

Global warming and the Arctic: a new world beyond the reach of the Grinnellian niche?

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Summary

The levels of CO₂ in the atmosphere have already far exceeded values attained at any other time over at least the past 650,000 years. Temperature increases due to rising greenhouse gases will be amplified in Arctic and subarctic regions, and winter warming will be enhanced relative to summer warming. Climate in large areas of high latitudes may have no analogue in current climates or those of the recent geological past. Experimental field manipulations and laboratory studies indicate that plants will exhibit complex responses in photosynthesis, growth rates, phenology and reproductive functioning due to this combination of increasing temperatures, changing seasonality and increasing levels of CO₂. The resulting changes in the abundance, distribution, growth rates and production of fruit and phenology of plant species will in turn impact animal populations. In predicting what the future biota of the 'New Arctic' will be like and developing appropriate conservation strategies, Grinnellian niche-based approaches are likely to be insufficient, and experimental ecological studies of organism response to specific anticipated changes in climate are crucial.

Key words: climate change, Arctic, subarctic, experimental plant ecology, Grinnellian niche.

Introduction

The impact of climate warming on the Arctic and adjacent subarctic regions has been the focus of much interest for several important reasons. The high latitudes of the northern hemisphere will probably warm more quickly and to a greater extent than other areas of the globe (Callaghan et al., 2005; IPCC, 2007a; IPCC, 2007b; IPCC, 2007c). This effect has been referred to as Arctic amplification. Global temperature trends from 1958 to 2008 show this pattern of Arctic amplification very well, with particularly enhanced warming over northern Asia and northwestern North America (Fig. 1). In turn, some of the environmental changes caused by the warming of the Arctic could produce positive feedbacks that will enhance global warming (Foley et al., 2003). For example, the albedo of boreal forest cover can be 25–50% lower than that of tundra (Bonan et al., 1995). The differences in albedo coupled with increased surface roughness mean that the boreal forest has a higher sensible heat flux than tundra regions. During the summer, the long-wave flux in the interior boreal forest of Eurasia averages around 10 W m⁻² higher than the tundra to the north (MacDonald et al., 2007). A significant replacement of Arctic tundra by forest would serve to significantly lower the planetary albedo and increase overall warming of the Earth.

Due to the phenomena of Arctic amplification, the Arctic can be considered a climatological 'canary in the coal mine' in terms of global warming. The case can also be made that the Arctic serves as a canary in the coal mine in terms of detecting ecological impacts of climate warming. The terrestrial environments of the Arctic and subarctic have low biodiversity, a simple and open vegetation structure, species distribution and trophic structures that are relatively easy to trace, and species that display a wide variety of morphological, physiological and behavioral adaptations to cold temperatures, and the pronounced seasonal shifts typical of high

latitude climates. Although the straightforwardness of Arctic communities can be overstated (Post et al., 2009), the relative simplicity of Arctic terrestrial ecosystems and their location in a region of amplified warming could aid in the early detection of changes in the biota related to global warming. Appreciable changes in Arctic terrestrial environments and biota may already be occurring in response to recent climate warming (Hinzman et al., 2005; Post et al., 2009). Some examples of such changes include increased radial growth and recruitment of conifers during the 20th century at many sites along the northern treeline (Hinzman et al., 2005; MacDonald et al., 2007), northward expansion of shrubs onto previously herb- and graminoid-dominated tundra in Alaska and the general pan-Arctic region (Hinzman et al., 2005; Tape et al., 2006), and declining populations of Arctic mammal species such as caribou (*Rangifer tarandus* L.) in several regions (Post and Forchhammer, 2008; Post et al., 2009).

In view of the amplified warming of the Arctic and possible biological changes already underway many outstanding questions revolve around what species will make up the Arctic flora and fauna in the future. In anticipating the eventual impacts of long-term climate warming on the geographical distribution of Arctic species, the easiest approach is to use the construct of the Grinnellian niche (Grinnell, 1917; Soberón, 2007) as a basis for extrapolating future conditions. In this approach the geographical distribution of a species is compared with the geographical distribution of climatic variables, such as mean July temperature and total annual precipitation, and a climatic envelope that corresponds with the distribution of the species in climatic space is determined or a linear model that relates selected climate variables to the presence, absence or abundance of the species is constructed. To estimate the future geographical distribution of a species the projected future distribution of the species' climatic envelope is mapped out or the derived model

