment of genetic responses of microorganisms to climate change is based on laboratory models as data from observations within Arctic terrestrial ecosystems are absent. Short generation times and impressive genetic plasticity of bacteria make them one of the favorite objects in theoretical studies of general population genetics. Because most mutations are deleterious, mutation rates are generally thought to be low and, consequently, mutator alleles should be counter-selected. However, up to 1% of natural bacterial isolates have been found to be mutators. A mutator can be viewed as behaving altruistically because, although it reduces individual fitness, it increases the probability of an adaptive mutation appearing. These results may help to explain observations that associate high mutation rates with emerging pathogens causing spontaneous epidemic outbreaks (Sniegowski et al., 1997; Wilke et al., 2001).

In the Arctic environment, intensive mutagenic actions are expected from UV radiation and also from aerosols and volatile chemical mutagens brought to the cool polar air from the mid- and low latitudes. The direct mutagenic effect is probably not strong, especially if we take into account the protecting shielding effects of soil particles and population mechanisms discussed above. However, possible mutants could lead to epidemic outbreaks that could have profound and unexpected consequences for the whole ecosystem.

Summary: Genetic responses of species to changes in climate and UV-B radiation

Arctic plants show the same range of genetic variation as temperate plants, ranging from comparatively high levels to very low levels. In widespread Carex taxa, levels of genetic variation were not related to climate, but were to a large extent explained by differences in glaciation history at the sampling sites: populations in areas deglaciated ca 10 000 years ago had significantly lower genetic variation than populations in areas deglaciated 60 000 years ago.

Plant species representing populations with relatively high levels of genetic variation usually have a large geographic distribution. On a microtopographical scale, extremely steep environmental gradients are frequent and ecotypic differentiation has been demonstrated over short distances for several widespread species. This heterogeneity, together with large phenotypic plasticity, is likely to contribute to resilience to change at the population and species levels. For plants with long-lived seed, further genetic variation related to former environments is preserved in the seed banks. Thus, there are several mechanisms for widespread Arctic plant species to respond to environmental change.

Experiments with plants from outside the Arctic have shown that increased UV-B may speed up genetic change and may lead to an increased tendency for mutations in future generations.
The present genetic differentiation of Arctic terrestrial animals that have been studied thoroughly, such as reindeer, lemmings and Arctic fox, reflects to a large extent historic processes and the presence of current migration barriers. For mammals with relatively restricted mobility such as lemmings, even small-scale barriers (e.g. large rivers) can form the borders between sub-species while a very mobile animal such as the Arctic fox shows little genetic structuring at the circumpolar scale. A species with high genetic/racial diversity has proved an ability to adapt to different environmental conditions in the past and is likely to do so also in the future.

There is a paucity of studies on Arctic animals that have addressed the potential for rapid adaptations to climatic change. Elsewhere, it was shown that northern boreal red squirrels were able to respond genetically within a decade to increased spring temperatures.

Up to 1% of natural bacterial isolates have been found to be mutators and high mutation rates are associated with emerging pathogens causing spontaneous epidemic outbreaks. In the Arctic, intensive mutagenic actions are expected from UV radiation and also from aerosols and volatile chemical mutagens. Although the effect is probably not strong, possible mutants could lead to epidemic outbreaks that could possibly have profound and unexpected consequences for the whole ecosystem.

### 3.6 Recent and expected changes in species distributions and potential ranges

Paleoecological research (Section 2) and observations over many decades demonstrate that the geographical ranges of terrestrial species in general can be correlated well with bioclimatic variables. Furthermore, the strength of these relationships is independent of trophic level (Huntley et al., 2003). Major climate related species distributions at the large scale include the limit of trees (associated with the isoline for mean July air temperatures of about 10 °C (Brockmann-Jerosch, 1919, discussed in Körner, 1999) and soil temperature of 7 °C (Körner, 1998)) and the limit of woody plants such as dwarf shrubs that are one indicator of the boundary of the polar deserts zone (Edlund and Alt, 1989). Such relationships suggest that species distributions at the macro geographical and landscape scale will change as temperature changes. Here, we assess the impacts of climate change on recent changes in species distributions and those expected in the future.

#### 3.6.1 Recent changes

Indigenous knowledge projects have documented recent changes in the ranges of caribou in relation to changes in weather based on hunters’ understandings of how environmental conditions affect seasonal caribou distribution patterns (Kofinas et al., 2002). Hunters’ explanations of caribou distributions may provide indications of potential range changes under scenarios of warming. For example, in the El Niño year of 1997/98, several thousand Porcupine Caribou over-wintered on the Yukon Coast in Arctic Canada. Hunters in Aklavik, Northwest Territories explained this phenomenon in terms of the Beaufort Sea ice pack, which was farther from the Yukon North Slope than in most years, resulting in warmer coastal temperatures and thus more abundant forage for caribou. In July of 1997, as the caribou moved into Canada from their Alaskan calving grounds, several large groups remained on the coast, taking advantage of the rich forage opportunities. A mild fall and the lack of icing events that push the caribou South for the winter kept the caribou in the area into October, as the animals could continue to access summer forage. The herd remained on the coast for the winter, and was reported to be in better condition than the herd wintering in the usual locations.
IK has also documented recent changes in the ranges of other animals in relation to changes in weather. In the Canadian Arctic, Inuit in communities such as Baker Lake report insects previously associated with areas South of the treeline (Fox, 2002). In more western regions, there are more frequent sightings of “mainland ducks” such as pintail ducks and mallard (Riedlinger, 2001).

Working in the Canadian Arctic, and using the "conventional science approach", Morrison et al. (2001) summarized the trends in data for breeding waders. Almost all Arctic breeding species are declining. The reasons for the trends were not always clear and probably of multiple origin. Long term monitoring in Finland has shown a substantial decline in the populations of many Arctic and sub-Arctic bird species over the past 20 years (Väisänen et al., 1998), but the trend is not always negative. Zöckler et al. (2003) found that almost half of the long distance Arctic breeding migrants studied are presently in decline. For many species there are still insufficient data available, and only a few (8%) show an increasing trend. In most cases, it is not easy to correlate trends with climate change. As the trends in some species are different outside and inside the Arctic region, there is an indication that factors of a more global nature are involved. An example is the drastic decline of the Ruff (Philomachus pugnax) in almost all breeding sites outside the Arctic in contrast to their stable or even increasing populations in some (but not all) northern Arctic areas (Zöckler, 2002). This coincides with the recent northern expansion of other wet grassland waders, such as Common Snipe in the Bolshemelzkaya tundra (Morozov, 1998), Black-tailed Godwit and Northern Lapwing Vanellus vanellus in northern Russia concomitant with a northward expansion of agriculture including sown meadows (Lebedeva, 1998). Several other bird species have recently been recorded in more northern locations in the Arctic (Zöckler et al., 1997) suggesting a general trend that some species are shifting their distribution in response to changing climate that is altering habitats. The emerging picture is that the Ruff is being forced to retreat to its core Arctic habitats through the effect of global climate change in combination with increasing nutrient enrichment on the quality of wet grassland habitats (Zöckler, 2002).

Table 6.7. Scenarios of habitat loss of breeding area in % for 23 Arctic water bird species applying two different circulation models (HadCM2GSa1 = moderate warming; UKMO = extreme warming); their globally threatened status (VU = Vulnerable as a globally threatened species, according to Collar et al. (2000); EN = suggested to be upgraded as Endangered as a globally threatened species; ! = suggested for inclusion into the Red List) based on Zöckler and Lysenko (2000)

<table>
<thead>
<tr>
<th>Species</th>
<th>HadCM2GSa1*</th>
<th>UKMO*</th>
<th>Red List</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tundra Bean Goose</td>
<td>76</td>
<td>93</td>
<td></td>
</tr>
<tr>
<td>Red-breasted Goose</td>
<td>67</td>
<td>85</td>
<td>VU</td>
</tr>
<tr>
<td>Spoon-billed Sandpiper</td>
<td>57</td>
<td>57</td>
<td>VU/EN</td>
</tr>
<tr>
<td>Emperor Goose</td>
<td>54</td>
<td>54</td>
<td>!</td>
</tr>
<tr>
<td>Ross's Gull</td>
<td>51</td>
<td>73</td>
<td></td>
</tr>
<tr>
<td>Red-necked Stint</td>
<td>48</td>
<td>68</td>
<td></td>
</tr>
<tr>
<td>Sharp-tailed Sandpiper</td>
<td>46</td>
<td>74</td>
<td></td>
</tr>
</tbody>
</table>
A recent global meta-analysis of plants claim that a climate change signal has been identified across natural ecosystems (Parmesan and Yohe, 2003). Range shifts of plants averaging 6.1 km per decade towards the poles and 6.1 meters per decades upwards have been identified in response to a mean advancement of spring by 2 to 3 days per decade. Although some northern treeline data were included, little information was available for Arctic ecosystems.

### 3.6.2 Expected future changes in species distributions

Species–climate response surface models based upon correlations between species ranges and bioclimatic variables are able to project scenarios of the recently observed range changes of at least some species of both birds (Zöckler and Lysenko, 2000) and butterflies (Hill et al., 1999; in press; Virtanen and Neuvonen, 1999). Related studies have shown that, at least in the case of butterflies, the extent to which species have realized their predicted range changes over the last 30–50 yr is strongly related to their degree of habitat restriction, generalist species being much more able to achieve the predicted range expansions than are specialist species (Warren et al., 2001).

Such models (Huntley et al., 1995; Hill et al., in press) simulated potential future ranges of Arctic species that are often markedly reduced in spatial extent compared to the species’ present ranges. The range limits of boreal and temperate species shift polewards in response to the same future climate scenarios. However, the large magnitude of the simulated range margin shifts results in many boreal species also exhibiting potential future ranges of reduced spatial extent because they are limited to the North by reaching the shore of the Arctic Ocean.

The extent to which Arctic plant species may suffer the rapid range reductions simulated by such models will depend principally upon two factors. Firstly, such reductions are likely to happen most rapidly in species that experience some physiological constraint at their southern range

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>E.U.</th>
<th>I.T.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little Stint</td>
<td>Calidris minutus</td>
<td>45</td>
<td>65</td>
</tr>
<tr>
<td>Curlew Sandpiper</td>
<td>Calidris ferruginea</td>
<td>41</td>
<td>70</td>
</tr>
<tr>
<td>Pectoral Sandpiper</td>
<td>Calidris melanotos</td>
<td>38</td>
<td>60</td>
</tr>
<tr>
<td>Dunlin</td>
<td>Calidris alpina</td>
<td>36</td>
<td>58</td>
</tr>
<tr>
<td>White-fronted Goose</td>
<td>Anser albirostris</td>
<td>36</td>
<td>57</td>
</tr>
<tr>
<td>Long-billed Dowitcher</td>
<td>Limnodromus scolopaceus</td>
<td>31</td>
<td>54</td>
</tr>
<tr>
<td>Great Knot</td>
<td>Calidris tenuirostris</td>
<td>31</td>
<td>42</td>
</tr>
<tr>
<td>Lesser White-fronted Goose</td>
<td>Anser erythropus</td>
<td>28</td>
<td>29</td>
</tr>
<tr>
<td>Barnacle Goose</td>
<td>Branta leucopsis</td>
<td>21</td>
<td>27</td>
</tr>
<tr>
<td>Western Sandpiper</td>
<td>Calidris mauri</td>
<td>19</td>
<td>21</td>
</tr>
<tr>
<td>Brent Goose</td>
<td>Branta bernicla</td>
<td>16</td>
<td>44</td>
</tr>
<tr>
<td>Knot</td>
<td>Calidris canutus</td>
<td>16</td>
<td>33</td>
</tr>
<tr>
<td>Greater Snow Goose</td>
<td>Anser caerulescens</td>
<td>14</td>
<td>46</td>
</tr>
<tr>
<td>Canada Goose</td>
<td>Branta Canadensis</td>
<td>13</td>
<td>22</td>
</tr>
<tr>
<td>Pink-footed Goose</td>
<td>Anser brachyrhynchus</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Sanderling</td>
<td>Calidris alba</td>
<td>5</td>
<td>25</td>
</tr>
</tbody>
</table>

*Value could be substantially higher as unclassified areas in this GIS analysis may contain different tundra types e.g. mountain tundra.
margin (e.g. the winter thermal constraint postulated for *Rubus chamaemorus* (Marks, 1978; Marks and Taylor, 1978) or the summer thermal constraints postulated for *Catharacta skua* (Furness, 1988)); species that have their southern range margin determined by biotic interactions are likely to be affected less rapidly. Secondly, such reductions very probably happen more rapidly where the northward migration of boreal or temperate species is not limited either by habitat availability or propagule dispersal. ‘Fugitive’ species of the early successional communities that characteristically follow disturbance of the boreal forests will have the required dispersal ability to achieve rapid poleward range expansions. Unless other factors, such as herbivore pressure or a lack of microsites for successful seedling establishment, exclude them then these species potentially will extend into the Arctic rapidly, forming transient ecosystems that will persist until the arrival of the more slowly expanding late successional boreal species.

Loss of habitat is a particularly important possibility that will constrain species ranges. The change in habitat that is most dramatic for many waterbirds is the loss of tundra habitat, varying between 39% and 57% (Harding et al., 2002; Paxton and Prentice, 1996). Vegetation models (Neilson and Drapek, 1998) applied with GIS distribution maps of water birds show a large variation in the impact of predicted changes in vegetation on 25 selected species (Zöckler and Lysenko, 2000). According to the HadCM2GAS1 model, 76% of Tundra Bean Geese (*Anser fabalis rossicus/serrirostris*) will be affected by the alteration of tundra habitats, whilst only 5% of the Sanderling will be affected. However, the Sanderling, in a similar way to many other high Arctic breeders, might even be affected more strongly, as southern tundra types will replace their specific high Arctic habitats. Whereas the more southerly breeding species can shift northwards, it is increasingly difficult for High Arctic breeders to compete. For two of the three water bird species which are considered globally threatened, namely the Red-breasted Goose (*Branta ruficollis*) and the Spoon-billed Sandpiper (*Eurynorhynchus pygmaeus*), 67% and 57% of their current breeding range is expected to change from tundra to forest, respectively (see summary in Table 6.7). This additional loss of habitat will place these two species at a higher risk of extinction. The Emperor Goose (*Anser canagica*), already in decline and with 54% of its small range affected, is highlighted as needing further conservation attention.

### 3.6.2.1 Geographical ranges of plants

Strong relationships between growth and temperature in the circumpolar ericaceous dwarf shrub *Cassiope tetragona* and the feather moss *Hylocomium splendens* can be used to model range changes. The growth of *C. tetragona* is strongly related to mean July temperature (Havström et al., 1995b) and that of *H. splendens* is related to mean annual temperature (Callaghan et al., 1997) throughout their northern ranges (Figure 6.14a). (Mean July and mean annual temperatures are to some extent equivalent to latitude as they decrease towards the North in the above examples.) The natural climatic warming from the beginning of the Little Ice Age to the present is the equivalent of only a minor shift in latitude for *C. tetragona*. On the other hand, scenarios of future warming would produce an equivalent greater displacement of latitude which, at the northern current ranges of the two species, could result in a northern range extension (Figure 6.14a). In contrast, at the southern edge of the ranges, future warming could not increase growth beyond the genetic capabilities of the species and the dynamics of the species at this part of their ranges would be potentially determined by the responses of competitors to warming. A similar
analysis for the moss *H. splendens* shows how a current alpine population would resemble a population from a lowland forested area under climatic warming (Figure 6.14b).

*Figure 6.14* a) The number of leaves produced per year in shoots of Cassiope tetragona as a function of the average July temperature b) Correlation between a growth parameter in *Hylocomium splendens* and mean annual temperature at seven Arctic/sub-Arctic sites. The boxes on the regression lines contain scenarios of growth for ACIA time slices resulting from temperature increases according to the five ACIA scenarios. The dotted line in a) depicts predicted growth probably outside the capability of the species. The expanded boxes to the right depict uncertainty ranges associated with each of the predictions. Filled circles denote populations for which scenarios have been applied.

At the landscape scale, plants are distributed in mosaics associated with microhabitats and the larger scale latitudinal range changes will be associated with initial changes in landscape mosaics. Cushion plants and other species characteristic of wind-exposed patches might become restricted in distribution by increased snow cover. In contrast, plants of snow beds might become more restricted if snow duration decreases. Wetland species will become restricted by drying and so on. Plants currently restricted to south-facing slopes and warm springs (to some extent analogs of future warmer habitats and hot spots of biodiversity) North of their main distribution areas, can provide “an inoculum” for rapid colonization of surrounding habitats when climate becomes warmer, although they themselves are likely to be displaced from their current niches by less diverse shrub-thicket communities. Examples include orchids, ferns and herbs in warm springs on West Greenland (although orchids and ferns are unlikely to become widely distributed), ericaceous dwarf shrubs in some inner fjords of Svalbard and the large shrub/small trees of the North Slope of Alaska.

### 3.6.2.2 Geographical ranges of animals

Often observed trends of migratory bird population numbers cannot easily be distinguished from local, site-related factors in and outside the Arctic, such as drainage, land use change, hunting and persecution by humans, as well as predation. Even among global factors, climate change is one in an array of impacts, such as eutrophication, often working in synergy with climate change and reinforcing the effect. In addition migratory birds are also heavily impacted by climate change outside the Arctic breeding grounds. Desertification, droughts and the loss of wetlands, the eutrophication of staging and wintering wetlands, changes in land use and application of chemicals and nutrients on wintering grounds, lead to changes in vegetation and biomass on coastal staging and wintering grounds. Sea level rise impacts on the extent of coastal staging and wintering grounds will be particularly harmful, and the hunting pressure on wintering waders in certain areas will also reduce bird populations.

The impact of climate change on migratory species has not been studied very much, although the recent trends in some species (e.g. Arctic geese) are well known (Madsen et al., 1999). Very little can be concluded about observed impacts of current climate variability on migratory birds, as existing monitoring programs are few (e.g. Soloviev et al., 1998) and often started only recently.
Analysis of Hadley Centre spring and summer data of temperature and precipitation over the last 50 years, interpolated over the currently known distribution areas of the White-fronted Goose (*Anser albifrons*) and the Taymyr population of the Knot (*Calidris canutus canutus*) in the Arctic, demonstrates a significant correlation between the mean June temperature and the juvenile percentage as a measure of breeding success. The Nearctic population of the Knot (*C. c. islandica*), as well as the Curlew Sandpiper (*Calidris ferruginea*) breeding on the Taymyr Peninsula, do not show such a correlation (Zöckler and Lysenko, 2000). Under the HadCM2GSa1 model, an increase of 1% CO$_2$/yr results in a moderate increase of the mean June temperature scenario in the Taymyr-breeding area of the White-fronted Goose which is likely to favor the goose population. The conditions for the Taymyr population are particularly favorable for the period around 2020. However, a considerable early cooling and lack of warming over today’s values by 2080 of the breeding grounds of the goose population in West Greenland is likely to lead to a drop in size of the fragile Greenland population. Although the ACIA climate scenarios differ from those used in Zöckler and Lysenko (2000), possible decreases in temperature in ACIA sub-region I are within the range of scenarios (Table 6.14). This study has to be interpreted in relation to other factors, such as other weather parameters, and natural predation which often fluctuates in 3-4 year cycles according to the abundance of the main prey, i.e. the lemming (see Section 4.1.4.2). Furthermore, hunting by humans, mainly outside the Arctic, and the effects of climate change, in particular sea-level rise outside the Arctic, need to be taken into account.

Investigations of the breeding wader population in NE Greenland for over 30 years showed that spring snow cover is the main factor governing initiation of egg-laying in High Arctic waders, such as Red Knot and other sandpipers, while temperature appears not to be important in June (Meltofte, 1985; 2000 and pers. comm.). In fact, waders breed earlier in the arid but cool far North of Greenland, than they do in the 'mild' South of the high Arctic zone because snow-cover is much deeper and extensive in the humid South. Predictions for northeast Greenland are cooler summers, later snowmelt, and less snow-free space to feed on for the arriving waders, leading to later breeding and smaller populations. Snow-cover must still be considered the prime regulating factor for initiation of egg-laying, but temperature - so important for determining invertebrate food availability (Chapter 7) - is involved as well, when sufficient snow-free habitat is already present.

Although global warming in synergy with global eutrophication will probably lead to an increase of biomass, a change in vegetation height and density and a general change in vegetation structure with shifts in species distribution that will have an enormous impact on water birds that are highly dependant on open landscapes and lightly vegetated breeding sites, it will provide opportunities for other birds with more southerly distribution, such as owls and woodpeckers. Some birds, like most goose species and also a few waders have demonstrated a certain ability to adjust to new and changing habitats (Lugert and Zöckler, 2001), but the majority of high Arctic breeding birds appears to be prone to be pushed to the edge with little habitat left.

### 3.6.2.3 Geographical ranges of microorganisms

Studies on geographical ranges of microbes related to extreme cold environments such as the Arctic, and also to climate change, are in their infancy. Contrary to plant and animal ecology, soil
microbiology still does not have a solution to the central biogeographical problem: are soil microorganisms cosmopolitan (widely distributed) or endemic (restricted to one location) species? Until we know the ranges of species, we cannot identify which bacteria might be threatened by climate change (Staley, 1997).

The prevailing hypothesis for bacterial biogeography is based on the axiom of the Dutch microbiologists Baas-Becking and Beijerinck, who stated, “Everything is everywhere, but the environment selects” (Beijerinck, 1913). This assumes that free-living bacteria are cosmopolitan in their geographic distribution; they are readily disseminated from one location on Earth to another by water and air currents or animal vectors such as birds that migrate between regions. Only recently has it been possible to rigorously test the cosmopolitan distribution of bacteria with unbiased molecular biological approaches. Studies outside the Arctic demonstrate that the cyanobacteria *Microcoleus chthonoplastes* is a cosmopolitan species (Garcia-Pichel *et al.*, 1996). Using different molecular biology techniques, Stetter *et al.* (1993) discovered that hyperthermophilic (“heat loving”) archaea isolated from Alaskan oil reservoirs showed a high degree of DNA-DNA reassociation with selected *Archaeoglobus*, *Thermococcus*, and *Pyrococcus* species. Stetter *et al.* concluded that the species were the same as those from European thermal marine sources. In a separate study, DNA-DNA reassociation of a strain isolated from North Sea crude oil fields showed 100% relatedness to an *Archaeoglobus fulgidus* strain from Italian hydrothermal systems (Beeder *et al.*, 1994). These two studies comprise some of the best evidence to date supporting the cosmopolitan hypothesis of Baas-Becking.

