

HERBIVORY-MEDIATED RESPONSES OF SELECTED BOREAL FORESTS TO CLIMATIC CHANGE

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Abstract. Recent efforts to project vegetation responses to climatic warming have emphasized the tight linkages between climate and vegetation distribution. Here we provide several examples indicating that the direct effects of climatic warming on boreal vegetation can be qualitatively different than the indirect effects mediated by climatic responses of herbivores. These herbivore-mediated vegetation responses to climatic warming will likely vary regionally. In southern Fennoscandia, we project that the climatically induced changes in animal populations should enhance the density of spruce at the expense of pine and broadleaved trees. In northern Fennoscandia we project reduced herbivory on broadleaved trees and increased herbivory on pine, leading to an increase in broadleaved trees and spruce and a reduction in pine. Climatic warming in interior Alaska may reduce herbivory on broadleaved trees and increase herbivory on evergreen spruce, thus reinforcing the impact of increased fire frequency.

1. Introduction

Global climate is warmer than at any time in at least the past 600 yr and is projected to continue to warm in the future (Kattenberg et al., 1996). However, projections of future climate are difficult, in part because of the large magnitude but uncertain nature of feedbacks from terrestrial processes to the atmosphere. Changes in plant community composition and disturbance regime strongly affect these terrestrial feedbacks to the atmosphere through changes in energy exchange (Bonan et al., 1992) and biogeochemistry (Smith and Shugart, 1993). The current correlation between climate and vegetation has been applied to General Circulation Model (GCM) simulations of past and future climate to simulate past and future changes in vegetation distribution (Prentice et al., 1992). However, an equilibrium approach is misleading if other determinants of future vegetation distribution, e.g., herbivores, fire, or human activities, have strong effects on vegetation composition that are independent of the climate-vegetation correlation. For example, human impacts on animal grazing and disturbance can have large effects on ecosystem structure



Climatic Change **48**: 427–440, 2001.

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and composition (Owen-Smith, 1988; Zimov et al., 1995) that are not predicted by climate.

Here we compare the potential interactive effects of herbivores and climate on the future tree-species of three boreal regions: northern and southern Fennoscandia and Interior Alaska. We suggest that the responses differ among regions and that the direct effects of climate on boreal vegetation often differ qualitatively from the indirect effects mediated by climatic responses of herbivores. Plant ecologists have often emphasized the importance of changes in summer climate in governing vegetation change, but changes in winter climate are expected to be more pronounced (Kattenberg et al., 1996; Prentice et al., 1992) and are likely to have stronger effects on animals than on plants.

2. Methodology and Assumptions

Our scenarios of future climate in boreal forest are based on the IPCC 'business as-usual' scenario (IS92a) of climatic change forced by continued increases in atmospheric CO₂ and other greenhouse gases with sulfate aerosols included (Houghton et al., 1990; Kattenburg et al., 1996). An intercomparison of 19 GCMs simulate current high-latitude air temperature within 2EC in all seasons (Tao et al., 1996) but simulate current high-latitude precipitation less well (Kattenburg et al., 1996; Serreze et al., 2000). These models generally agree qualitatively in temperature projections of IPCC scenarios but differ in both direction and magnitude of projected future changes in precipitation (Serreze et al., 2000). There is often, however, agreement in the regional pattern of precipitation changes (e.g., greater increase in coastal areas like Scandinavia than in continental regions like interior Alaska and eastern Siberia). Because of the discrepancies among GCM projections, we rely primarily on regional climate projections, where they are available, based on the assumption that authors have selected GCMs that adequately simulate current climate patterns in their region. In Scandinavia, climate projections are based on the Kettunen et al. (1987) and GCM (Kellomäki et al., 1994; Kellomäki and Kolström, 1994) and the UKMO GCM (Sykes et al., 1995). In Alaska, climate simulations are based on the UKMO, GISS, GFDL, and CCC GCMs (Maxwell, 1992), with regional patterns for the interior boreal forest simulated by the ARC-SyM regional model (Lynch et al., 1995) with lateral boundary conditions provided by the UKMO GCM. In Siberia we rely on the summary projections of the IPCC GCM intercomparison (Figures 6.10 and 6.11 in Kattenburg et al., 1996).

