

Response of arctic terrestrial ecosystems to recent climate change: biophysical and habitat changes in northern Alaska

Udo Schickhoff, Hamburg

Abstract. Average arctic temperatures increased at almost twice the global average rate in the past 100 years, and Alaska and northern Asia, together with the Antarctic Peninsula, have been the most rapidly warming regions of the globe over the past several decades. The observed warming in the Arctic in the latter half of the 20th century appears to be without precedent since the early Holocene. Global warming is currently impacting Alaskan arctic terrestrial ecosystems in multifarious ways. This paper reviews the impacts of climate change on physical systems and illustrates the response of terrestrial ecosystems to climate and related environmental changes, focussing on changes in vegetation.

Climate warming causes cascading effects on arctic physical systems including permafrost warming and thawing, extensive thermokarsting, increasing active layer depths, warming and drying topsoils, altered carbon release, increasing river discharge, melting of glaciers and ice sheets, reductions in sea ice extent, rising sea level, increasing coastal erosion, earlier snowmelt and diminishing snow-covered areas. Some of the affected physical processes imply important feedbacks to the climate system. Climate change has substantially affected arctic terrestrial ecosystems, both directly and indirectly via physical feedbacks. The response of ecosystems includes significant vegetation changes. In northern Alaska, a considerable increase in the abundance and extent of shrubs in tundra areas has been detected over the past decades. Warming experiments confirm the increasing dominance of deciduous shrubs in the Alaskan tundra under experimental and observed climate warming. The increase of shrub biomass is associated with a widespread advance of trees into tundra ecosystems, reflecting more favourable growth conditions for woody species. Changes in land, ice and snow cover are likely to act as a positive feedback to radiative forcing and enhance atmospheric warming. At the plant community scale, changing site conditions under climate warming greatly affect species compositions. Altered floristic compositions will have implications for nutrient availability, element accumulations, carbon cycling, trace-gas exchange, and other ecosystem processes and thus change ecosystem structure and function.

1 Introduction: climate change in northern Alaska and other arctic regions

Northern Alaska and other arctic regions provide increasing evidence of ongoing impacts of climate change on species, communities and ecosystems (HINZMAN et al. 2005), corroborated by observations based on local knowledge of long-time residents in the Arctic (KRUPNIK & JOLLY 2002). The climate has warmed substantially since the end of the Little Ice Age to present, only interrupted by a cooling trend in many regions between 1940 and about the mid-1960s, but even then large areas (e.g., southern Canada, southern Eurasia) experienced significant increases in temperature (MCBEAN et al 2005). From 1850 to 1950, the Arctic warmed to the highest temperatures in 400 years

(OVERPECK et al. 1997). Air temperature appears to have increased throughout the Arctic during most of the 20th century. Average arctic temperatures increased at almost twice the global average rate in the past 100 years, and the Arctic (together with the Antarctic) experienced the greatest regional warming on earth in recent decades (TRENBERTH et al. 2007, ANISIMOV et al. 2007). Average annual temperatures have risen by about 2-3 °C since the 1950s and in winter up to 4 °C (MCBEAN et al. 2005). The most recent warming (exceeding 1 °C/decade since 1980) is strongest over the interior portions of northwestern North America and northern Asia. It is strongest in winter and spring, and smallest in autumn. The instrumental record of land-surface air temperature is qualitatively consistent with other climate records in the Arctic such as temperatures in the marine Arctic (SERREZE et al. 2000; POLYAKOV et al. 2003) or surface temperatures derived from satellite thermal infrared measurements (COMISO 2003).

In Alaska, observed data indicate that over the last 50 years mean annual surface temperatures have increased by 3-5 °C with some of the largest increases occurring along the Alaskan North Slope (Alaska Climate Impact Assessment Commission 2008). Summer warming in arctic Alaska has accelerated from about 0.15 to 0.17 °C per decade (1961-1990 and 1966-1995) to about 0.3 to 0.4 °C per decade (1961-2004; Fig. 1) (SERREZE et al. 2000; CHAPIN et al. 2005a). Alaska and northern Asia, together with the Antarctic Peninsula, have been the most rapidly warming regions of the globe over the past several decades (TURNER et al. 2007). The observed warming in the Arctic in the latter half of the 20th century appears to be without precedent since the early Holocene (MANN & JONES 2003).