However, 3-chlorobenzoate–degrading bacteria isolated from soils in six regions on five continents (Fulthorpe *et al.*, 1998) were found to have restricted/unique ranges. Also, plant species have been reported to harbor their own unique symbiotic species of fungi associated with leaves, bark, roots, etc (Hawkesworth, 1991), so, by definition, the existence of endemic plants should imply the existence of respective microbial symbionts. Therefore, Arctic microbial communities may consist of a mixture of species, some of which are endemic and some of which are cosmopolitan.

**Summary: Recent and expected changes in species distributions and potential ranges**

Monitoring of distribution ranges with a spatial representation as good as for temperate latitudes is not available for the terrestrial Arctic region. Indigenous knowledge projects have documented recent changes in the ranges of caribou in relation to changes in weather. Hunters’ explanations of caribou distributions may provide indications of potential range changes under scenarios of warming temperatures, such as overwintering of caribou in coastal areas during warm winters. Other Arctic indigenous observations include insects previously associated with areas South of the treeline and more frequent sightings of “mainland ducks”. In contrast, almost all Arctic breeding species are declining. The reasons for the trends are not always clear and probably of multiple origins, although there are suggestions of a general trend that some species are shifting their distribution in response to changing climate that is altering habitats.

Quantitative monitoring of conspicuous and popular species such as birds and butterflies has demonstrated that many formerly southern species are quickly approaching the Arctic regions and some have already entered. Arctic birds, especially Arctic-breeding water and waders, that can be counted on staging and wintering grounds, show mostly declining population trends; some of them have declined dramatically. It can be suspected that these changes result from the combined action of eutrophication and habitat loss on wintering and staging sites as well as concurrent climate change although separating the relative contributions of these factors is difficult. Based on climate models,
quite dramatic reductions of the populations of tundra birds can be predicted as generally warmer climate is likely to increase vegetation height and the Arctic’s landmass will probably decrease in extent.

Species–climate response surface models are able to predict the recently observed range changes of at least some species of both birds and butterflies. At least in the case of butterflies, the extent to which species have realized their predicted range changes over the last 30–50yr is strongly related to their degree of habitat restriction, generalist species being much more able to achieve the predicted range expansions than are specialist species. Simulated potential future ranges are often markedly reduced in spatial extent compared to the species’ present ranges. The range limits of boreal and temperate species shift polewards but the large magnitude of the simulated range margin shifts, however, results in many boreal species exhibiting potential future ranges of reduced spatial extent because they are limited to the North by reaching the shore of the Arctic Ocean. Species that experience some physiological constraint at their southern range margin are likely to be affected sooner than those that are affected by biotic relationships such as competition by immigrant species. Loss of habitat, such as tundra ponds for many Arctic birds, is a particularly important possibility that will very probably constrain species ranges. In contrast, plant populations that are outliers of more southern regions and restricted to particularly favorable habitats in the Arctic, may spread rapidly during warming. Models of a moss and dwarf shrub growth along latitudinal gradients show considerable potential for range expansion in the North, but considerable uncertainty, in relation to ACIA scenarios of warming.

Probably the great majority of microorganisms detected in northern ecosystems such as free-living bacteria are cosmopolitan in their geographic distribution, are readily disseminated from one location to another and the environment selects those that can proliferate. However, some species, particularly symbionts with endemic plants, can themselves be candidates for endemic status.
4. Effects of changes in climate and UV on structure and function of Arctic ecosystems in the short- and long-term perspectives

The previous section assessed the responses of individual species to changes in climate and UV-B radiation. Here we assess the responses of species aggregated into communities and ecosystems. The two main attributes of ecosystems that respond to environmental change are structure and function. We assess each separately although the two attributes strongly interact.

We define ecosystem structure in terms of:
- Spatial structure such as canopy structure, and habitat
- Trophic interactions and
- Community composition in terms of biodiversity

and we define ecosystem function in terms of:
- Carbon and nutrient cycling including dissolved organic carbon (DOC) export
- Soil processes
- Controls of trace gas exchange processes
- Primary and secondary productivity
- Water and energy balance

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) scales: processes at the landscape and regional scales will be covered in sections 5 and 7. Also, community responses to climate and UV change presented here include affects on the diversity of plant growth forms in terms of biomass contribution, but details of impacts on biodiversity in terms of organism survival and population dynamics are included earlier in section 3.

4.1 Effects of changes in climate and UV on ecosystem structure

4.1.1 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 (Plate 6.1-6.4). 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 (Chernov and Matveyeva, 1997; Walker et al., 1989).

Plate 6.1 Forest tundra vegetation represented by the Fennoscandian mountain birch forest, Abisko, northern Sweden.
Plate 6.2 Zonal tussock tundra near Toolik Lake, Alaska, with large shrubs/small trees of Salix in moist sheltered depressions.
Plate 6.3 Polar semidesert dominated by Dryas octopetala, Ny Ålesund, Svalbard.
Plate 6.4 Polar desert, Cornwallis Island, Northwest Territories, Canada.
Plate 6.5 Polygonal wet tundra near Prudhoe Bay, Alaska.
Plate 6.6 Racomitrium/Empetrum heath in Iceland (showing erosion).
Plate 6.7 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.

Plate 6.8 Thermokarst scenery in the Russian Tundra, New Siberian Islands.

According to Bliss and Matveyeva (1992), 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 characterized by white spruce Picea glauca in Alaska, birch in Fennoscandia (Plate 6.1), 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 (Hustich, 1983). 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 6.2). 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 semi desert communities (Plate 6.3) 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 6.4). 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 6.5) 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 (Matveyeva and Chernov, 2000).

The classification of vegetation described above has geographical connotations and cannot be applied easily to reconstructions of past vegetation throughout the circumpolar North (Kaplan et al., 2003). A recent classification of tundra vegetation at the biome level (Walker, 2000) has been proposed by Kaplan et al. (2003; Table 6.8, Figure 6.2).


<table>
<thead>
<tr>
<th>Biome</th>
<th>Definition</th>
<th>Typical taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low- and high-shrub tundra</td>
<td>Continuous shrubland, 50 cm to 2 m tall, deciduous or evergreen, sometimes with tussock-forming graminoids and true mosses, bog mosses and lichens</td>
<td>Alnus, Betula, Salix, Pinus pumila (in eastern Siberia), Eriophorum, Sphagnum</td>
</tr>
<tr>
<td>Erect dwarf-shrub tundra</td>
<td>Continuous shrubland 2 to 50 cm tall, deciduous or evergreen, with graminoids, true mosses, and lichens</td>
<td>Betula, Cassiope, Empetrum, Salix, Vaccinium, Poaceae, Cyperaceae</td>
</tr>
</tbody>
</table>
Prostrate dwarf-shrub tundra  Discontinuous “shrubland” of prostrate deciduous dwarf-shrubs 0 to 2 cm tall; true mosses and lichens

Cushion forb, lichen, and moss tundra  Discontinuous cover of rosette plants or cushion forbs with lichens and true mosses

Graminoid and forb tundra  Predominantly herbaceous vegetation dominated by forbs, graminoids, true mosses, and lichens

1 “true” mosses exclude the genus *Sphagnum*

Within the biomes or zonal vegetation types, there are “intrazonal habitats” which are frequently associated with variations in soil moisture and snow accumulation and which have a microclimate that deviates from the general macroclimate associated 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 understorey of mosses and liverworts but lack fruticose lichens (Matveyeva and Chernov, 2000). 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 6.5). Diversity “focal points/hot spots” Walker, M. D. (1995) and “oases” (Edlund and Alt, 1989; Svoboda and Freedman, 1994) 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 6.6).

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 understorey 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 (Chapin *et al*., 1995; Bret-Harte *et al*., 2001) and sexual reproduction (Molau and Larsson, 2000), although range expansion will depend on geographical barriers such as mountains and seas (Table 6.14). Recent warming in Alaska has caused substantial increase in shrub density and size in moist tundra of northern Alaska (Sturm *et al*., 2001b). In areas where shrubs are absent, shrubs are likely to exhibit time lags in migration into new habitats (Chapin and Starfield, 1997). 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 (Chapin et al., 1996; Bret-Harte et al., 2001) and to reduce overall litter quality (Hobbie, 1996) 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 (Matveyeva and Chernov, 2000). 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 (Torn and Chapin, 1993; Joabsson and Christensen, 2001). 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 (Section 5.3.2), which are characterized by the absence of woody plants.

4.1.2 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 in Section 3; here we emphasize overall community structure and species interactions.

4.1.2.1 Plant communities

Nutrient addition is the environmental manipulation that has strongest effect on the productivity, canopy height and community composition of Arctic plant communities (Press et al., 1998a; Jonasson et al., 2001; van Wijk et al., 2003; Figure 6.15). 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 (c.f. the Paddus and Slätta 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 (Parsons et al., 1994; Press et al., 1998b). Similarly, in northern Alaska addition of nitrogen and phosphorus increased productivity and turnover within three years (Chapin et al., 1995). 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 (Figure 6.16). After nine 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 (Chapin et al., 1995; Bret-Harte et al., 2001; Shaver et al., 2001). 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 (Shaver et al., 1998; Jonasson et al., 1999b). In polar semi deserts, nutrient addition generally had a negative effect on vascular plants, due to enhanced winter kill, but stimulated the growth of mosses (Robinson et al., 1998), 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.

Figure 6.15. 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 (van Wijk et al., 2003).

Water additions to simulate increased precipitation have generally had only minor effects on total biomass and production (Press et al., 1998a).

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 (Arft et al., 1999; Shaver and Jonasson, 2000; Jonasson et al., 2001; van Wijk et al., 2003; Figure 6.15). 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 (Robinson et al., 1998; Arft et al., 1999). In the low Arctic, community biomass and nutrient mass changed little in response to warming in two Alaskan tussock sites (Chapin et al., 1995; Hobbie and Chapin, 1998) and in two wet sedge tundra sites (Shaver et al., 1998), 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 (Chapin and Shaver, 1985a; b; Chapin et al., 1995), similar to a pattern observed in the sub-Arctic Swedish forest floor vegetation (Press et al., 1998b). The responses to warming were much stronger in the Swedish treeline heath and in the fellfield (Jonasson et al., 1999b). 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 understorey through the treeline heath to the cold, high altitude fellfield where the response to warming was of the same magnitude as the response to fertilizer addition (Jonasson et al., 2001). 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 (van Wijk et al., 2003: Figure 6.15).

Figure 6.16 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 (Chapin et al. 1995). 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.

4.1.2.2 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 (Hodkinson et al., 1998). Species with rapid life cycles (Aphids and Collembola) responded demographically more quickly than species (e.g. mites) with slow life cycles (Coulson et al., 1996). 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 (Hodkinson et al., 1998) and to anoxic conditions in winters due to ice crust formation following episodes with mild weather (Coulson et al., 2000). Ice crust formation during the winter may increase over-winter mortality by 50% in Collembola (Coulson et al., 2000). Also freezing-thawing events in spring may cause differential mortality among species, thus altering community composition (Coulson et al., 1995). 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.

Compared to the high Arctic, sub-Arctic invertebrate communities at Abisko responded less to experimental warming (Hodkinson et al., 1998). 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 (Ruess et al., 1999a;b).

4.1.2.3 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 effect on the biomass (Jonasson et al., 1996; 1999b; Michelsen et al., 1999, Schmidt et al., 2000). In some cases, however, a combination of carbon and nutrient addition has led to a pronounced increase of both microbial biomass and nutrient content (Schmidt et al., 2000). 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 semi
desert led to substantial increase in microbial biomass C and microbial activity (Illeris et al., 2003).

Data on effects of growing-season ecosystem warming of 2-4°C over 5 (Jonasson et al., 1999b; Ruess et al., 1999) and 10 (Jonasson and Michelsen, unpublished) 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 (see Section 4.2.1.1).

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 (Giblin et al., 1991; Jonasson et al., 1999b; Schmidt et al., 1999; 2002). In contrast, pronounced increases of both bio- and nutrient mass have been reported in autumn (Jaeger et al., 1999; Lipson et al., 1999; Bardgett et al., 2002), 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 (Schmidt et al., 1999; Grogan and Jonasson, 2003), despite soil temperatures below 0°C (Clein and Schimel, 1995; see Section 3.3.3.1). It is followed by a sharp biomass decline in the transition between winter and spring (Brooks et al., 1998; Bardgett et al., 2002; Grogan and Jonasson, 2003), which may (Brooks et al., 1998) or may not (Larsen et al., 2002; Grogan and Jonasson, 2003) coincide with a decrease also in microbial N and an increase of mineralised N, indicating a pronounced transformation of microbial N to soil inorganic N (Giblin et al., 1991; Schmidt et al., 1999). 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 (Schimel and Chapin, 1996), and microbes access nutrients efficiently only when the sink strength for nutrients in plants is low (Jonasson et al., 1999b).

Laboratory experiments have shown that the spring decline of microbial mass is a likely effect of repeated freeze-thaw cycles (Schimel and Clein, 1996). Indeed, Larsen et al. (2002) 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 (Johnson et al., 2002). Although these rhizosphere bacteria are a relatively small component of the below ground microbial biomass, they are likely to be particularly responsive to environmentally induced changes in below ground 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 (Gehrke et al., 1995). 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. (1995). 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 (Moody et al., 2001). 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.

4.1.3 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 (Myneni et al., 1997; 2001; Figure 6.17), although changes in satellites and sensor degradation may contribute to this trend (Fung, 1997). Aerial photographs show a general increase in shrubbiness in Arctic Alaska (Sturm et al., 2001b) and 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 (Shaver et al., 2001). In Scandinavia, recent decadal changes in vegetation are affected more strongly by cyclic abundance of lemmings than by climatic trends (Laine and Henttonen, 1983).

Figure 6.17 Changes in greeness (depicted by NDVI) of northern vegetation between 1981 to 1991 (Myneni et al., 1997).

4.1.4 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 (Chernov, 1995). 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 (Batzli et al., 1980; Oksanen et al., 1997; Wiklund et al., 1999) while the abundance of phytophagous (plant-eating) insects relative to plant biomass is low on Arctic tundra (Strathdee and Bale, 1998). Large predators such as wolves, wolverines and bears are less numerous in the tundra than in the boreal forest (Chernov and Matveyeva, 1997) 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) (Batzli, 1975; Wiklund et al.,
1999) 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.

4.1.4.1. Plant-herbivore interactions

Changes in climate, UV-B, CO$_2$, 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 (Haukioja, 1980; Jefferies et al., 1994). 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. (1983; Coley et al., 1985), 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. Jonasson et al., 1986; Iasson and Hester, 1993; Jefferies et al., 1994) the abundance of secondary chemicals is often strongly responsive to changes in environment including temperature, light, and nutrient availability (e.g. Laine and Henttonen, 1987; Haukioja et al., 1998; Graglia et al., 2001b). In a widespread Arctic shrub species, Betula nana, Graglia et al. (2001b) 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 (Gwynn-Jones, 1999). 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 CO$_2$ concentrations can also affect plant tissue quality and consequently herbivory (Agrell et al., 1999). Enriched CO$_2$ 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 CO$_2$ 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 (Bylund, 1999; Neuvonen et al., 1999). In *Epirrita autumnata*, eggs laid on birch twigs in autumn cannot tolerate winter temperatures lower than \(-36^\circ C\). For this reason *Epirrita* is destroyed in portions of the terrain (e.g. depressions) where winter temperatures get lower than this critical minimum (Tenow and Nilssen, 1990; Virtanen and Neuvonen, 1999). 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 *Operopthera brumata* to extend their geographic distributions into continental areas with cold winters (Tenow, 1996). 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 (Bale et al., 2002). 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 (Tenow, 1972; 1996). 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 lead to more or less permanent tundra (Kallio and Lehtonen, 1973; Lehtonen and Heikkinen, 1995). There are no population outbreaks in *E. epirrita* further South in Fennoscandia, most likely due to high abundance of generalist parasitoids that keep the moth populations below outbreak levels (Tanhuaanpää et al., 2001). 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 (Buck and Callaghan, 1999; Lavola et al., 1997; 1998). 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 (Buck, 1999). 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 (Batzli et al., 1980; Oksanen et al., 1997;Wiklund et al., 1999). 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 (Chernov and Matveyeva, 1997). 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 (Batzli, 1975; Section 3.3.2.1). Lemming peak densities exceed 200 individuals per ha in the most productive *Lemmus* habitats both in Siberia and North
America (Batzli, 1981) and the standing crop of lemmings may approach 2.6 kg dry 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 (Batzli, 1993). 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 goose near breeding colonies). Moreover, lemmings destroy much more vegetation than they ingest and after population peaks typically 50% of the above-ground biomass has been removed at snow melt (Turchin and Batzli, 2001). In unproductive snowbeds, which are favored winter habitats of *Lemmus lemmus* (Kalela, 1961), up to 90-100% of the moss and graminoid present during the winter may be removed (Koskina, 1961). 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 non-cyclic 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 (Chernov and Matveyeva, 1997). 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 dry w ha\(^{-1}\) (Batzli, 1981) on their summer pastures and usually < 10% of the vegetation is taken (Jeffries *et al.*, 1994). The only cases where reindeers have been shown to have large impacts on the vegetation seem to be in unusual circumstances (stranding on islands; Klein, 1968) or under human intervention (e.g. removing top predators or introductions to islands) where overshooting reindeer populations have lead to destruction of the vegetation, degradation of habitats and subsequent population crashes.

Although the cooling since the mid 1970’s in the Hudson Bay region has affected the reproduction of snow geese, the mid-continental population is currently growing at 5% per year (Skinner *et al.*, 1998). 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 subspatacea* (Jeffries *et al.*, 1995). 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 (Shultz 1969), production cycles inherent in food plants (Tast and Kalela, 1971), induced chemical defense in plants (Haukioja, 1991) and recurrent overgrazing (Oksanen et al., 1981). The empirical evidence is mixed. There is at least partly supporting evidence for induced chemical defense in the *Epirrita*-birch system (Ruohomäki et al., 2000) and for overgrazing in the *Lemmus*-plant system in unproductive tundra habitats (Turchin et al., 2000). There is little evidence, however, for mechanisms involving nutrient cycling and chemical defense in the case of lemmings and voles (Anderson and Jonasson, 1986; Jonasson et al., 1986). 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, Charles Elton 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 (Turchin and Hanski 1997, Gilg et al. 2003). 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 (Ims and Steen, 1990; Ims and Andreassen, 2000). The impacts of bird predators have a strong seasonal component since most migrate South for the winter (Ims and Steen, 1990). 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 (Batzli, 1981). In the Karup Valley in Greenland the combined impact of different predators both limited population growth and caused population crashes in collered lemmings (Gilg et al., 2003). 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 (Heske et al., 1993). Using the same methodology, Reid et al. (1995), Wilson et al. (1999) and Gilg (2002) showed that predation was the predominant mortality factor in populations of Collared lemmings at various localities in northern Canada and eastern Greenland.

**4.1.4.2 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) (Batzli,
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 (Erlinge et al., 1999; Predavec et al., 2001), the highly mobile avian predators can track lemming population peaks in space. Mammal lemming and vole specialists 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 (MacLean et al., 1974). In lemming low years weasel and ermine reproduction frequently fails and mortality rate increases (Hanski et al., 2001; Gilg et al., 2003). On coastal and inland tundra habitats where bird colonies are lacking, the Arctic fox also exhibits the population dynamics typical of a lemming specialist (Angerbjörn et al., 1999). 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 (Sutherland, 1988; Bety et al., 2002). Recently observed increased predation pressure on waterbirds in various Arctic region might reflect a change of the lemming cycle in response to climate change with secondary effects on predators and waterbirds as an alternative prey (Summers and Underhill, 1987; Soloviev et al., 1998). Thus a large part of the tundra vertebrate community cycle is in a rhythm dictated by the lemming populations (Stenseth and Ims, 1993; Chernov and Matveyeva, 1997).

This rhythm is likely to be disrupted by future variation in snow properties (e.g. snow season length, snow density and snow cover thickness) (Yoccoz and Ims, 1999). 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 (Hansson and Henttonen, 1988). 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 (Post et al., 1999), but more extensive snow patches give relief from insect pests (Section 3.4.2.1). 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”; Moran, 1953), 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 (Henttonen and Wallgren, 2001) (see Figure 6.12 in Section 3). 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 middle of 1980s) in the northern taiga (Henttonen et al., 1987; Hanski and Henttonen, 1996; Henttonen, 2000), and are still prevailing. For predators that specialize in feeding on small rodents, the lack of cyclic peak abundance of small rodents, especially in the spring (Oksanen et al., 1997), 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 (Angerbjörn *et al*., 2001). In Alaska a similar decrease in cyclicity of lemmings occurred in the 1970s (Batzli *et al*., 1980).

Large predators such as wolves, wolverines and bears are less numerous in the tundra than in the boreal forest (Chernov and Matveyeva, 1997). 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) (Krebs *et al*., 2003).

4.1.4.3 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 (Gauslaa, 1984), 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 (Skinner, 2002). 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 (Killick and Warden, 1991). Species and strains of the fungus *Metarhizium* are important agents of insect disease but some, particularly high latitude strains, are sensitive to UV-B (Braga *et al*., 2001a; b).

Parasitism is perhaps the most successful form of life, but until recently certainly underestimated, especially in the Arctic regions (Henttonen and Burek, 2001; Hoberg *et al*., 2003). 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 (Fedorov *et al*., 1999a; b). The impact seems to be at least as profound on the helminth parasites of Arctic rodents (Haukisalmi *et al*., in press; Hoberg *et al*., 2003). 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 (Kutz et al., 2002). 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 (1990) 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 (Irvine et al., 2000). Recently Albon et al. (2002) 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 (Chapter 14).

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 (Section 3.4.2.1). 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.

4.1.4.4 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. (1999b) 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 solubilisation 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 several-fold and should constitute an important plant nutrient source (Jonasson et al., 1999a; 2001).

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 (Read et al., 1989), 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 non-existing. 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 (Ruess et al., 1999a; b). If so, the release rate of plant available nutrients is likely to increase (e.g. Ingham et al., 1985), which may explain the enhanced nutrient sequestration by plants in warmer soils rather than pulse sequestration after microbial dieback.

### Summary: Effects of changes in climate and UV on the structure of Arctic ecosystems

Changes in climate and UV will very probably affect three important attributes of ecosystem structure: spatial structure such as canopy structure and habitat, trophic interactions and community composition in terms of biodiversity. Ecosystem structure varies along a latitudinal gradient from the treeline to the high Arctic polar deserts. Along this gradient there is a decreasing complexity of vertical canopy structure and ground cover ranging from the continuous and high canopies (>2m) of the forest tundra in the South to the low canopies (ca 5 cm) that occupy less than 5% of the ground surface in the polar deserts. Within each Arctic vegetation zone there are often outliers of more southerly zones. Changes in distribution of vegetation in relation to climate warming are likely to occur by local expansion of these intra-zonal communities and northward movement of zones. Satellite measurements, aerial photographs and indigenous knowledge already show a recent increase in shrubbiness of parts of the Arctic.