For vegetation projections in the absence of large changes in herbivore abundance we rely on regional analyses of the responses of individual tree species to climate (Beuker et al., 1996) and on projected patterns of vegetation change simulated for a 2 × CO₂ climate by the BIOME3 model (Prentice et al., 1992; Sykes and Prentice, 1995). These simulations assume that biomes and species shift to maintain their current correlation with climate. In Alaska we assume that vegetation will

change in the same way as during the last thermal maximum 6000 yr BP (Brubaker et al., 1995). A transient model of forest response to gradual warming in Alaska and associated changes in fire regime simulates vegetation responses to warming that are similar to those in the paleorecord (Starfield and Chapin, 1996).

Our projections of the responses of herbivores to climatic change are based on variations in herbivore abundance associated with geographic and interannual variations in climate as described in the cited references. We infer the resulting effects on vegetation from studies that document vegetation responses to exclusion of mammalian herbivores or the impacts on vegetation of local variation in herbivore density.

Short-term temporal fluctuations in herbivore abundance and their effects on vegetation may not reflect long-term, climate-induced changes in animal abundance, which are also influenced by feedbacks resulting from changes in plant tissue quality and impacts of predators and diseases; these are more difficult to project. In the scenarios that we present, we include only those feedbacks that are well documented. As in any scenario of future change, there are inevitably other feedbacks and processes that we have not considered and which could cause the actual future to differ from the scenarios that we project.

We first present plausible scenarios of climatic effects on vegetation in four boreal regions with (and without) considering changes in herbivore impacts, based on evidence from the literature. Finally we consider the impact of some of our major underlying assumptions.

3. Southern Fennoscandia

In southern Fennoscandia, IPCC scenarios of climatic warming associated with continued increases in anthropogenic CO₂ emissions (IS92a, the business-as-usual scenario) is projected to lead to higher winter air temperatures, increased precipitation, a loss of permanent winter snow cover, lower winter soil temperatures (due to lack of insulation by snow), and a growing season that extends into autumn (Kellomäki et al., 1994) (Figure 1). Mean annual temperature is expected to rise about 2 °C, with the effective temperature sum (threshold 5 °C) increasing from 1300 to 1700 degree-days at Helsinki (Kellomäki et al., 1994). Little or moderate change is expected in summer temperatures (Kellomäki and Kolström, 1994). Because winter temperature has little direct effect on growth of dominant tree species, and autumn growth is curtailed by photoperiod rather than temperature, we expect little direct vegetation response to this climate change. Provenance trials have shown that wood production in Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) show little relationship to regional variation in summer climate in southern Fennoscandia (Beuker et al., 1996).

In contrast to weak climatic effects on tree growth, winter conditions strongly influence the density and impact of vertebrate herbivores. A reduction in snow