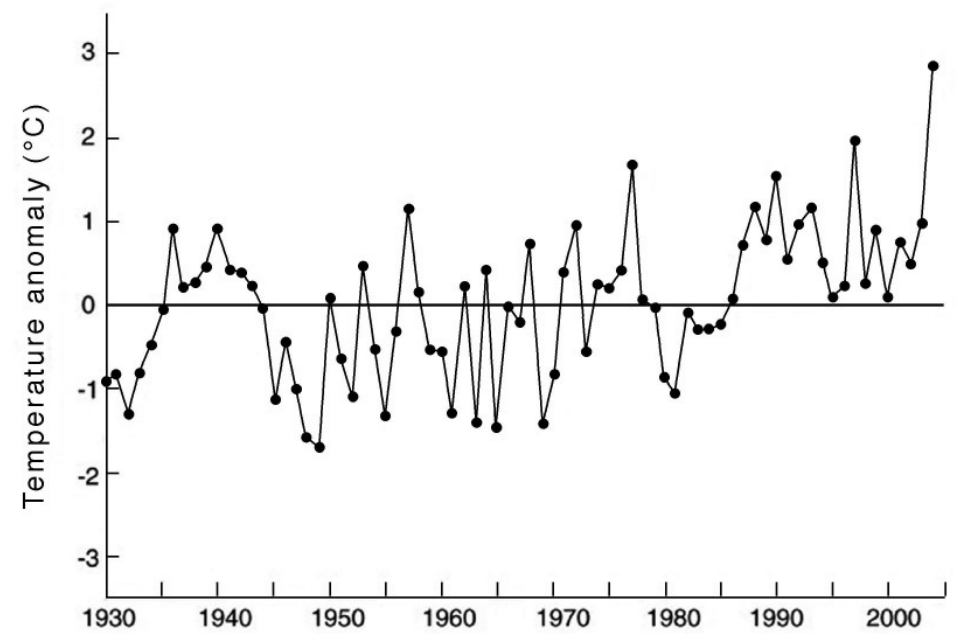


Fig. 1: Air temperature anomaly (deviation from the long-term mean) in Alaska, 1930-2004 (after CHAPIN et al. 2005a)

At the same time, precipitation in the Arctic shows signs of an increase over the past century. However, the trends are small, highly variable in space, and highly uncertain because of deficiencies in the precipitation measurement network. In the past 40 years, precipitation increased by about 2 % per decade (MCBEAN et al. 2005). Increases in precipitation primarily occur during the autumn and winter season (SERREZE et al. 2003) with an additional fraction of liquid precipitation at the cost of the fraction falling as snow (cf. FØRLAND & HANSEN-BAUER 2003). There have been significant positive trends in annual precipitation (up to 20 % increase) over Alaska and in Canada north of 55° N (KARL et al. 1993; MEKIS & HOGG 1999). Average Alaskan precipitation has increased in all seasons. SERREZE & FRANCIS (2006) concluded that a substantial portion of the recent climate change is circulation-driven, and that the Arctic is in the early stages of a manifestation of a human-induced greenhouse signature.

Globally, 2005 was the warmest year on record with a sustained period of warming in the Arctic during 2000-2005. 1998 and 2002-2004 are the next warmest years in the series since 1850 (TRENBERTH et al. 2007). Global warming is currently impacting Alaska and will continue to impact in a number of ways. This paper first reviews the impacts of climate change on physical systems including change in soil moisture, permafrost melt, greenhouse gas exchange between polar landscapes and the atmosphere, sea ice and glacier retreat, increasing discharge of arctic rivers, rising sea level, coastal erosion, and increased storm severity. It also outlines related effects such as infrastructure damage and relocation of villages. Subsequently, it illustrates the response of terrestrial ecosystems to climate and related environmental changes, focussing on vegetation dynamics. Apart from an increase in greenness and biological productivity, considerable changes in species' ranges and abundances and also in the position of treelines in northern Alaska have been observed. Knowing how the structure and function of arctic terrestrial ecosystems are responding to recent climate change is of fundamental importance for the understanding of the future state of the Earth system (HINZMAN et al. 2005). Understanding the system response is also vital in terms of adaptation planning.

Since polar regions act as an important cooling system for the globe by reflecting incoming radiation from ice, snow, and clouds and by transferring the heat transported poleward by the atmosphere and oceans back to space, they play a key role in the global climate system. Climate-driven changes in the terrestrial cryosphere and hydrology such as degrading permafrost and decreasing surface albedo will have cascading effects on key regional bio-physical systems, and cause global climatic feedbacks. At the same time, these changes are affecting socio-economic systems in the north. Arctic human communities are already adapting to climate change, but both external and internal stressors might exceed their adaptive capabilities. Polar regions are thus singled out as areas of special concern: they are extremely vulnerable to current and projected climate change, and have the greatest potential to affect global climate and thus human populations and biodiversity (ANISIMOV et al. 2007).

2 Impacts of climate change on physical systems

Enhanced rates of temperature increase have inevitable consequences for cryospheric processes. Unequivocally, the physical processes of climate-permafrost interactions are affected, and observations of permafrost change are increasing. Precise measurements in boreholes indicate a general increase in arctic permafrost temperatures during the last 50 years (ROMANOVSKY et al. 2002). On the North Slope of Alaska, permafrost temperatures in boreholes rose by 2-4 °C during the last 50-100 years (LACHENBRUCH & MARSHALL 1986), and showed a recently accelerating warming. Borehole temperature data from the Alaskan Arctic Coastal Plain and Alaskan Arctic Foothills indicate permafrost warming by about 3 °C since the late 1980s (CLOW & URBAN 2002). Long-term monitoring of deep wells in a N-S transect across the North Slope from Prudhoe Bay to the Brooks Range (Fig. 2) likewise reveals a clear warming trend over the last 25 years (HINZMAN et al. 2005). Measurements on Barter Island and in the Arctic National Wildlife Refuge (ANWR) confirm the warming trend documented for the central and western Alaskan Arctic. Near Kaktovik (Barter Island) and in the northern ANWR, permafrost warmed 1.5 to 3 °C from 1985 to 2004 (OSTERKAMP & JORGENSEN 2006). Concomitantly, discontinuous permafrost further south is warming and thawing. The magnitude of warming at the discontinuous permafrost surface amounts to 0.5 to 1.5 °C (OSTERKAMP & ROMANOVSKY 1999).

