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Permalink

https://escholarship.org/uc/item/4m48z1dn

Journal

Global Change Biology, 6(S1)

ISSN

1354-1013

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Publication Date

2000-12-01

DOI

10.1046/j.1365-2486.2000.06022.x

Global Change Biology (2000) **6** (Suppl. 1), 211–223

Arctic and boreal ecosystems of western North America as components of the climate system

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Abstract

Synthesis of results from several Arctic and boreal research programmes provides evidence for the strong role of high-latitude ecosystems in the climate system. Average surface air temperature has increased 0.3 °C per decade during the twentieth century in the western North American Arctic and boreal forest zones. Precipitation has also increased, but changes in soil moisture are uncertain. Disturbance rates have increased in the boreal forest; for example, there has been a doubling of the area burned in North America in the past 20 years. The disturbance regime in tundra may not have changed. Tundra has a 3–6-fold higher winter albedo than boreal forest, but summer albedo and energy partitioning differ more strongly among ecosystems within either tundra or boreal forest than between these two biomes. This indicates a need to improve our understanding of vegetation dynamics within, as well as between, biomes. If regional surface warming were to continue, changes in albedo and energy absorption would likely act as a positive feedback to regional warming due to earlier melting of snow and, over the long term, the northward movement of treeline. Surface drying and a change in dominance from mosses to vascular plants would also enhance sensible heat flux and regional warming in tundra. In the boreal forest of western North America, deciduous forests have twice the albedo of conifer forests in both winter and summer, 50–80% higher evapotranspiration, and therefore only 30–50% of the sensible heat flux of conifers in summer. Therefore, a warming-induced increase in fire frequency that increased the proportion of deciduous forests in the landscape, would act as a negative feedback to regional warming.

Changes in thermokarst and the aerial extent of wetlands, lakes, and ponds would alter high-latitude methane flux. There is currently a wide discrepancy among estimates of the size and direction of CO_2 flux between high-latitude ecosystems and the atmosphere. These discrepancies relate more strongly to the approach and assumptions for extrapolation than to inconsistencies in the underlying data. Inverse modelling from atmospheric CO_2 concentrations suggests that high latitudes are neutral or net sinks for atmospheric CO_2, whereas field measurements suggest that high latitudes are neutral or a net CO_2 source. Both approaches rely on assumptions that are difficult to verify. The most parsimonious explanation of the available data is that drying in tundra and disturbance in boreal forest enhance CO_2 efflux. Nevertheless, many areas

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of both tundra and boreal forests remain net sinks due to regional variation in climate and local variation in topographically determined soil moisture. Improved understanding of the role of high-latitude ecosystems in the climate system requires a concerted research effort that focuses on geographical variation in the processes controlling land–atmosphere exchange, species composition, and ecosystem structure. Future studies must be conducted over a long enough time-period to detect and quantify ecosystem feedbacks.

Keywords: arctic, boreal forest, carbon balance, energy exchange, methane flux, vegetation change

Introduction

Arctic and boreal ecosystems play a crucial role in the Earth System for several reasons: (i) they occupy a large proportion (22%) of the terrestrial surface; (ii) their structure and functioning are sensitive to subtle changes in climate; (iii) many of these functional changes have large effects on the atmosphere. Consequently, there have been several major North American research programmes that have studied the role of high latitudes in the climate system (Table 1). Together these programmes cover several major types of atmospheric feedbacks (CO_2, CH_4, and water/energy exchange), the major biomes (tundra, boreal forest, and boreal wetlands), spatial variability in land–atmosphere exchanges, and long-term changes in ecological processes that regulate these exchanges. However, each programme, by itself, has been limited in either its temporal or its geographical perspective. This special issue is the product of two workshops that sought to integrate the major findings of these research programmes. The objective of the workshops was to synthesize information on the temporal and spatial variation in the controls over land–atmosphere exchanges of water, energy, CO_2 and CH_4 in the high-latitude ecosystems of western North America. This paper provides an overview of these high-latitude climate feedbacks, based on the workshops and on the papers in this special issue. We refer readers to other papers in this issue and to results from Eurasia (Schulze *et al*. 1999) for detailed documentation.

The land surface is coupled to the atmosphere through two fundamentally different mechanisms (Fig. 1). The exchanges of long-lived greenhouse gases (e.g. CO_2, CH_4) affect the atmosphere primarily at the global scale. These materials become globally mixed within a year, and their effects seldom change local radiative forcing by more than a few percent. Changes in high-latitude CO_2 and CH_4 fluxes are potentially important because of the large carbon stores and extensive areas of poorly aerated soils (Hobbie *et al*. 2000; Walker 2000). Any substantial change in regional carbon stocks or CH_4 fluxes from wetlands could substantially alter the global budgets of these species. The radiative effects of CO_2 and CH_4 initiate a warming which puts more water vapour in the atmosphere, predominantly from tropical regions, further enhancing the atmospheric warming.

