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Published in:
Ambio

2004

Link to publication

Citation for published version (APA):

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Effects of Changes in Climate on Landscape and Regional Processes, and Feedbacks to the Climate System

Terry V. Callaghan, Lars Olof Björn, Yuri Chernov, Terry Chapin, Torben R. Christensen, Brian Huntley, Rolf A. Ims, Margareta Johansson, Dyanna Jolly, Sven Jonasson, Nadya Matveyeva, Nicolai Panikov, Walter Oechel, Gus Shaver, Sibyll Schaphoff and Stephen Sitch

Biological and physical processes in the Arctic system operate at various temporal and spatial scales to impact large-scale feedbacks and interactions with the earth system. There are four main potential feedback mechanisms between the impacts of climate change on the Arctic and the global climate system: albedo, greenhouse gas emissions or uptake by ecosystems, greenhouse gas emissions from methane hydrates, and increased freshwater fluxes that could affect the thermohaline circulation. All these feedbacks are controlled to some extent by changes in ecosystem distribution and characteristics by large-scale movement of vegetation zones. Indications from a few, full annual measurements of CO₂ fluxes are that currently the source areas exceed sink areas in geographical distribution. The little available information on CH₄ sources indicates that emissions at the landscape level are of great importance for the total greenhouse balance of the circumpolar North. Energy and water balances of Arctic landscapes are also important feedback mechanisms in a changing climate. Increasing density and spatial expansion of vegetation will cause a lowering of the albedo and more energy to be absorbed on the ground. This effect is likely to exceed the negative feedback of increased C sequestration in greater primary productivity resulting from the displacements of areas of polar desert by tundra, and areas of tundra by forest. The degradation of permafrost has complex consequences for trace gas dynamics. In areas of discontinuous permafrost, warming, will lead to a complete loss of the permafrost. Depending on local hydrological conditions this may in turn lead to a wetting or drying of the environment with subsequent implications for greenhouse gas fluxes. Overall, the complex interactions between processes contributing to feedbacks, variability over time and space in these processes, and insufficient data have generated considerable uncertainties in estimating the net effects of climate change on terrestrial feedbacks to the climate system. This uncertainty applies to magnitude, and even direction of some of the feedbacks.

INTRODUCTION

Biological and physical processes and phenomena in the Arctic system operate at various temporal and spatial scales to impact large-scale feedbacks and interactions with the earth system (1). Understanding these processes at multiple scales is critical because the complex interactions between physical, biological, and human dimensions on system performance cannot be predicted by simply applying a different scale to existing results. Therefore, a multidisciplinary and quantitative approach is necessary to understand and predict the response of the Arctic system to variability in temperature and moisture. The large scale, interrelated processes described here include:

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

Paleoclimatic studies (2) and studies of the contemporary Arctic together (1) have identified four potential feedback mechanisms between the impacts of climate change on the Arctic and the global climate system:

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

In the past, three of the potential feedbacks have been generally positive and only one negative. Some of the feedbacks such as energy and water exchange operate at local to regional scales whereas others, particularly trace gas fluxes, have the potential to operate at regional to global scales. In this paper, we assess the impacts of changes in climate (but not UV for which data are unavailable) on ecosystem processes at the larger scale. We explore the implications of these changes for feedbacks from terrestrial ecosystems to the climate system, but we do not calculate changes in forcing (3). Nor do we consider freshwater discharge (Chapters 6 and 8 in reference 3) and methane hydrate feedbacks (Chapters 6 and 9 in ref. 3). This paper is part of an holistic approach to assess impacts of climate change on Arctic terrestrial ecosystems (3, 4).