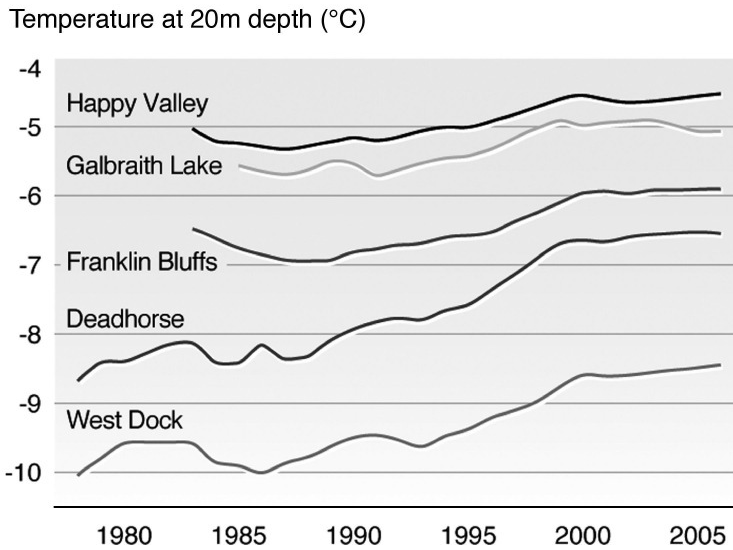


Fig. 2: Temperatures measured at 20 m depth in permafrost boreholes on the North Slope of Alaska display broad-scale warming over recent decades (after <http://maps.grida.no/go/graphic/trends>, updated from OSTERKAMP 2003)

Thawing of ice-rich permafrost results in a marked subsidence of the surface, leading to the development of extensive areas of thermokarst terrain and to dramatic changes in the ecosystem. Thermokarst can occur with warming even in very cold climates such as the North Slope of Alaska, because massive ice is very close to the ground surface.

Extensive thermokarsting and creation of new water-filled surface depressions was recently observed on the coastal plain in northern Alaska (JORGENSEN et al. 2003). However, in regions over thin permafrost, where a talik penetrates the permafrost and connects with subpermafrost groundwater, surface ponds may also shrink and surface soils may become drier as the permafrost degrades (cf. HINZMAN et al. 2005). In interior Alaska, boreal forests on badly drained sites underlain by ice-rich permafrost are currently replaced by wet sedge meadows, bogs, and thermokarst ponds and lakes (JORGENSEN et al. 2001). Thaw subsidence can reach several meters. HINZMAN et al. (2005) point out that much of the discontinuous permafrost in Alaska is both warm and ice-rich, making it highly susceptible to thermal degradation.

The detrimental impact thawing permafrost has on the infrastructure built upon it will greatly affect socio-economic systems. As frozen ground thaws, many existing buildings, roads, pipelines, airports, and industrial facilities are likely to be destabilized, requiring substantial rebuilding, maintenance, and investment. Transportation and industry on land will increasingly be disrupted by the shortening of the periods during which ice roads and tundra are frozen sufficiently to permit travel (INSTANES et al. 2005).

In view of future climate change, a key concern of permafrost thawing is the feedback to the global climate system through potential emission of greenhouse gases. Changes in temperature and thickness of the active layer (seasonally thawed layer overlying permafrost) and associated soil moisture dynamics are critical in this respect since most ecological, hydrological, biogeochemical, and pedogenic processes take place within the active layer. Conclusive evidence of increases in active layer thickness is lacking so far, at least for northern Alaska. However, a marked delay in active layer freezing resulting from relatively milder winters in recent years is currently observed (HINZMAN et al. 2005). The permafrost base has been thawing at a rate ranging up to 0.04 m per year in Alaska since 1992 (LEMKE et al. 2007). It is projected that the depth of seasonal thawing may increase on average by 15-25 % by the middle of the century and by 50 % in the northernmost locations (ANISIMOV & BELOLUTSKAIA 2004; WALSH et al. 2005).

Warming and permafrost thawing potentially alters the carbon balance substantially. The trajectories of soil carbon flux are largely influenced by soil moisture dynamics, in particular by the water table position. HINZMAN et al. (2005) provided evidence that the surface water balance (precipitation minus potential evapotranspiration) significantly declined for both the Alaskan coastal plain (on average 2.0 mm/yr) and interior regions (on average 5.5 mm/yr) between 1960 and 2001. A long-term drying trend in northern Alaska corresponds to observations by local residents. Lowering the water table can markedly increase the CO₂ emission rates from soil. Increased emissions of carbon will likely lead to positive climate forcing (SITCH et al. 2007). Arctic areas that have warmed and dried are generally a carbon source. After having accumulated carbon during most of the Holocene, Alaska became a net carbon source when regional warming began in the 1970s (OECHTEL et al. 1994). As plant- and ecosystem-scale feedbacks increased carbon uptake by plants, the strength of this source declined (OECHTEL et al. 2000). Currently there is a trend toward carbon release in the short term, whereas long-term trends depend on the balance between increased primary production and uncertain trends in respiration (CHAPIN et al. 2005b). Climate warming also enhances methane release from arctic

wetlands since methane efflux responds positively to soil moisture and summer soil temperatures. Thawing of permafrost in peatlands and frozen organic matter accelerates biochemical decomposition. Increasing areas of wetlands and thaw lakes as a result of warming and thawing of permafrost further increases methane efflux, creating another positive feedback to climate change (CHRISTENSEN et al. 2004).