The land surface directly affects the atmosphere at the local to regional scale through the energy and water vapour transferred to the atmosphere (Fig. 1). These exchanges cause large proportional changes in the heat and moisture content of the overlying atmosphere, and therefore directly influence local air temperature and the

Table 1 Major North American high-latitude research programmes and their major focus

Research programme	Biome studied	Duration of intensive fieldwork	A major focus
ABLE IIIA	Tundra	1 y	Landscape pattern of CO_2 and CH_4 flux
BOREAS	Boreal forest	4 y	Regional scaling of climate feedbacks
Northern Wetlands	Boreal wetlands	2 y	Geographical variation in CO_2 and CH_4 flux
FLUX	Tundra	3 y	Regional scaling of climate feedbacks
ATLAS	Tundra	4 y	Circumpolar scaling of climate feedbacks
IBP	Tundra	4 y	Site-specific controls over biogeochemical cycles
LTER (ARC)	Tundra	20+ y	Site-specific long-term changes in ecological processes
LTER (BNZ)	Boreal forest	30+ y	Site-specific long-term changes in ecological processes
PALE	Tundra/ boreal forest	20,000+ y	Palaeoecological changes in community composition

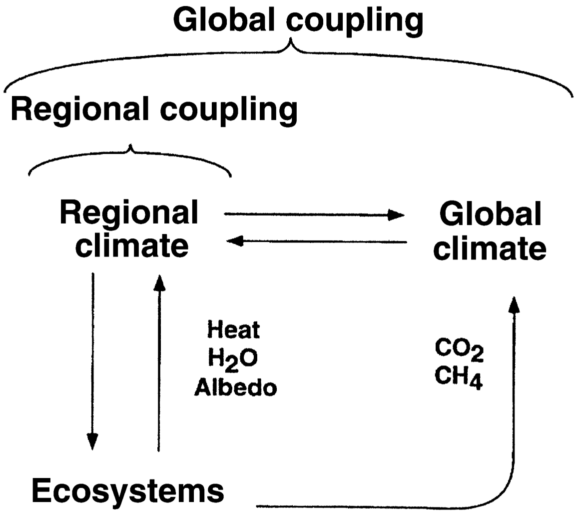

Fig. 1 The processes that couple high-latitude ecosystems to regional climate (through albedo and water/energy flux) and to global climate (through CO_2 and CH_4 flux).

moisture available for precipitation. These high-latitude effects on the atmosphere could also affect global climate through atmospheric telecommunication among regions.

An assessment of the role of high-latitude ecosystems as components of the climate system requires knowledge of the temporal and spatial patterns of temperature, precipitation, and relevant land-surface properties, and the factors regulating exchanges of trace gases, water, and energy. Given the large spatial and temporal variation in both atmospheric and land-surface properties, the greatest challenge in assessing atmospheric feedbacks is to identify a relatively small number of variables to which these feedbacks are most sensitive. We hypothesize that water, energy, CO_2, and CH_4 exchanges differ in their environmental sensitivities and therefore exert varying temporal and spatial influences on the earth's climate system.

Changes in environment and land surface

Environment

Surface air temperatures measured at the high-latitude weather stations of western North America have warmed 0.31 ± 0.03 °C per decade during the twentieth century (Keyser *et al.* 2000). The warming trend is greatest for spring minimum temperatures (0.47 °C per decade) and is broadly consistent with projections of the response of this region to altered greenhouse forcing (McGuire *et al.* 2000; Serreze *et al.* 2000) and/or to global changes in land use (Chase *et al.* 2000). The twentieth century warming in the Arctic is the largest in 400 years (Overpeck *et al.* 1997). However, the NCEP reanalysis of temperature in the lowest 1500 m of the atmosphere shows different regional patterns from the surface record: thus the trends in surface temperature over the past 30 years may reflect regional processes rather than a general global warming induced by increased radiative forcing (Chase *et al.* 2000).

The spring warming in the high latitudes of western North America has advanced the onset of bud-break by 1.1 days per decade and lengthened the growing season by 2.6 days per decade (Keyser *et al.* 2000). However, this pattern is not globally uniform, with warming in western North America and Siberia coinciding with a cooling trend in eastern Canada (Serreze *et al.* 2000). Regional variation in the magnitude of warming also depends on changes in the movements of air masses and storm tracks (Fleming *et al.* 2000). High-latitude regions also differ in their sensitivity to large-scale variations, such as El Niño and the North Atlantic Oscillation. Future warming cannot therefore be uniformly projected to the circumpolar region.

High-latitude precipitation has increased in the twentieth century, primarily during winter and spring (Serreze *et al.* 2000). Because both temperature and precipitation have increased in western North America, the net effect of these changes on soil moisture or atmospheric moisture transport are uncertain. There has been no temporal trend in water transport into or out of high-latitude regions during the twentieth century (Serreze *et al.* 2000). Thus even the signs of trends in plant-available moisture associated with recent regional warming are not known, although they do appear to have been small. The limited capacity of atmospheric models to simulate precipitation, the large underestimation of precipitation at high-latitude weather stations, and the current lack of any long-term data on soil moisture are currently the largest impediments to understanding the long-term ecological consequences of high-latitude climatic change.

The local and regional patterns of current temperature and precipitation are poorly known because of the paucity of weather stations at high latitudes and their concentration at low elevations and along the coast (Fleming *et al.* 2000). This problem has been addressed at the global scale using topographically sensitive interpolation routines to produce gridded climate maps at half-degree resolution (McGuire *et al.* 2000). The same procedure applied at a fine scale (1 km) in Alaska produced maps of regional temperature and precipitation suitable for modelling of ecological processes at regional scales (Fleming *et al.* 2000). These interpolations had no directional biases in representation of temperature and precipitation, although the spatial pattern of these data is least certain where the station density is lowest and is sensitive to the nonrepresentative distribution of weather stations (Fleming *et al*. 2000). Obtaining surface temperature data by remote sensing would require a polar-orbiting satellite and careful atmospheric corrections.

Sharp discontinuities in ecosystem structure, such as the forest–tundra boundary, are hypothesized to influence, and to be influenced, by temperature strongly (Pielke & Vidale 1995; Eugster *et al*. 2000). However, this hypothesis has not been empirically tested.

In summary, recent trends in high-latitude temperature and precipitation are regionally variable, but there has been a strong surface-warming trend in western North America. Regional patterns of precipitation are uncertain because the processes determining precipitation are more complex and occur at a more local scale.