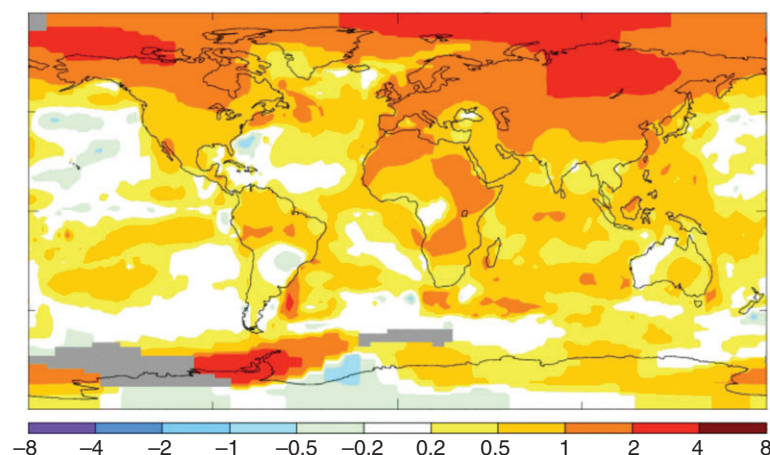


Fig. 1. Arctic amplification of recent temperature trends as captured by a map of the change in annual surface temperature from 1958 to 2008 (data and mapping algorithm from NASA Goddard Institute for Space Studies).

relating the species abundance to selected climate variables is applied. This then forms the basis for inferring the future distribution of the species. This approach can be applied to individual species, or at a meta-level, to plant functional types, biomes or overall biodiversity. One such projection comes from the IPCC Fourth Assessment Report (Anisimov et al., 2007). Here a northward extension of the boreal forest biome is projected across large areas of the Arctic by 2100 (Fig. 2). In a number of areas the expanded forest and woodland will extend to the Arctic coastline and the continental tundra biome will be completely replaced. A displacement of the forest–tundra ecotone of this magnitude would impact not just Arctic vegetation and planetary albedo but also habitat conditions for a variety of sedentary and migratory animals. Such projections of northern forest expansion have led Fischlin et al. to declare that by 2100 there would be a 50% increase of existing tundra and similar scale declines in breeding habitat for various bird species (Fischlin et al., 2007).

However, a number of studies suggest that species' responses to projected climate change are likely to incorporate far more physiological, phenological, behavioral and synecological complexity than is captured by a simple Grinnellian niche approach. In addition, it is very likely that the climatic conditions expected for the Arctic in the near future will have no analogue in the past several million years – which will mean that these conditions will represent new challenges in terms of evolution and adaptation for Arctic species. A simple Grinnellian niche approach for predicting future species distributions is based on interpolation from an assumed static species–climate relationship. Such an approach may mislead us on the impacts of climatic conditions, which have no current analogue or do not incorporate the synecological impacts of interspecific differences in responses to unprecedented climate states. Finally, levels of CO₂ in the atmosphere that are unprecedented over the span of most current Arctic plant species may redefine niche breath on some climatic axes. There is an urgent need for more hard data on the full range of morphological, physiological and phenological responses that may occur in the face of specific anticipated changes in climatic variables. It is important to know how species, which currently co-exist, may display differential responses to such climatic changes. Because the developing climates may have no current counterpart, much of the required data will need to come from detailed experimental manipulation studies in the lab and field. In terms of warming, Arctic species and ecosystems can often be experimentally manipulated in a relatively straight-forward manner through the use of passive- and active-heating techniques. Indeed, under the auspices of the International Tundra Experiment (ITEX) such studies have a

long history of coordinated pan-Arctic effort (Arft et al., 1999). Experimental manipulations in addition to direct observational studies of Arctic ecosystems, which are now experiencing some of the greatest magnitudes of climate warming, can provide insights into the variety of morphological, physiological and phenological responses to increasing temperatures in the Arctic. Some of these insights will also certainly be applicable to more complex systems elsewhere.

In the following sections I outline the uniqueness of the projected Arctic climate compared with today and the Arctic climates of the recent past. I will then look at some recent experimental manipulation studies of important Arctic–subarctic plants that illustrate the broad range and complexity of morphological, physiological and phenological responses that will occur and, in some cases, even alter long-standing fundamental niches relative to climatic axes.