IMPACTS OF RECENT AND CURRENT CLIMATE ON CARBON FLUX

There are two complementary approaches to solve the carbon flux inventory problem; bottom-up and top-down approaches. The first is based on the long-term monitoring of gas emissions within networks of field stations or sites that cover the main types of habitats. At its simplest, the total circumpolar emission is estimated from the number and area of the types of northern...
ecosystems differentiated in terms of easily mapped features like vegetation, soil properties, relief, geomorphology and the characteristic annual exchange of CO₂ and CH₄ from each ecosystem. The data on CO₂ and CH₄ fluxes come from three main groups of available techniques that operate at different spatial scales: (i) closed and open top chambers (0.1–1 m²); (ii) micrometeorological towers based on eddy covariance and gradient methods (10–10000 m²); and (iii) aircraft sensing (up to tens and hundreds of km²). All three groups of techniques have their own advantages and disadvantages. However, the continuous measurements with towers seem to be the most appropriate to provide reliable information on temporal variation of gas emission at the ecosystem and landscape spatial levels.

Recent Changes in CO₂ Flux

Recent variations in Arctic climate have had profound effects on some ecosystem and regional-level carbon fluxes and, in general, they reflect the recent spatial variability in climate change. Here, we restrict our assessment to carbon in the active layer of soils and in plants. We do not consider carbon in permafrost and methane hydrates (Chapters 6 and 9 in ref. 3).

The North Slope of Alaska has seen a secular rise in temperature (Fig. 1 in ref. 1)(2), increase in length of the growing season, and decrease in available soil moisture (5–9) over the last 3–4 decades. This has resulted in a change from North Slope Arctic ecosystems being a sink for carbon through the Holocene (10) to a source of carbon to the atmosphere beginning in the mid-1970s to early 1990s (6–8) (Fig. 1 in Callaghan et al. (1)). However, as there has been a secular change in climate, with progressive warming, drying, and lengthening of the growing season, there has been physiological, community, and ecosystem level adjustment that has reduced the rate of carbon loss from North Slope ecosystems (Fig. 1 in Callaghan et al. (1)). Also other, wetter parts of the North Slope are not showing the same source function (11).

The swings in carbon balance are very large, from a net summer CO₂ uptake of from about 25 g C m⁻² yr⁻¹, to a summertime loss of over 225 g C m⁻² yr⁻¹. If these fluxes held worldwide for wet coastal and moist tussock tundra, this would result in a net loss of up to 0.3 Gt C yr⁻¹ from these two ecosystem types alone.

In NE Greenland, the recent climatic history is different to that of Alaska. Here there has been no significant trend towards higher temperatures (5) and integrating for all vegetation types shows that the Zackenberg valley is a small net sink with a large uncertainty range of 2.3 ± 16.2 g C m⁻² yr⁻¹. This integrated study of the valley shows that satellite (Landsat) derived carbon flux estimates are in good agreement with ground-based eddy correlation flux measurements covering all the dominant vegetation types in the valley. The Landsat-method estimated a mid-day uptake rate in August 1997 of 0.77 g C m⁻² d⁻¹ for the valley as a whole whereas the ground-based measurements showed 0.88 g C m⁻² d⁻¹ (12). The measured annual balance in the valley varies from significant uptake in the intensively studied fen areas in the order of 18.8 ± 6.7 g C m⁻² yr⁻¹ to net C losses in the dry heath (12–14).

Like Alaska, northern Scandinavian areas have seen warming in recent years. The ecosystem carbon balances there vary between a sink of between 15 and 25 g C m⁻² yr⁻¹ in a sub-Arctic Swedish peatland (Friborg pers. comm.). Similarly, in Finland, a net annual uptake of about 20 g C m⁻² yr⁻¹ has been reported for a subarctic fen at Kaamanen (15). Six years of continuous measurements at this fen show marked interannual variation in the CO₂ balances (sinks from 4 to 52 g C m⁻² yr⁻¹), mainly reflecting the variations in the spring temperatures and the timing of the snow melt (Aurela, pers. comm.). Work on fluxes in a high Arctic barren tundra on Svalbard show a very limited source of around 1 g C m⁻² yr⁻¹ (16). Overall, the synthesis of regional C flux information from measurements at several sites in northern Europe and Greenland (the LAPP project; 17) indicates a general picture of Arctic landscapes as being remarkably similar in their C flux during the peak summer but with the length of the growing season and the shoulder season fluxes (Fig. 1 in Callaghan et al. (18)) being the key determinants for the net annual fluxes. This causes substantial interannual variability at the individual sites and a general uncertainty associated with the current status of the circumpolar North as a source or a sink for carbon.