The impacts of permafrost degradation include drainage patterns, surface wetness and hydrological processes in general which are primarily controlled by the presence or absence of permafrost, but also by the thickness of the active layer and the total thickness of the underlying permafrost. Hydrological processes impacted by degrading permafrost in northern Alaska include gradual or catastrophic drainage of lakes, increased winter stream flows, decreased summer peak flows, changes in stream water chemistry, and fluvial geomorphological processes (HINZMAN et al. 2005). Arctic rivers have increased their discharge to the Arctic Ocean over the past decades, primarily due to increases in winter discharge (PETERSON et al. 2002). SHIKLOMANOV et al. (2000) calculated time series of river discharge from individual drainage areas between 1921 and 1999 based on hydrometeorological observations and found positive trends for the Asian and northern American regions (linear trend of $0.7 \text{ km}^3/\text{yr}$ each). Stream monitoring stations in central and northern Alaska show statistically significant trends. Rivers on the North Slope display increasing trends in runoff over the period of record (20-30 years), even when their basins are non-glacierized (HINZMAN et al. 2005). Increasing runoff is a common feature of basins with a substantial glacial component, presumably due to increases in glacier melt. On many rivers the spring discharge pulse is now occurring earlier. Earlier break-up and later freeze-up have combined to lengthen the ice-free season of rivers and lakes by up to three weeks since the early 1900s (WALSH et al. 2005).

The Arctic Ocean is extremely sensitive to changes in discharge because it receives more discharge per unit ocean volume than any other ocean. Continued increase of low-density fresh water input into the Arctic Ocean and finally into the North Atlantic could disrupt the thermohaline circulation and may trigger major climatic shifts in Europe and the North Atlantic Region (cf. CURRY & MAURITZEN 2005; BINDOFF et al. 2007). The total annual river inflow to the Arctic Ocean is expected to increase by approximately 10 to 30 % by the late 21st century (WALSH et al. 2005).

An additional source of future freshwater input will be from melting of circumpolar glaciers, ice caps and ice sheets. Negative mass balances and glacier retreat have been observed throughout Alaska. ARENDT et al. (2002) analysed 67 glaciers in northern, southern and southeastern Alaska and neighbouring Canada and observed increased and accelerating melting. Nearly all of the glaciers displayed increased thinning compared to earlier measurements collected between 1950 and 1995. CALKIN et al. (1998) ascertained a 30 % reduction in length of the Grand Union glacier (Seward Peninsula) between 1950 and 1990. Considerable reductions in glacier volume and length have also been detected for glaciers in the Brooks Range (NOLAN et al. 2005). Extrapolating the average thinning rate (1.8 m/yr) of 28 glaciers between the mid-1990s and 2000-2001 to all glaciers in Alaska results in a volume change equivalent to a sea-level rise of $0.27 \pm 0.1 \text{ mm/yr}$ (WALSH et al. 2005). The rapid wastage of Alaskan glaciers represents about half the estimated loss of mass by glaciers worldwide (MEIER & DYURGEROV 2002), and the

largest glacial contribution to sea-level rise yet deduced from measurements (ARENDT et al. 2002). It is generally agreed that the retreat of glaciers will continue across arctic glaciers with a consequent impact on global sea level.

Impacts of climate warming on cryospheric processes include an apparent reduction in coverage and thickness of sea ice in the Arctic. Sea ice is another highly important variable in an assessment of arctic change since potential effects of changing sea ice cover on climate, ecosystems, and infrastructure are large. Satellite data show a continuation of the 2.7 ± 0.6 % per decade decline in annual mean arctic sea ice extent since 1978 (LEMKE et al. 2007). The rate of decrease is accelerating in recent years, corresponding to a decrease in perennial sea ice of about 9 % per decade (COMISO 2002; CAVALIERI et al. 2003). The extent of Arctic sea ice reached an all time low in September 2007, shattering the previous record in 2005 by 23 %. It was also 39 % below the long-term average from 1979 to 2000 (Alaska Climate Impact Assessment Commission 2008). The impacts of decreasing extent and thickness of sea ice on surface energy and moisture budgets are substantial and are affecting climate at least locally and regionally. A loss of sea ice means an increase in open water and thus greater absorption of solar energy, leading to increased warming in the ocean and accelerating ice loss (albedo-temperature feedback). Greater expanses of open water enhance atmospheric humidity and cloudiness, resulting in an increase in precipitation, and could also strengthen low-pressure systems as they move across the arctic seas (WALSH et al. 2005). Wave generation is affected as well since the wind stress acting directly on the ocean is increasing. Reductions in sea ice extent, a rising sea level and more intense wave generation will increase coastal erosion that currently threatens many coastal villages (CHAPIN et al. 2005b), especially during high wind events. Some villages have already begun relocation plans. Vulnerability to storms is likely to increase in low-lying coastal areas as the ice-free season lengthens. Average wind speeds at the northern Alaskan coast, particularly in winter, the intensity of summer cyclones as well as coastal erosion rates have increased in recent decades (HINZMAN et al. 2005).

Changes in snow cover have generally substantial hydrological implications and influence many other physical and biological processes. The snow-covered area has diminished by nearly 10 % since the early 1970s over both North America and Eurasia so that the total extent of northern hemisphere snow during spring and summer was lower in the 1990s than at any time in the past 100 years (WALSH et al. 2005). The disappearance of snow cover at Barrow, northern Alaskan coast, presents a consistent trend of earlier snowmelt (Fig. 3).

Regression analysis indicates that the snowmelt date has advanced by about 10 days since 1941 (HINZMAN et al. 2005). Earlier melt is consistent with lower total snow accumulation in winter and rising March and April temperatures in recent decades. A decrease in snow cover will considerably reduce the surface albedo, leading to enhanced absorption of solar radiation and warming of the ground – an important positive feedback to climate warming. Rapid warming of frozen soils in spring and later snow accumulation in autumn also results in a longer period of soil microbial activity. Accordingly, carbon emissions increase and may not be fully offset by photosynthetic uptake of plants.