A new world – uniqueness of the future Arctic climate

One of the challenges in anticipating and managing the impacts of future climate warming is the fact that climate regimes will develop over this century that have no analogue today or in the recent geological past. It is also likely that some existing climatic regimes will disappear altogether. Saxon et al. calculated that by 2100 about 53% of the United States of America (including Alaska) could experience climatic conditions that have no modern counterpart today, even with significant reductions in greenhouse gas emissions over this century, while 63.1% of the United States of America will have non-analogue climatic conditions if moderate increases in emissions occur (Saxon et al., 2005).

Climate change is a normal part of the Earth's environment. If we go back into the recent geological past can we find analogues for projected Arctic climate? Over the past million years – the period spanning the existence of most extant species of plants and animals in the Arctic – there have been extended periods (millennia) when the climate at high latitudes has warmed or cooled relative to the 20th century. In addition, there have been large shifts in the global atmospheric concentrations of greenhouse gases such as CO₂ and CH₄. Some of the best long-term records of such variations actually come from the Arctic and Antarctic. The sources of these climatic and atmospheric histories are the chemical records from ice cores. Taken together these records show that over the recent geological past Arctic and Antarctic temperatures have varied significantly. The variation in annual mean temperature has been around 8°C in Antarctica and on the scale of 20°C in Greenland between the ice-age conditions of glacial periods and warm interglacial periods such as we have experienced over the past 12,000 years of the Holocene epoch (Alley,

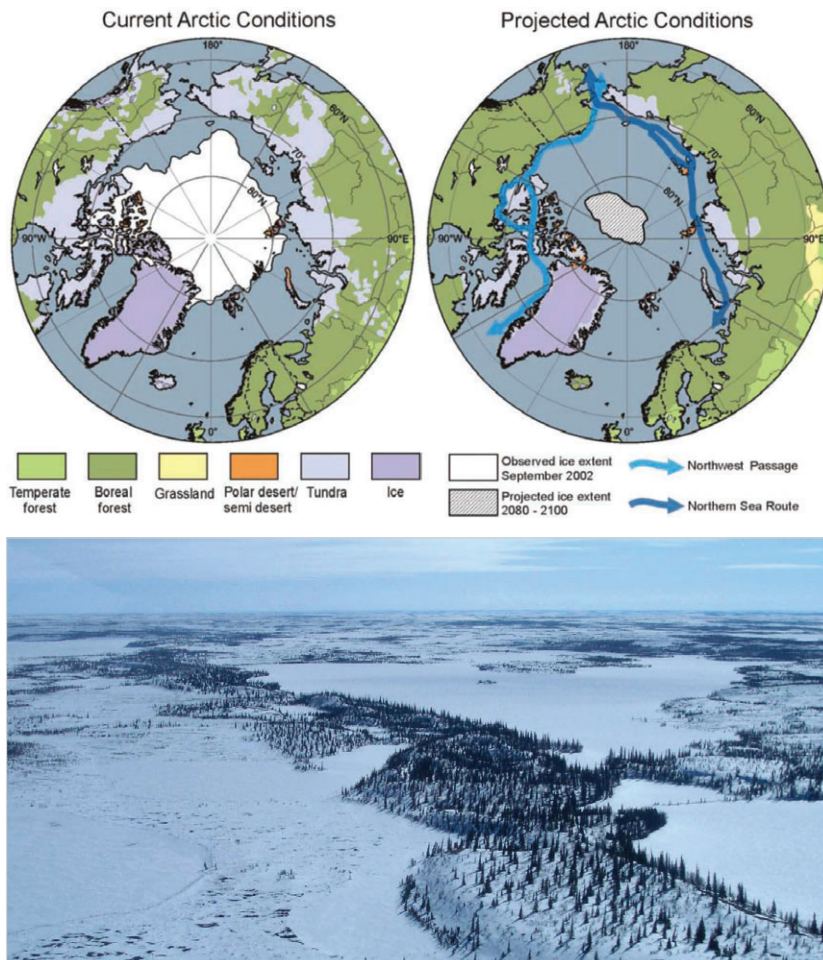


Fig. 2. Treeline expansion from present conditions to those anticipated at 2100 by the IPCC Fourth Assessment Report [map from Anisimov et al. (Anisimov et al., 2007) – courtesy of the IPCC; picture courtesy G. M. MacDonald].