SOUTHERN FENNOSCANDIA

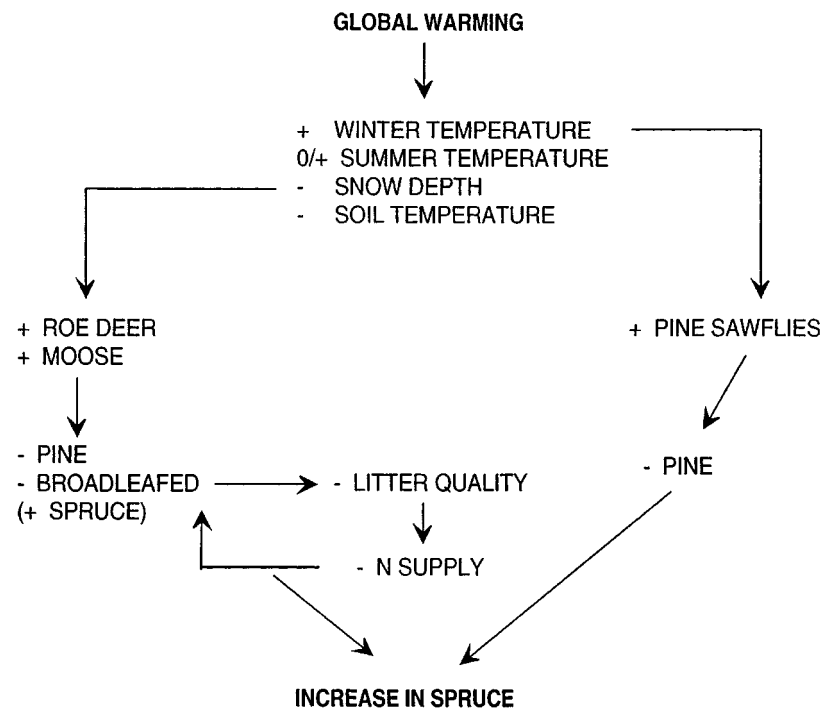


Figure 1. Effects of climatic warming on those biotic interactions likely to influence forest composition in southern Fennoscandia.

cover increases the survival and activity of moose (*Alces alces*) (Andersson, 1971; Loisa and Pulliainen, 1968) and roe deer species (Borg, 1970; Cederlund, 1982) but depresses vole populations by increasing predation rates by small mustelids (Hanski et al., 1991; Hansson and Henttonen, 1985). Moose browse preferentially on Scots pine and broadleaved deciduous species like rowan, aspen and birches, resulting in increased densities of spruce (Bergström and Hjeljord, 1987) (Figure 1). Moose exclosure experiments show that moose reduce broadleaved deciduous species (Hjeljord, 1994) (Danell, pers. comm.). Increased populations of roe deer may also favor spruce. Voles show feeding preferences similar to those of moose and roe deer, but have less dramatic effects on vegetation.

We expect that the projected scenarios of climatic change in southern Fennoscandia would decrease the cover of dwarf shrubs (especially *Vaccinium myrtillus*) and increase the cover of grass due to increased winter browsing by moose and roe deer (Cederlund et al., 1980). Moreover, decreased snow cover would reduce protection of *Vaccinium* from low winter temperatures, leading to increased winter mortality, especially of aboveground parts (Havas, 1971).

The projected climate warming would likely cause an increase in forest insect pests that overwinter in trees and frequently experience population crashes in years of extremely low winter temperatures. Pine sawfly (*Neodiprion sertifer*) is the most serious folivorous pest of Scots pine in Fennoscandia. It overwinters in the egg stage in trees, and cold-hardiness of eggs varies between -30 and -36 °C (Austarå, 1971). Projected increase in winter temperatures (Kattenberg et al., 1996) would increase winter survival of eggs and hence promote forest damage (Virtanen et al., 1996). Similarly, the winter moth *Operophtera* spp., is a severe pest of birch (*Betula pubescens*) forests on the Atlantic coast of Norway and recently on broadleaved forests on Karelian Isthmus in the subcontinental boreal forest zone (Tikkanen et al., 1998). The cold-hardiness of its eggs is -36 °C (MacPhee, 1967). As with pine sawfly, increased winter temperatures would increase winter survival of *Operophtera* eggs and consequently defoliation of broadleaved forests (Virtanen et al., 1996; Tikkanen et al., 1998).

Because leaves of moose-browsed plants are more palatable than leaves of unbrowsed plants to insect herbivores (Danell and Huss-Danell, 1985), the interaction between moose and insects should be synergistic. The low decomposition rate of spruce compared to pine or broadleaved litter (Pastor et al., 1988) would reduce decomposition and nitrogen mineralization as spruce dominance increases. Low nutrient availability reduces the growth of pine and broadleaved trees more than that of spruce, reinforcing the vegetation change to a greater dominance of spruce.