Disturbance regime

The area of North American boreal forest burned annually has doubled in the last 20 years (0.28% in the 1970s to 0.57% in the 1990s), in parallel with the recent warming trend (Kasischke *et al*. 1999). The trends in fire regime in Russia may be similar, but known biases in reporting fires make the published record difficult to interpret. As discussed below, these changes in fire regime could have a larger effect on boreal feedbacks to the atmosphere than any direct ecological responses to temperature and precipitation. The satellite record has the potential to reconstruct fire regime over the past 30 years. However, longer-term reconstruction of fire regime, which is equally important for assessing current trends in high-latitude carbon budgets, requires an analysis of stand age distributions. These data are only sparsely available at the pan-arctic scale (Kurz & Apps 1993).

The underlying causes of fire regime are poorly understood. For example, fire probability increases predictably with drought (a function of precipitation and temperature), but is equally sensitive to vegetation distribution and fire control effort (Baker 1992). The increasing proportion of nonflammable early successional vegetation associated with increased fire frequency would reduce fire probability. Human activities increase the number of fires but reduce fire size in areas where fire suppression is effective. The magnitude of these effects, their geographical variation, and their future trajectory are unknown. However, in principle, these determinants of fire regime could be modelled at regional and global scales (Kittel *et al*. 2000).

Other disturbance agents, such as insects, pathogens and logging, can be just as important as fire in their ecological impact (Malmström & Raffa 2000). However, insect and pathogen species differ greatly in their scale of disturbance and the environmental thresholds required to trigger large outbreaks. Logging also varies regionally in extent and is strongly influenced by accessibility to markets and other economic factors. Therefore, modelling of these biotic disturbances is most tractable at the regional scale, where the biological attributes of hosts, insects, pathogens, and humans can be explicitly considered. The potential invasion of insects and pathogens in response to regional warming, and potential resultant changes in forest harvest, constitute some of the biggest surprises that could modify current projections of high-latitude feedbacks to climate substantially (Malmström & Raffa 2000). There are important interactions between the probability of fire and these other sources of disturbance.

The changes in ecosystem properties and drainage caused by melting of ice-rich permafrost (thermokarst), triggered by warming or disturbance, could substantially alter the impacts of high-latitude ecosystems on the atmosphere (Hobbie *et al*. 2000; Rouse 2000). For example, thaw-lake formation caused by melting of ice-rich loess sediments in Siberia may contribute 25% of high-latitude winter accumulation of CH_4 in the atmosphere (Zimov *et al*. 1997). Thermokarst has not been incorporated into large-scale models of high-latitude ecological or atmospheric change, despite its large effects on ecosystem processes and trace-gas fluxes.

Ecosystem properties

One of the most surprising results of this synthesis is that the ecosystem properties influencing the atmosphere during summer generally differ more strongly within either boreal forest or tundra than between these biomes, as described in the next sections. Therefore, an understanding of ecosystem impacts on the atmosphere requires knowledge of the distribution of vegetation *within* as well as between biomes.

The distribution of the major tundra vegetation types is governed most strongly by latitudinal gradients in climate and secondarily by topographic variation in soil moisture (Walker 2000). The vegetation patterns associated with latitude and continents have been documented in a vegetation map, whose precise boundaries are currently being refined (Walker 2000). However, while major topographic patterns associated with mountain ranges, coastal plains, and broad lowlands are captured in global maps, local topographic variation at the subpixel scale ($< 1\,km^2$) has not yet been incorporated into models of land–atmosphere exchange. In contrast to most biomes, most of the sensitivity of tundra vegetation to geological substrate reflects simple pH differences and can be modelled readily from an understanding of the balance between disturbance and landscape development. Disturbances such as glaciation, wind erosion, frost action and animal activity increase the exposure of unweathered soils and reduce the abundance of acid-producing mosses and organic matter. This offsets the gradual decline in pH that occurs during paludification and landscape development (Walker 2000). Although this pH effect occurs throughout the pan-arctic region and strongly affects all land–atmosphere exchanges (Walker *et al*. 1998; Oechel *et al*. 2000; Walker 2000), its ecological effect has been modelled only qualitatively (Zimov *et al*. 1995) because of the lack of geographically explicit field data (McGuire *et al*. 2000).

In contrast to tundra, the geographical pattern of major boreal ecosystem types is associated more strongly with topography and disturbance than with climate. For example, boreal wetlands and conifer forests are extensive throughout a broad latitudinal belt, but their distribution and aerial extent are determined by topography rather than by macroclimate. Macroclimate has its greatest effect on tree density, height, and productivity, rather than on the type of predominant vegetation. In boreal lowlands, variation in pH associated with disturbance and hydrology exerts a stronger effect than climate on vegetation composition. In boreal uplands of western North America, fire and other stand-replacing disturbances trigger the replacement of conifers by less flammable broadleaf deciduous forests.

The complexity of factors governing the distribution of high-latitude vegetation constitutes a major challenge to predicting its future distribution in response to climatic change. The two most widely applied assumptions used in projecting future vegetation feedbacks to climate are (i) that vegetation will not change (null model) and (ii) that vegetation will change instantaneously to remain in equilibrium with the new climate (Kittel *et al*. 2000). These two assumptions represent unrealistic boundary conditions. Two types of models have been developed to provide scenarios of transient vegetation change in response to changing climate.

1 Frame-based models simulate the movement of specific ecosystem types and associated disturbance regimes in response to changing climate. These are relatively simple, rule-based models that incorporate climate–disturbance interactions and time lags associated with migration, but allow no flexibility in the species composition of an ecosystem.