Experimental manipulation of environmental factors expected to change at high latitudes show that some of these factors have strong effects on the structure of Arctic ecosystems, but the effects are regionally variable. Nutrient addition has the strongest effect on the productivity, canopy height and community composition of Arctic plant communities. Nutrients also increase biomass turnover, so biomass may or may not respond to nutrient addition. 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 and always to greater responses than after water addition. Plant growth response increased from a climatically, relatively mild forest understory through a treeline heath to a cold, high altitude fellfield. A 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. Warming experiments in the high Arctic had a greater effect on the fauna above ground than below ground and than on fauna in the sub-Arctic. Freeze-thaw events in spring were important and will probably cause differential mortality among species, thus altering community composition. In general, Arctic invertebrate communities are very likely to respond rapidly to change. In contrast long-term data on effects of summer warming of ecosystems by 2-4°C have not shown appreciable changes in microbial biomass and nutrient stocks. This suggests that temperature increase alone is unlikely to have any strong impact on microbial C and nutrient sequestration. Manipulations simulating enhanced UV-B radiation and a doubling of atmospheric CO₂ for 7 years altered the use of labile carbon substrates used by gram-negative bacteria suggesting a change in community composition. UV-B radiation also affects the structure of fungal communities. So far, no change in plant community structure has been found in the Arctic in response to manipulations of UV-B and CO₂.

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. Small herbivorous rodents of the tundra (mainly lemmings) are the main trophic link between plants and carnivores. Small rodent population cycles with peak densities every 3-5 years induce strong pulses of disturbance, energy and nutrient flows, and a host of indirect interactions throughout the food web. Lemming population cycles are crucial for nutrient cycling, structure and diversity of vegetation and for the viability of a number of predators and parasites that are specialists on rodent prey/hosts. Trophic interactions are likely to be affected by climate change. Ice crusting
in winter may render vegetation inaccessible for lemmings, deep snow may render rodent prey less accessible to
snow surface predators, and increased plant productivity due to warmer summers may dominate the food web
dynamics. Long-term monitoring of small rodents at the border of the Arctic region in Fennoscandia provides
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. These include the Arctic fox, snowy owls, buzzards
and skuas.

In sub-Arctic forests, a few insect defoliators such as the autumnal moth *Epirrita autunnata* that exhibit cyclic peak
densities at approximately 10 year intervals are dominant actors in the forest food web. Insects can devastate large
tracts of birch forest at outbreak densities, and play a crucial role in forest structure and dynamics. Trophic
interactions with either the mountain birch host plant or its insect parasitoids, are the most plausible mechanisms
generating cyclic outbreaks in *Epirrita*. Climate is likely to alter the role of *Epirrita* and other insect pests in the
birch forest system in several ways. Warmer winters may act to increase survival of eggs and expand the range of the
insects into areas outside their present outbreak ranges. Alternatively the distribution range and activity of natural
enemies like parasitic wasps is likely to keep the insect herbivore populations below outbreak densities.

Climate change is likely to also 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. 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. There are large uncertainties about the outcome of the
potential spread of new trophic interactants, especially pests and pathogens into the Arctic.

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. The incidence of new diseases from increasing mobility of pathogens with a southern
distribution is a possibility but UV-B could possibly reduce the impact of viral and fungal pathogens.

Microbe-plant interactions can be competitive for nutrients and also mutualistic through mycorrhizal associations.
Warming will probably affect both types of relationship but information is scarce.

### 4.2 Ecosystem function

#### 4.2.1 Biogeochemical cycling: dynamics of carbon (C) and nutrients

##### 4.2.1.1 General introduction

Arctic ecosystems are characterized by low primary productivity, low element inputs, and slow
element cycling yet they tend to accumulate organic matter, C, and other elements because
decomposition and mineralization processes are even more strongly limited than productivity by
the Arctic environment, particularly the cold, wet soil environment (Jonasson et al., 2001). Because of this slow decomposition, the total C and element stocks of wet and moist Arctic
tundra frequently equal and may exceed the stocks of the same elements in much more productive systems of temperate and even tropical latitudes (Table 6.9).

*Table 6.9. Comparisons of average carbon pools (g m⁻²) in Arctic and alpine tundra with the
neighboring boreal zone and the world’s average for all terrestrial ecosystems. The results are
also expressed as the total amount of carbon in these biomes, together with the world’s total. The
soil pools do not include organic C in permafrost, beneath the seasonally-thawed active layer
(from Jonasson et al., 2001, after data in McGuire et al., 1997).*
Low Arctic sites with warmer and dryer soils, and extremely unproductive high Arctic polar deserts and semi deserts, have smaller organic matter accumulations (Table 6.10). Most of the organic matter and element accumulation occurs in soils, while large accumulations of vegetation mass are limited by a lack of tall woody plant forms such as trees, by selection for slow-growing, low, compact plant forms, and by low productivity and low availability of soil-available elements such as N or P. Typically, the majority of the vegetation mass consists of roots and below ground stems, with above ground plant mass accounting for less than one third, and sometimes only 5-10 per cent, of the total.

In addition to the large C stocks within the seasonally-thawed, upper active layer of soil (Table 6.10), an equally large pool of organic C may be held in the upper permafrost, within 1-2 m of the surface (Michaelsen et al., 1996). While these frozen C stocks are not actively involved in C cycling on a seasonal or yearly basis, in the long term they do represent an important C sink, and they may be of particular importance if climate changes lead to greater soil thaw or to loss of permafrost (Chapter 5).

<table>
<thead>
<tr>
<th>Area</th>
<th>Soil</th>
<th>Vegetation</th>
<th>Soil:Veg.</th>
<th>Total carbon (10^{12} kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(10^6 km)</td>
<td>(g m^{-2})</td>
<td>(g m^{-2})</td>
<td>ratio</td>
<td>Soil</td>
</tr>
<tr>
<td>Arctic and Alpine tundra</td>
<td>10.5</td>
<td>9200</td>
<td>550</td>
<td>17</td>
</tr>
<tr>
<td>Boreal woodlands*</td>
<td>6.5</td>
<td>11750</td>
<td>4150</td>
<td>2.8</td>
</tr>
<tr>
<td>Boreal forest</td>
<td>12.5</td>
<td>11000</td>
<td>9450</td>
<td>1.2</td>
</tr>
<tr>
<td>Terrestrial total</td>
<td>130.3</td>
<td>5900</td>
<td>7150</td>
<td>0.8</td>
</tr>
</tbody>
</table>

*approximates to forest tundra


<table>
<thead>
<tr>
<th>Soil organic matter</th>
<th>Vegetation biomass</th>
<th>NPP</th>
<th>Soil:Vegetation</th>
<th>Soil:NPP</th>
<th>Veg:NPP</th>
<th>% of total area</th>
</tr>
</thead>
<tbody>
<tr>
<td>(g/m^2)</td>
<td>(g/m^2)</td>
<td>(g/m^2/y)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>High Arctic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polar desert</td>
</tr>
<tr>
<td>Semi-desert</td>
</tr>
<tr>
<td>Wet sedge/mire</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Low Arctic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Semi-desert</td>
</tr>
<tr>
<td>Low shrub</td>
</tr>
</tbody>
</table>
Although

4.2.1.2 Spatial variability

Although the productivity of the most productive tundra may rival that of highly productive shrub and marsh systems at lower latitudes, most Arctic systems lie at the low end of the global productivity range. What is striking is the wide range of variation (about three orders of magnitude) of NPP, and standing stocks of organic matter in soils and vegetation within the

<table>
<thead>
<tr>
<th>Wet sedge/mire</th>
<th>38750</th>
<th>959</th>
<th>220</th>
<th>40</th>
<th>176</th>
<th>4.3</th>
<th>16</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tall shrub</td>
<td>400</td>
<td>2600</td>
<td>1000</td>
<td>0.2</td>
<td>0.4</td>
<td>2.6</td>
<td>3</td>
</tr>
<tr>
<td>Tussock/ sedge dwarf shrub</td>
<td>29000</td>
<td>3330</td>
<td>225</td>
<td>8.7</td>
<td>129</td>
<td>16</td>
<td>17</td>
</tr>
</tbody>
</table>

The largest body of information on organic matter, C, and nutrient budgets of a wide range of Arctic ecosystems comes from the International Biological Program’s Tundra Biome Program, which took place during the late 1960s and early 1970s (Bliss et al., 1981). Since then, research on Arctic element cycling has tended to focus on controls over individual biogeochemical processes rather than on comparisons of overall budgets and element stocks. The recent surge of interest in climate change and feedbacks from the Arctic to the globe has highlighted the relevance and utility of those earlier studies, particularly as currently only a few sites are under study at the whole-system level.

Microbes in Arctic soils contain only one or a few percent of the ecosystem C pool. However, the proportions of ecosystem N and P are appreciably higher due to high concentration of N and P in the microbial tissue compared to the concentration in plants and soil organic matter (SOM) (Jonasson et al., 1999a). The proportions of microbial biomass and nutrient content of the total amount in the soil organic matter are similar to the proportions in non-Arctic ecosystems but, due to the low plant biomass in the Arctic, appreciably higher than the proportion in the vegetation. Data from various Arctic and sub-Arctic sites have shown that microbes commonly contain appreciably less C, slightly less or comparable amounts of N and much higher amounts of P than the entire plant biomass (Cheng and Virginia, 1993; Jonasson et al., 1996; 1999a; Hobbie and Chapin, 1996; Schmidt et al., 2002).

Nutrient mineralization rates are low, however, typically ten-fold lower than in the boreal region. The low rate is mainly due to low soil temperatures, and it leads to low supply rate of nutrients to the plant available pool and nutrient-constrained plant productivity in most Arctic ecosystems (Nadelhoffe et al., 1992). The combination of low mineralization rates and high proportion of nutrients in microbes compared to plants leads to possible competition for nutrients between microbes and plants at periods of rapid microbial growth (Kaye and Hart, 1997). However, microbes are likely also to release a pulse of nutrients during periods of population decline when the cells are lysed and nutrients are leached (Giblin et al., 1991; Jonasson et al., 2001). To predict the microbial effects on the nutrient constrained plant productivity by environmental changes, it is essential therefore not only to understand how the microbial processing rate of the organic matter will change, but also to understand the controls of microbial population sizes and how changes in the populations affect nutrient cycling and interact with plant processes (see also Section 4.1.4.4).

4.2.1.2 Spatial variability

Although the productivity of the most productive tundra may rival that of highly productive shrub and marsh systems at lower latitudes, most Arctic systems lie at the low end of the global productivity range. What is striking is the wide range of variation (about three orders of magnitude) of NPP, and standing stocks of organic matter in soils and vegetation within the
Arctic (Table 6.10). In general, productivity and organic matter stocks decrease with temperature and precipitation from South to North, but local variation in productivity in relation to topography is dramatic (often 10-100 fold). Among the most important correlates of topographic variation in productivity are the duration and depth of winter snow cover and degree of protection from winter wind damage, as well as variation in soil moisture, soil thaw, and soil temperature. Local variation in these factors can be nearly as great as that across a wide range of latitudes (Billings, 1973; Shaver et al., 1996; Jonsson et al., 2001). Local variation in productivity is also associated with dramatic shifts in the relative abundance of plant functional types including both vascular and nonvascular plants (Section 3; Section 4.1). Because of this dramatic local variability, primary production and organic matter accumulation are distributed in a mosaic fashion across the Arctic, with a higher frequency of more productive sites (usually wet or moist lowlands) at lower latitudes.

The spatial distribution of productivity and organic matter in the Arctic is broadly predictable in relation to temperature, soil moisture and other soil factors such as pH, topography and snow cover (D. Walker et al., 1998; 2002; M. Walker et al., 1989; 1994). The proximate controls on C cycling in these ecosystems, however, are much more closely tied to the inputs and turnover of other elements, especially N and P (Shaver et al., 1992). Because N and P inputs (by deposition, fixation, or weathering) are low, even where rapid photosynthesis is possible C cannot be stored in organic matter any faster than the rate of N or P accumulation. Thus, for example, in the Canadian high Arctic where a large portion of the surface is bare ground, C fixation and accumulation is closely tied to low, wet areas where anaerobic soil conditions favor N fixation (Gold and Bliss, 1995). In other Arctic systems, such as Alaskan wet and moist tundras, the total amounts of N and P in soil organic matter may be very high but, due to slow rates of decomposition, the availability of these elements to plants is low, thus leading to low productivity despite high element and soil organic matter stocks (Giblin et al., 1991).

4.2.1.3 Temporal variability

Year-to-year variation in biogeochemical cycles has received little attention in the Arctic, although a few multiyear records of ecosystem C exchange, N deposition, and C and N losses at the watershed or catchment level do exist (Oechel et al., 2000a; Hershey et al., 1997; Kling et al., 2000; Steiglitz et al., 2000). Clearly, the trend over the Holocene, at least, has been one of overall accumulation of elements in organic matter since the loss of the glacial ice cover, but the variation in rates of accumulation (or loss) at the scale of years to decades is particularly poorly understood.

The net C balance of Arctic ecosystems, as in any terrestrial ecosystem, may be positive or negative depending on the time scale over which it is measured and the environmental conditions during the measurement period. This dynamic balance is called Net Ecosystem Production (NEP) and is defined as the difference between two large, opposing fluxes, Gross Ecosystem Production (GEP, or gross ecosystem photosynthesis) and Ecosystem Respiration (R_{E}), both measured in units of C mass or moles per unit area and time. Ecosystem Respiration (R_{E}) has two major components, R_{A} (autotrophic or plant respiration) and R_{H} (heterotrophic or animal plus microbial respiration). Each of these components of NEP has different relationships to current temperature, moisture, and light conditions. Because they are measured at the whole-system level, all three
components are also a function of the current functional mass or surface area of organisms as well as the organisms’ current nutritional status. Thus, for example, even though NEP must be positive over the long term for the large C accumulations in tundra ecosystems to occur, on a daily or seasonal basis NEP swings from strongly negative (at “night”, even under the midnight sun, or in winter) to strongly positive (at midday in midsummer). These daily and seasonal fluctuations have been measured at an increasing number of Arctic sites in recent years (Oechel et al., 2000a; Vourlitis and Oechel, 1997; 1999; Søgaard et al., 2000; Nordström et al., 2001).

NEP may also vary sharply among years, and may be either positive or negative on an annual basis. Recent work in Alaska (Oechel et al., 2000a) indicates that although C was accumulating in wet and moist tundras in the 1960s and 1970s, (i.e. “negative” C balance) during much of the 1980s and 1990s there was a net loss of C from these ecosystems in both winter and summer (i.e. “positive” C balance). In the late 1990s the summer C balances turned again so that the ecosystems were net sinks, but it is not yet clear whether the C balances for the full year have returned to net C accumulation (Figure 6.18; see also Section 5.1.1). It also is not clear whether the shifts in NEP that have occurred over the past 40 years, from C sink to C source and are related in any direct way to weather, because the entire period has been one of general warming in northern Alaska (Section 5). Modeling studies (e.g., McKane et al., 1997; Clein et al., 2000; McGuire et al., 2000) suggest that in the short term (within one or a few years) the response of R_{e} (both R_{A} and R_{H}) to temperature is more rapid than the response of GEP, leading to a short-term loss of C (negative NEP) with warming. In the long term, however, the interaction between temperature and soil nutrient availability might increase GEP sufficiently to cause an eventual return to net C accumulation (positive NEP). There is also evidence from manipulation experiments (Shaver and Chapin, 1991; Shaver et al., 1998) and latitudinal gradients (Callaghan and Jonasson, 1995) that air warming can result in soil cooling after long periods. The mechanism is that air warming leads to increased leaf area indices that intercept a greater proportion of incoming radiation before it reaches the soil surface, thereby leading to soil cooling.

Figure 6.18. Long term trends in summer net CO₂ flux, temperature, and precipitation for Alaskan coastal wet sedge tundra (Oechel et al., 1993; 2000b).

Species and functional type composition of the vegetation are keys to long-term change in productivity, because of differences in nutrient use and allocation, canopy structure, phenology, and relative growth rates among plants (Chapin et al., 1993; Hobbie, 1995). Large differences exist, for example, in the rate at which tundra plants can respond to changes in weather and climate, due to differences in allocation to stems versus leaves or to secondary chemistry versus new growth (Shaver et al., 2001), in the ability to add new meristems (Bret-Harte et al., 2001), and in the constraints on the amount of growth that can be achieved by a single meristem within a single year (i.e., determinate versus indeterminate growth). Species and functional types also differ in their phenology of growth and thus in their ability to take advantage of a change in the timing and duration of the growing season. For example, moss-dominated ecosystems in Iceland have limited ability to respond to climate change without a complete change to a vascular plant-dominated community (Jónsdóttir et al., 1995) whereas shrubs and small trees already present in sheltered, moist depressions on the North Slope of Alaska seem to be already expanding their distribution (Sturm et al., 2001b).
The chemical composition of primary productivity (leaves versus wood, secondary chemistry, species composition) is important as a long-term feedback on productivity and its responsiveness to climate change. It is also important in terms of both animal community composition and secondary (herbivore) productivity. C:N ratios, lignin and protein content, and tannin, resin, and phenolic content are all important in determining forage quality (Section 4.1.4.1) and the susceptibility of plant litter to decomposition, and thus the remineralization of essential limiting nutrients like N and P (Hobbie, 1996).

Despite the critical importance of NPP together with NEP and considerable research on these parameters, additional field measurement and focused process studies are needed to resolve issues relating to the different methodologies used for measuring NPP and NEP (Williams et al., 2000; Hobbie et al., 2000). Also, results from different methodologies need to be reconciled (see Section 6.1.1.2).

N and P budgets were developed for several Arctic sites during the IBP studies 30 years ago (Chapin et al., 1980) but complete documentation of inputs and outputs of any element other than C has not been attempted since then for any Arctic site. Part of the problem is that individual N and P inputs and outputs in Arctic ecosystems, such as N fixation, N deposition, denitrification, rock weathering, or losses in streamflow (discussed below), are even smaller than the amounts annually recycled by mineralization of organic matter (Figure 6.19; Nadelhoffer et al., 1991; Shaver et al., 1992; Peterson et al., 1992), except perhaps in the high Arctic (Gold and Bliss, 1995). Thus, very long-term records are needed to evaluate the significance of interannual variation in N and P budgets, while most studies of the component processes last only 1-3 years.

Figure 6.19. Nitrogen budget for wet sedge tundra at Barrow Alaska (Shaver et al., 1992; adapted from Chapin et al., 1980). Numbers in boxes are N stocks in g m\(^{-2}\); numbers in parentheses are N fluxes in g m\(^{-2}\) y\(^{-1}\).

4.2.1.4 Inputs/outputs, primary production and NEP

The dominant C input to Arctic ecosystems is by photosynthesis of vascular and nonvascular plants which in total sums to Gross Ecosystem Production, GEP. The relative (apparent) importance of various controls on primary production differs depending on whether one looks at the leaf level, the canopy level or the whole vegetation, and at daily, seasonal, or decadal time scales (Williams et al., 2001). Carbon inputs at the leaf level are clearly limited in the short term by generally low irradiance and consequent low temperatures during usually short, and late, growing seasons (Figure 6.8), despite a wide range of specific photosynthesis-related adaptations to the Arctic environment (Section 3). Photosynthesis of Arctic plants is also often sensitive to changes in CO\(_2\) (in the short term), moisture conditions, and snow (UV effects are variable and comparatively small). Although Arctic plants in general are well-adapted to the Arctic climate, there still is considerable variation in the responses of photosynthesis to microclimate among plant functional types. In the longer term and at the level of whole vegetation canopies, however, C inputs are limited by generally low canopy leaf areas, leaf phenology/duration, and light interception (Williams et al., 2001). Canopy leaf area is low because low soil nutrient availability, particularly N, limits the ability of the vegetation to develop a large,
photosynthetically efficient leaf area (Williams and Rastetter, 1999), and it also limits the ability of the vegetation to use newly-fixed C in new growth, because growth requires adequate supplies of multiple elements in addition to C (Shaver et al., 1992; Jonasson et al., 2001). It is also low because of the low stature of the vegetation, which prevents development of a multilayered canopy. Other environmental factors such as wind and soil disturbance also limit C gain. Storage of photosynthate and nutrients acquired in previous years plays a key role in determining current year's productivity (Chapin and Shaver, 1985b).

Carbon outputs from Arctic ecosystems occur via a wider array of processes and are regulated very differently from C inputs (Section 4.2.2). The dominant form of C loss is as CO2, produced by both plants and soil biota. Autotrophic or plant respiration (R4) typically accounts for about half of GEP on an annual basis (Williams et al., 2000; 2001) but follows a very different seasonal and daily pattern (discussed above). Heterotrophic respiration (Rit), mostly by soil organisms, accounts for most of the other half although in the long term the sum of these two must be slightly less than GEP if C is to accumulate in soil organic matter. Rit includes both CO2 and CH4, the latter produced anaerobically in wet soils (Section 4.2.2). Much of the CH4 produced in Arctic soils is oxidized to CO2 before it reaches the atmosphere; net CH4 emission thus is normally only a fraction of CO2 emission in Arctic soils (less than 5%), but methane is a much more powerful greenhouse gas than CO2. Other aspects of carbon balance are important yet difficult to quantify. Examples are plant root respiration, the sloughing of dead material from roots, root exudation, and the growth and respiration of microorganisms intimately associated with plant roots.

Most of the respiratory CO2 and CH4 losses from Arctic systems move directly to the atmosphere. A significant fraction of these gases, however, travels in dissolved forms in soil water, eventually moving into streams and lakes where they are released to the atmosphere (Kling et al., 1991; 1992). Additionally, soil and surface waters contain significant amounts of dissolved organic forms of C, much of which is eventually consumed by aquatic microbes, producing more CO2 (Chapter 7). Together, these losses to aquatic systems may add up to a significant component of the net C balance of Arctic systems. Synoptic, simultaneous analysis of aquatic C losses at the same time, place, and scale as direct atmospheric exchanges has not been completed, but estimates of aquatic C losses suggest that these may equal as much as 20-30 percent of GEP.