2000; Kawamura et al., 2007). The amount of CO_2 in the atmosphere has varied by about 100 p.p.m. (parts per million) by volume, decreasing during glacial periods and increasing during interglacials (Petit et al., 1999; Lüthi et al., 2008). The temperature shifts between glacial and interglacial periods that have typified the Earth's climate over the past two million years are driven by natural cyclical changes in the Earth's orbit. Warm interglacials like the Holocene occur during periods when orbital factors produce higher amounts of insolation in the high northern latitudes during summer. During these times winter insolation in the northern hemisphere is lower (Berger and Loutre, 1991; Huybers, 2006). During the last major interglacial period, about 130,000 years ago, summer insolation was at a peak in the Arctic and the region experienced summer temperatures that were actually some 4–5°C warmer than Holocene temperatures (Cape Last Integrated Project Members, 2006). Earlier in the Holocene summer insolation was higher than present and between 12,000 and about 3000 years ago, and many parts of the Arctic experienced summer temperatures that were on average slightly higher (~1–3°C) than the past 3000 years (Kaufman et al., 2004).

Although the Arctic has experienced relatively warm periods in the recent geological past, these climates do not provide a true analogue for projected conditions. First past warm periods in the Arctic have been associated with increased summer insolation and increased summer temperatures. Winter insolation has been lower during recent previous warm periods. Projections for future climate warming due to increasing greenhouse gases suggest a different seasonal pattern of warming. It is projected that winter temperatures will increase much more markedly than summer temperatures in

the Arctic over the 21st century (Fig. 3). By the end of this century winter [December–January–February (DJF)] temperatures in the Arctic may increase by over 7°C, while summer temperatures [June–July–August (JJA)] may only increase by 2–4°C (IPCC, 2007b). The seasonal pattern of warming is completely the reverse of warming during earlier warm periods in the Arctic when temperatures were enhanced in the summer relative to the winter. For example, climate model results (Renssen et al., 2005) suggest that during the warmer early to mid-Holocene period, some 9000 years ago, it is likely that summer temperature increases over the land were equal to or greater than winter increases, particularly southward from the Arctic coastline and into the subarctic (Fig. 3). Second, the magnitude of winter and annual warming will exceed known natural warming of the Holocene over large parts of the Arctic and subarctic (Fig. 3) or previous interglacials. So, in terms of the seasonal pattern of warming and the magnitude of annual and winter warming, the conditions projected for the Arctic by the end of this century will probably have no analogue over the past 12,000 years to two million years.

Although levels of atmospheric CO_2 have shifted by values of 100 p.p.m. in the recent geological past, at no time over the past 650,000 years (the period for which we have good ice-core records) have levels exceeded ~280–300 p.p.m. by volume (Petit et al., 1999; Lüthi et al., 2008). At present we are experiencing a concentration of 390 p.p.m., and we may witness concentrations of between 500 p.p.m. and 900 p.p.m. by the end of the century (IPCC, 2007a). The current values of CO_2 in the atmosphere exceed anything experienced over at least the past 650,000 years. At 2100 we may