2 Dynamic vegetation models simulate the changes in relative abundance of plant functional types, i.e. generic plant types that may represent several ecologically similar species (Kittel *et al*. 2000). These models allow changes in community composition, as is frequently observed in the palaeorecord, but are currently too complex to include realistic disturbance regimes or time lags. The major challenges for modelling of vegetation change will be to include realistic representation of topography, which is currently lacking from all of these models, disturbance, and feedbacks to the atmosphere. Because within-biome variability in vegetation has such a strong impact on the atmosphere (see below), these modelling developments are critical to the development of plausible scenarios of high-latitude climate and the role of high latitudes in the global climate system.

Energy feedbacks

Albedo

The greatest biome differences in energy exchange occur in winter and spring, when snow-covered tundra and boreal wetlands have an albedo that is three- to six-fold greater than boreal forest, and therefore absorb correspondingly less radiation and warm the atmosphere less than does boreal forest. This difference in albedo is particularly important in spring, when solar radiation is high. Simulations suggest that the northward movement of treeline 6000 years ago could have accounted for half of the regional warming that occurred at that time, the rest resulting from an increase in solar input (Foley *et al*. 1994). Recent measurements show that albedo of boreal forest in winter is much less (0.11–0.21) than assumed previously for weather forecast modelling (0.6–0.8), which may explain why weather forecast models have underestimated boreal winter air temperatures by ≈15 °C (Baldocchi *et al*. 2000). Therefore, biome differences in winter may be even more important than these simulations have suggested. Within the boreal forest, deciduous stands have twice the winter albedo of the darker coniferous stands (Baldocchi *et al*. 2000). Consequently, any increase in fire frequency, forest harvest or other boreal disturbances that increase the proportion of unforested lands or deciduous forests, would reduce spring energy absorption and could offset the spring warming trend that is now so pronounced in western North America (Keyser *et al*. 2000).

In contrast to winter, there is greater variation in summer albedo within either tundra or boreal forest than between the two biomes (Eugster *et al*. 2000). Thus the current use of a single parameter set for tundra and another for boreal forest in the land-surface packages of climate models seems inappropriate. For example, in boreal forest, the summer albedo of deciduous stands is about twice that of conifer forests, just as in winter (Baldocchi *et al*. 2000). There are also large differences in albedo between pine and spruce forests. In the tundra, summer albedos are variable. However, the average tundra albedo is similar to that of deciduous forest, except where there is standing water or bare soil, where albedo drops by about 40% (Eugster *et al*. 2000).

Energy partitioning

As with summer albedo, there is greater variation in summer energy partitioning within either tundra or boreal forest than between the two biomes (Eugster *et al.* 2000). For example, evaporation and transpiration (as a proportion of net radiation) are 50–80% higher in deciduous than conifer forests, and nearly 90% of the precipitation in deciduous stands is returned to the atmosphere by transpiration (Baldocchi *et al.* 2000). Much (30–90%) of the evaporation in conifer forests comes from the forest floor rather than the trees because the sparse tree canopy allows radiation to penetrate to the forest floor. Here radiation drives evaporation from mosses, which lack stomatal control of water loss (Baldocchi *et al.* 2000). A combination of low leaf area, low stomatal conductance, which is a consequence of low leaf nitrogen content and low photosynthetic capacity, and cold anaerobic soils, constrain water loss from the conifer tree canopy. Because the conifer canopy has a high absorption of radiation, due to its low albedo, and a low transpiration rate, most of the energy is dissipated as sensible heat. Sensible heat flux of boreal conifer canopies is typically two- to three-fold greater than that of deciduous forests, leading to thermal convection which results in a deep planetary boundary layer. This process entrains dry air from the upper atmosphere across the top of the planetary boundary layer, which reduces the moisture content of the lower atmosphere. The resulting dry conditions cause stomates to close, forming a positive feedback that promotes high sensible heat flux and low transpiration. Thus, there are many factors, ranging from tree physiology and canopy structure to atmospheric mixing, that account for the sharp differences in energy partitioning between deciduous and conifer forests in the boreal zone. The deciduous conifer (larch) and evergreen conifer (pine and spruce) forests of Siberia have high sensible heat fluxes similar to those of western North American conifers (Schulze *et al.* 1999).

The spatial variability in energy partitioning in tundra is less pronounced than in boreal forest and occurs for different reasons. The large topographic variation in surface moisture and vegetation within tundra causes evaporation and transpiration to dominate in wet areas and sensible heat flux to dominate in dry areas (Eugster *et al.* 2000; Rouse 2000). This contrasts with the boreal forest where transpiration dominates in the well-drained deciduous-dominated forests. In areas of intermediate moisture, the vegetation structure of tundra mediates energy partitioning. Shrubs reduce the penetration of radiation to the freely evaporating moss surface and therefore increase sensible heat flux at the expense of evaporation and ground heat flux (McFadden *et al.* 1998; Eugster *et al.* 2000). Climate also has an important direct effect on energy partitioning in tundra. The low surface temperatures and high humidity of the arctic coast minimize evapotranspiration and create a strong surface-to-air temperature gradient that drives sensible heat flux (Rouse 2000). As a result of regional climatic variation, energy partitioning can differ as much between coastal and interior wetlands as between structurally different vegetation types. In tundra 10–20% of net radiation is partitioned into ground heat flux during summer, due to the sparse canopy shading and steep thermal gradient between the ground surface and permafrost (Eugster *et al.* 2000). This contrasts with temperate and tropical ecosystems, where average daily ground heat flux is close to zero.

Role of energy exchange in the climate system

The research summarized above provides a basis for assessing the sensitivity of the high-latitude climate system to changes in components of the energy budget. The greatest sensitivity in energy exchange *per unit area* is to variation in albedo during late winter. For example, if warming caused an earlier snow-melt or advancement of forest into tundra, this would generate a positive feedback, whereas increased boreal fire frequency or logging would cause a negative feedback to warming. Some of these potential land-surface responses to regional warming, such as earlier snowmelt and increased fire frequency, would occur rapidly, whereas treeline advance would occur following long time lags (Chapin & Starfield 1997).