Wintertime CO2 losses are a second major gap in our knowledge of C losses from Arctic ecosystems. Although wintertime CO2 losses have long been recognized (Coyne and Kelley, 1971), more recent research indicates that these losses are not only larger than was thought earlier, but also that they may be the product of significant respiratory activity during the wintertime (Oechel et al., 1997; Hobbie et al., 2000; Welker et al., 2000; Fahnestock et al., 1999; Section 3.3.3.1) in which recently fixed carbon is respired (Grogan et al., 2001).

Inputs and outputs of N have been relatively little-studied in the Arctic, largely because early work suggested they were small relative to standing N stocks and internal recycling, and thus were less important, at least on a short-term basis (Shaver et al., 1992). In the long term, however (e.g., on a scale of several decades or more), understanding of N inputs and outputs is essential to understanding how the total pool sizes of N change over time. Changes in standing stocks of N
are closely tied to the accumulation or loss of organic matter and C in the Arctic (Gold and Bliss, 1995).

N enters Arctic ecosystems by atmospheric deposition and by microbially-mediated N fixation (Figure 6.19). N deposition rates are low in the Arctic relative to other parts of the world, mostly because the atmosphere is cold enough that it cannot hold the high concentrations of N species such as nitrate (NO$_3^-$) that fall on lower latitudes. Thus N deposition can account for only about 5\% or less of the annual plant N uptake requirement in Alaskan wet sedge tundra (Chapin et al., 1980), although this might increase with increased industrial activity at lower latitudes. In regions such as northern Scandinavia that are subject to N deposition from lower-latitude anthropogenic sources, however, N deposition may be greater than 0.1 g m$^{-2}$ y$^{-1}$, which if continued for many years is sufficient to affect plant growth and productivity (Back et al., 1994). N fixation rates are usually assumed to be of similar magnitude, although the only relatively recent studies (Chapin and Bledsoe, 1992; Lennihan et al., 1994) indicate that, at least in the high Arctic, N fixation might account for more than 10\% of plant requirements with the remaining 90\% supplied by recycling from the soils.

N losses are also poorly-known. There have been no recent, published studies of denitrification in the Arctic; although anaerobic soils might be expected to have high potential for denitrification, the generally low rates of nitrate production in tundra soils suggest that this is also a small component of the annual N budget. Possible spring losses of N in the form of N$_2$O have been suggested (Christensen et al., 1999a) but not yet verified in the Arctic. N losses in streams have been monitored at several locations, and are of roughly the same magnitude as N deposition (Hershey et al., 1997).

### 4.2.1.5 Responses to climate change

Responses of element cycles in Arctic ecosystems to climate change factors have been studied in multiyear manipulation experiments in several contrasting ecosystem types (Shaver and Jonasson, 2000; Dormann and Woodin, 2002; Figure 6.20). These experiments include manipulations of air temperature, CO$_2$, light, water (both excess and deficit), nutrients and UV-B radiation. One common observation from these experiments is that although short-term responses to single factors like CO$_2$ or warming are measurable and often significant, these responses are often not sustained due to other limitations. A general conclusion is that nutrient limitation dominates the multiyear responses and is linked to changes in other factors (e.g., temperature and water) through their indirect effects on nutrient mineralization and availability to plants. In wet systems, water table depth and soil drainage are critical variables limiting nutrient turnover in the soil; increases in C turnover in these systems are not linked to increases in C accumulation because increased C accumulation requires increased N and/or P supply (Shaver et al., 1998; Oechel et al., 1998; 2000a). A large pool of nutrients exists in organic matter, and may drive large changes in organic matter stocks if the nutrients can be mineralized and not leached from the system. Similarly, short-term increases in photosynthesis and growth in response to high CO$_2$ are often not sustained due to nutrient limitation (Gruulke et al., 1990; Oechel et al., 1994; Hartley et al., 1999; see Section 3).
The results of several manipulation experiments indicate that nutrient mineralization stimulated by increased soil temperatures will probably not be sustained in the long term. Warming of soil causes an immediate increase in soil respiration in laboratory studies, but few Arctic field studies have shown increased mineralization rates in response to air warming (but see Schmidt et al., 1999) and longer-term field studies show an acclimation to increased temperature (Hartley et al., 1999; Luo et al., 2001). Some studies have shown soil cooling in response to air warming in experiments (Shaver and Chapin, 1991) and along latitudinal gradients (Callaghan and Jonasson, 1995). Air warming stimulates leaf area development (Myneni et al., 1997) and greater LAI would be expected to intercept thermal radiation before it reaches the soil, leading to soil cooling. In addition, organic matter in lower soil profiles is less responsive to temperature increases than surface layers (Christensen et al., 1999b; Grogan et al., 2001), again suggesting that any temperature-induced mineralization is likely to be transitory.

Overall, however, multi year experiments suggest that the most responsive Arctic ecosystems to climate change will probably be those in which the environmental change is linked to a large change in nutrient inputs or soil nutrient turnover, and/or large changes in leaching or erosional losses of soil-available nutrients (Figure 6.19). Effects of UV on overall organic matter cycling are generally unknown, but not unimportant. Recent work by Niemi et al. (2002) showed that UV-B decreased methane emissions from a peat land in northern Finland while three studies show an effect on UV-B on Sphagnum growth (Searles et al., 1999; Gehrke et al., 1995; Sonesson et al., 2002) with potential implications for carbon sequestration. Long term responses of biogeochemical cycling to increased CO$_2$ and UV-B are small in magnitude but are likely to lead to longer term changes in biogeochemical cycling and ecosystem structure (Sections 3.4.3; 4.1.2.3). However, most of our understanding of UV responses is based on species- and tissue-level research.

4.2.1.6 Biodiversity and species effects on biogeochemistry

Does the species or growth form composition of the vegetation have any impact on biogeochemistry of Arctic ecosystems, or is biogeochemistry largely regulated by climate and resource availability irrespective of species composition? Although only partial answers to this question are currently available, there are at least five main mechanisms by which species composition are likely to have important consequences for biogeochemistry. These are:

1. Species composition will probably affect the rate of change in ecosystems in response to environmental change, through differences in species potential growth, reproduction, and dispersal rates (e.g., Bret-Harte et al., 2001)
2. Species are likely to affect nutrient availability and C cycling through differences in the 
turnover of elements in their living tissues and in the decomposability of their dead parts 
(Hobbie, 1998; Quested et al., 2003)
3. Species will probably affect element accumulations in living plants through differences in 
their biomass allocation patterns and in the element concentrations and element ratios in 
their biomass (Shaver et al., 2000; Bret-Harte et al., 2002; Quested et al., 2003)
4. Species are likely to differ in their effects on snow accumulation and snowmelt, surface 
energy balance, and soil temperature regimes, with important feedbacks on element cycles 
(Sturm et al., 2001a; McFadden et al., 2001)
5. Physiological mechanisms, for example species of wetlands that act as conduits for 
methane transport from soil to air (Figure 6.21) Öqvist and Svensson, in press; Joabsson 
and Christensen, 2001; Niemi et al., 2002))

All five of these species effects have been documented in Arctic systems, although it is often 
uncertain how to scale up from small experimental communities to larger units of the landscape.

Species richness or diversity itself is likely to also affect biogeochemistry of Arctic ecosystems, 
although the magnitude of the effect is hard to judge. There is a weak positive correlation 
between productivity and vascular species richness in Arctic vegetation, but, like most 
vegetation, richness declines when productivity is increased artificially by fertilizer addition or 
other disturbance (Gough et al., 2000). Recent evidence suggests that Arctic plants obtain their N 
from diverse sources in the soil (Michelsen et al., 1996; 1998; Nadelhoffer et al., 1996) and that 
the relative abundance of different species reflects different abilities to acquire the different 
forms of N (McKane et al., 2002). These latter studies suggest that diversity will probably 
increase productivity in Arctic vegetation by increasing total uptake of different forms of a 
strongly limiting element, N. Partial support for this conclusion comes from experiments 
involving removal of individual species from Arctic vegetation, in which the remaining species 
failed to increase in abundance (Fetcher, 1985; Jonasson, 1992; Shevtsova et al., 1995; 1997).

Figure 6.21 Seasonal mean methane emission from a high Arctic fen in NE Greenland 
(Zackenberg) plotted against leaf biomass of Eriophorum scheuchzeri, Dupontia psilosantha, 
Carex subspathacea and total leaf biomass of the three species. The regression lines represent 
linear fits. The figure shows that the minor constituents of the total vascular plant biomass 
(Carex and Eriophorum) seem to be "driving" net methane emissions from the site suggesting 
that shifts in vascular plant species composition alone could lead to significant effects on trace 
gas exchange (Joabsson and Christensen, 2001).

Vascular plants affect directly the substrate availability for methanogens and have the capability 
to transport gases between the anaerobic parts of soils and the atmosphere (Bubier and Moore, 
1994; Joabsson et al., 1999; Joabsson and Christensen, 2001; Niemi et al., 2002). Different 
vascular plant species have different effects, however, and the vascular plant species composition 
in wet tundra ecosystems may be a key determinant for the scale of CH₄ emissions (Figure 6.21; 
Joabsson and Christensen, 2001; Ström et al., 2003). Changes in species composition per se 
caused by climate warming – and increased UV-B radiation – are likely to cause a change in CH₄ 
emissions adding to the direct effect of a changing soil climate (Niemi et al., 2002) (see Section 
4.2.2.).
4.2.1.7 Role of disturbance

Disturbances are expected to increase with climatic warming, mainly through thermokarst (Section 5.2) and possibly also through increased fire in some northern ecosystems, and insect pest outbreaks in sub-Arctic forests (Section 4.1.4.1). In general, physical disturbance to Arctic ecosystems results in greater soil warming and permafrost thawing, which tend to increase soil organic matter and nutrient turnover. Typically, productivity of the vegetation increases dramatically although soil respiration also increases. It is not yet clear whether the increased plant growth is sufficient to compensate for losses of soil organic matter. In the long term, however, Arctic landscapes should gain OM in both soils and vegetation on disturbed sites. The timing and trajectory of these changes are key unknowns for future research.

4.2.2 Soil processes and controls over trace gas exchanges

4.2.2.1. Diversity of trace gases

During the last decade, trace gases, their production, emission and consumption have attracted considerable attention from the scientific community. The reason is that

i) most of these gases belong to the category of “radiatively active”, i.e. they affect heat balance and induce the “greenhouse” effect responsible for climate instability and warming

ii) the atmospheric concentration (mixing ratios) of these gases underwent remarkably fast changes after the industrial revolution (e.g. atmospheric methane has been growing with an annual rate of 0.8-1% which can have a significant impact on the biosphere even beyond the greenhouse effect)

iii) most trace gases are intermediate or end products/substrates of key biogeochemical processes, and this is why monitoring these gas species can be used for early detection of any anomaly in ecosystem functioning.

Table 6.11 lists the major trace gases and their potential impacts on ecosystems. Not all of the listed gases are of primary importance for Arctic terrestrial ecosystems. In the present review, our attention will be restricted to CO₂, (Section 4.2.1) CH₄ and N₂O.

Table 6.11. Trace gases produced in tundra soils and their potential impacts on terrestrial ecosystems. (abbreviations: OM = organic matter; GHG = greenhouse gas; NMHC = non-methyl hydrocarbons)

<table>
<thead>
<tr>
<th>Gas species</th>
<th>Main soil source</th>
<th>Main soil sink</th>
<th>Environmental control on “source-sink” balance</th>
<th>Impact</th>
<th>Reference related to the Arctic</th>
</tr>
</thead>
<tbody>
<tr>
<td>CH₄</td>
<td>Methanogenesis</td>
<td>Uptake by</td>
<td>Temp</td>
<td>GHG</td>
<td>Whalen and</td>
</tr>
</tbody>
</table>
### 4.2.2.2. Soil and ecosystem processes responsible for gas emissions

<table>
<thead>
<tr>
<th>Compound</th>
<th>Process Description</th>
<th>Variables</th>
<th>Emissions</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>N$_2$O</td>
<td>Denitrification Nitrification</td>
<td>Temp</td>
<td>GHG</td>
<td>Christensen et al., 1999a</td>
</tr>
<tr>
<td>CO</td>
<td>Anaerobic decomposition of OM, airborne pollution</td>
<td>Temp</td>
<td>Photo-chemical reactions in atmosphere, toxicity</td>
<td>Conrad, 1996; Whalen and Reeburgh, 2001</td>
</tr>
<tr>
<td>H$_2$</td>
<td>Fermentation, Pollution</td>
<td>Temp</td>
<td>GHG, ozone and aerosol formation within plant canopy</td>
<td>Conrad, 1996</td>
</tr>
<tr>
<td>NMHC (terpene and isoprene derivates)</td>
<td>Plants and microorganisms (bacteria, fungi)</td>
<td>Temp</td>
<td>Phytotoxicity</td>
<td>Guenther et al., 1993; Isidorov et al., 1983; Isidorov and Jdanova, 2002</td>
</tr>
<tr>
<td>Methylated halogens (methyl-Bromide, methyl-Iodide etc)</td>
<td>Soil affected by oceanic water</td>
<td>Soil hydrology and location within landscape relative to oceanic line shore</td>
<td>Ozone depletion, Phytotoxicity</td>
<td>Dimmer et al., 2001. Data for Irish peatland ecosystems</td>
</tr>
<tr>
<td>Dimethyl-sulfide</td>
<td>Hydrolysis and uptake as a S-source by plants</td>
<td>Soil hydrology and location within landscape relative to oceanic line shore</td>
<td>Phytotoxicity</td>
<td>Legrand, 1995</td>
</tr>
<tr>
<td>Sulfur oxides (SO$_2$, SO)</td>
<td>Fuel combustion: airborne contamination of soil</td>
<td>Temp</td>
<td>Acid rain, Phytotoxicity</td>
<td>Conrad, 1996</td>
</tr>
<tr>
<td>Ammonia</td>
<td>Airborne soil contamination</td>
<td>Temp</td>
<td>Plant productivity</td>
<td>Conrad, 1996</td>
</tr>
</tbody>
</table>
Trace gas exchange with the atmosphere occurs through a set of coupled soil/ecosystem processes, including

(i) production of substrate(s) for processing by trace gas-producing organisms
(ii) conversion of substrate to respective gaseous species in parallel with gas consumption (Table 6.12)
(iii) mass-transfer of produced gas to the free atmosphere, which includes three main mechanisms: molecular diffusion, vascular gas transfer (i.e. through plant “conduits”), and ebullition (i.e. bubble formation).

Table 6.12. Examples of soil processes where trace gases are formed or consumed

<table>
<thead>
<tr>
<th>Gas species</th>
<th>Reaction-Source</th>
<th>Reaction-Sink</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO₂</td>
<td>Oxidative decomposition of dead OM: OM+O₁ → CO₂+H₂O+'Ash'</td>
<td>Photosynthesis (plant and green bacteria): CO₂+H₂O → CH₃OH+O₂</td>
</tr>
<tr>
<td></td>
<td>Oxidation of root exudates</td>
<td>Soil chemosynthesis (nitrifying, H₂, Fe²⁺ and S oxidizing bacteria)</td>
</tr>
<tr>
<td></td>
<td>Fermentations: CH₃O → CO₂+VFA + H₂</td>
<td>Carbonate formation and leaching</td>
</tr>
<tr>
<td>CO</td>
<td>Fermentation</td>
<td>Activity of carboxidobacteria: CO + 1/2 O₂ → CO₂</td>
</tr>
<tr>
<td></td>
<td>O₂-limited oxidation reactions</td>
<td>Spontaneous chemical oxidation</td>
</tr>
<tr>
<td>CH₄</td>
<td>Methanogenesis</td>
<td>Methanotrophy</td>
</tr>
<tr>
<td></td>
<td>CO₂ + H₂ → CH₄ or CH₃COO(acetate) → CH₄</td>
<td>CH₄ + CO₂ + H₂O</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Photochemical reactions with OH•, Cl•…</td>
</tr>
<tr>
<td>N₂O</td>
<td>Nitrification: NH₄⁺ → NO₃⁻ + 1% N₂O</td>
<td>The same reactions when completed</td>
</tr>
<tr>
<td></td>
<td>Denitrification NO₃⁻ → N₂O → N₂</td>
<td></td>
</tr>
<tr>
<td>NO</td>
<td>Nitrate reduction</td>
<td>NO oxidation</td>
</tr>
<tr>
<td></td>
<td>NO₃⁻ → NO</td>
<td></td>
</tr>
<tr>
<td>Isoprene</td>
<td>Secondary metabolic reactions in plants: pyruvate → isoprene Fermentations</td>
<td>Microbial oxidation</td>
</tr>
<tr>
<td>(C₅H₈)</td>
<td></td>
<td>Formation of phyogenic aerosol and sedimentation</td>
</tr>
</tbody>
</table>

Substrates are formed through one of three processes: (i) decomposition (hydrolytic breakdown of plant litter, oxidation, fermentation); (ii) nitrogen mineralization, and (iii) photosynthesis + photorespiration. However, the starting point for almost all substrates is the primary production of organic matter through plant photosynthesis or (occasionally) bacterial chemosynthesis. There are two main flows of C-substrates from plants: (i) via plant litter formation with lignocellulose as a main resistant component; and, (ii) continuous supply of readily available C monomers (root and foliage exudation). The chain of events leading to the formation of immediate precursors of trace gases can be long and intricate (Panikov, 1999). It is worthwhile to note that the most successful simulation models of trace gas emissions include vegetation or primary productivity modules.

4.2.2.3 Trace gas transport
There are three main transport mechanisms: (i) molecular diffusion, (ii) vascular transport of gas through plant roots, and (iii) ebullition. Vascular transport can be described as a diffusion process through plant root aero-parenchyma, which is a continuous network of gas-filled channels. Vascular transport is two or three orders of magnitude more rapid than diffusion in water. Ebullition is probably the most difficult process to simulate and describe mathematically due to its stochastic nature. In northern soils, ebullition and vascular transport were shown to be the major transport mechanisms accounting for up to 98% of the total emissions (Christensen et al., 2003a).

4.2.2.4. Environmental controls on CH₄ fluxes

Methane is produced from anaerobic decomposition of organic material in waterlogged, anaerobic, parts of the soil. Wet and moist tundra environments are known to be significant contributors to atmospheric CH₄ (Fung et al., 1991; Bartlett and Harriss, 1993). Methane is formed through the microbial process of methanogenesis which is controlled by a range of factors most notably temperature, the persistence of anaerobic conditions, gas transport by vascular plants as well as supply of labile organic substrates (Schimel, 1995; Whalen and Reeburgh, 1992; Joabsson and Christensen, 2001; Ström et al., 2003). Figure 6.22 shows the variety of controls on CH₄ formation rates at different spatial and temporal scales. Methane is, however, not only being produced but also consumed in the aerobic parts of the soil. This takes place through the microbial process of methanotrophy which can even take place in dry soils with the bacteria living off the atmospheric concentration of CH₄ (Whalen and Reeburgh, 1992; Panikov, 1999; Christensen et al., 1999a; Sjögersten and Wookey, 2002). Methanotrophy is responsible for the oxidation of an approximated 50% of the CH₄ produced at depth in the soil and as such is as important a process for net CH₄ emissions as the process of methanogenesis is in itself. The anaerobic process of methanogenesis is much more responsive to temperature than CH₄ uptake, so soil warming in the absence of any other changes will accelerate emission (which is the difference between production and consumption), in spite of the simultaneous stimulation of the two opposing processes.

Figure 6.22 Controls on methanogenesis (redrawn from Davidson and Schimel, 1995).

Apart from temperature, water regime, and plant cover, methanogenic bacteria are strongly affected by biological interactions within the soil community. Competition with acetogenic, and sulfidogenic bacteria for H₂ (the outcome of this competition depends on the affinity to H₂, the temperature, and density of the various populations) determines the pattern of gas formation not only quantitatively, but also in qualitative terms. For example, ecosystems can be a source of CH₄ (if methanogenic bacteria prevail), or H₂S and other sulfides (under the domination of sulfate reducing bacteria), or acetic acid (if a large population of acetogens is present).

Early empirical models of northern wetland/tundra CH₄ exchanges suggested sensitivity to climate change (Roulet et al., 1992; Harriss et al., 1993). A simple mechanistic model of tundra methane emissions including the combined effects of temperature, moisture and active layer depth also suggested significant changes in CH₄ emissions as a result of climate change (Christensen and Cox, 1995). More complex wetland methane emission models suggest that winter processes have a strong influence on net annual emissions of CH₄ (Panikov and Dedysh,
2000). Variations in CH$_4$ emissions at the large regional-global scale are driven largely by temperature (Harriss et al., 1993; Crill et al., 1992) with important modulating effects of the vascular plant species composition superimposed (Christensen et al., 2003b; Ström et al., 2003). An initial warming is, hence, expected to lead to increased CH$_4$ emissions, the scale of which though depends on associated changes in soil moisture conditions and the secondary effects of changes in vegetation composition (Section 5.1.2).

4.2.2.5 Controls on N$_2$O fluxes

The simulation of N$_2$O emission requires consideration of the combined N and C cycles, because the substrates of denitrification include electron acceptors (nitrate) as well as oxidizable C substrates. The ecosystem-atmospheric fluxes of N$_2$O are associated with fundamental transformations of nitrogen in the soils, namely the processes of nitrification and denitrification. Very few field studies of N$_2$O fluxes are available from the Arctic (Christensen et al., 1999a) but very small releases of N$_2$O are expected from Arctic soils due to their general nutrient limitation. One issue of potential great importance in the Arctic though is early spring fluxes of N$_2$O. Denitrification has been found to take place even below the freezing point (Dorland and Beauchamp, 1991; Malhi et al., 1990). During freezing and thawing, carbon is liberated and this may increase denitrification activity in the soil (Christensen and Christensen, 1991). During the spring thaw of the soil, significant parts of the annual emission of N$_2$O can take place (Papen and Butterbach-Bahl, 1999). The early spring fluxes may also explain the significant potential N$_2$O production measured in fertilized plots on a sub-Arctic heath (Christensen et al., 1999a) on soils that showed no emissions from control plots. Hence, as with CH$_4$, the winter and “shoulder” season processes are generally very important but at the same time the least well understood.

4.2.3 Water and energy balance

Arctic ecosystems exhibit the largest seasonal changes in energy exchange of any terrestrial ecosystem because of the large changes in albedo from late winter, when snow reflects most incoming radiation, to summer when the ecosystem absorbs most incoming radiation. About 90% of the energy absorbed during summer is transferred to the atmosphere, with the rest transferred to the soil in summer and released to the atmosphere in winter (Eugster et al., 2000). Consequently, Arctic ecosystems have a strong warming effect on the atmosphere during the snow-free season.