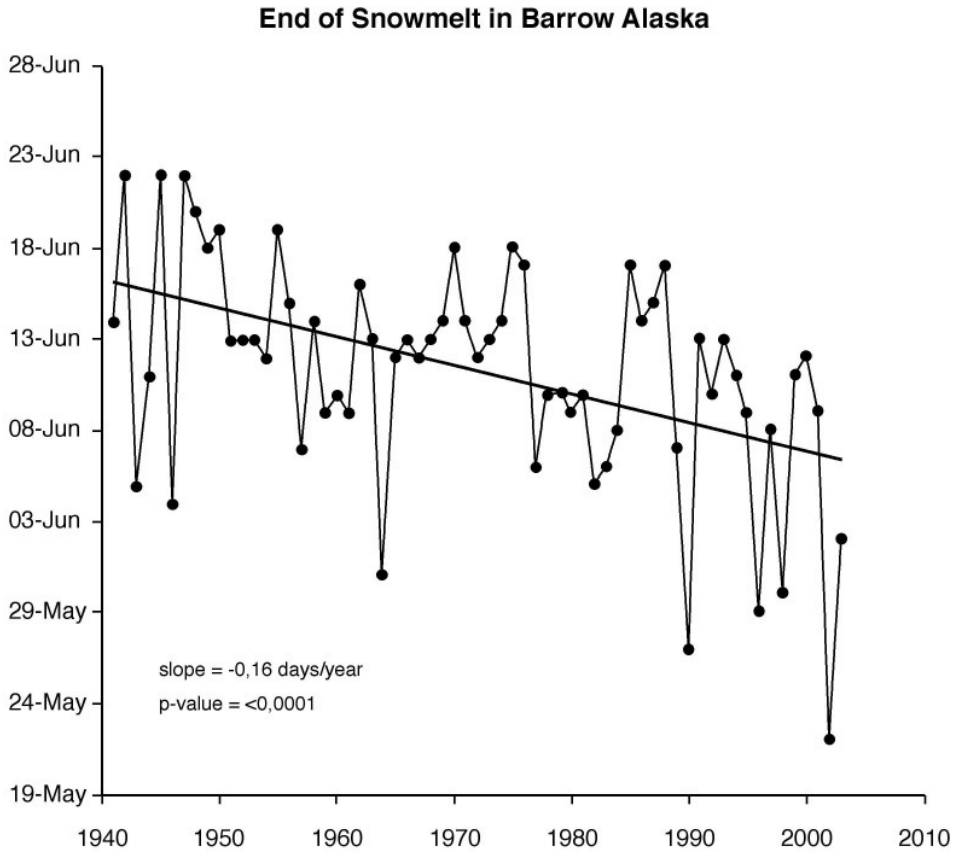


Fig. 3: End of snowmelt in Barrow, Alaska, 1941-2004. The time series was compiled from direct snow depth measurements, proxies estimated from radiometric (albedo) and air temperature measurements (after HINZMAN et al. 2005, updated from STONE et al. 2002)

3 Response of terrestrial ecosystems to climate change

Polar regions are often considered to show particular sensitivity and rapid, visible ecosystem responses to ongoing climate warming and related environmental changes. Current arctic species have characteristics that have enabled them to pass various environmental filters associated with the arctic environment such as freezing tolerance (WALKER, M.D. 1995). However, 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. Thus, arctic species will probably change their distributions rather than evolve significantly in response to warming (CALLAGHAN et al. 2005). Evidence from the past indicates that geographic ranges of terrestrial species in general are well correlated with bioclimatic variables and that arctic

species are extremely vulnerable to climate alterations. It has been predicted that 21st century climate change will dominate the major factors affecting biodiversity in the Arctic (SALA & CHAPIN 2000).

Actually, the substantial changes in many of the drivers that shape polar physical and biological processes are having profound effects on ecosystems, being reflected inter alia in significant vegetation changes. Changes in relative abundances of arctic plant species have been increasingly documented in recent years. In northern Alaska, a considerable increase in the abundance and extent of shrubs in tundra areas has been detected with comparisons between historical and contemporary photographic imagery. Using 202 pairs of old (taken between 1945 and 1953) and new oblique aerial photographs, TAPE et al. (2006) found that alder (*Alnus crispa*), willow (*Salix alaxensis*, *S. pulchra*, *S. glauca*), and birch (*Betula nana*, *B. glandulosa*) have been increasing in size and abundance on the North Slope of Alaska, colonizing areas where previously there were no large shrubs. 87 % of the pairs of photographs analysed showed a detectable increase in shrubs reflected in expanding shrub patch boundaries, in-filling of shrub patches, and growth of individual shrubs. The results confirm previous repeat photography studies (STURM et al. 2001a) as well as indigenous observations across much of the North American Arctic (KRUPNIK & JOLLY 2002). Moreover, TAPE et al. (2006) present plot and remote sensing evidence for shrub expansion also in Canada, Scandinavia, and parts of Russia.