Plausible changes in summer energy exchange vary in both magnitude and direction, depending on the original vegetation type and the scenario of change in climate and disturbance regime (Eugster *et al.* 2000). In the absence of vegetation change, regional warming might reduce moisture availability, increase sensible heat flux, and deepen the planetary boundary layer, inducing a positive feedback to warming. Rising atmospheric CO_2 would magnify this effect, by reducing stomatal conductance, particularly in deciduous stands, due to their greater sensitivity of stomatal conductance to atmospheric CO_2 (Ellsworth 1999; Tognetti *et al.* 1999). However, both a dry environment (Hogg & Hurdle 1995) and drought-induced increase in fire frequency (Van Cleve *et al.* 1991) would likely augment the abundance of early successional deciduous forests, leading to increased transpiration and reduced sensible heat flux – a large negative feedback to warming. In addition, smoke particles from fires might cause cooling by reducing solar energy input, as observed with tropical biomass burning. In tundra, by contrast, if warming caused either a continued expansion of shrubs in upland tundra or a drying of wetlands, this would probably increase sensible heat flux and act as a positive feedback to warming. Regions with a different dominant vegetation, such as the larch forests of Siberia (Schulze *et al*. 1999), or different climatic trends, as in eastern Canada, would probably differ in response to environmental change (Eugster *et al*. 2000).

In summary, in the absence of vegetation change, land–atmosphere energy exchange would probably act as a positive feedback to regional temperature changes throughout high-latitude regions. The principles underlying these positive feedbacks are well understood and amenable to modelling. In western North America, warming might be enhanced by vegetation change in tundra but offset by logging or fire-induced vegetation change in boreal forest. The magnitude of these potential changes is poorly known but many of the effects are likely to be large and variable, depending on the initial vegetation type. The biggest impediment to projections of future energy feedbacks to climate is the uncertainty of future disturbance rates in boreal forest and the limited ability to model them at large scales.

Regional changes in energy exchange will probably interact with the carbon cycle by changing disturbance regime, regional temperature and precipitation, and the depth of the boundary layer. For example, the shallower boundary layer in deciduous compared to coniferous forests would cause seasonal changes in atmospheric CO_2 concentration to be more pronounced (diluted over a smaller volume of air). Thus, any increase in area of deciduous forest due to enhanced disturbance would exaggerate the seasonal variation in atmospheric CO_2 concentration (Randerson *et al*. 1999; Zimov *et al*. 1999).

Trace-gas feedbacks

Methane

Methane production occurs only by anaerobic processes in strictly anoxic environments, such as in wetlands and ponds (Reeburgh *et al*. 1998). When the water table is near the soil surface in wetlands, or the landscape unit is flooded permanently, the potential for methane oxidation is minimized, and there are large CH_4 fluxes from the ecosystem (Bartlett & Harriss 1993; Moore & Roulet 1995). Under saturated conditions, soil temperature becomes an important control over methane flux (Harriss & Frolking 1992). Future emissions of methane from high-latitude ecosystems therefore depend on the aerial extent of these saturated environments. A combination of atmospheric and hydrological modelling based on digital elevation models will be useful in estimating the areas with a high potential for emissions.

Landscape disturbance caused by the melting of permafrost and the creation of thermokarst features creates shallow, flooded surfaces with large carbon inputs that can lead to high methane emissions (Zimov *et al*. 1997). The activities of beavers in the boreal forest also transform uplands and riparian areas into large sources of CO_2 and CH_4 (Roulet *et al*. 1997).

Boreal and tundra wetlands account for between 30 and 40 Tg $CH_4\,y^{-1}$ (Bartlett & Harriss 1993), or approximately 10% of the annual atmospheric burden. CH_4 is significant as a greenhouse gas because of its high radiative efficiency compared to that of CO_2 (Isaksen *et al*. 1992) and accounts for approximately 15% of current radiative forcing. Thus changes in CH_4 emissions from northern ecosystems would impact the global methane budget (Gorham 1995; Moore *et al*. 1998).

Carbon dioxide

The arctic and boreal forest contain 25–35% of the global stock of soil carbon, which, if released by respiration in warmer drier soils, could provide a large positive feedback to global warming (Keyser *et al*. 2000; McGuire *et al*. 2000). Alternatively the nutrients released from this decomposition and the warmer temperatures might stimulate production and enhance carbon storage (Shaver *et al*. 1992; McKane *et al*. 1997). The net contribution of high-latitude ecosystems to net CO_2 flux has been estimated variously as a source of 0.2 Pg to a sink of 1 Pg. These numbers are substantial compared to the average CO_2 accumulation in the atmosphere of 3.5 Pg, so the current range in uncertainty in high-latitude CO_2 flux is climatically important. Differences among studies in estimates of current high-latitude CO_2 flux reflect differences in approach and assumptions for extrapolation more than discrepancies in the underlying data. Here we provide a simplified overview to place these assumptions in perspective. Two general approaches have been used.