Vegetation profoundly influences the water and energy exchange of Arctic ecosystems. In general, ecosystems with high soil moisture have greater evapotranspiration than dry ecosystems, as in any climatic zone. Arctic ecosystems differ from those at lower latitudes, however, in that there is no consistent relationship between CO$_2$ flux and water vapor flux, because vascular plants account for most CO$_2$ flux, whereas mosses account for most water vapor flux (McFadden et al., in press). This contrasts with other major biomes on Earth, where these two fluxes are strongly correlated (Schulze et al., 1994; Kelliher et al., 1995).

Within tundra, vegetation strongly influences winter energy budget through its effects on snow depth and density. Shrubs increase the snow depth by reducing the velocity of blowing snow and reducing sublimation rates; models suggest that in northern Alaska this shrub-induced reduction
in sublimation can increase ecosystem-scale winter snow accumulation by 20% (Sturm et al., 2001a). Shrubs also cause snow to accumulate within shrub patches and to be depleted from shrub-free zones, increasing the spatial heterogeneity of snow depth. Snow within shrub canopies is deeper and less dense, which reduces heat transfer through the snow-pack and increases winter soil temperatures by 2°C relative to adjacent shrub-free tundra. Warmer soil temperatures beneath shrubs may increase winter decomposition and enhance nutrient availability, forming a positive feedback that promotes shrub growth (Sturm et al., 2001a).

Midsummer vegetation feedbacks to regional climate are determined largely by midsummer patterns of water and energy exchange (Chapin et al., 2000a). Midsummer albedo is greatest in sedge communities, whose standing dead leaves reflect much of the incoming radiation (McFadden et al., 1998, Chapin et al., 2000a). Evergreen forests and forest tundra, in contrast, have a particularly low albedo because of the dark absorptive nature of evergreen leaves and the effectiveness of complex forest canopies in capturing light (Chapin et al., 2000b; Eugster et al., 2000). Deciduous-dominated tundra and forest tundra canopies are intermediate in albedo and therefore in the quantity of energy which they absorb and transfer to the atmosphere (Baldocchi et al., 2000; Chapin et al., 2000b). A larger proportion of the energy transfer to the atmosphere occurs as sensible heat flux in forests, forest tundra, and shrub tundra than in wet tundra (Lafleur et al., 1992; Boudreau and Rouse, 1995; McFadden et al., 1998; Chapin et al., 2000a; Eugster et al., 2000).

All Arctic ecosystems exhibit greater ground heat flux during summer (5-15% of net radiation) than do temperate ecosystems (generally close to zero), due to the strong thermal gradient between the ground surface and permafrost and the long hours of solar radiation (Chapin et al., 2000a). Ground heat fluxes are reduced in tundra ecosystems with a large leaf area, which shades the ground surface (McFadden et al., 1998), or where the ground cover is highly insulative, as with Sphagnum mosses (Beringer et al., 2001a). Grazing and other processes causing surface disturbance increase ground heat flux and thaw depth (Walker et al., 1998). Future changes in vegetation driven by climate change are very likely to profoundly alter regional climate.

**Summary: Effects of changes in climate and UV-B on ecosystem function**

Arctic ecosystems tend to accumulate organic matter and elements despite low inputs because organic matter decomposition is very slow. As a result, soil-available elements like N and P are key limitations to increases in C fixation and further biomass and organic matter accumulation. Key issues for prediction of whole-system responses to climate change include the importance of C-nutrient interactions, the interactions of C and nutrient cycles with temperature, water, and snow cover, the magnitude of DOC and DIC losses in soil water, and the magnitude and role of wintertime processes. Most disturbances are expected to increase C and element turnover, particularly in soils, which may lead to initial losses of elements but eventual, slow recovery. Individual species and species diversity have clear impacts on element inputs and retention in Arctic ecosystems but their magnitude relative to climate and resource supply is still uncertain. Similarly, the current information on long-term effects of CO₂ and UV-B on whole ecosystems indicates that direct effects of these variables will be probably small relative to changes in soil resources and element turnover. Indirect effects of CO₂ and UV-B are likely to be more important at the ecosystem level, such as through changes in species composition.

The most important trace gases in Arctic ecosystems are CO₂ and CH₄. Trace gas exchange with the atmosphere occurs through a set of coupled soil ecosystem processes. Wet and moist tundra environment are known to be significant contributors to atmospheric CH₄. However, methane is also consumed in aerobic parts of the soil. Methane emissions from the ecosystems are a balance between production and consumption. Production is more
responsive to warming than consumption. Soil warming in the absence of any other changes will very likely accelerate emissions. Winter processes and vegetation type also affect CH₄ emissions. N₂O emissions are also sensitive to winter conditions and potential winter warming.

Arctic ecosystems exhibit the largest seasonal changes in energy exchange of any terrestrial ecosystem because of the large changes in albedo from late winter, when snow reflects most incoming radiation, to summer when the ecosystem absorbs most incoming radiation. Vegetation profoundly influences the water and energy exchange of Arctic ecosystems. Vascular plants account for most CO₂ flux, whereas mosses account for most water vapor flux; albedo during the period of snow cover declines from tundra to forest tundra to deciduous forest to evergreen forest; shrubs and trees increase snow depth which in turn increases winter soil temperatures; ground heat fluxes ecosystems with a large leaf area and insulating moss carpets reduce ground heat fluxes and conserve permafrost. Future changes in vegetation driven by climate change are very likely to profoundly alter regional climate.
5. Effects of changes in climate on landscape and regional processes and feedbacks to the climate system

Biological and physical processes and phenomena in the Arctic system operate at various temporal and spatial scales to impact large-scale feedbacks and interactions with the earth system. Understanding these processes at multiple scales is critical because the complex interactions between physical, biological, and human dimensions on system performance cannot be predicted by simply applying a different scale to existing results. Therefore, a multidisciplinary and quantitative approach is necessary to understand and predict the response of the Arctic system to variability in temperature and moisture. The large scale, inter-related processes described here include:

- Ecosystem processes extrapolated to the landscape or regional scale, for example trace gas exchange, water and energy exchange and disturbance
- Changes in ecosystem distribution and abundance in the landscape
- Changes in vegetation zonation, e.g., treeline movement
- Interactions between terrestrial and freshwater ecosystems
- Regional feedbacks

Paleoclimate studies and studies of the contemporary Arctic together have identified four potential feedback mechanisms between the impacts of climate change on the Arctic and the global climate system:

1. Albedo (reflectivity)
2. Greenhouse gas emissions and/or uptake through biological responses to warming
3. Greenhouse gas emissions from methane hydrates released from thawing permafrost
4. Increased freshwater fluxes that could affect thermohaline circulation.

In the past, three of the potential feedbacks have been generally positive and only one negative.

Some of the feedbacks such as energy and water exchange operate at local to regional scales whereas others, particularly trace gas fluxes, have the potential to operate at regional to global scales. In the following section, we assess the impacts of changes in climate (but not UV for which data are unavailable) on ecosystem processes at the larger scale. We explore the implications of these changes for feedbacks from terrestrial ecosystems to the climate system, but we do not calculate changes in forcing (Chapter 4). Nor do we consider freshwater discharge (Chapters 5, 7) and methane hydrate feedbacks (Chapter 5).

5.1 Impacts of recent and current climate on carbon flux

There are two complementary approaches to solve the carbon flux inventory problem - bottom-up and top-down approaches. The first is based on the long-term monitoring of gas emissions within networks of field stations or sites that cover the main types of habitats. At its simplest, the total circumpolar emission is estimated from the number and area of the types of northern ecosystems differentiated in terms of easily mapped features like vegetation, soil properties, relief, geomorphology and the characteristic annual exchange of CO₂ and CH₄ from each ecosystem.
The data on CO₂ and CH₄ fluxes come from three main groups of available techniques that operate at different spatial scales: i) closed and open top chambers (0.1 - 1 m²), ii) micrometeorological towers based on eddy covariance and gradient methods (10-10,000 m²), and iii) aircraft sensing (up to tens and hundreds of km²). All three groups of techniques have their own advantages and disadvantages. However the continuous measurements with towers seem to be the most appropriate to provide reliable information on temporal variation of gas emission at the ecosystem and landscape spatial levels.

### 5.1.1 Recent changes in CO₂ - flux

Recent variations in Arctic climate have had profound effects on some ecosystem and regional level carbon fluxes and, in general, they reflect the recent spatial variability in climate change. Here, we restrict our assessment to carbon in the active layer of soils and in plants. We do not consider carbon in permafrost and methane hydrates (Chapter 5).

The North Slope of Alaska has seen a secular rise in temperature (Figure 6.18, Weller, 2000), increase in length of the growing season, and decrease in available soil moisture (Oechel et al., 1993; 1995; 2000a; Serreze et al., 2000) over the last 3-4 decades. This has resulted in a change from North Slope Arctic ecosystems being a sink for carbon through the Holocene (Marion and Oechel, 1993) to a source of carbon to the atmosphere beginning in the mid 1970s to early 1990s (Oechel et al., 1993; 1995; 2000a) (Figure 6.18). However, as there has been a secular change in climate, with progressive warming, drying, and lengthening of the growing season, there has been physiological, community, and ecosystem level adjustment that has reduced the rate of carbon loss from North Slope ecosystems (Figure 6.18). Also other more wet parts of the North Slope are not showing the same source function (Harazono et al., 2003). The swings in carbon balance are very large, from a net summer CO₂ uptake of from about 25 g C m⁻² y⁻¹, to a summertime loss of over 225 g C m⁻² y⁻¹. If these fluxes held world wide for wet coastal and moist tussock tundra, this would result in a net loss of up to 0.3 GtC y⁻¹ from these two ecosystem types alone.

In NE Greenland, the recent climatic history is different than that of Alaska. Here there has been no significant trend towards higher temperatures (Weller, 2000) and integrating for all vegetation types shows that the Zackenberg valley is a small net sink with a large uncertainty range of 2.3±16.2 g C m⁻² yr⁻¹. This integrated study of the valley shows that satellite (Landsat) derived carbon flux estimates are in good agreement with ground-based eddy correlation flux measurements covering all the dominant vegetation types in the valley. The Landsat-method estimated a mid-day uptake rate in August 1997 of 0.77 g C m⁻² d⁻¹ for the valley as a whole whereas the ground-based measurements showed 0.88 g C m⁻² d⁻¹ (Søgaard et al., 2000). The measured annual balance in the valley varies from significant uptake in the intensively studied fen areas in the order of 18.8±6.7 g C m⁻² yr⁻¹ to net C losses in the dry heath (Søgaard et al., 2000; Christensen et al., 2000; Nordstroem et al., 2001).

Like Alaska, northern Scandinavian areas have seen warming in recent years. The ecosystem carbon balances there vary between a sink of between 15 and 25 g C/m²/yr in a sub-Arctic Swedish peatland (Friborg pers. com). Similarly, in Finland, a net annual uptake of about 20 gC/m-2yr-1 has been reported for a subarctic fen at Kaamanen (Aurela et al 2002). Six >years of
continuous measurements at this fen show marked interannual variation in the CO2 balances (sinks from 4 to 52 gC/m²/yr), mainly reflecting the variations in the spring temperatures and the timing of the snow melt (Aurela pers. com). Work on fluxes in a high Arctic barren tundra on Svalbard show a very limited source of around 1 g C/m²/yr (Lloyd, 2001). Overall, the synthesis of regional C flux information from measurements at several sites in northern Europe and Greenland (the LAPP project; Laurila et al., 2001) indicates a general picture of Arctic landscapes as being remarkably similar in their C flux during the peak summer but with the length of the growing season and the shoulder season fluxes being the key determinants for the net annual fluxes. This causes substantial interannual variability at the individual sites and a general uncertainty associated with the current status of the circumpolar North as a source or a sink for carbon.

Recent work in East European tundra indicates a substantial current source function of the northeastern European tundra areas (Heikkinen et al., submitted). When combined with the areas of the northern Alaska tundra mentioned above that also have a source function, source areas (East European tundra, Svalbard and Alaska) may exceed the sink areas (NE Greenland, N Scandinavia). However, data are available for only a limited geographical extent of the Arctic.

There may be a correlation with recent climatic history in areas that have seen a significant warming and drying: these areas experienced at least a temporary release of CO2 while others that have not seen the same extent of warming and drying or have possibly experienced a warming and wetting and they remain atmospheric CO2 sinks and may even become large sinks. Any real synthesis of the available information from the circumpolar North is, however, not as yet available but is underway.

New models and approaches make estimation of current and future global carbon balance possible. The modeling approach has been used to predict recent change from carbon sink to source status (Clein et al., 2000; McGuire et al., 2000). The TEM (Terrestrial Ecosystem Model) has been used to estimate current carbon fluxes, and those in the future while the model “Hybrid v4.1”, (Friend et al., 1997) has been used to predict vegetation and carbon pool changes at high latitudes for the period 1860-2100 (White et al., 2000). Under current conditions, there is a simulated mix of carbon sinks and sources, that reflect variation in current and past climate. Under contemporary conditions, McGuire estimates circumpolar carbon fluxes to average a small sink of 17 gC/m²/yr (McGuire et al., 2000). The standard deviation around this number, however, is estimated at 40 g C/m²/yr. This uncertainty range is comparable to the LPJ model outputs referred to in section 5.4.1 (Sitch et al., 2003) and the calculation of current sink status correspond to the predictions by White et al. (2000).

Although a conclusion is that source areas currently exceed sink areas, there is great uncertainty about the current CO2 balance of the Arctic due to geographically inadequate measurements and inadequate representation of ecosystem dynamics in current models.

5.1.2 Current circum-Arctic CH₄ fluxes

Probably the most intensive studies and the longest observations of methane fluxes were obtained in North America, mainly within the central Alaskan and North Slope sites at Barrow, Atqasuk,
Toolik Lake, and Prudhoe Bay (Whalen and Reeburgh, 1990; 1992; Christensen, 1993; Vourlitis et al., 1993; Morrissey et al., 1992). In the North of Eurasia including Russia, the extensive measurements of gas emission was initiated from late 1980 and followed either as short-term measurements across geographical transects or as a long time-series of fluxes at one site. The first approach is illustrated by chamber measurements of CH₄ (and CO₂) fluxes across the Russian Arctic (Christensen et al., 1995; 1998). The second approach is realized in a number of field stations where gas fluxes are measured mainly during the summer season (Panikov et al., 1995; 1997; Zimov et al., 1993; Wagner et al., 2003).

The general tendencies of spatial and temporal flux variation can be formulated as follows. Firstly, there are evident temperature related variations: even within northern wetlands the highest net fluxes occur in warmer soils, the maximal values being attained in the boreal zone. This trend is especially evident in respect to methane, the gas emission increasing along the sequence Barrow-Toolik Lake-Fairbanks, or Taimyr - Surgut - Tomsk. Seasonal variations also follow a temperature dynamics curve, although winter, autumn and spring emissions are often measurable (Sections 3.3.3.1 and 4.2.1.4). A transect of seasonal measurements of CH₄ emissions from five different wetland sites from NE Greenland over Iceland and Scandinavia to Siberia also showed a clear positive relationship with the mean seasonal temperatures of the sites (Christensen et al., 2003b). Secondly, there is always enhanced emission from wetland patches covered by vascular plants (Eriophorum, Carex, Menyanthes) as compared with pure Sphagnum lawn (the effects of vascular plants; section 4.2.2.3 and 4.2.2.4). Thirdly, variations in water table affect CH₄ (and CO₂) emission in opposite ways, methane fluxes being stimulated and carbon dioxide suppressed by an increase in the water table. However, the range of fluxes varies so widely that uncertainty in regional/global estimates remains too large and is very much dependent on site specific features of a particular study. For example, extensive measurements by various techniques over the Hudson Bay Lowland (Roulet et al., 1994) lead to the conclusion that northern wetlands are modest sources of atmospheric methane (average July emission as low as 10-20 mg CH₄/d/m²). On the other hand, Alaskan wet meadow and shrub/tussock tundra have average summer emissions up to 100-700 mg CH₄/d/m² (Whalen and Reeburgh, 1992; Christensen, 1993). The uncertainty in regional/global estimates that follows from these differences in actual measured fluxes is very frustrating and calls for alternative ways to solve the problem of scaling up fluxes. One such alternative solution can be the inverse modeling approach.

In the top-down inverse modeling approach, the information on temporal and spatial variation of CH₄ and CO₂ emissions from soils are deduced from observation data on gas mixing ratios in air (obtained from a network of NOAA/CMDL field stations scattered over the globe, mainly in oceanic regions far from industrial impacts). These data are fitted to a three-dimensional atmospheric transport model, which is combined with a tropospheric background chemistry module and accounts for all essential sources and sinks of gases. The model is validated against an “internal standard” such as methyl chloroform. Presently available results of inverse modeling (Hein et al., 1997) do not deviate significantly from data obtained by the bottom-up approach. The contribution of high latitude regions (>60 °N) to the global methane source was less than 13% or 70 Tg/year, and northern wetlands are responsible for emissions of less than 30 Tg of CH₄ per year. At first sight, such a conclusion contradicts the latitudinal gradient of atmospheric methane that has a well expressed maximum in the North. But the build-up of methane in air over
high latitudes is explained also by a low content of OH and, hence, lower rates of temperature-controlled photochemical reactions that break down the atmospheric CH₄.

5.1.3 Relative contribution of CH₄ and CO₂ to carbon budget and their importance

The formation of CO₂ and CH₄ are a result of aerobic and anaerobic decomposition respectively. The ratio of respired CO₂ to CH₄ is hence an indication of how reduced the soil environment is. An increasingly reduced soil environment (i.e. higher CH₄/CO₂ ratio) also leads to slower overall decomposition rates as the anaerobic decomposition is less efficient in absolute C terms compared to aerobic decomposition. This is what generally leads to a build up of stored organic carbon in wet tundra soils as the net primary production is not normally limited by wet soil conditions to the same extent as the respiration.

The net CH₄/CO₂ ratio of the total respiration is also a function of the amount of CH₄ that is oxidized in the aerobic soil layers above a given anaerobic zone of production and even the possible atmospheric CH₄ uptake that takes place in some dry tundra soil environments. The CH₄/CO₂ ratio or the % contribution of CH₄ to the total respired carbon varies from <1% in dry ecosystems to >20% in extreme cases in wet tundra ecosystems. Typical annual average contributions of CH₄ to the total C flux lies in the range 2-10% for wet tundra and northern wetlands (e.g. Clymo and Reddaway, 1971; Svensson, 1980; Klinger et al., 1994; Christensen et al., 1996; Svensson et al., 1999).

It is very important in a climate change context to note that the relative contribution of CH₄ as a greenhouse gas to the total radiative forcing is much stronger on a per molecule basis than CO₂ (Chapter 4). The so-called global warming potential (GWP) indicates how many times stronger a given greenhouse gas is to CO₂ on a per molecule basis and this is dependent on a particular time horizon. For example over a 100 year time horizon, the GWP of CH₄ is 23 and with a 20 year horizon it is 63 (Houghton et al., 2001).

From a global warming perspective it is, hence, not very informative only to look at the carbon balance of any ecosystem if this exchanges CH₄ or other greenhouse gases such as N₂O (Christensen and Keller, 2003). Calculations have shown that ecosystems such as the huge western Siberian lowlands, despite being strong sinks for carbon, are sources of radiative forcing due to the considerable CH₄ emissions (Friborg et al., 2003). Data are, however, scarce when it comes to full annual budgets from tundra regions of both CO₂ and CH₄ fluxes. Figure 23 shows calculations based on accumulated continuous eddy correlation measurements of CO₂ and CH₄ fluxes in the Zackenberg valley during 1997 (Friborg et al., 2000; Søgaard et al., 2000). The figure illustrates that a net carbon accumulation (“minus” in the accumulated budget) during the season is completely cancelled out in effect if CH₄ is calculated and added as CO₂ equivalents using the 20 yr time horizon. Using the 100 yr time horizon the ecosystem is still a small sink of CO₂ equivalents at the end of the growing season. However, given the autumn and winter fluxes which are entirely sources but are not in the figure, the annual total will probably add up to a source as well.
Figure 23. Accumulated carbon and greenhouse warming potential from CO₂ and CH₄ exchanges calculated as CO₂ equivalents throughout the summer of 1997 at Zackenberg, Northeast Greenland (data from Friberg et al., 2000; Søgaard et al., 2000).

In general, due to the predominantly wet soil conditions in the most productive tundra areas, there are significant CH₄ emissions there. It is most likely that, at the landscape, regional and global scales, the tundra represents a source of radiative forcing due to CH₄ emissions being the most important greenhouse gas driving the ecosystem influence on atmospheric radiative forcing.

5.2 Current circum-Arctic water and energy balances

Arctic ecosystems exhibit the largest seasonal changes in energy exchange of any terrestrial ecosystem because of the large changes in albedo from late winter, when snow reflects most incoming radiation (albedo about 0.7), to summer when the ecosystem absorbs most incoming radiation (albedo about 0.15). This change in albedo combined with the greater incoming solar radiation in summer than in winter cause much greater energy absorption in summer than in winter. About 90% of the energy absorbed during summer is transferred to the atmosphere, with the rest transferred to the soil in summer and released to the atmosphere in winter (Eugster et al., 2000). Also, snow within shrub canopies is deeper and less dense, which reduces heat transfer through the snowpack and increases winter soil temperatures by 2°C relative to adjacent shrub-free tundra. Consequently, Arctic ecosystems have a strong warming effect on the atmosphere during the snow-free season, and any increase in the duration of snow-free conditions results in a strong positive feedback to regional climate warming (Foley et al., 1994; Bonan et al., 1995).

Climate influences the partitioning of energy between sensible and latent flux. Cold moist air from coastal oceans, for example, minimizes latent heat flux (evapotranspiration), as does extremely warm dry air, which can induce stomatal closure (Eugster et al., 2000; Rouse, 2000); evapotranspiration is therefore greatest at intermediate temperatures. Conversely, sensible heat flux is a larger proportion of the energy transfer to the atmosphere when air is cold and moist or when drought limits stomatal conductance under dry conditions. Heat that is conducted into the ground during summer is released to the atmosphere in winter, with any seasonal imbalance causing changes in permafrost temperature and probability of thermokarst (Osterkamp and Romanovsky, 1999).

There are large regional differences among Arctic ecosystems in energy exchange and partitioning. Albedo during the period of snow cover is extremely high in tundra and declines with increasing development of a plant canopy above the snow from tundra to shrub tundra, to forest tundra to deciduous forest to evergreen forest (Betts and Ball, 1997). These differences in albedo are an important feedback to climate during spring, when the ground is snow-covered, and incoming radiation is high. As a result of differences in albedo and sensible heat flux, forests at the Arctic treeline transfer about 5 W m⁻² more energy to the atmosphere than does adjacent tundra (Beringer et al., 2001b). This vegetation difference in energy transfer to the atmosphere is an order of magnitude less than the heating contrast which had been hypothesized to be required for treeline to regulate the position of the Arctic Front (Pielke and Vidale, 1995). Thus, the
location of the Arctic front is more likely to govern the position of treeline than the other way around (Bryson, 1966).