In summary, although projected climatic changes should have little direct effect on plant growth in southern Fennoscandia (Beuker, 1994), these projected changes in climate would likely induce changes in animal populations that would greatly enhance the density of spruce at the expense of pine and broadleaved trees. This is consistent with the paleorecord, in which pine arrived first after the retreat of continental glaciers and was gradually displaced by spruce (Sauer, 1988).

4. Northern Fennoscandia

In northern Fennoscandia, the IPCC business-as-usual climatic scenario projects increases in summer and winter air temperature by $2-3$ °C and in the effective temperature sum from 1000 to 1500 degree days (Kellomäki et al., 1988). Annual precipitation is projected to increase, causing greater winter snow accumulation and therefore higher winter soil temperatures.

Experimental warming during summer has no effect on nutrient availability or growth of tundra plants in northern Fennoscandia (Parsons et al., 1994; Jonasson et al., 1993; Havström et al., 1993) or growth of treeline birch (Sveinbjörnsson, 1992). However, provenance trials with conifers growing in different climates show that warming associated with this climate scenario could lead to a 300% increase in wood production of Norway spruce in northern Finland, but only a 60% increase in Scots pine (Beuker et al., 1996). Climate change simulations suggest that the

NORTHERN FENNOSCANDIA

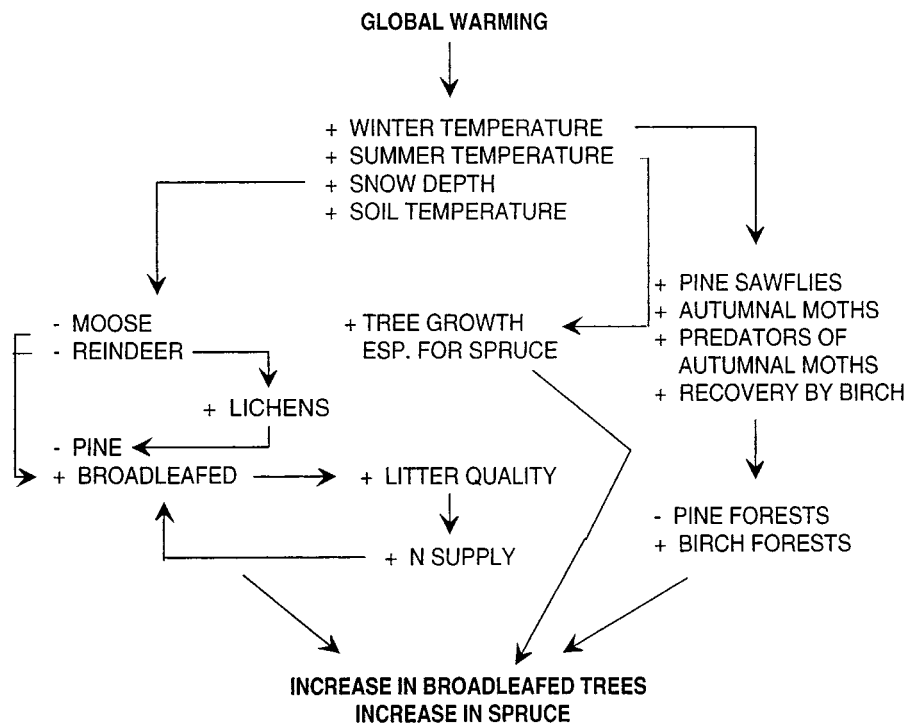


Figure 2. Effects of climatic warming on those biotic interactions likely to influence forest composition in northern Fennoscandia.

growth of pubescent birch (*Betula pubescens*) would be three times greater in this climatic scenario than at current temperatures (Kellomäki and Kolström, 1994).

Due to the sensitivity of moose population densities and activity to snow depth (Andersson, 1971; Loisa and Pulliainen, 1968), the increased winter snow depth projected by this scenario would likely reduce the negative effect of moose on recruitment of mountain ash, other broadleafed trees, and Scots pine. Thus, there would be increases in broadleafed trees due to decreased moose browsing and in Norway spruce due to increased summer temperature (Figure 2).