One approach uses the seasonal or interannual changes in the quantity of CO_2 in the atmosphere with atmospheric transport models to estimate the spatial distribution of surface sources and sinks. This 'inverse' approach has generally concluded that mid-northern latitudes were a net carbon sink during the 1980s and early 1990s (Tans *et al*. 1990; Ciais *et al*. 1995; Fan *et al*. 1998; Bousquet *et al*. 1999; Rayner *et al*. 1999). At high northern latitudes, these models give a wider range of estimates, with some analyses pointing to a net source (Ciais *et al*. 1995; Fan *et al*. 1998) and some to a sink (Bousquet *et al*. 1999; Rayner *et al*. 1999). The greatest sources of uncertainty in these analyses are model parameterizations of atmospheric mixing, including the strength of the seasonal and diurnal boundary layer, moist convection, and interhemispheric transport (Denning *et al*. 1995). In addition, most of the observations used to constrain the atmospheric inversions are surface measurements, with very little known about the vertical profiles of CO_2 and $^{13}CO_2$. The sparse density of sampling stations results in relatively coarse spatial resolution, making it difficult to distinguish between north-temperate and boreal sources and sinks. For example, a large north-temperate sink (Fan *et al*. 1998) and a small arctic source (Ciais *et al*. 1995) could produce an atmospheric pattern similar to that of a net boreal sink.

The second general approach is to sum the fluxes that have been estimated in different locations, stratified by ecosystem type, climate zone, time of season, nutrient availability, stand age, disturbance type, etc., and to weight these flux estimates by the appropriate areas (Clein *et al*. 2000; McGuire *et al*. 2000; Oechel *et al*. 2000). This approach has either concluded that high latitudes are a net carbon source or that it is uncertain whether high-latitudes are a carbon source or sink. Because there is insufficient information about all the factors that influence flux, simplifying assumptions must be made about which factors are most important and what relationships exist between controlling factors and flux. The greatest sources of uncertainty are the availability of underlying data and the validity of the simplifying assumptions on which these extrapolations are based. The papers in this issue provide new information that identifies many of these sources of uncertainty.

Disturbance often causes an abrupt reduction in carbon stocks, after which carbon accumulates gradually until it approaches some steady-state value (Odum 1959) (Fig. 2). The shape and time-course of this curve reflect the magnitude of carbon loss during disturbance and the subsequent factors controlling plant production and decomposition. At the regional scale, net carbon exchange depends on disturbance frequency and the magnitudes and rates of change in carbon stocks associated with disturbance and subsequent recovery (Schulze & Heimann 1998; Schulze *et al*. 1999; Harden *et al*. 2000). If there was a constant disturbance frequency followed by recovery to the same steady-state carbon stock, regional net carbon flux would equal zero, regardless of the frequency or magnitude of disturbance, the rate of recovery, or the final carbon stock. It is the *change* in these parameters that determines net CO_2 flux. Thus, we expect no consistent relationship between net regional carbon flux and climate or ecosystem type unless there has been a consistent change in one or more of the underlying processes. Any nonzero regional carbon flux must reflect deviations from these steady-state assumptions. High-latitude carbon balance therefore depends on the relative sensitivity of disturbance frequency, decomposition and production to environmental change.

While there is substantial evidence of increased carbon uptake at the onset of the growing season (Keeling *et al*. 1996; Randerson *et al*. 1999; Keyser *et al*. 2000), there is much greater uncertainty concerning the annual budget. A positive correlation between CO_2 uptake and spring temperature anomalies during the 1980s and early 1990s suggests that photosynthesis has increased during May and June in response to anomalously high spring temperatures (Randerson *et al*. 1999). This increase in photosynthesis could drive a high-latitude carbon sink. It is also possible, however, that strong negative feedbacks from increased respiration and fire frequency later in the growing season, cause boreal and arctic ecosystems to remain in balance or lose carbon on annual timescales (Zimov *et al*. 1999). Evidence for a carbon source comes from the observation that fire frequency has doubled in the last 20 years in western North America (Kasischke *et al*. 1999), with large carbon emissions associated with fire and subsequent decomposition (Kasischke *et al*. 1995; Hobbie *et al*. 2000). However, Scandinavia has a long history of disturbance that could contribute to current CO_2 sink activity (phase t_2 of Fig. 2). Sink activity could be stimulated by nitrogen deposition (Kauppi *et al*. 1992) and by warming-induced increases in nitrogen mineralization (McGuire *et al*. 1992; Shaver *et al*. 1992). These changes in nitrogen supply could make boreal NPP more responsive to increased atmospheric CO_2 (Schimel 1995; Hobbie *et al*. 2000). Simulations suggest that the *direct* temperature effects on the boreal carbon balance may be small because warming-enhancement of NPP is balanced by increased decomposition (Keyser *et al*. 2000). These environmental effects on stand-level carbon balance and fire regime vary regionally due to regional variation in recent temperature trends. They also vary locally along topographic gradients, with peatlands likely to have slower decomposition and less frequent fires than upland forests (Harden *et al*. 2000; Hobbie *et al*. 2000). The impacts of thermokarst have not been adequately incorporated into carbon-balance models at either the stand or regional levels. The associated change in soil moisture and vegetation would likely have strong effects on carbon balance (Hobbie *et al*. 2000; Keyser *et al*. 2000). In summary, the major uncertainties in boreal carbon balance reflect insufficient data on stand age distributions following disturbance, on the time course of stand-level carbon exchange after disturbance, and on the sensitivity of this carbon exchange to nitrogen deposition, CO_2 concentration, soil moisture, and thermokarst.