5.3 Large scale processes affecting future balances of carbon, water and energy

In this section, we assess the effects of climate change on permafrost degradation and vegetation re-distribution as a prerequisite for assessing changes in feedbacks from future terrestrial ecosystems to the climate system.

5.3.1 Permafrost degradation

Soil carbon storage is greatest where the drainage is slight and the limited precipitation is held near the surface by permafrost and modest topography. This results in ponds, wetlands, and moist tundra with a saturated seasonal active layer that limits microbial activity. Increases in the active layer can cause subsidence at the surface, a lowering of the soil water table (Hinzman et al., in press), and, potentially, thermokarst erosion (Hinzman et al., 1997). This can drain surrounding areas, often increasing the decomposition rate of soil organic matter which accelerates the loss of below ground carbon stores (Oberbauer et al., 1991; 1996) and results in a change in plant communities and their abilities to sequester atmospheric CO$_2$. Initially, increased soil decomposition rate can increase mineralization rates (Rastetter et al., 1997) and result in increased net primary productivity (Section 4.2.1.5). However, continued thawing of permafrost and increased drainage of surface water in areas with low precipitation could lead to a drying process, a decrease in NPP and even desertification (Section 5.3.2.1).

Full permafrost disintegration in subarctic discontinuous permafrost regions may in some cases show a rather different response. Monitoring of changes in permafrost distribution in subarctic Sweden as part of the Circumpolar Active Layer Monitoring Program (CALM: Brown et al., 2000), shows that permafrost loss causes mires to shift from ombrotrophic moss and shrub-dominated systems to minerotrophic wet vascular plant dominated systems (Svensson et al., 1999; Christensen et al., in press). This, in turn, leads to a significant lowering of soil redox potentials, an increase in anaerobic decomposition, and increased methane emissions. Wet minerotrophic soils and vegetation are in general associated with the highest methane emissions in subarctic and Arctic tundra environments. Discontinuous permafrost regions are considered some of the most vulnerable to climate warming, so with the predicted warming over the next 100 yrs effects such as the one listed above are expected to be strong.

Permafrost degradation and disintegration will therefore, have major effects on ecosystem C balances and methane emissions. The rate of permafrost thawing, the amount of ground surface subsidence and the response of the hydrologic regime to permafrost degradation all depend on numerous site characteristics. Changes in hydrological regime will also alter the soil thermal regime. In areas of significant topographic variations, flowing water can carry heat into drainage channels causing increased soil temperatures and increased active layer thickness (Kane et al., 2001; Hastings et al., 1989). In regions with minor topographic variations, subtle differences in
elevation can create cooler, saturated wetlands (as mentioned above) or markedly drier, warmer uplands (Rovansek et al., 1996).

5.3.2 Changes in circumpolar vegetation zones

While climate-driven changes in the structure and the distribution of plant communities affect trace gas fluxes and water and energy at the landscape scale (Section 4.2), changes in the location and extent of broad vegetation zones is a longer term integrative process that is likely to potentially lead to regional and even global impacts on feedbacks to the climate system (Harding et al. 2002; Chapin et al., 2000a; Betts, 2000; McGuire et al., 2002). Such vegetation zone changes will probably also affect permafrost dynamics (Chapter 5), biodiversity (Section 3.2) and ecosystem services (Vlassova, 2002). Past climate-driven changes in vegetation zones such as forest and tundra (Section 2; Payette et al., 2002) lead us to expect that future climate-warming will result in vegetation and ecosystem change, but predicting future changes is complex and relies on modeling.

5.3.2.1 Dynamics of the treeline and changes in the areas of tundra and taiga vegetation

The latitudinal treeline or tundra-taiga boundary is an exceptionally important transition zone in terms of global vegetation, climate feedbacks, biodiversity and human settlement.

The treeline stretches for more than 13,000 km around the northern hemisphere and through areas that are experiencing different types of environmental change for example, cooling, warming, marginal temperature change and increasing compared with decreasing land use. However, climate is only one of a suite of environmental factors that are now changing and a critically important challenge is to determine how human impacts in the ecotone will modify the zone’s expected response to climate (Vlassova, 2002).

The lack of standardization of terminology and the wide variation in methodology applied to locate, characterize and observe changes in the boundary have resulted in a rather poor understanding of even the current location and characteristics of the boundary. Particular areas of uncertainty include the Lena Delta of Siberia (Callaghan et al., 2002) and forests in Iceland that have been subjected to major environmental and land use changes since colonization by people from 1100 years ago. One of the major problems in the current studies of the latitudinal “treeline” is the concept of “line” inappropriately applied to the transition from forest, through an area dominated by forest in which patches of tundra occur, to tundra in which patches of forest occur, and then eventually to tundra without trees. Often there are East-West gradients related to the presence of a river valley, bogs, mires, uplands etc. which also confound the concept of a linear.

Dynamics of the boundary

Current and projected changes in the location of the tundra-taiga boundary should be seen in the context of the longer term past cooling trend during which the treeline has been at its lowest locations for several thousands of years (see Section 2.4). Examples of recent treeline advance include upward displacements of the sub-Arctic treeline of 40 m during the 20th Century in
northern Sweden (Sonesson and Hoogesteger, 1983; Kullman, 1979; Emanuelsson, 1987; Rapp, 1996), an increase in shrub growth in Alaska (Sturm et al., 2001b), and an increase in shrubbiness and larch advance in the Northeast Russian European Arctic (Katenin, unpublished). In contrast, other studies show a surprising displacement to the South of the tundra-taiga boundary (Crawford et al., 2003; Vlassova, 2002; Kozhevnikov, 2000). Part of this is a counter-intuitive response to warming in which increasing oceanicity together with permafrost thawing and water-logging have led to paludification and the death of treeline trees (Skre et al., 2002). Part is associated with human activities including mining, farming, forestry, that have led to ecosystem degradation in the forest tundra zone and the movement of its northern boundary southwards in some locations (Vlassova, 2002). In the Archangelsk region and the Komi Republic, the southern border of the forest tundra zone now lies 40 to 100 km further South than when previously surveyed. One report claims that human-derived tundra now covers about 470-500,000 km² of the forest tundra stretching from Archangelsk to Chukotka (Vlassova, 2002), although it is likely that this estimate includes deforestation in some of the northern boreal forest zone.

Although records of recent changes in the location of the latitudinal treeline are surprisingly rare, there is good evidence of increased growth of current northern forests. Comparisons of the greenness index (NDVI) from satellite images show that May to September values for the northern hemisphere between 55 and 75 °N increased by 12.5 to 9.3% respectively (Myneni et al., 1997; Figure 6.17). The increases were larger in North America than in Eurasia. The increased greenness was associated with an increase in growing season length of 4.3 to 3.8 days for the circumpolar area mainly due to an earlier start of the growing season.

Predicting future changes in the tundra-taiga boundary

In order to model changes in the location of the tundra-taiga ecotone and estimate future areas of tundra to the North and taiga to the South, it is necessary to understand the causes of the treeline. Opinions on the mechanisms controlling the location of the treeline vary greatly. Some researchers see the limit of tree growth as a universal mechanism related to a specific process such as sink limitation (Körner, 1998; 1999) or carbon limitation (Nojd and Hari, 2001). Others see a range of possible mechanisms that operate in different places and at different times (Sveinbjörnsson et al., 2002). These physiological mechanisms are in turn affected by environmental factors such as incident radiation, temperature, wind, moisture and soil nutrients, which exert their impacts on tree reproduction, seedling establishment and the growth and physiology of mature trees. Extreme conditions such as ice crystal abrasion and soil movement also directly damage tree tissues such as conifer needles and displace individuals. Diseases, pests, fires and human activities all exert some control on the treeline at certain places and at certain times (Chapter 13).

Models of vegetation redistribution resulting from global change operate on more general mechanisms such as biogeography and biogeochemistry. Most current global vegetation models and regional models suggest that a major part of the tundra (between 11 and 50% according to location) will be displaced by an advance of the boreal forest over the period in which atmospheric CO₂ will double (Skre et al., 2002; Harding et al., 2002; Kaplan et al., 2003; Tables 6.13 and 6.14; Figure 6.31). Treeline is predicted to advance in all sectors of the Arctic, and even
in Greenland and Chukotka where only fragments of forest exist today (Kaplan et al., 2003). However, this rate, or type, of forest response has been recorded less than would be expected even though temperature has already risen dramatically in some areas.

*Figure 6.24 Simulated potential vegetation for 2090-2100 with the HADCM2-SUL GCM using the IS92a greenhouse-gas scenarios (Kaplan et al., 2003). (See Figures 6.2 and 6.4 for the legend)*

The observations of the latitudinal treeline noted above that show a recent southern displacement of the treeline suggest that there will very probably not be a general northwards displacement of the latitudinal treeline throughout the circumpolar region as the models suggest. In addition to possibilities of paludification (Crawford et al., 2003) and local human activities displacing treelines southwards, permafrost thawing, surface water drainage and drying of soils in areas of low precipitation are likely to lead to the formation of tundra steppe-like vegetation (Yurtsev, 2001). Increased disturbance such as pest outbreak, thermokarst, and fire are likely to also locally affect the direction of treeline response. In addition, some tree species show reduced responsiveness to increases in temperature with increasing continentality of their location and decreased precipitation (Linderholm et al., submitted; Chapter 13): this suggests that increased temperatures in combination with no comparative increase in precipitation will probably lead to reduced tree growth and/or change in species and lack of treeline advance. Even in areas expected to undergo warming with none of the moderating factors listed above, it is uncertain if the rate of tree migration can keep up with the rate of increases in expected warming. Past tree migration rates were generally in the order of 0.2 to 0.4 km yr\(^{-1}\) but could reach 4.0 km yr\(^{-1}\) (Section 2; Payette et al., 2002). Such rates would suggest that those areas of the Arctic that have warmed substantially in the last 30 years should have already seen an advance of treeline of about 6 to 120 km. Such observations have not been recorded in the Arctic, although Parmesan and Yohe (2003) claim to have identified a poleward displacement of species ranges of 6.1 km/10 years globally.

Overall, it is likely that treeline will show many different responses throughout the circumpolar North according to different degrees of warming associated with various changes in precipitation, permafrost dynamics, land use and tree species migration potential.

### 5.3.2.2 Predicting future changes in the areas of tundra and polar desert

Projections of changes in vegetation in the northern areas of the Arctic have been made by the LPJ model (Sitch et al., 2003; Tables 6.13 and 6.14) for the ACIA process. Although the results and interpretations are preliminary, model runs for B2 scenarios of the CCC, GFDL, HadCM3 and ECHAM4 GCMs are consistent in showing a decrease in the area of polar desert that will be replaced by northward moving tundra (Table 6.13). Compared with a starting date of 1960, the area of the Arctic covered by polar desert is predicted to decrease by 17.6% (range 14 to 23%) by 2080. In this model, the two vegetation zones were defined by plant functional types: woody species for the tundra, and absence of woody species for the polar desert. In the Biome 4 model simulations by Kaplan et al. (2003), and driven by the HADCM2-SUL GCM using the IS92a greenhouse gas scenario, 5 tundra biomes were constructed (Table 6.8). The most significant changes appear to be a significant northward advance of the cold evergreen needleleaf forest that
is particularly dramatic in the region of Arctic Russia between Chukotka and the Taymyr peninsula. This greatly reduces the area of tundra. However, low and high shrub tundra in the Canadian Arctic Islands remains as a wide zone and displaces prostrate dwarf shrub tundra (Figures 6.2 and 6.24). Earlier modeling by White et al. (2000) predicted that the area of tundra would be halved by forest expansion by 2100.

### 5.4 Projections of future balances of carbon, water and energy exchange

Because the Arctic contains huge stores of carbon in the soil and permafrost (see Section 4.2 above), and because the Arctic has capacity for unlimited additional storage or significant loss (Billings et al., 1982; 1984), it can be a major positive or negative feedback on increasing trace gas concentrations in the atmosphere and on global warming. Loss of CO\(_2\) from Arctic ecosystems could lead to enormous positive feedbacks on global warming by release to the atmosphere of the estimated 250 GtC from the large Arctic soil pool (Lal et al., 2000; Oechel and Billings, 1992; Oechel et al., 1993; 1995; 2000a; Billings et al., 1982; Billings, 1987). In addition, an increasing snow-free period (Engstrom et al., 2002; Keyser et al., 2000), increasing shrub cover (Sturm et al., 2001a; b; Silapaswan et al., 2001), and the northerly migration of treeline (Lloyd et al., 2002) would act to decrease Arctic albedo and further increase regional warming (Bonan et al., 1992; Thomas and Rowntree, 1992; Foley et al., 1994; McFadden et al., 1998; Chapin et al., 2000a; 2000b). Below, we assess likely changes in balances of carbon, water and energy exchange in relation to vegetation change.

#### 5.4.1 Projected changes in carbon balance

Using the vegetation distribution model, BIOME 3, for current and 2 x CO\(_2\) scenarios, changes in extent of the Scandinavian, Central northern Siberian and Eurasian tundra areas were calculated as between 10\% and 35\% as a result of displacement by taiga (Harding et al., 2002). This process was calculated to significantly increase CO\(_2\) draw-down and to significantly reduce CH\(_4\) emissions with a net result in favor of carbon sequestration in the biosphere of a magnitude that would alter the radiative forcing of the Earth. Using another model, McGuire et al. (2000) estimate circumpolar mean carbon uptake to increase from a current 12 g C/m\(^2\)/yr to 22 g C/m\(^2\)/yr by the end of the period (2100) because NPP is increasing more than respiration throughout the period (McGuire et al., 2000). It should be noted, however, that throughout the 200 year model run, the standard deviation always crosses the zero line (McGuire et al., 2000). White et al. (2000) produced comparable results from their Hybrid v4.1 model, predicting that high latitude terrestrial ecosystems would remain a sink for carbon.

The Dynamic Global Vegetation Model (DGVM) LPJ (Sitch et al., 2003) was used to produce ACIA-exclusive estimates for future changes in Arctic carbon storage and fluxes based on four different GCM outputs. The results and analyses are preliminary but indicate a consistent net further sink of the Arctic in 2080 compared to 2000 with global Arctic C stores varying between +12 Gt C and +31 Gt C depending on the climate scenario used.

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**TEXT IN ITALICS FOR A TEXT BOX**

The Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ) combines process-based, large-scale representations of terrestrial vegetation dynamics and land-atmosphere carbon and water exchanges in a modular framework. Features include feedback through canopy conductance between photosynthesis and transpiration and...
interactive coupling between these fast processes and other ecosystem processes including, resource competition, tissue turnover, population dynamics, soil organic matter and litter dynamics and fire disturbance. Ten plant functional types (PFTs) are differentiated by physiological, morphological, phenological, bioclimatic and fire-response attributes. Resource competition and differential responses to fire between PFTs influence their relative fractional cover from year to year. Photosynthesis, evapotranspiration and soil water dynamics are modeled on a daily time step, while vegetation structure and PFT population densities are updated annually.

Within the biosphere model (Sitch et al., 2003), the raw GCM 1900-2100 climatologies were not used directly. The present-day climate simulated by GCMs is not yet good enough to use directly to drive a biosphere model, therefore the anomaly approach was used. The data were downscaled from the GCM specific grid onto one at 0.5 degree resolution. GCM climate anomalies were normalized to the 1961-1990 observed average monthly CRU climatology (CRU CL 1.0: New et al. 1999).

Figure 6.25 shows the predicted carbon storage anomalies as predicted by LPJ and table 6.14 shows further details of the regional subdivision of these outputs.

Figure 6.25 Carbon storage anomalies (kg C/m²) between 1960-2080 predicted by LPJ-DJVM using emissions from the SRES B2 within four GCM (Sitch et al., 2003).

There are great uncertainties associated with these estimates due to the complex differential response of NPP and respiration to the climate drivers (temperature, precipitation), which themselves are highly spatially variable and interact. But the general response of the model seems to be as follows. In areas with no or little vegetation (e.g. polar desert), increasing CO₂ and temperature (e.g. increasing growing season), lead to increased vegetation growth and northward plant migration, leading to an increase in future carbon stocks. This seems to be a general pattern acting through increased productivity throughout the Arctic, all else being equal (see NPP predictions in Table 6.13). However, increased temperature leads also to increased heterotrophic (soil microorganism) respiration. Therefore areas, which at present contain large soil carbon stocks will release larger amounts of carbon from the soil as the respiration is responding to a warmer climate. Whether these areas are net sources or sinks depends on the balance between increased productivity (hence increased biomass and litterfall), due to increased CO₂/ longer growing seasons, and temperature enhanced respiration. When LPJ is forced with the climate prediction of ECHAM4 which produces very large temperature increases, respiration is enhanced more than productivity. Over the entire Arctic, carbon storage is balanced, due to northward migration of plants etc, with carbon loss in areas which experience large temperature changes and have large stocks of soil carbon. On the whole the result is that all runs with the model agree on an increased carbon gain. The "warmest" GCM, ECHAM4, predicts overall the lowest carbon gain, and the "coldest" CCC the highest carbon gain.

Table 6.13. Average and ranges of the drivers and responses of a leading Dynamic Global Vegetation Model, the LPJ model (Sitch et al., 2003) to the forcing of outputs from four different climate models (CCC, GFDL, HadCM3, Echam4) run for the Arctic (i.e. terrestrial >60°N).

<table>
<thead>
<tr>
<th>Temperature change (°C)</th>
<th>Average</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>2100-2000</td>
<td>5.0</td>
<td>4.7-5.7</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Precipitation change (mm/yr)</th>
<th>Average</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>2100-2000</td>
<td>42.9</td>
<td>9.04-78.0</td>
</tr>
</tbody>
</table>
The current estimated circumpolar emissions of CH₄ are in the range 20-60 Tg CH₄/yr. These have a significant potential for feedback to a changing climate. Large-scale CH₄ flux models are currently not as advanced as general carbon cycling models and few allow for climate change scenario-based projections of changes in the future. Early attempts to assess and model tundra CH₄ emissions driven by climate change all indicated a potential increase in emissions (Roulet et al., 1992; Harriss et al., 1993; Christensen and Cox, 1995) but more recent improved mechanistic models (Walter and Heimann, 2000; Granberg et al., 2001) have not yet been followed up by full coupling to GCM predictions to assess the circumpolar CH₄ emissions in the future. A critical factor is not only the mechanistic responses of soil processes but also the geographical extent of wetlands and how these may change in the future. There is, however, little doubt that with climate scenarios of warming and wetting of the Arctic soils, there will undoubtedly be increases in CH₄ emissions while with warming and drying there will be few changes or a decline of emissions relative to the current scale.

Lakes and streams cover large portions of many Arctic landscapes and, due to low evapotranspiration, runoff is a major component of Arctic water budgets. These surface freshwaters contain large amounts of dissolved organic and inorganic C that is carried into them by soil and groundwater flow from the terrestrial portions of their watersheds (Kling et al., 1992; 2000). The inorganic C is largely CO₂ produced by soil and root respiration. Organic C concentrations in soil-water, groundwater, and surface waters are typically several times greater than inorganic C concentrations and are a major source of respiratory CO₂ produced in lakes and streams, thus adding to their already high dissolved inorganic C content.
Because the dissolved CO₂ in surface waters is typically supersaturated with respect to the atmosphere, and the surface area and flow of freshwater is large, surface waters of Arctic landscapes lose large amounts of CO₂ to the atmosphere (Kling et al., 1991; Chapter 7). Estimates of CO₂ emissions from surface waters are as large as 20-25% of gross landscape CO₂ fixation and thus may be a major component of landscape C balance that is not accounted for in studies that include terrestrial CO₂ fluxes only. Similar large CO₂ losses also occur in freshwaters of boreal, temperate, and tropical landscapes (Cole et al., 1994), but they are generally not considered in landscape-level C budgets. At present, little is known of controls over these CO₂ losses or how they might change with changes in climate or water balance. Attempts to measure the losses directly have yielded inconsistent results (Eugster et al., in press).

### 5.4.2 Projected changes in exchanges of energy and water

Many of the likely changes in water and energy exchange that occur in response to projected future warming will likely act as a positive feedback to warming. Earlier disappearance of snow from the tundra will lead to a decline in albedo and an increase in regional warming (Bonan et al., 1992; Thomas and Rowntree, 1992). Similarly, an expansion of forest will lead to a reduction in albedo, because trees mask a snow-covered surface. In areas where forest expansion occurs, this will lead to significant heating of the lower atmosphere (Section 4.2.3 and Section 5.2). Paleoclimate modeling experiments have shown that the northward movement of treeline 6,000 yr BP accounted for half of the climatic warming that occurred at that time (Foley et al., 1994). Although the current Arctic treeline appears relatively stable or to be retreating in some areas of human impact (Callaghan et al., 2002; Vlassova, 2002; Section 5.3.2.1), any future northward advance of treeline will likely contribute to regional warming or treeline retreat would contribute to regional cooling, particularly in late spring due to the large differences in albedo between snow-covered tundra and adjacent forest.

A positive feedback (leading to increased warming) of displacement of tundra by trees and shrubs will tend to offset the negative feedback (leading to cooling) due to increased carbon sequestration at the local level (Harding et al., 2002), but the climate forcing by energy and water exchange operates primarily at the regional scale, where the energy exchange occurs, whereas the negative feedback due to atmospheric carbon sequestration will likely vary between regions and will contribute to warming through changes in the globally mixed pool of atmospheric CO₂. Models suggest that forests in the eastern Canadian Arctic would show a net negative feedback through sequestration of carbon whereas forests in Arctic Russia would have a net positive feedback to climate through decreased albedo (Betts and Ball, 1997; Betts, 2000). This complex balance between opposing feedbacks indicates that encouraging forest to displace tundra as an appropriate mitigation strategy against global climate change should take into account the local feedback.

An important contributing factor to the effect of vegetation change on albedo is the characteristics of the plant canopy in terms of canopy height relative to snow height, leaf duration, and leaf optical properties. The greatest changes in albedo will occur after increases relative to tundra vegetation in the order of dark, evergreen boreal trees such as pine and spruce> deciduous conifer trees such as larch> deciduous angiosperm trees such as birch > low shrubs such as willows and dwarf birch.