Reindeer are a dominant large mammalian herbivore in northern Fennoscandia that depend on lichens as their primary winter food. Increased winter snow depth would reduce lichen availability and consumption by reindeer during winter, probably reducing reindeer numbers. Lichens inhibit pine recruitment (Brown and Mikkola, 1974), so that increased lichen biomass expected in response to declining reindeer densities could reduce pine recruitment. Over-dense reindeer populations browse preferentially on mountain birch, willow, poplar and mountain ash dur-

ing summer (Helle, 1994). Reduced reindeer numbers would, therefore, increase the proportion of broadleaved trees. Because the ground would be snow-covered now and in the future, we expect no large climatically driven changes in vole populations (Hansson and Henttonen, 1985).

The northern treeline of birch in Fennoscandia is controlled by population outbreaks of the geometrid moth *Epirrita autumnata* (Kallio and Lehtonen, 1973). Here climatic warming should have conflicting effects on the interactions between *Epirrita* and birch. Warmer winters would increase egg survival of *Epirrita*, especially in river valleys and lower altitudes (Nilsson and Tenow, 1990; Niemelä, 1979), but also increase the abundance and northern distribution of ground-nesting ants, which are effective predators on *Epirrita* (Laine and Niemelä, 1980) and would promote summer recovery of birches from defoliation (Haukioja et al., 1985). We expect that the net result of these multiple effects to be an increase in the abundance of birch because temperature effects on ant predation and summer recovery of birches from defoliation exceed the effects of increased winter survival of *Epirrita*. The warmer winters should also increase the survival of pine sawflies, just as in the south, reducing pine growth and survival (Virtanen et al., 1996).

Spruce is a shade-tolerant tree that displaces deciduous species in late succession. Its growth is not strongly affected by competition with deciduous trees, and it is less palatable to herbivores, so we expect that its direct response to climate warming (Beuker et al., 1996) and its avoidance by herbivores would lead to increased abundance in the warmer climate projected.

In summary, we expect that climatic warming in northern Fennoscandia would stimulate growth of all tree species, especially spruce, but would reduce herbivory on broadleaved trees and increase sawfly herbivory on pine, leading to an increase in broadleaved trees and spruce and a reduction in pine. The increase in broadleaved trees should enhance nitrogen mineralization (Hobbie, 1992), producing a nutritional environment favoring broadleaved species.

5. Interior Alaska

GCMs simulate an increase in winter temperatures and to a lesser extent in summer temperatures in Interior Alaska in the 'business-as-usual' scenario of climatic change (Maxwell, 1992). These projections are consistent with observations during the past 30 years (Chapman and Walsh, 1993; Serreze et al., 2000). The climate of interior Alaska is more continental than that of Scandinavia, and precipitation is projected to increase less than in Scandinavia. This might result in drier soils in summer due to increased evapotranspiration (Kane et al., 1992) but an increase in winter snow when storms move inland from the ice-free North Pacific Ocean (Kattenburg et al., 1996). Warm dry summers in Alaska are typically associated with positive anomalies in the Arctic Oscillation (AO) and a weakening of the Aleutian low pressure center south of Alaska – a situation that has occurred consistently

since 1989 (Serreze et al., 2000) and might persist with climatic warming. A major secondary effect of warm dry summers is high fire frequency which has increased in central Canada (Flannigan and Van Wagner, 1991) and is projected to increase with warming in Alaska (Kasischke et al., 1995). Increased fire frequency would increase the proportion of early successional birch (*Betula resinifera*) and aspen (*Populus tremuloides*) forests (Yarie, 1981; Starfield and Chapin, 1996).

We expect relatively modest changes in plant growth in response to climatic warming. On south-facing slopes any beneficial effects of increased temperature and associated increase in nitrogen mineralization will be counterbalanced by increased drought, the climatic factor that most strongly limits growth of white spruce (*Picea glauca*) in interior Alaska (Yarie, 1981). On north-facing slopes productivity and nitrogen cycling in black spruce (*Picea mariana*) forests is temperature-limited (Van Cleve et al., 1983). However, this species grows slowly under all circumstances (Chapin et al., 1983), so we expect modest increases in productivity in response to climatic warming and no major vegetation change except as a result of altered fire regime.