In contrast to the boreal forest, the disturbance regime of tundra has probably not changed significantly so that regional carbon balance primarily reflects the sensitivity of stand-level carbon balance to environment (McGuire *et al*. 2000; Oechel *et al*. 2000). The trend toward warmer, drier soils in Alaska led to net carbon efflux, particularly

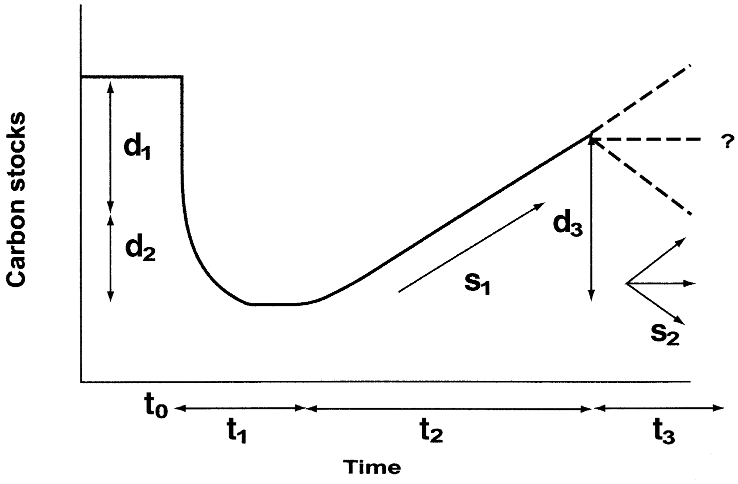

Fig. 2 Generalized time-course of carbon stocks in an ecosystem following disturbance. There are four qualitatively different patterns of change in carbon stocks during a disturbance cycle: (i) A rapid decrease in carbon stock directly caused by the disturbance (d_1) at time zero (t_0); (ii) a continued net loss of carbon following disturbance (d_2 over time period t_1) because decomposition exceeds NPP; (iii) an increase in carbon stocks in vegetation and soils (d_3 during time period t_2) because NPP exceeds decomposition; and (iv) a steady-state period during which carbon stocks change in response to climate variability but not to successional processes (t_3). The rate of carbon accumulation differs between t_2, when carbon generally increases (s_1) and the period of steady-state (t_3), when the changes in carbon stock are variable depending primarily on climate (s_2).

in well-drained tundra (Oechel *et al.* 1993), presumably because decomposition is inhibited by high soil moisture (Oechel *et al.* 1993; Hobbie *et al.* 2000). This net carbon efflux would shift to a net carbon gain, as nutrients released by this decomposition are incorporated into plant biomass, which stores more carbon per unit of nitrogen than does soil (Shaver *et al.* 1992; McKane *et al.* 1997). Finally, changes in temperature and nutrient availability would likely alter community composition, which has effects on carbon storage that are at least as strong as those due to changes in environment (Hobbie *et al.* 2000). The time course of these changes is poorly known.

The regional and pan-arctic patterns of carbon exchange simulated by models depend on underlying assumptions. Simulations and measurements of instantaneous carbon exchange are sensitive primarily to radiation, temperature, leaf area index and leaf nitrogen (Oechel *et al.* 2000; Williams *et al.* 2000). These models of short-term carbon dynamics use leaf area or NDVI as inputs, because of the widespread availability of these data. The biogeochemical controls over leaf area are represented implicitly. These models frequently show a strong sensitivity of CO_2 flux to temperature, because short-term changes in temperature cause a change in the balance between photosynthesis and respiration. Biogeochemical models, in contrast, explicitly simulate changes in plant biomass and biogeochemistry. These models indicate greater sensitivity of carbon exchange to soil moisture and drainage than to temperature because of the sensitivity of nitrogen cycling to drainage (Clein *et al.* 2000; McGuire *et al.* 2000). However, there are still substantial uncertainties concerning the link between decomposition and nitrogen supply at high latitudes (Clein *et al.* 2000; Hobbie *et al.* 2000). Thus long-term changes in carbon dynamics might show environmental sensitivities that differ from those of short-term carbon exchange measurements and experiments against which these models are calibrated. Because of the substantial regional variation in climate and disturbance regime, any pan-arctic extrapolations of conclusions about the role of tundra in the global carbon balance will need to consider regional variation in causal factors and the timescale of ecosystem response to these factors (Shaver *et al.* 1992; McGuire *et al.* 2000).

Another important uncertainty in estimating high-latitude carbon balance is the magnitude and controls over winter respiration. Until recently, winter respiration was assumed to be negligible. However, a summary of recent measurements shows that winter respiration accounts for an average of 20% of the annual belowground respiration in high-latitude studies (Hobbie *et al.* 2000; Oechel *et al.* 2000). Although this respiration is clearly temperature-sensitive (Zimov *et al.* 1996; Oechel *et al.* 2000), it is probably controlled by different processes from summer respiration (Hobbie *et al.* 2000). Finally, given the importance of species effects on production and decomposition (Hobbie *et al.* 2000), the understanding of high-latitude carbon exchange must include the long-term dynamics of vegetation and disturbance, which are only beginning to be incorporated into biogeochemical models (Kittel *et al.* 2000).

The next steps

The high-latitude climate system is vulnerable to change because it is sensitive to many factors that