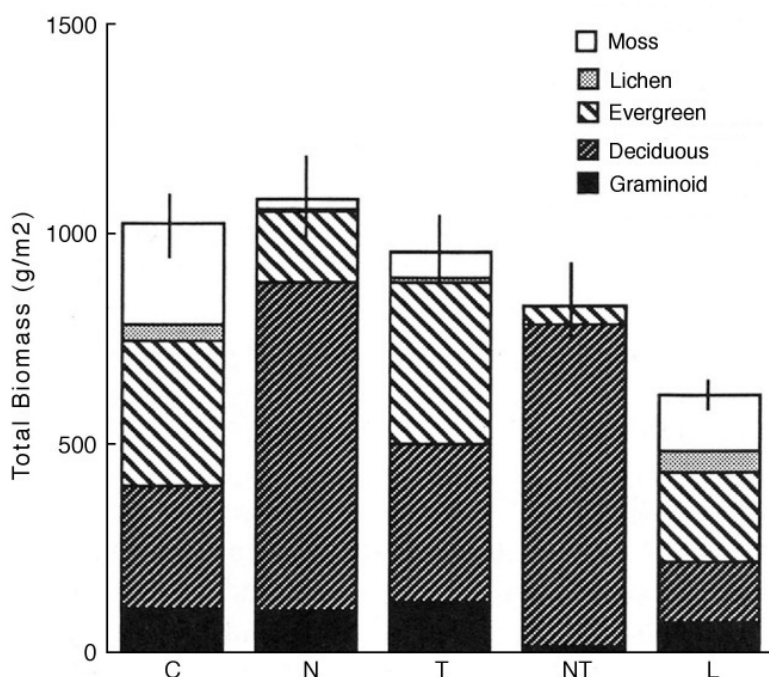


Fig. 4: Total biomass (excluding roots) of plant functional groups in arctic tussock tundra after 9 years of different environmental manipulations: control (C), nutrient addition (N), greenhouse that raised summer air temperature by 3 °C (T), fertilized greenhouse (NT), and shading to reduce light by 50 % (L) (after CHAPIN et al. 1997)

The observed increase in shrub cover in the Alaskan tundra is consistent with anticipated increases in shrub cover due to a warmer climate (STURM et al. 2001b), remote sensing analyses (HOPE et al. 2003; STOW et al. 2004), results of manipulation experiments (CHAPIN et al. 1995, 1997; BRET-HARTE et al. 2001; HOLLISTER 2003; VAN WIJK et al. 2004; WALKER, M.D. et al. 2006), and dynamic vegetation modelling (EPSTEIN et al. 2000, 2004). CHAPIN et al. (1995) manipulated light, temperature, and nutrients in moist tussock tundra in northern Alaska to determine how changes in these parameters might affect community and ecosystem processes (Fig. 4). After 9 years, a strong dominance of deciduous shrubs (mainly *Betula nana*) was associated with a loss of 30-50 % of the species in the nutrient and nutrient-temperature treatments (cf. NT treatment in Fig. 4). Nutrient addition increased biomass and production of deciduous shrubs, but reduced growth of evergreen shrubs and nonvascular plants. Elevated temperature enhanced shrub production too, but reduced production of nonvascular plants. From these results the authors predicted that increased nutrient availability caused indirectly by climate warming should increase the abundance of deciduous shrubs – a shift in dominance which is actually being observed. The large decline in other functional groups points to the sensitivity of tundra ecosystems to climate warming and to potentially profound ecosystem consequences. A recent metaanalysis on plant community measurements from standardized warming experiments (WALKER, M.D. et al. 2006), conducted at 11 locations across the tundra biome and started in the early 1990s, confirms the increasing dominance of deciduous shrubs under experimental and observed climate warming. Warming increased height and cover of deciduous shrubs and graminoids, decreased cover of mosses and lichens, and decreased species richness, diversity and evenness. It is predicted that warming will cause a decline in biodiversity across a wide variety of tundra, at least in the short term. The results of this metaanalysis provide rigorous experimental evidence that recently observed increases in shrub cover are in response to climate warming. A future increase in shrub biomass at the expense of other plant functional types is also suggested by simulations of climate warming using a dynamic tundra vegetation model (EPSTEIN et al. 2000). After 200 simulation years, climate warming associated with increased nitrogen mineralization and growing season length resulted in the formation of novel, stable plant communities with deciduous shrubs as the dominant plant functional type. Using the same model, but focussing on decadal time scales, EPSTEIN et al. (2004) found that the likely changes in tundra plant community composition with warming will be an increase in shrubs and a decline in mosses and lichens. Decreasing lichen biomass and increasing vascular plant biomass following warming was also reported from several other warming experiments (CORNELISSEN et al. 2001). The decline in nonvascular plants (see also HOLLISTER 2003; VAN WIJK et al. 2004) will have profound ecosystem consequences since mosses and lichens are a large component of arctic plant diversity and controllers of ecosystem processes. Mosses insulate the soil and thus strongly influence the soil thermal regime. Lichens are critical to the over-winter nutrition of caribou.

Recent warming in northern Alaska has not only been accompanied by the increase of shrub biomass, but also by a widespread advance of trees into tundra ecosystems. The latitudinal treeline has advanced by 10 km or more, converting about 2 % of tundra to forest in the past 50 years (LLOYD et al. 2003). The density of white spruce (*Picea glauca*) has increased at arctic treelines in NW-Alaska (SUAREZ et al. 1999), range expansions have been also observed in the Brooks Range (COOPER 1986), the White

Mountains and the Alaska Range (LLOYD & FASTIE 2003). The fact that forest age becomes progressively younger when crossing from forest into tundra is a direct evidence for treeline advance. The widespread nature of treeline advance in Alaska strongly suggests that this represents a directional response to regional climate change (HINZMAN et al. 2005). Growth patterns of individual spruce trees at treeline, however, are varied and complex and rarely a linear response to higher temperatures. At certain treeline sites, increased warmth may also induce drought stress and decreased forest productivity (cf. BARBER et al. 2000; LLOYD & FASTIE 2002).