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"DO NOT CIRCULATE OR CITE"
The vegetation changes expected to occur in northern Alaska in response to climatic warming are calculated to increase summer heating of the atmosphere by 3.7 W m\(^{-2}\) (Chapin et al., 2000a). This warming is equivalent to the unit-area effect of a doubling of atmospheric CO\(_2\) or a 2% increase in solar constant (i.e., the difference that caused a switch from a glacial to an interglacial climate), two forcings that are known to have large climatic effects (Kattenberg et al., 1996). Regional climate simulations suggested that a conversion from moist tussock tundra to shrub tundra would cause a 1.5-3.5°C increase in July mean temperature on the Alaskan North Slope, reflecting greater sensible heat fluxes to the atmosphere from the shrub-dominated ecosystem. Thus vegetation changes of the sort that have recently been observed (Sturm et al., 2001b) are very likely to have large positive feedbacks to regional warming, if the increased shrub cover were extensive. This vegetation-climate feedback requires only modest increases in shrub density to enhance sensible heat flux (McFadden et al., 1998).

The transition from tundra to forest also affects evapotranspiration and the water storage capacity of the biosphere such that freshwater run-off via rivers to the Arctic Ocean may decrease (Harding et al., 2002).

Other human activities also have impacts on the local climate of the forest tundra. Deforestation, as a result of industrial activities or forestry, increases wind speeds; pollution leads to earlier snow melt and increased temperatures, and the northern extension of farming and settlements in general induce permafrost thawing (Vlassova, 2002).

Summary: Effects of changes in climate on landscape and regional processes and feedbacks to the climate system

Biological and physical processes in the Arctic system operate at various temporal and spatial scales to impact large-scale feedbacks and interactions with the earth system. There are four main potential feedback mechanisms between the impacts of climate change on the Arctic and the global climate system: albedo, greenhouse gas emissions or uptake by ecosystems, greenhouse gas emissions from methane hydrates, and increased freshwater fluxes that could affect the thermohaline circulation. All these feedbacks are controlled to some extent by changes in ecosystem distribution and character and particularly by large scale movement of vegetation zones. However, it is difficult to assess the consequences of the interacting feedbacks, and even of individual feedbacks.

There are currently too few full annual measurements available to give a solid answer to the question as to whether the circumpolar Arctic is an atmospheric source or a sink of CO\(_2\) at the landscape scale. Indications are, however, that currently the source areas exceed sink areas in geographical distribution. CH\(_4\) sources are also lacking study but the available information indicates emissions at the landscape level that are of great importance for the total greenhouse balance of the circumpolar North. In addition to the effect of greenhouse gases the energy and water balances of Arctic landscapes encompasses important feedback mechanisms in a changing climate. Increasing density and spatial expansion of the vegetation cover will cause a lowering of the albedo and more energy to be absorbed on the ground that is likely to exceed the negative feedback of increased C sequestration in greater primary productivity. The degradation of permafrost has complex consequences. In areas of discontinuous permafrost, warming, will lead to a complete loss of the permafrost. Depending on local hydrological conditions this may in turn lead to a wetting or drying of the environment with subsequent implications for GHG fluxes. Models projecting vegetation change in response to future climate change scenarios indicate a 7-18% decrease in the area occupied with polar desert and a 4-11% northward migration of the treeline over the coming 80 years. This in turn leads to an increased carbon storage over this same period due to productivity being stimulated more than respiration. However, this balance critically depends on the degree of warming predicted. With warmer climate change scenarios the heterotrophic respiration is stimulated more and the carbon gained will be less. There are very few models available
for projections of future CH₄ emissions but the importance of these emissions for the total greenhouse gas balance and functioning of the circumpolar Arctic will be huge.

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Will the Arctic become a source of carbon, or remain a sink?

There is not yet a definitive answer to this question, although past opinions favored the hypothesis that the tundra will switch from being a sink for carbon during recent millennia to becoming a source under future warming scenarios, based mainly on the response of increased soil respiration to warming relative to increases in photosynthesis. At a recent meeting of experts on carbon dynamics in the Arctic, the following authoritative consensus statements were made.


- The available flux data show large interannual variability. Arctic terrestrial ecosystems are a patchwork, with some regions being sources of carbon to the atmosphere (mostly dry and mesic ecosystems) and some regions sinks (mostly wet tundra). Currently indications are that source areas exceed sink areas.
- The available data indicate that when considering both CO₂ and CH₄ the Arctic region is a source of radiative forcing.
- Contrary to the data from ground-based measurements current global carbon models indicate a small carbon sink function of the Arctic. This apparent discrepancy is, however, within the uncertainty range of the data and model outputs.
- The recent remote sensing record indicates a greening of the Arctic suggesting increased photosynthetic activity and net primary productivity but does not address the below-ground processes i.e. respiration.
- Future projections from global models of vegetation and soil responses to climate change suggest that the enhanced production of vegetation will exceed increases in decomposition, thereby resulting in net C sequestration. Large uncertainties include the response of heterotrophic respiration, nutrient cycling, permafrost dynamics, land-cover change and scaling issues.
- Experimental data indicate that warming enhances carbon loss under dry soil conditions and carbon sequestration under wet soil conditions. Thus, future responses to regional warming will depend substantially on changes in soil moisture.
- Recent observations indicate that cold season greenhouse gas emissions contribute substantially to the annual budget.

The new, but uncertain, insights from these statements are that the Arctic is already a source of carbon and radiative forcing, and that it is likely to become a weak sink of carbon during future warming. Other aspects, not including in the consensus statements include uncertainties due to:

- Potential complex flux patterns over long time periods during which acclimation of carbon fluxes to warming leads to transient trends within millenia-long smoothing of shorter term dynamics.
- Probable increased physical and biotic disturbance during warming that might increase carbon emissions particularly if carbon storage shifts from tundra soils to invading forests.
- The various feedbacks between changing vegetation, soil temperatures, quality and quantity of litter and biodiversity of decomposer organisms.

Many uncertainties remain and it should be noted that the carbon we consider is that in the active layer in the soil and in vegetation, and not that trapped in permafrost and methane hydrates.
6. Uncertainties and recommendations

6.1 Uncertainties

Our current understanding of ecological processes and changes driven by climate and UV-B is strong in some geographical areas and in some disciplines, but is weak in others. Although the strength of our predictions has increased dramatically recently with increased research effort in the Arctic and the introduction of new technologies, our current understanding is constrained by various uncertainties: here, we focus on these uncertainties, rather than strengths of our knowledge, and recommend ways in which uncertainties can be reduced.

6.1.1 Uncertainties due to methodologies and conceptual frameworks

6.1.1.1. Uncertainties in methods of predicting impacts of changes in climate and UV-B on species and ecosystems

Each method has advantages and strengths and has lead to the important and extensive current knowledge base. However, each method also has uncertainties which need to be identified so that methods can be refined and uncertainties quantified.

The use of paleo analogs to infer future changes under-represents the differences between past changes and those likely to occur in the future due to a) differences in the starting state of the environment and biota, and b) the different nature of past and likely future changes. Major differences are the role of people, e.g. extent of land use impacts, current and future stratospheric ozone destruction, and trans-boundary pollution that are probably unprecedented.

Using geographical analogs can indicate where communities and species should be in a warmer world, but they do not tell us at what rate species can relocate or if new barriers to dispersal such as fragmented habitats will prevent potential distributions from being achieved.

Observations and monitoring provide essential data on changes as they occur and can be used to test hypotheses and model predictions, but they have little predictive power in a changing climate during which many biotic responses are non-linear.

Experiments that simulate future environments of CO₂, UV-B, temperature, precipitation, snow depth and snow duration etc., all have artifacts, despite attempts to minimize them. It is difficult in field experiments to include simulations of all likely eventualities: in warming experiments, it is very difficult to identify separate effects of seasonal warming and extreme events while most experiments are small in spatial extent, and are short-term in the context of the life cycles of Arctic plants and animals. It is also difficult to identify the complex interactions among all the co-occurring environmental change variables and ecological processes determined in experiments in one geographical area may not relate sufficiently to other areas because of different ecological conditions and histories.

Indigenous knowledge, although a valuable contributor to our understanding (section 6.2.2.1), is more qualitative than quantitative, and often characterized by relatively coarse measures (i.e.……
monthly and seasonal change rather than daily or weekly). The information available is sometimes limited to phenomena that fall within the cycle of subsistence resource use, and is more likely to be diachronic (long time series of local information) and not synchronic (simultaneously observed). It is often difficult to assign particular environmental changes to individual changes in biota, to determine mechanisms of change, and distinguish climate-related change from other changes occurring in the environment. Indigenous knowledge is variable between and within communities, and interpretation and verification processes are as important as collection and documentation. It is a knowledge system.

Uncertainties can be reduced when information from several methods converge. This chapter accepts all methodologies, knowing their limitations, and qualifies the information we present by the methodologies used to obtain it.

6.1.1.2 Uncertainties in measuring primary production and controlling factors

Key unknowns about primary productivity in the Arctic include root production and turnover and below ground allocation processes in general, including allocation to mycorrhizae and exudation. Also poorly understood are long-term (multiyear to multidecade) interactions between the C cycle and nutrient cycles, in which relatively slow changes in soil processes and nutrient availability interact with relatively rapid changes in photosynthesis in response to climate change. One major unknown is the control on dispersal, establishment and rate of change in abundance of species and functional types that are not now present or common in Arctic vegetation (e.g., trees and tall shrubs) that are more productive than current Arctic species.

There are two major approaches to assess NEP, a) classic weighing of biomass and b) round year CO₂ flux recording, but these are not always compatible. A particular gap in our estimates is the lateral transport of organic C from one ecosystem to another. The two methodologies give opposite results when accounting for the input of allochthonous OM (organic matter produced outside) to a particular ecosystem: CO₂ flux measurement gives negative NEP due to increased CO₂ emission from soil to atmosphere, while weighing gives a higher accumulation of organic C in the soil. Also, current estimates of buried C released to ecosystems due to soil erosion and thermokarst are poor (see plates 6.6 and 6.8).

6.1.1.3 Uncertainties due to difficulties in studying microorganisms

We have a limited understanding of microbes that are critically important in many ecosystem processes. Knowledge of microbial diversity and function has been strongly constrained by lack of development in methodology and conceptual frameworks.

Bacteria and even more-advanced microscopic yeasts and fungi cannot be characterized by visual observation alone due to their very simple shapes (rods, spheres, filaments). Typically, microbial strains must be cultivated in pure culture to reveal their various functional features and an appreciable amount of laboratory work is required to differentiate a microbe from close relatives. Only a small fraction of soil microorganisms are able to grow on artificial laboratory media, and less than 1% of the cells observed with a microscope form colonies on the plate. The main reasons for this “Great Plate Count Anomaly” (Staley and Konopka, 1985) include i) metabolic stress of ‘famine-to-feast’ transition occurring when cells are brought from soil to artificial,
nutrient rich media; ii) inadequacy of cultivation conditions compared with the natural environment, and iii) metabolic interactions/cooperation in natural communities that are broken after cells have been separated by plating (Panikov, 1995). This technical problem has resulted in an underestimation of diversity in natural habitats. Fortunately, new cultivation approaches are being developed that are helping to overcome this problem (Staley and Gosink, 1999). However, it is not presently possible to make a fair comparison between the numbers of species of animals and plants versus bacteria given that these groups are defined differently (Staley, 1997).

6.1.1.4 Uncertainties due to incomplete databases

Length of time series of data. Although many long time series of relevant data, e.g. on species performance and phenology, exist, most information relates to short time series. This is a particular problem in the Arctic where complex population dynamics (e.g. cycles) need to be understood over periods long enough to allow trends to be separated from underlying natural dynamics. Also, observations of trace gas emissions require annual observations over time periods long enough to encompass significant climate variability. Experiments are usually too brief to capture stable responses to environmental manipulations and to avoid artifacts that are disturbance responses. Long time series of data are also necessary in order to identify extreme events and non-linear system changes.

Geographical coverage and spatial scaling. The ecosystems and environments in the Arctic are surprisingly variable yet generalizations to the circumpolar Arctic are often made from few plot level studies. Sometimes, particular experiments, for example CO\textsubscript{2} and UV-B manipulations or observations are restricted to a few m\textsuperscript{2} of tundra at just one or two sites. Uncertainties due to generalizing and scaling up are thus significant. The International Biological Programme (IBP: 1960’s and early 1970’s) and the International Tundra Experiment (ITEX) are exceptional examples of how standardized experiments and observations can be implemented throughout the Arctic.

Coverage of species and taxa. Chapin and Shaver (1985a) and others have demonstrated the individualistic responses of species to experimental environmental manipulations, including climate, while Dormann and Woodin (2002) have shown the inadequacy of the concept of “plant functional types” to generalize plant responses to such experiments. An approach has to be adopted to measure responses of a relevant range of species to changes in climate, and particularly UV-B. Plants studied were generally at their northernmost distributional limits and well adapted to high UV-B levels characteristic of southern parts of their ranges. Greater responses would be expected from species at their southern distributional limits where increased UV-B would exceed levels in the plants’ recent “memory”.

Some species and taxonomic groups are particularly difficult to study, or have little socio-economic value, and so are underrepresented in databases. Examples are mosses, lichens, soil fauna and flora and microorganisms (see 6.1.1.3).

6.1.1.5 Uncertainties due to nomenclature and concepts

The restricted use of appropriate language often generates uncertainties. The nomenclature of vegetation and plant community types allows us to model changes in the distribution of these
assemblages of species in a changed climate, but constrains our understanding of changes in the *structure* of the assemblages which is likely to happen because assemblages of species do not move *en bloc*. This problem limits our understanding of novel future communities (Chapin and Starfield, 1997) and non-analogue communities of the past and emphasizes the uncertainties due to the lack of ability of quantitative models to predict qualitative changes in systems. Similarly, the concept of “line” to denote the limit of species’ distributions such as treeline, is inadequate to express the gradient of changes from one zone to another that can occur over 10’s of km.

The concept of ”species” is particularly difficult in the context of microorganisms as discussed above, and even as applied to flowering plants. The traditional view that there are few rare and endemic Arctic plant species is challenged by recent studies of the flora of Wrangel Island and Beringia (Table 6.14; 6.15) but it is not known to what degree plant taxonomy is problematic (although the Pan Arctic Flora Project is addressing this problem). Such problems need to be resolved before we can assess the impacts of climate change on biodiversity.

### 6.1.2 Uncertainties due to surprises

Perhaps the only certainty in our assessment of impacts of changes in climate and UV on terrestrial ecosystems is that there will be surprises. It is difficult by definition to predict surprises. However, the possibility that climate *cooling* will occur because of a change in thermohaline circulation, is potentially the most dramatic surprise that could occur.

#### 6.1.2.1 Regional cooling

The potential for a negative feedback arising from an increased freshwater flux to the GIN (Greenland, Icelandic and Norwegian) seas and Arctic basin, leading to a consequent partial or complete shut down of the thermohaline circulation of the global oceans, remains an area of considerable uncertainty; (Chapter 5 and 8). Such an event would lead to marked and rapid regional cooling in at least Northwest Europe. This region at present enjoys an anomalously warm climate given its latitude (50°–72°N), enabling agriculture to be practiced and substantial settlements maintained at far higher latitudes than in any other Arctic/sub-Arctic region. Such cooling would qualitatively alter terrestrial ecosystems (Fossa, 2003), agriculture and forestry over very large areas of Fennoscandia and Europe.

#### 6.1.2.2 Mutations

Mutations are expected from UV radiation and also from aerosols and volatile chemical mutagens brought to the cool polar air from the mid- and low latitudes. The direct mutagenic effect is probably not strong, especially if we take into account the protecting shielding effects of soil particles and adaptive mechanisms discussed above. However, possible microbial mutants could lead to epidemic outbreaks that could have profound and unexpected consequences for the Arctic and elsewhere.

#### 6.1.2.3 Desertification

Several approaches suggest an increase in productivity of Arctic vegetation with climate warming and a long term net sequestration of CO₂. However, the complex interactions among
warming, permafrost dynamics, hydrology, precipitation and soil type are generally lacking from our understanding. Desertification is a plausible outcome in some areas where scenarios suggest that permafrost will thaw, drainage will increase, warming will occur and precipitation will not increase substantially. In areas of sandy soil and loess deposition, such as areas of eastern Siberia, there is a particular risk of desertification. In the polar deserts, herb barrens and heaths of northern Greenland, plant productivity is strongly correlated with precipitation and increased evapotranspiration could lead to a similar process (Heide-Jørgensen and Johnsen, 1998). Locally, impacts of overgrazing and disturbance through human impacts can accelerate the process. A clear example of the effect of warming and drying on Alaskan tundra carbon balance is shown in section 5, but the possible wider geographical scale of this process is unknown.

6.1.2.4 Changes in current distributions of widespread and rare species

Climate change could have counter-intuitive impacts on species distributions. Currently rare Arctic plant species, particularly those that are northern outliers of species with more southerly distributions, could expand during initial phases of climate warming. In contrast, currently widespread species, particularly lichens and mosses, could become more restricted in their abundance during warming. It is necessary to reassess the concept of “threatened species” in the context of climate and UV change (see section 7 and chapter 10).

6.1.3 Uncertainties due to lack of validation of models

During the IBP period (late 1960s early 1970s) tundra research was characterized by extensive field observations but a general lack of modeling capability. Currently, a technological revolution has stimulated model generation and remote sensing of ecosystem change. However, in some cases, validation is insufficient. Models that predict NPP at a global or circum-Arctic level are insufficiently validated as recent measurements of NPP are rare and restricted to few localities. Also, lack of inter-comparison between models and existing observations lead to potential error in prediction: modeled displacement of the tundra by the boreal forest currently fails to relate to current observations of the southwards retreat of the treeline in some areas and the expansion of “pseudotundra” in parts of Russia due to permafrost degradation, paludification and human activities.

6.1.4 Uncertainties due to the use of ACIA scenarios

The future climate scenarios for ACIA were the B2 scenarios, but A2 scenarios have been used to a limited extent as a plausible alternative (Houghton et al., 2001) (Chapter 1). A2 scenarios have a greater economic emphasis, while B2 have a greater emphasis on environmental concerns: each has considerable uncertainties (Chapter 4). In the present chapter, the B2 scenarios were mainly used to model changes in vegetation and carbon storage. Use of A2 scenarios would have resulted in higher temperatures than for those of B2 runs for a particular time period. The A2 changes would occur earlier by 5-10 years for the time slice 2050 and by 10-20 years for time slice 2080. Potential impacts on ecosystems would thus occur faster.

The major implication for ecosystems of a faster rate of temperature change is an increased mismatch between the rate of habitat change and the rate at which species can relocate to occupy new habitats in appropriate climate envelopes. The overall, generalized, difference between the
B2 and A2 scenarios would be an increased risk of disturbance and disease in species that, under the A2 scenario, cannot relocate quickly enough. There would also be an increased mismatch between initial stimulation of soil respiration and longer-term vegetation feedbacks that would reduce carbon fluxes to the atmosphere under an A2 scenario.

The present-day climate simulated by GCMs is not yet good enough to use directly to drive a biosphere model, therefore the anomaly approach was used within the biosphere model (Sitch et al., 2003). Data were downscaled from the GCM specific grid onto one at 0.5 degree resolution and GCM climate anomalies were normalized to the 1961-1990 observed average monthly CRU climatology (CRU CL 1.0: New et al., 1999).

6.2 Recommendations to reduce uncertainties

6.2.1 Thematic recommendations and justification

The following section contains important thematic topics that require particular research. For each topic, we summarize the state of knowledge and important gaps, and give recommendations to fill these gaps (in italic font).

Mechanisms of species responses to changes in climate and UV-B. Changes in microbe, animal and plant populations are triggered by trends in climate and UV, exceeding thresholds and by extreme events, particularly during winter. However, information is uneven and dominated by trends in summer climate. We need appropriate scenarios of extreme events and to deploy long-term experiments simulating extreme events and future winter processes in particular. We also need a better understanding of thresholds relevant to biological processes.

Biodiversity changes. Some groups of species are very likely to be at risk from climate change impacts, and the biodiversity of particular geographic areas such as Beringia are at particular risk. We do not know if currently threatened species might proliferate under future warming or which currently widespread species might decrease in abundance. We need to reassess the nature of threats to species, including microbes, from long-term climate and UV-B change simulation experiments. We also need to identify and monitor currently widespread species that are likely to decline under climate change, and to redefine conservation and protection in the context of climate and UV change.

Relocation of species. The dominant response of current arctic species to climate change, as in the past, is very probably relocation rather than adaptation. Relocation possibilities are very likely to vary according to region and geographical barriers. Some changes are already occurring. However, our knowledge of rates of relocation, impact of geographical barriers, and current changes is poor. We need to measure and predict rates of species migration by combining paleo-ecological information with observations from indigenous knowledge, environmental and biodiversity monitoring and experimental manipulations of environment and species.

Vegetation zone redistribution. Forest is very likely to replace a significant proportion of the tundra and will very probably have a great effect on the composition of species. However, several processes including land use and permafrost dynamics are expected to modify the
modeled response of vegetation redistribution related to warming. We need to develop and link models of climate, hydrology (permafrost), ecosystems and land use. These models need to be based on improved information on the current boundaries of major vegetation zones, defined and recorded using standardized protocols.

**Carbon sinks and sources in the Arctic.** Current models suggest that the Arctic’s vegetation and active-layer soils will be a sink for carbon in the long-term because of the northward movement of vegetation zones that are more productive than those they displace. Model output needs to be reconciled with observations that show that tundra C source areas currently exceed C sink areas, although the measurements of circum-Arctic C balance are very incomplete. Also, it is not known to what extent disturbance will reduce the C sink strength of the Arctic. We need to establish long-term, annual carbon monitoring throughout the Arctic; to develop models capable of scaling ecosystem processes from plot experiments to landscapes; to develop observatories, experiments and models to relate disturbance such as desertification to carbon dynamics; to improve the geographical balance of observations by increasing high Arctic measurements. We also need to combine estimates of ecosystem carbon flux with estimates of carbon flux from thawing permafrost and methane hydrates.

**UV-B and CO$_2$ impacts.** Enhanced CO$_2$ and UV-B have subtle but long-term impacts on ecosystem processes that reduce nutrient cycling with the potential to decrease productivity. However, these are generalizations from very few plot-scale experiments, and it is difficult to understand impacts that include large herbivores and shrubs. We need long-term experiments on CO$_2$ and UV-B effects on a range of Arctic ecosystems interacting with climate; short-term experiments stimulating repeated episodes of high UV exposure; long-term experiments that determine the consequences of high CO$_2$ and UV-B for herbivores and short-term screening trials to identify the sensitivity of a wide range of species, including soil microbes, to current and predicted UV-B levels.