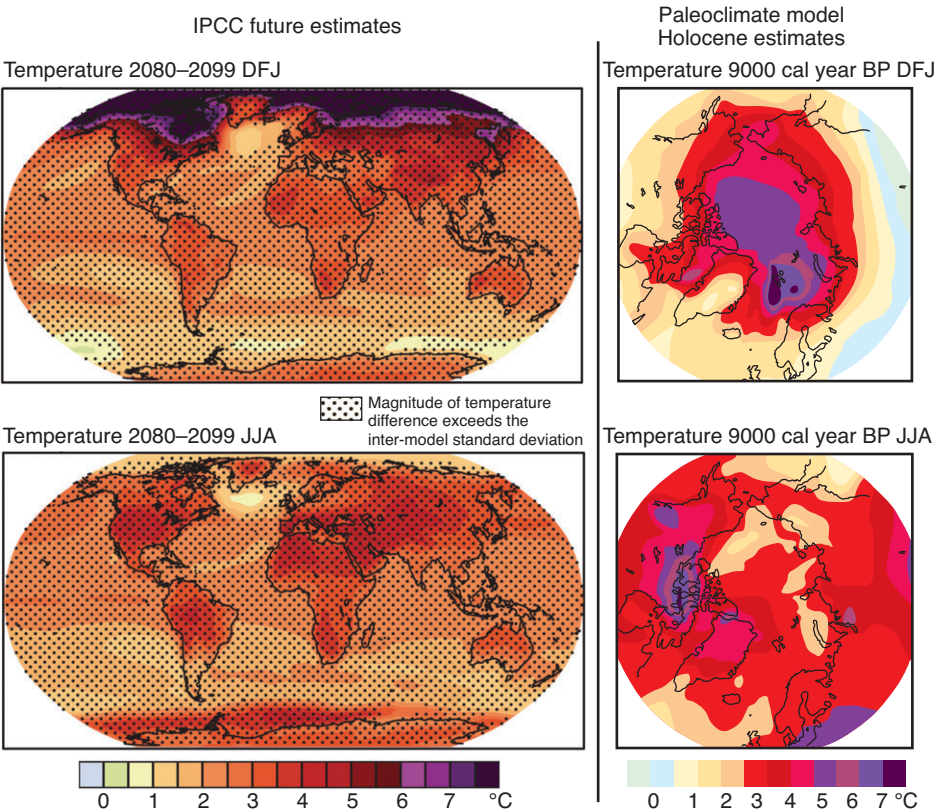


Fig. 3. Projected temperature changes in winter [December–January–February (DJF)] versus summer [June–July–August (JJA)] from the IPCC Fourth Assessment Report [(IPCC, 2007b) – courtesy of the IPCC] and paleoclimate model estimates of winter (DJF) and summer (JJA) temperature departures from 20th century conditions at 9000 calendar years before 1950 AD [redrawn from results of Renssen et al. (Renssen et al., 2005)]. BP is years before present (with present being AD 1950).

experience concentrations that are double to triple the highest natural levels experienced in the recent geological past. This non-analogue situation in terms of CO₂ concentrations is not only a driver of climate change but could have important direct consequences for the physiological functioning of Arctic plants through its impact on photosynthesis and water-use efficiencies.

In terms of climate and the composition of the atmosphere, the Arctic of 2100 will be a new world for the plant and animal species of the region.

Experimental insights on plant responses to the new Arctic climate

The increasing temperatures in the Arctic, the pronounced warming of the winter relative to the summer and the increasing levels of atmospheric CO₂ can all produce responses in Arctic plant species, which in turn will affect animal populations. The results of some

recent experimental manipulation studies of the response of Arctic plants to climate warming and elevated CO₂ illustrate the complexity of such responses – and the usefulness of such experimental manipulations for anticipating the future.

White spruce [*Picea glauca* (Moench) Voss] and black spruce [*Picea mariana* (P. Mill.) B.S.P.] are common at the northern treeline across North America. They are the most northerly distributed coniferous tree species of the North American boreal biome and their northern ranges basically determine the ultimate location of the boreal forest–tundra ecotone. This ecotone can extend over tens to hundreds of kilometers between closed-crown boreal forest to the south and totally treeless tundra to the north. The location of the treeline zone generally corresponds with the geographical area between the 12.5°C and 10°C July mean temperature isotherms. Many studies have examined the climatic controls on treeline (e.g. Black and Bliss, 1980; Stevens and Fox, 1991; James et al., 1994;

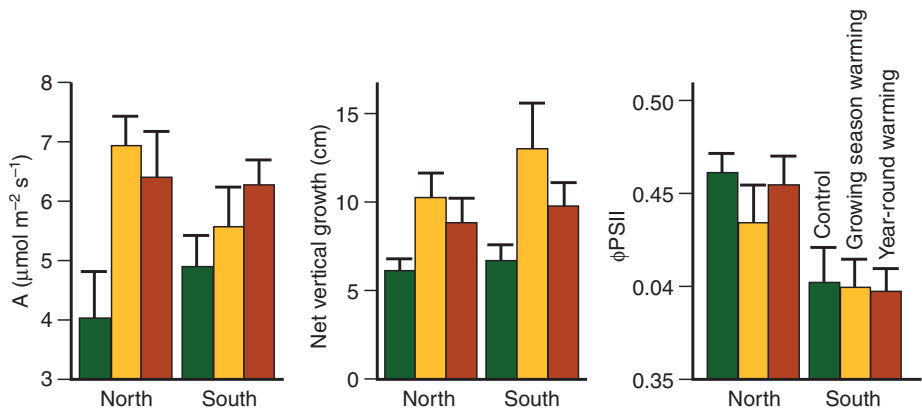


Fig. 4. Impact of open growth chamber experimental field manipulation that produced passive warming of treeline spruce seedlings (*Picea glauca*) at treeline in the Yukon Territory of Canada [redrawn from data from data from Danby and Hik (Danby and Hik, 2007)]. Seedlings were located on either north- or south-aspect slopes at the subalpine treeline. Responses shown are net photosynthesis [A ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)], vertical growth (cm) and Photosystem-II (ΦPSII).