An increased proportion of early successional postfire stands would increase the abundance of snowshoe hares (Wolff, 1980), which browse preferentially on willows (Bryant et al., 1983), reducing the competition for broadleaved tree species and spruce (Figure 3). Although early successional postfire habitat also favors moose, the projected increase in snow depth would likely have a net detrimental effect on moose, allowing saplings of broadleaved trees to escape to the canopy.

The drought associated with dry summer soils reduces photosynthesis and growth of white spruce (Yarie, 1981), reducing their resistance to bark beetles (Lorio, 1986), thus increasing frequency of bark beetle outbreaks (Mattson and Haack, 1987) and reducing abundance of spruce (Figure 3). The last three decades of warm weather (Chapman and Walsh, 1993) allowed spruce bark beetles to complete their life cycle in one, rather than two, years in southern Alaska, contributing to extensive areas where spruce has been eliminated by bark beetles (Holsten, 1990). Bark beetle outbreaks also increase the probability of fire and, therefore, the proportion of broadleaved forests in the landscape. Also insect defoliator populations might respond to climatic warming in North America's boreal forests. In particular circumstances severe spruce budworm outbreaks could destroy the ability of tree populations to renew themselves (Fleming and Wolney, 1995; Fleming, 1996). Warm dry summers in the subarctic are associated with an increase in the phenolic content of aspen and birch (Jonasson et al., 1986; Bo and Hjeljord, 1991; Irons, unpubl.), reducing their nutritional value to insect defoliators (Bryant et al., 1993) and moose (Bo and Hjeljord, 1991), which may promote the competitive advantage of birch.

In summary, projected summer warming in interior Alaska would likely have modest effects on plant growth but would reduce herbivory on broadleaved trees and increase herbivory on evergreen spruce, thus reinforcing the impact of increased fire frequency. The shift toward broadleaved species would increase net

INTERIOR ALASKA

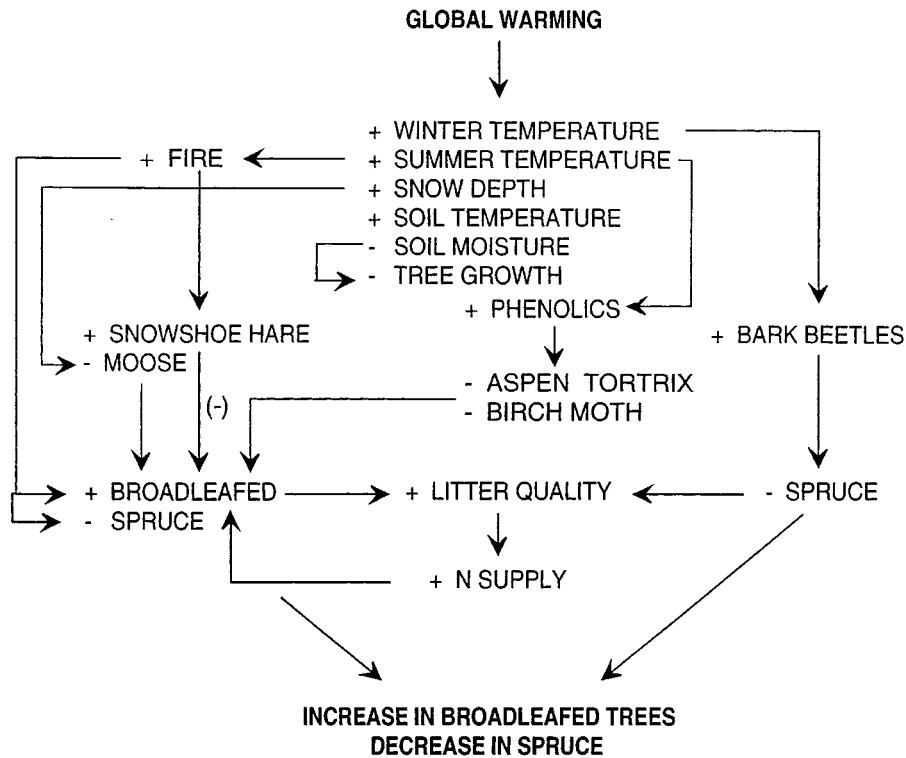


Figure 3. Effects of climatic warming on those biotic interactions likely to influence forest composition in interior Alaska.