**Local and regional feedbacks.** Displacement of tundra by forest will very probably lead to a decrease in albedo with a potential for local warming whereas carbon sequestration will probably increase with potential impacts on global greenhouse gas concentration. However, the timing of the processes and the balance between the processes are very uncertain. How local factors such as land use, disturbance, tree type and possible desertification will affect the balance, are also uncertain. We need long-term and annual empirical measurements, analysis of past remotely sensed images and collection of new images together with the development and application of new models that include land use, disturbance and permafrost dynamics.

**6.2.2 Recommendations for future approaches to research and monitoring**

No one approach is adequate and confidence is increased when results from different approaches converge (Section 6.1.1). We recommend the maintenance of current approaches and development of new approaches and even paradigms, for example when defining “threatened species” and “protected areas”. Some important approaches are highlighted below.

**6.2.2.1 Reducing uncertainty by increasing and extending the use of indigenous knowledge**
Arctic Indigenous peoples retain strong ties to the land through subsistence economies and they are “active participants” in ecosystems (sensu Bielawski, 1997). Unlike a scientist, a hunter is not bound in his observations by a project time line, budget, seasonality, or logistical constraint (Krupnik, 2000; Riedlinger and Berkes, 2001). Subsistence activities occur on a daily basis, year after year, and throughout the winter period when many scientists are South in home institutions. Indigenous peoples of Arctic regions therefore possess a substantial body of knowledge and expertise related to both biological and environmental phenomena. Such local expertise can highlight qualitative changes in the environment and provide pictures of regional variability across Arctic regions that are difficult to capture using coarser scaled models.

We present some of the first efforts at linking western science and IK to expand the range of approaches that inform the current assessment. However, the potential is far greater including for example local scale expertise, information on climate history, generation of research hypotheses, community monitoring and community adaptation (Riedlinger and Berkes, 2001).

6.2.2.2 Monitoring

Long term environmental and biological monitoring have been undervalued but are becoming increasingly necessary to detect change, to validate model predictions and results from experiments, and to substantiate measurements made from remote sensing. Present monitoring programs and initiatives are too scarce and are scattered randomly. Data from the Arctic on many topics are often not based on organized monitoring schemes, are geographically biased and are not long-term enough to detect changes in: - species’ ranges, natural habitats, animal population cycles, vegetation distribution, and carbon balance. More networks of standardized, long-term monitoring sites are required to better represent environmental and ecosystem variability in the Arctic and particularly sensitive habitats. Because there are interactions among many co-varying environmental variables, monitoring programs should be integrated. Observatories should have the ability to facilitate campaigns to validate output from models or ground-truth observations from remote sensing. There should be collaboration with Indigenous and other local peoples’ monitoring networks where relevant. It would be advantageous to create a decentralized and distributed, ideally web-based meta-database from the monitoring and campaign results, including relevant Indigenous knowledge.

Monitoring also requires institutions, not necessarily sited in the Arctic, to process remotely sensed data. Much information from satellite and aerial photographs exists already on vegetation change, such as treeline displacement, and on disturbances such as reindeer over-grazing and insect outbreaks. However, relatively little information has been extracted and analyzed.

Monitoring carbon fluxes has gained increased significance since the signing of the Kyoto Protocol. Past temporal and spatial scales of measurement used to directly measure carbon flux have been a poor match for the larger scale of Arctic ecosystem modeling and extrapolation. It remains a challenge to determine if flux measurements and model output are complementary. The technological difficulties in extrapolating many non-linear, complex, interacting factors that comprise fluxes at hundreds to thousands of square kilometers over time, space, and levels of biological and environmental organization in the Arctic have been significant (Oechel et al. 2000b; 1998). Research is needed to better understand how the complex system behaviors at the meter scale relate to larger spatial scales that can be efficiently modeled and evaluated at the
regional and circumpolar scale. To do this, extensive long-term and year round eddy covariance sites and other long-term flux sites, including repeated aircraft flux measurements and remote sensing (Oechel et al., 2000a) provide the basis for estimating pan Arctic net ecosystem CO₂ exchanges. Currently, the pan Arctic region is disproportionately covered by current and recent measurements, with Canadian and high Arctic regions particularly poorly represented.

6.2.2.3 Long-term and year-round approach to observations and experiments

Many observations and experiments are short term (<5 years) and they are biased towards the summer period often because of commitments of researchers to institutions outside the Arctic during wintertime. However, throughout this assessment it has become clear that long-term and year-round measurements and experiments are essential to our understanding of the slow and complex responses of Arctic organisms and ecosystems to climate change.

Long-term (>10 years) observations and experiments are required to:

- Enable transient responses to be separated from possible equilibrium responses
- Increase the chances that disturbances, extreme events and significant inter-annual variation in weather can be included in the observations
- Allow possible thresholds for responses to be experienced

Year-round observations are necessary to understand the importance of winter processes in determining the survival of Arctic species and the function of Arctic ecosystems. Such observations are necessary to recognize the expected amplification of climate warming in wintertime and to redress the current bias of experiments to summer-only warming. For microbes, it is particularly important to understand changes in winter respiration and nutrient mobilizations during freeze-thaw in spring and late autumn.

It is important to improve the appropriateness of the timing of our observations and experiments. For example, current information on impacts of increased UV-B is mainly derived from general summer enhancements or filtration of UV-B although future increases in UV-B are likely to be highest in spring and during specific events. Also, frequency of observations can be fitted to the rate of change of the species/processes. Decadal measurement may suffice for some variables such as treeline movement.

6.2.2.4 Increasing the complexity and scale of environmental and ecosystem manipulation experiments

Single factor manipulation experiments now have limited applicability because it is clear that there are many interactive affects among co-occurring environmental change variables. There is need for well-designed large, mutifactorial environmental (e.g. climate, UV-B and CO₂) and ecosystem manipulation (e.g. species removal and addition) experiments that are long term and seek to understand annual, seasonal and event-based impacts of changing environments. The complexity of appropriate treatments and time scales is vast but the spatial scale is also a significant challenge as it is important to have manipulations that can be related to larger plants (e.g. trees, shrubs) and animals (e.g. reindeer).
6.2.2.5 Assessing the impacts of cooling on ecosystems

Warming scenarios dominate the approaches of predicting responses of ecosystems to future climates. However, cooling in some areas remains a possibility. As the impacts of cooling on terrestrial ecosystems and their services to people are likely to be far more dramatic than warming, it is timely to reassess the probabilities of cooling from GCMs and the appropriateness of assessing cooling impacts on ecosystems.

6.2.2.6 Modeling responses of Arctic ecosystems to climate and UV-B change and communicating results at appropriate geographical scales

High resolution models are needed at the landscape scale for a range of landscape types that are expected to experience different future envelopes of climate and UV-B. Modeling at the landscape scale will simulate local changes that relate to plot scale experiments and can be validated by results of experiments and field observations. Also, visualization of model results presented at the landscape scale will enhance the understanding of the changes and their implications by local peoples and decision-makers. A particular challenge is to provide scenarios for changes in climate and UV-B at the scale of 10’s of meters.

6.2.3 Funding requirements

It is inappropriate here to comment on levels of funding required to fulfill the recommendations discussed above. However, it is appropriate to highlight two essential aspects of funding.

1. Current short-term funding is inappropriate to support research into long-term processes such as ecosystem responses to climate change and UV-B impacts. A stable commitment to long-term funding is necessary.

2. Funding possibilities that are restricted to single nations or at best few nations, make it extremely difficult to implement coordinated research that covers the variability in ecosystems and expected climate change throughout the circumpolar North, even though the instruments for coordination exist for example within IASC, ICSU, IGBP. Limitation of international funding possibilities leads to geographical biases and gaps in important information. Circum-Arctic funding is required so that coordinated projects can operate at geographically appropriate sites over the same time periods.
7. Synthesis: Scenarios of expected changes in the four ACIA subregions for 2020, 2050 and 2080.

This synthesis draws on information in the chapter that can be assessed within the four ACIA subregions. Most of the information is therefore based on model output. Details of the subregions and the logic determining them are presented in Chapter 1 while details of the models that generate the climate and UV-B scenarios are presented in Chapters 3 and 4 respectively. Many of the details relating to vegetation and carbon dynamics are derived specifically for this section from the LPJ model (Sitch et al., 2003), details of which are presented in the text box of section 5.4.1. Other aspects of the assessment that cannot currently be divided into the subregions are summarised within and at the end of the various chapter sections.

7.1 Environmental characteristics

The four ACIA sub-regions (Chapter 1) differ greatly in their geography and climatology which leads to variation in future possibilities for the relocation of species and ecosystems, and differences in scenarios of future changes in climate and UV-B radiation (Table 6.14).

Geographically, zone IV has a far greater extent of land at high latitudes compared with other zones. This could potentially support northward migration of Arctic biota even if the Canadian high Arctic archipelago and the glacial landscape of Greenland together with lack of suitable soils will, to some extent, pose problems to migration. Relatively narrow tundra zones in some parts of regions III and I could, under sea level rise and boreal forest expansion northwards, disappear with forest reaching the shore of the Arctic Ocean (Figure 24). Sub-region I contains the relatively isolated high Arctic Islands of Svalbard, and the islands of Iceland and the Faroe Islands that might experience delayed immigration of southern species during warming. Both Iceland and the Faroe Islands have equivocal positions within classifications of the Arctic: the northern part of Iceland and the alpine zones of the Faroe Islands (Fossa, 2003) have the strongest Arctic characteristics and climate warming can lead to altitudinal displacement of tundra-like vegetation in both areas, and displacement from the northern coastal area in Iceland. The imbalance of species loss and replacement by species invading more slowly to islands is expected to lead to an initial loss in diversity (Heide-Jørgensen and Johnsen, 1998).

The 5 ACIA scenarios of temperature change show complex patterns with time, some from initial cooling to substantial warming. The data used for the modeling of vegetation zone displacement and carbon storage used a different baseline period (2000) than the ACIA scenarios (1980-1999) and excluded the NCAR CSM. Also, the data for the LPJ model are cited for 2100, rather than 2080, as in the case of the ACIA scenarios (see section 5). It is therefore difficult to compare the results, even though both approaches had four GCMs in common and used the same emissions scenario.

Changes in UV-B radiation are expected to vary among sub regions, but only over the next 20 years. By 2050, stratospheric ozone repair is expected to reduce UV-B radiation to relatively low levels above present with no differences among sub regions. Of course, this repair depends entirely on the success of management and regulation. In the near future however, UV-B increases are expected to be greatest in sub region IV, follow by I and II (Taalas et al., 2000).
The projected shifts in thickness of the soils’ active layer above the permafrost shows increases of 20-60% by 2071-2100 (compared to the IPCC baseline, 1961-1990). The largest percentage increases are in northern Siberia and the interior of the Alaka-Yukon Region. In general, the largest relative changes in the active layer occur in those regions where the active layer is presently shallow (Chapter 5). Degradation of continuous to discontinuous permafrost and the disappearance of discontinuous permafrost will occur at the southern boundaries of each of the zones.

### 7.2 Vegetation zones and carbon balance

Region I, Arctic Europe, East Greenland, European Russian North and North Atlantic, includes many high Arctic areas but these are separated from terrestrial ecosystems of lower latitudes by barriers of open sea. The possibilities for future species relocation are limited, even though moderate warming is predicted here (Table 6.14). In contrast, Region II, Central Siberia, has continuous landmasses from the tropics to the high Arctic. This region is currently warming, and scenarios show that future warming will be greater here than elsewhere. The possibilities for responses in ecosystem distribution, structure and carbon balance are therefore considerable. This is shown by large predicted increases in taiga which displaces tundra in particular, and also in decreases in polar desert which is displaced to some extent by northward movement of the tundra (Table 6.14). There is also a northwards displacement and reduction in prostrate dwarf-shrub tundra, particularly in Yakutia and the Taymyr Peninsula together with a displacement of erect dwarf shrub tundra from much of the Russian Arctic by low and high-shrub tundra that expands markedly there (Figures 6.2 and 6.24). Region III, Chukotka, Bering Sea, Alaska, western Canadian Arctic, is an area with little high Arctic and large maritime influence. Increases in temperature and precipitation are expected to be moderate as are changes in vegetation (Table 6.14). Region IV, Northeast Canada, Labrador Sea, Davis Strait, West Greenland, is a region of fragmented landmasses that are often strongly glaciated or have recently become deglaciated. This area has experienced recent cooling, but a warming trend is expected over the period from the current time to 2100. Increases in temperature and precipitation are expected to lead to relatively small increases in taiga (compared with other sub regions) but a particularly large loss of polar desert of about 36% by 2080.

In terms of carbon storage, all sub regions are predicted to accumulate carbon, largely because of the replacement of bare ground by tundra. Consequently, the greatest carbon gain is expected to occur in Region IV (Table 6.14; Figure 6.25). In contrast, the smallest gains – but still gains – are expected in Region I which has the smallest expected increase in temperature.

### 7.3 Biodiversity

Biodiversity is affected by habitat fragmentation. Scenarios of all projected human infrastructure development on Arctic flora and fauna suggest that these impacts in the Arctic extend for 4 – 10 km away from the infrastructure (Nellemann et al., 2001). This is a much wider zone of impact than in other regions of the earth. Nellemann et al. (2001) calculated that 50 to 80% of the Arctic could be impacted by infrastructure development by 2050. Of course, infrastructure development varies among ACIA sub regions and this remains to be characterized. However, threats to flora
and fauna will be increased by the additive or even possible interactive effects of development of infrastructure and climate change.

The number of rare endemic vascular plant species in the Arctic varies greatly between the subregions (Table 6.1; 6.15). Region I including the European Arctic has relatively little land mass and supports only 2 of the rare endemic vascular plant species. Region IV in West Greenland and Northeast Canada that contains a significant proportion of the high Arctic contains 8% of the species and central Siberia contains 18%. In complete contrast over 70% of the species are found in Beringia. 24 species are found on Wrangel Island (Talbot et al., 1999). A recent modification (Talbot and Murray, 2001) of the list of threatened Arctic plant species (CAFF Atlas of rare endemic vascular plants of the Arctic; Talbot et al., 1999) adds a further 63 plant species, but data have not yet been compiled on the ACIA sub regional distributions. Although tables 6.14 and 6.15 shows clear sub regional differences in the distribution of rare and endemic plant species, and also a surprisingly high number of these species, it should be born in mind that the taxonomic treatment of species is likely to vary from region to region and there is uncertainty about the taxonomic status of some of the species.

It is not clear to what extent the rarity of the species listed in Tables 6.7 and 6.14 will be affected by climate change as many other factors determine rarity. However, the species concentrated in small areas such as Wrangel Island are particularly at risk from any future climate warming and species invasion.

*Figure 6.26. Threats to current conservation using protected areas from climate change. A map of current protected areas in the Arctic (CAFF, 2001) has been overlain by a map of changes in vegetation derived from Kaplan et al. (2003) and Figures 6.2 and 6.24.*

The likely impacts of climate change on biodiversity in terms of threatened species require us to conceive new concepts of “threatened species” and “protection” of currently perceived threatened species (Figure 6.26; Chapter 10). The numbers of species currently perceived as threatened vary between sub regions. Sub region III contains significantly more rare plant species and threatened animal and plant species than other sub regions. Although temperature and precipitation changes are likely to be less in this sub region than in others, the vulnerability of the biodiversity of this area is likely to be considerable. Northwards expansion of dwarf shrub and tree dominated vegetation into an area such as Wrangel Island that is rich in rare endemic species could result in the loss of many plant species. Although some of these might not be considered vulnerable because they are currently in “protected” areas, this protection is against local human activities such as hunting, infrstructur development etc., and protection cannot extend to changes in climate and UV-B radiation. It is possible that some plant species, particularly outliers of more southerly distributions, might experience population expansion or reproduction and recruitment to populations leading to initial expansion in response to warming. However, displacement of herbaceous species by woody immigrants is a probability in the long term in mesic areas. In contrast to the possibility that some threatened species might proliferate in a warmer climate, some currently widespread species might become less abundant and even “threatened”.

The greatest long-term threat to Arctic diversity is the loss of Arctic habitat (Section 2.6). In locations where the tundra zone is narrow, boreal forest moves northward from the South and the
ocean moves southward due to sea-level rise, there is very likely to be, over a period of centuries, a loss of Arctic ecosystems and the species that characterize them.

Table 6.14. Summary baseline information for the four sub regions. Average and ranges (in brackets) of the drivers and responses of a leading Dynamic Global Vegetation Model, the LPJ model (Sitch et al., 2003) to the forcing of outputs from four different climate models (CCC, GFDL, HadCM3, Echam4) run for the ACIA sub-regions (Chapter 4).

<table>
<thead>
<tr>
<th>Region</th>
<th>Expected environmental changes</th>
<th>Ecosystem processes predicted by LPJ model</th>
<th>Landscape processes predicted by LPJ model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Annual Temperature from the ACIA Scenarios</td>
<td>NPP (Pg C/yr) See table 6.12 for the total of the Arctic</td>
<td>% change in areas of vegetation Taiga v tundra***</td>
</tr>
<tr>
<td></td>
<td>Baseline 1980-1999</td>
<td>1960s</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td>2020 (change from baseline)</td>
<td>2080s</td>
<td>1.8</td>
</tr>
<tr>
<td></td>
<td>2050 (change from baseline)</td>
<td>% change</td>
<td>46.3</td>
</tr>
<tr>
<td></td>
<td>2080 (change from baseline)</td>
<td>NEP</td>
<td>Change in C storage (Pg C) See table 6.12 for the total of the Arctic</td>
</tr>
<tr>
<td></td>
<td>Precipitation change used for the LPJ Model (mm/month)</td>
<td>Veg C</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Baseline 1980-1999</td>
<td>Soil C</td>
<td>-0.1</td>
</tr>
<tr>
<td></td>
<td>2020 (change from baseline)</td>
<td>Litter C</td>
<td>-0.02</td>
</tr>
<tr>
<td></td>
<td>2050 (change from baseline)</td>
<td>Total C</td>
<td>0.04 (-0.7-0.8)</td>
</tr>
<tr>
<td></td>
<td>2080 (change from baseline)</td>
<td>Change in albedo (due to vegetation change)</td>
<td>2050++</td>
</tr>
<tr>
<td></td>
<td>Precipitation change used for the LPJ Model (mm/yr)</td>
<td>2080++</td>
<td>-0.1 to 0.01</td>
</tr>
<tr>
<td></td>
<td>Baseline 1980-1999</td>
<td>UV-B change Mean for 2010-2020</td>
<td>0 to 10% increase</td>
</tr>
<tr>
<td></td>
<td>2020 (change from baseline)</td>
<td>Mean for 2040-2050</td>
<td>0 to 2% increase</td>
</tr>
<tr>
<td></td>
<td>2050 (change from baseline)</td>
<td>Permafrost</td>
<td>?</td>
</tr>
<tr>
<td></td>
<td>2080 (change from baseline)</td>
<td>Habitat fragmentation</td>
<td>?</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Region I</th>
<th>Region II</th>
<th>Region III</th>
<th>Region IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctic Europe, East Greenland, European Russian North and North Atlantic</td>
<td>Central Siberia</td>
<td>Chukotka, Bering Sea, Alaska, western Arctic Canada</td>
<td>Northeast Canada, Labrador Sea, Davis Strait, West Greenland</td>
</tr>
<tr>
<td>Temperature change (°C)</td>
<td>Expected environmental changes</td>
<td>Ecosystem processes predicted by LPJ model</td>
<td>Landscape processes predicted by LPJ model</td>
</tr>
<tr>
<td>2020-1999</td>
<td>3.9 (3.6-4.4)</td>
<td>4.4 (4.0-4.8)</td>
<td>5.0 (4.5-5.5)</td>
</tr>
<tr>
<td>Baseline 1980-1999</td>
<td>3.9 (3.6-4.4)</td>
<td>4.4 (4.0-4.8)</td>
<td>5.0 (4.5-5.5)</td>
</tr>
<tr>
<td>Precipitation change used for the LPJ Model (mm/yr)</td>
<td>2020-1999</td>
<td>2020-1999</td>
<td>2020-1999</td>
</tr>
<tr>
<td>Baseline 1980-1999</td>
<td>3.9 (3.6-4.4)</td>
<td>4.4 (4.0-4.8)</td>
<td>5.0 (4.5-5.5)</td>
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</tbody>
</table>
Biodiversity

<table>
<thead>
<tr>
<th></th>
<th>2080-1960</th>
<th>-4.2 (-5.9 - -3.2)</th>
<th>-11.4 (-14.6 - -10)</th>
<th>-13.2 (-16.6 - -11.4)</th>
<th>-35.6 (-47.8 - -25.9)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No of rare endemic vascular plant species****</td>
<td>2</td>
<td>18</td>
<td>69</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Threatened vascular plant species (occurring at 1 unprotected location)****</td>
<td>1</td>
<td>4</td>
<td>11</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Threatened animal species*****</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

* only a proxy as the change is derived from functional characteristics of the vegetation produced by the model rather than predictions of specific vegetation composition per se. For a proper vegetation distribution estimate it would be more appropriate to use a proper biogeographical model such as BIOME4.
** based on percentage increase in woody plants produced by LPJ.
***based on the percentage reduction in bare ground produced by LPJ.
**** extracted from Talbot et al, 1999
*****Zöckler
++ Betts, (conference proceedings, Rovaniemi, using IS92a scenario).

Acknowledgements

Many individuals and organizations kindly contributed information to this assessment and we are grateful to all. In particular, we thank the Steering Committees of the IASC projects on the Tundra-Taiga Interface and Feedback from Arctic Terrestrial Ecosystems. ITEX participants also gave support. We thank Dr Anders Michelsen for information on Arctic mycorrhizal associations and Jed Kaplan (MPI Jena) for providing unpublished estimates of the past and potential future extent of tundra derived from simulations made using the BIOME 4 model. We are grateful to Håkan Samuelsson and Chris Callaghan for help with some of the figures. Terry Callaghan and Margareta Johansson are very grateful to the Swedish Environmental Protection Agency (Naturvårdsverket) for funding to allow them to contribute to the ACIA process. Participation of K. Laine and E. Taulavuori have been facilitated by financial support from the Academy of Finland and Thule Institute, University of Oulu. Phycology research in the Arctic by J. Elster and colleagues has been sponsored by two grants; the Natural Environment Research Council (LSF-82/2002), and the Grant Agency of the Ministry of Education of the Czech Republic (KONTAKT - ME 576). We are grateful to A. Katenin for providing part of Figure 3 from Russian sources. Finally, we are grateful to the ACIA leadership, integration team and chapter liason Pål Prestrud for guidance and encouragement.
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External Review January2004

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