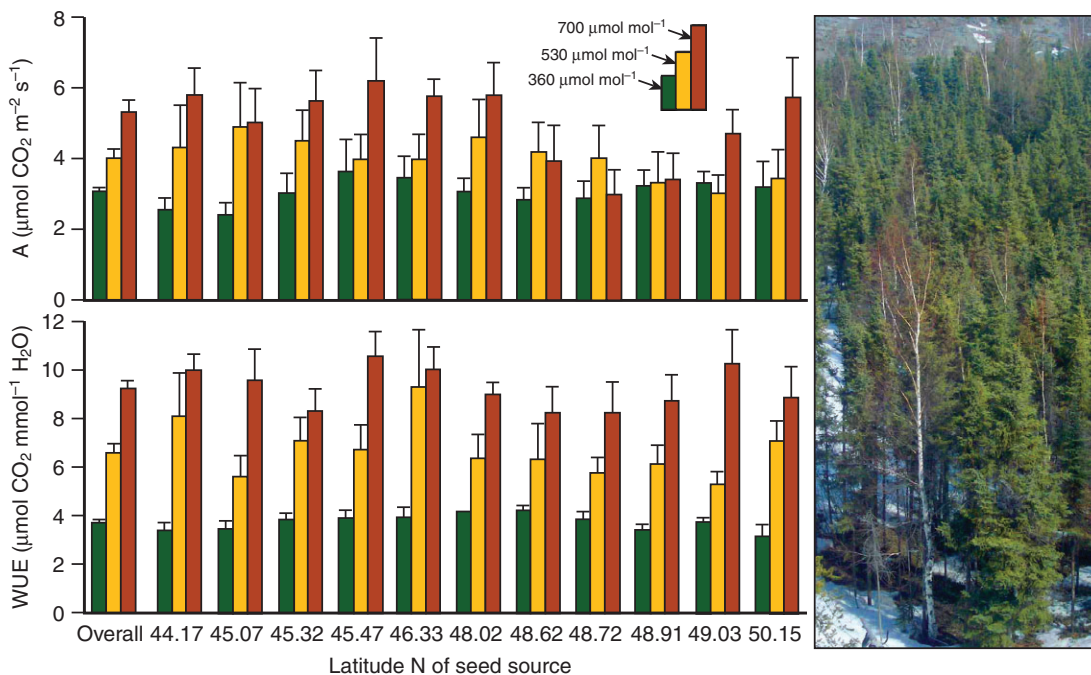


Fig. 5. Response of spruce (*Picea glauca*) to ambient ($360 \mu\text{mol mol}^{-1}$) and elevated levels of CO_2 in greenhouse experimental manipulations [redrawn from results from Dang et al. (Dang et al., 2008); photo courtesy of G. M. MacDonald]. Responses shown are net photosynthesis [A ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)] and water-use efficiency (WUE) ($\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$).

Körner, 1998; Sveinbjörnsson, 2000; Grace et al., 2002). The results of such studies support a general contention that northward limits of trees are dictated by summer air and soil temperatures that are too cold and a growing season that is too short for trees to conduct adequate photosynthesis and utilize glucose to meet growth and reproductive requirements. Rates of northern conifer photosynthesis and respiration decline sharply between 20°C and 5°C . In addition to energetics, the lower threshold for conifer tissue growth lies at temperatures between 3°C and 10°C , and prolonged temperatures of greater than 6°C are generally required for bud formation. Lower cardinal germination temperatures of 15°C have been identified as an important determinant of germination timing and success in some treeline conifers. Inadequate warming of soils in the growing season decrease nitrogen uptake and can further limit growth.

How will spruce trees and thus the forest–tundra ecotone respond to projected warming and increasing levels of CO_2 ? Danby and Hik conducted recent experimental manipulations of summer and annual temperatures for individual white spruce seedlings growing at the subalpine treeline in the Yukon Territory of Canada using open-top chambers (Danby and Hik, 2007). The results of their study provide an example of the species' physiological and morphological responses to warming temperatures. The chambers produced increased growing season air temperatures of approximately 1.8°C on a north-facing site and 1.0°C on a south-facing site. All seedlings in the chambers experienced higher photosynthetic gains and rates of vertical growth than control seedlings, although this impact was stronger for trees on the north-aspect site (Fig. 4). These results suggest a robust and anticipated positive response to warming, which would accelerate and accentuate the northward movement of the treeline. However, the seedlings in the open-top chambers also displayed Photosystem-II efficiencies that were either equal to or less than control seedlings. Furthermore, radial growth as measured by tree-rings was observed to decrease during the warmest years in some of the seedlings growing in the open-top chamber relative to the control seedlings. Increased moisture stress as a result of high temperatures may be a factor limiting both Photosystem-II efficiencies and radial growth (Danby and Hik, 2007). Interestingly,