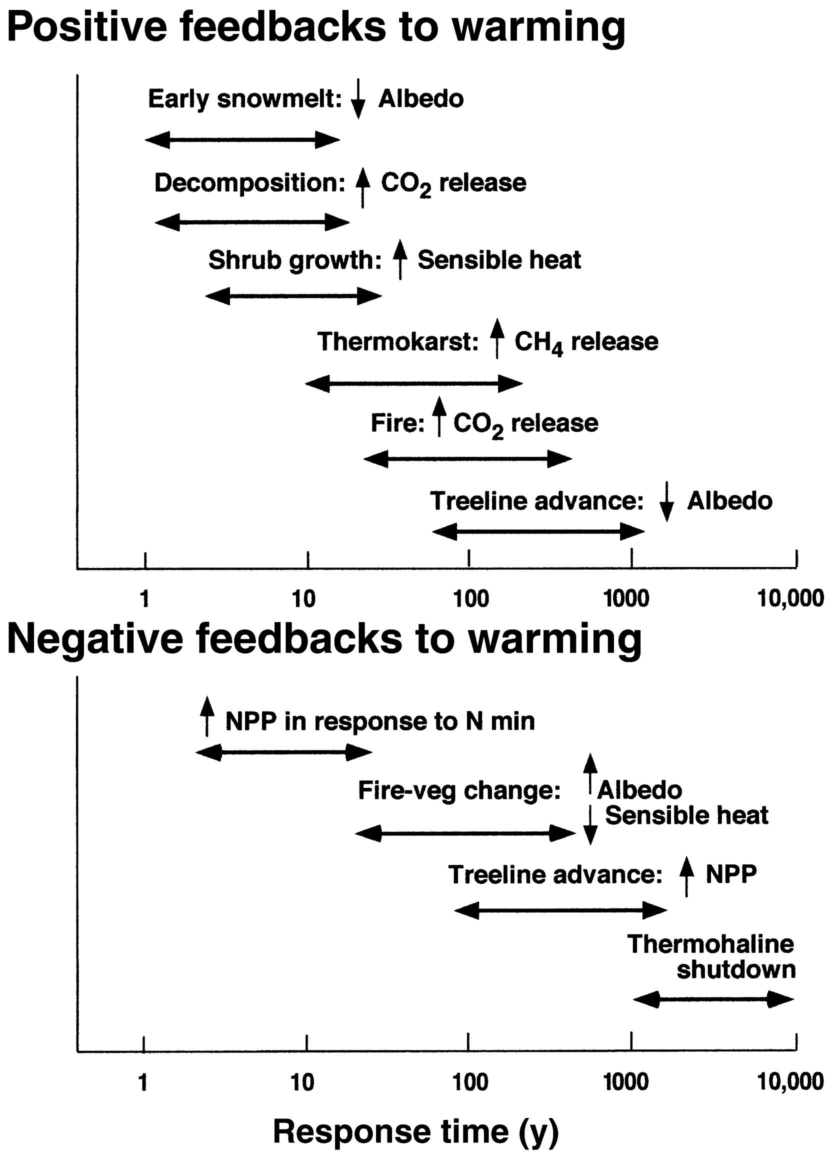

Fig. 3 The response times over which different positive and negative feedbacks from high-latitude ecosystems to the atmosphere are most pronounced.

differ in temporal and spatial scale (Fig. 3). Changes in the global climate system will continue to be communicated to high latitudes in ways that are regionally variable and differ in time lag. Short-term changes in terrestrial snow cover, sea ice cover, fire regime, and vegetation composition can rapidly affect the climate system. Longer time lags are associated with the northward migration of forests and changes in regional hydrology. Together these changes could alter regional hydrology and freshwater input to the Arctic Ocean. Rivers that enter the Arctic Ocean originate largely from boreal watersheds and are therefore sensitive to the balance or precipitation and evapotranspiration in that biome (Serreze *et al.* 2000). The salinity and outflow from the Arctic Ocean to the North Atlantic strongly influence the quantity of North Atlantic Deepwater formation and the strength of the thermohaline circulation (Serreze *et al.* 2000), which exerts an important influence on global climate.

Despite the long history of integrated ecosystem research programmes at high latitudes (Table 1), many gaps remain in the understanding of the role of high-latitude feedbacks in the climate system. In part, these gaps reflect the lack of any concerted effort that focuses on the underlying process controls over broad spatial gradients in climate, species composition, and ecosystem structure during a long enough time period to detect and quantify ecosystem feedbacks. Long-term studies of transects along sharp gradients in climate and ecosystem structure planned by the International Geosphere-Biosphere Programme (IGBP) provide one model for such an integrated effort. The major gaps that were identified by our synthesis of arctic and boreal research in North America were:

1 Uncertainty in the recent and future disturbance rates in the boreal forest and their effects on energy partitioning and carbon exchange.

2 Inadequate inclusion of fine-scale ecosystem properties, such as topography and disturbance regime, in global models of vegetation change and feedbacks to climate.

3 Uncertainty in the relationship between climate and soil moisture/thaw, as a basis for future projections of these soil properties.

4 Uncertainty in the time course of ecosystem controls over net carbon flux following changes in climate or disturbance, as controlled by the coupled interactions of plant and soil processes.

5 Uncertainty in the patterns and causes of high-latitude precipitation.

This paper has identified several critical science questions in arctic and boreal research. However, to quantify the contribution of high-latitude ecosystems to overall global biospheric dynamics, the greatest limiting factor is the lack of geographically extensive measurements that can be used to characterize the entire region in even the most fundamental ways. The boreal forest and tundra cover roughly 26 million km^2 (Schlesinger 1997), and most of this area is populated sparsely and has little road access. Information that is routinely available in temperate regions, such as biome distribution, soils, and climatology, is poorly quantified for high latitudes due to this remoteness and lack of a history of management-orientated research. For example, the circumpolar frequency of standard weather stations is < 1 per 100,000 km^2 in some areas. The exceptionally cold temperatures and freeze/thaw cycles ruin many monitoring instruments or make deployment difficult. Remote sensing approaches seem a logical way to address some of these deficiencies, yet the dark winters, low summer sun angles and persistent cloud covers make regular optical remote sensing challenging. Future research requires innovative new approaches to solve these problems. For example, a synthetic aperture radar that could monitor the entire circumpolar surface condition every 2–3 days without reliance on solar illumination or clear skies is now possible (Running *et al*. 2000), as are automated stations that relay data by telemetry from remote field sites. Broader regular sampling of the spatial heterogeneity of the system is an essential component of future high-latitude science.

Acknowledgements

We thank: the U.S. National Center for Ecological Analysis and Synthesis for sponsoring the workshops that led to this regional synthesis; the BOREAS, FLUX, ATLAS and LTER research programmes, which provided much of the data on which the syntheses were based; and the National Science Foundation (OPP-9523396) and National Aeronautics and Space Administration (TE/97–0032) for financial support for the workshops.

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