nitrogen mineralization (Van Cleve et al., 1983; Flanagan and Van Cleve, 1983), causing increased growth of broadleafed species.

6. Management Implications

The climatic impacts on herbivores and subsequent effects on vegetation that we have delineated could have important economic, social, ecological consequences and feedbacks to climate. Decreased reindeer densities in northern Fennoscandia would adversely affect the reindeer industry, which is an important economic and cultural base of northern Saami people. Spruce, which we project to become more abundant in both northern and southern Fennoscandia, is characterized by large soil and plant carbon pools and could increase carbon storage. By contrast in Alaska, an increase in fire frequency and abundance of broadleafed forest stands would reduce carbon storage. In addition, evergreens such as spruce have lower spring

albedo than deciduous trees (Betts et al., 1997) promoting heat transfer to the atmosphere. The low canopy conductance of evergreens (Schultze et al., 1994) also enhance heat flux and reduces moisture transport to the atmosphere, providing a positive feedback to local warming but reducing moisture available for precipitation. Neither the herbivore impact, nor its implications for biosphere-atmosphere interactions can be uniformly extrapolated to the circumpolar boreal zone but must account for regional variations in climate, vegetation, and herbivores.

To what extent might management decisions modify the predictions we have made? In southern Scandinavia, where both forests and large mammals are intensively managed, high browsing pressure on young pines may lead foresters to plant more spruce seedlings and thus speed the dominance of spruce. Due to the popularity of game management policies that maintain high moose populations, it is unlikely that policies would be instituted to reduce moose populations. In northern Fennoscandia, where a decline in reindeer numbers would have a severe negative impact on the local Saami economy, winter feeding to substitute for pastures covered by deep snow is economically viable only under rare conditions of short duration, so it is unlikely that management would introduce mechanisms to prevent the decline in large mammals that we project. However, direct planting of spruce in managed forests could increase the abundance of spruce more rapidly than we have projected. In Alaska, the main management option might be more extensive fire control, which could offset the expected trend toward reduced abundance of white spruce stands.

Over the long term, migration of temperate species into the boreal zone will alter the projections we have made (Prentice et al., 1992; Sykes and Prentice, 1995). However, during the 50–200 yr time lag before this occurs (Starfield and Chapin, 1996), both climate and herbivores can strongly influence forest composition and rates of migration through both seed dispersal and trophic interactions. Similarly, human activities will likely affect rates of migration of plants and animals and disturbance regimes. Thus, even in the long term, the role of animals in determining forest composition should be considered.

In conclusion, the direct effects of climatic warming on northern ecosystems may be less dramatic and qualitatively different than effects mediated by herbivores and fire over the next 50–200 yr, such that estimates of future vegetation cannot be reasonably projected without considering the role of animals. Other ecosystems in which herbivores play a crucial role include grasslands and savannas (Owen-Smith, 1988) and tundra (Zimov et al., 1995), which together with boreal forest account for 60% of the terrestrial biosphere. Thus, although animals may account for only a small proportion of the carbon flow through most ecosystems (Odum, 1959), they are critical controllers of current and future ecosystem structure and function and cannot be ignored in efforts in scenarios of future vegetation and its feedbacks to global processes.

Acknowledgements

We thank M. Power, S. Kellomäki, and H. Hänninen for critical review of the manuscript and Swedish Environmental protection Board, the Swedish Natural Science Research Council, and the U.S. Long-Term Ecological Research Program for funding the research that led to these generalizations.

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(Received 20 November 1997; in revised form 6 March 2000)