seedlings on the south-aspect site also had increased needle mortality over the winter, which may be related to increased desiccation. In recent decades adult trees in some treeline white spruce stands in the Yukon appear to be experiencing decreased rates of radial growth that may be attributable to growing moisture stress as temperatures have increased (D'Arrigo et al., 2004). This unexpected shift of radial growth rates in adult trees in the northern boreal forest away from sensitivity to low temperatures towards greater sensitivity to moisture stress has been observed by tree-ring studies at other sites in North America and Eurasia. In addition to its impact in terms of decreasing adult growth rates, increasing moisture stress due to higher temperatures may be important through its impact on reproductive success. Field and experimental studies of black spruce moisture relationships have shown moisture stress and subsequent seedling mortality to be a critical factor in limiting reproductive success at treeline (Black and Bliss, 1980). How significantly increasing moisture sensitivity might depress rates of northern forest extension remains uncertain but these results suggest that a shift to great moisture sensitivity may attenuate the response of spruce to warming in some regions.

A further complication in anticipating the rates and magnitudes of treeline response to climate warming, particularly in terms of growth rates and moisture relationships, is the direct impact of increasing levels of atmospheric CO_2 . Experimental manipulations in greenhouses (Dang et al., 2008) show that increased CO_2 fertilization from $360 \mu\text{mol mol}^{-1}$ (close to ambient atmospheric concentration) to $530 \mu\text{mol mol}^{-1}$ and $700 \mu\text{mol mol}^{-1}$ produced increased rates of water-use efficiencies for white spruce seedlings from a wide geographical range of provenances in Ontario, Canada (Fig. 5). The impact of CO_2 fertilization on growth and photosynthetic gain was more variable depending upon seed provenance but rates at $530 \mu\text{mol mol}^{-1}$ and $700 \mu\text{mol mol}^{-1}$ were typically equal to or higher than rates at $360 \mu\text{mol mol}^{-1}$ (Fig. 5). The ubiquitous response of increasing water-use efficiency as levels of CO_2 increased, coupled with the positive influence on growth rates, suggests that the higher levels of this atmospheric gas projected for the future may serve to not only increase rates of spruce

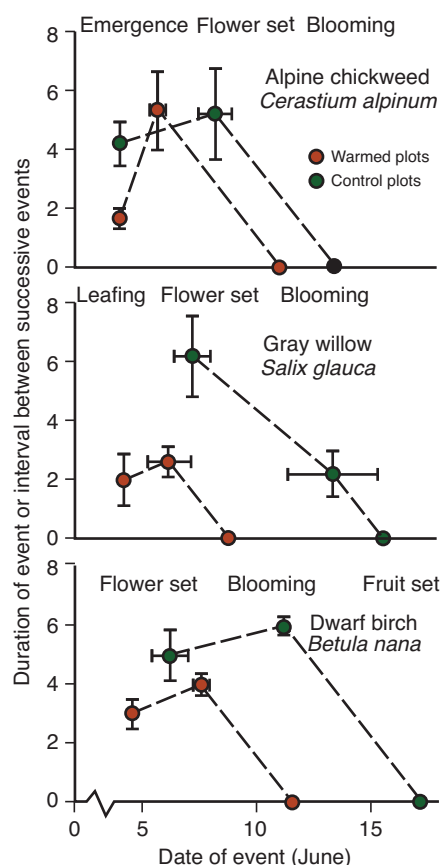


Fig. 6. Phenological impact of experimental surface heating (MJ) of a tundra herb and two shrubs in West Greenland using open-top chambers [redrawn from results from Post et al. (Post et al., 2008); photo courtesy of G. M. MacDonald].



growth but may also partially mitigate increasing moisture stress produced by higher temperatures. Changing sensitivity to moisture stress due to increasing levels of atmospheric CO₂ could be seen as representing an alteration of fundamental niche characteristics relative to moisture and temperature axes.