Expansion of shrub tundra and advancing treelines reflect more favourable growth conditions under current warming and the associated lengthening of the growing season. Warming seems to be generally favourable to the growth, development, and reproduction of most arctic plant species, particularly those with high phenotypic plasticity, although other limiting factors such as nutrients and soil moisture may modify plant responses to warming (CALLAGHAN et al. 2005). Analyses of the northern hemisphere NDVI (normalized difference vegetation index; index of vegetation greenness) over the last two decades correspond to expanding growing seasons, increasing primary productivity and aboveground biomass (MYNENI et al. 1997). The increased greenness was associated with an increase in growing-season length of between 3.8 and 4.3 days for the circumpolar area, mainly due to an earlier start of the growing season. SHABANOV et al. (2002) observed similar increases in the onset and length of the growing season in high northern latitudes between 1981 and 1994 using NDVI values and attributed these increases to winter and annual warming of near-surface temperature. In arctic Alaska, JIA et al. (2003) confirmed a long-term trend of increase in vegetation greenness and determined a NDVI increase by 16.9 % since 1981, corresponding approximately to a 171 g/m² increase in aboveground plant biomass for Alaskan tundra between 1981 and 2001. The analysis of changes for four specific vegetation types yielded the result that the temporal changes in peak and time-integrated greenness were greatest in areas of moist nonacidic tundra (Fig. 5). Likewise, an increasing NDVI trend in the 1990s for the Kuparuk river watershed and the entire North Slope of Alaska was reported by STOW et al. (2003) and HOPE et al. (2003).

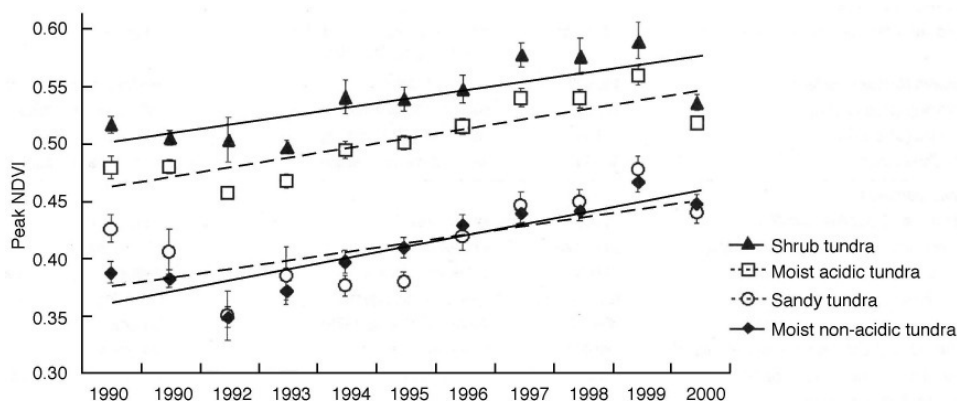


Fig. 5: Trend in Normalized Difference Vegetation Index in Alaskan Arctic Tundra, 1990-2000 (after JIA et al. 2003)

As evident from palaeoecological studies, the dominant response of arctic species to climate change is very likely to be relocation rather than adaptation (CALLAGHAN et al. 2005). At the landscape scale, changes in species abundances and distributions will probably result in forests replacing a significant proportion of the tundra, and in expansions of shrub tundra into regions now occupied by sedge tundra or polar desert. The treeline is projected to move north in all sectors of the Arctic (KAPLAN et al. 2003). According to the Lund-Potsdam-Jena (LPJ) dynamic global vegetation model (SITCH et al. 2003) the increase in taiga area in northern Alaska and neighbouring regions will amount to about 12 % until 2080 (CALLAGHAN et al. 2005). Extensive changes in land cover may significantly alter regional water and energy balances and feedback to the climate system. Decreased albedo due to changes in vegetation, the extension of snow-free and ice-free periods on terrestrial and lake surfaces, and reduction in the area occupied by glaciers and continental ice sheets in high latitudes may act as a positive feedback to radiative forcing and enhance atmospheric warming (HINZMAN et al. 2005). Warming and drying of tundra soils in parts of Alaska have already changed the carbon status of these areas from sink to source (see above), providing an additional positive feedback to warming.

At the plant community scale, a biome shift from tundra to forest or from sedge tundra to shrub tundra will have a great effect on the composition of species. In addition, species compositions of plant communities will be greatly influenced by changing abiotic site conditions under climate warming. As established for riparian willow communities (SCHICKHOFF et al. 2002) and for tussock tundra communities (M.D. WALKER et al. 1994; WALKER, D.A. & M.D. WALKER 1996), edaphic conditions (esp. soil moisture, soil pH) and factors pertaining to topography, disturbance regime and landscape evolution largely control spatial patterns and floristic compositions of vegetation units. Soil moisture appears to be a key abiotic variable for the differentiation of plant communities. Decreases in soil water availability as observed for the Alaskan arctic tundra during past decades (see above) will have inevitable consequences for the species composition of communities and will result in novel species assemblages. The same holds true for increases in soil water availability, e.g. at thermokarst sites. SCHUUR et al. (2007) analysed thermokarst sites in the Alaskan tundra and ascertained a change in plant species composition from graminoid-dominated to shrub-dominated tundra along a gradient of ground subsidence. Changes in dominant plant communities in the Alaskan Arctic during the Late Glacial period and Holocene are believed to have been caused to a great extent by changes in soil moisture (MANN et al. 2002). Changes in other site factors under climate warming such as nutrient supply will also have far-reaching consequences for species compositions as can be deduced from experimental manipulations (e.g., VAN WIJK et al. 2004). The shifts in dominances of plant functional types described above indicate that species abundances and floristic compositions of plant communities have already changed in response to climate and environmental alterations. Moreover, recent climate warming has facilitated the invasion of exotic plant species into polar regions (FRENOT et al. 2005). In the Arctic, maritime regions and inland areas with road and rail connection are already affected (CHAPIN et al. 2005b).