Experimental warming experiments also indicate that the responses of different plant species will incorporate a high degree of individuality, which may alter community dynamics between plants and between plants and herbivores. In one enlightening experiment Post et al. used passive open top growth chambers to experimentally increase May and June temperatures for Arctic shrub communities in West Greenland (Post et al., 2008). Over the two year experiment the mean temperatures in the chambers were ~2.02–1.48°C warmer than adjacent control plots. The researchers found that the increased temperatures in the growth chambers produced significantly accelerated phenology in terms of budding and reproduction (Fig. 6) for the species studied (chickweed – *Cerastium alpinum* L.; gray willow – *Salix glauca* L. and dwarf birch – *Betula nana* L.). However, the amount of acceleration varied markedly for different species and between different stages within the same species. Animals and insects adapted to current tempos and inter-specific patterns of bud development, leafing, flowering and fruiting could find the timing of these events both in absolute and relative terms significantly altered as climate change progresses. Indeed, it has been argued that caribou population decline in regions such as West Greenland may reflect a developing trophic mis-match between caribou and browse species as the phenologies of the latter change in the face of current warming (Post and Forchhammer, 2008).

As Arctic winters will warm more than summers, it is also possible that extreme winter warming events will become more common. Experimental manipulation experiments show that these

changes in the winter season may have profound impacts on Arctic plants and the animal species that depend on them. Bokhorst et al. deployed infrared heat lamps and soil heating cables in a shrub community in northern Sweden to simulate the impact of a prolonged extreme heating event in March (Bokhorst et al., 2008). Air temperatures were raised roughly 10°C compared with control plots while in selected plots soil temperatures were raised by about 5°C. The researchers found that all three of the shrub species studied (bilberry – *Vaccinium myrtillus* L., crowberry – *Empetrum hermaphroditum* Lange ex Hagerup and lingonberry – *Vaccinium vitis-idaea* L.) exhibited sensitivity to the heating, which became manifest in the following spring. The bilberry plants experienced delayed bud formation by up to three weeks in the following June, greatly reduced flowering and almost no berry production (Fig. 7). Crowberry also showed delayed timing of bud development but no significant decline in berry production. By contrast, lingonberry plants did not display a delay in bud development but did have reduced flowering and significantly reduced berry production on sites where the air, but not the soil, was warmed. Interestingly, spring plant growth and photosynthesis rates did not reveal any response to the winter warming. All three of these species produce berries, which are important for Arctic and subarctic animals. The results of the experimental manipulations demonstrate that extreme winter warming events can impact phenology and berry production and that these impacts display interspecific differences. All of these effects could have important consequences for animal species that depend upon the timing or magnitude of berry production.

Conclusions

Taken together, the unprecedented climate projected for the Arctic by the end of this century and these examples of the significant

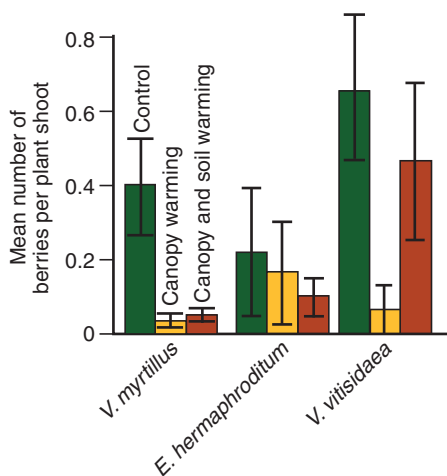


Fig. 7. Impact of experimental heating using infrared lights and soil cables to simulate an extreme winter warming event on berry production in a subarctic shrub community in northern Sweden [redrawn from results from Bokhorst et al. (Bokhorst et al., 2008)].

impacts, and the inter-specific differences in these impacts, on growth, reproductive capacity, phenology, photosynthesis and water usage suggest that anticipating the response of Arctic and subarctic vegetation communities to increased temperatures will need to incorporate more than current empirical relationships between species' distributions and the present climate. Experimental studies underscore the importance of considering not just direct temperature responses but also shifting moisture sensitivities, individualistic species' responses and the complication of the direct impacts of CO₂ fertilization on growth rates and moisture relationships. The latter phenomenon potentially represents a change of the fundamental niche of the species in terms of sensitivity to moisture stress because the fundamental composition of the atmosphere has changed to a new state unprecedented in the span of species that have never before experienced atmospheric concentrations of CO₂ greater than about 280 p.p.m.

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