A change in species composition of communities is synonymous with a change in ecosystem structure and function. E.g., species-specific growth rates, reproduction and dispersal rate potential affect ecosystem process rates in response to environmental

change. An increase in trees and shrubs will affect ecosystem structure and function because of their potential to dominate the canopy and reduce light availability to understory species and to reduce overall litter quality and rates of nutrient cycling (CALLAGHAN et al. 2005). Changes in species composition will affect nutrient availability, element accumulations and carbon cycling since species show specific differences in the turnover of elements in their living tissues, biomass element concentrations and in the decomposability of their dead parts (SHAVER et al. 2000). Species also affect element cycles through specific effects on soil temperature regimes, surface energy balance or snow accumulation and snowmelt, and through specific physiological mechanisms that influence trace-gas exchange between soils and the atmosphere (e.g., JOABSSON & CHRISTENSEN 2001). Species richness or diversity itself impacts biogeochemistry of arctic ecosystems as well. A weak positive correlation between productivity and vascular species richness, attributed to more complementary and increasing total uptake of different nutrients, was found in most studies (e.g., GOUGH et al. 2000; MCKANE et al. 2002).

Evidence for animal responses to climate change is increasing, albeit largely pertaining to conspicuous vertebrates such as caribou/reindeer and lemmings. Climate-related changes are likely to cause cascading impacts on plants and animals, e.g., displacing species and disrupting important food chains. Climate change will alter the access to food sources, breeding grounds, and historic migration routes for arctic terrestrial animals. E.g., ice-crust formation on the tundra as a result of freeze-thaw events during winter makes vegetation inaccessible to herbivores and may severely limit forage availability for large ungulates such as caribou (*Rangifer tarandus*) and muskox (*Ovibos moschatus*) (KLEIN 1999). Caribou numbers have been reported to decrease in years when there are many freeze-thaw cycles (THORPE et al. 2001), that are likely to increase with more short-term fluctuations in temperature. Winter survival rates of small mammals such as tundra voles (*Microtus oeconomus*) are likewise considerably affected by the frequency of freeze-thaw cycles (AARS & IMS 2002). Moreover, ice-crust formation creates unfavourable conditions for animals living under the snow, and affects invertebrates such as soil-dwelling springtails (Collembola) by inducing conditions of anoxia. Many invertebrates such as insects respond positively to higher temperatures in terms of population growth and are likely to expand their ranges northward under continued climate warming (CALLAGHAN et al. 2005).

In general, species ranges of animals are projected to shift northward on both land and sea, bringing new species into the Arctic while limiting some species currently present. E.g., possibly in response to changes in climate or prey abundances, the red fox (*Vulpes vulpes*) has already expanded into the Arctic, probably at the expense of the Arctic fox (*Alopex lagopus*) (HERSTEINSSON & MACDONALD 1992). Moose (*Alces alces*) have expanded from the boreal forest to the arctic tundra in Alaska and Canada, exemplifying that the observed expansion of tundra shrubs favours the range expansion of herbivores with wide dietary flexibility (CHAPIN et al. 2005b). On the other hand, the increases in arctic plant biomass, height, and density pose a threat to arctic wetland birds. Arctic birds, especially arctic-breeding water birds and waders, show mostly declining populations, possibly due to eutrophication and habitat loss on wintering and staging sites and concurrent climate change (CALLAGHAN et al. 2005). Some seabirds as well as some marine mammals such as polar bears (*Ursus maritimus*) and ice-inhabiting seals

are negatively affected through the reductions in sea ice and drastically shrinking marine habitats. Regional warming is believed to have contributed to recent northward range extensions of anadromous fish such as salmon (*Oncorhynchus* spp., *Salmo* spp.) (BABALUK et al. 2000).

4 Concluding remarks

Northern Alaska and other arctic regions have experienced accelerating climate change in the past decades, resulting in major ecological impacts. In addition to the impacts of climate change that are amplified in arctic regions, human activities have simultaneously been causing many other stresses affecting ecosystems and biota in the Arctic, including air and water contamination, overfishing, increasing levels of UV-B radiation due to ozone depletion, habitat alteration and pollution due to oil, gas and other resource extraction, and increasing pressure on land and resources related to the growing human population. The sum of these impacts that are largely caused from outside arctic regions threatens to exceed the adaptive capacity of some arctic plant and animal populations and ecosystems. The induced changes in the Arctic, however, will reverberate back to the global community. Changes taking place in the Arctic provide to the society a preview of changes that may be expected in lower latitudes in future. Detailed information on arctic climate change and its impacts have to be disseminated in order to raise awareness among a broader public and get it involved in working toward a sustainable future.

5 References

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Address of the author

Prof. Dr. Udo Schickhoff
Institute of Geography
University of Hamburg
Bundesstr. 55
20146 Hamburg, Germany

e-mail: schickhoff@geowiss.uni-hamburg.de

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