Recent work in East European tundra indicates a substantial current source function of the northeastern European tundra areas (19). When combined with the areas of the northern Alaska tundra mentioned above that also have a source function, source areas (East European tundra, Svalbard, and Alaska) may exceed the sink areas (NE Greenland, N Scandinavia). However, data are available for only a limited geographical extent of the Arctic.

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

New models and approaches make estimation of current and future global carbon balance possible. The modeling approach has been used to predict recent change from carbon sink to source status (20, 21). The Terrestrial Ecosystem Model (TEM) has been used to estimate current carbon fluxes, and those in the future while the model “Hybrid V4.1”, (22) has been used to predict vegetation and carbon pool changes at high latitudes for the period 1860–2100 (23). Under current conditions, there is a simulated mix of carbon sinks and sources, that reflect variation in current and past climate. Under contemporary conditions, McGuire estimates circumpolar carbon fluxes to average a small sink of 17 g C m⁻² yr⁻¹ (21). The standard deviation around this number, however, is estimated at 40 g C m⁻² yr⁻¹. This uncertainty range is comparable to the LPJ model outputs referred to in section 5.4.1 (24) and the calculation of current sink status corresponds to the predictions by White et al. (23).

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

CURRENT CIRCUM-ARCTIC CH₄ FLUXES

Probably the most intensive studies and the longest observations of methane fluxes were obtained in North America, mainly within the central Alaskan and North Slope sites at Barrow, Atqasuk, Toolik Lake, and Prudhoe Bay (25–29). In the north of Eurasia including Russia, the extensive measurements of gas emission was initiated from late 1980 and followed either as short-term measurements across geographical transects or as a long time-series of fluxes at one site. The first approach is illustrated by chamber measurements of CH₄ (and CO₂) fluxes across the Russian Arctic (30, 31). The second approach is realized in a number of field stations where gas fluxes are measured mainly during the summer season (32–35).

The general tendencies of spatial and temporal flux variation can be formulated as follows. Firstly, there are evident temperature related variations: even within northern wetlands the highest net fluxes occur in warmer soils, the maximal values being attained in the boreal zone. This trend is especially evident in respect to methane, the gas emission increasing along the sequence Barrow-Toolik Lake-Fairbanks, or Taimyr – Surgut – Tomsk. Seasonal variations also follow a temperature dynamics curve, although winter, autumn and spring emissions are often measur-
able (1, 18). A transect of seasonal measurements of CH\textsubscript{4} emissions from five different wetland sites from NE Greenland over Iceland and Scandinavia to Siberia also showed a clear positive relationship with the mean seasonal temperatures of the sites (36). Secondly, there is always enhanced emission from wetland patches covered by vascular plants (\textit{Eriophorum, Carex, Menyanthes}) as compared with pure Sphagnum lawn (the effects of vascular plants; (18)). Thirdly, variations in the watertable from industrial impacts). These data are fitted to a three-dimensional atmospheric transport model, which is combined with a tropospheric background chemistry module and accounts for all essential sources and sinks of gases. The model is validated against an “internal standard” such as methyl chloroform. Presently, available results of inverse modeling (38) do not deviate significantly from data obtained by the bottom-up approach. The contribution of high latitude regions (> 60\degree N) to the global methane source was less than 13\% or 70 Tg yr\textsuperscript{-1}, and northern wetlands are responsible for emissions of less than 30 Tg of CH\textsubscript{4} yr\textsuperscript{-1}. At first sight, such a conclusion contradicts the latitudinal gradient of atmospheric methane that has a well-expressed maximum in the North. But the build-up of methane in air over high latitudes is explained also by a low content of OH and, hence, lower rates of temperature-controlled photochemical reactions that break down the atmospheric CH\textsubscript{4}.

Relative Contributions of CH\textsubscript{4} and CO\textsubscript{2} to Carbon Budget and Their Importance

The formation of CO\textsubscript{2} and CH\textsubscript{4} are a result of aerobic and anaerobic decomposition, respectively. The ratio of respired CO\textsubscript{2} to CH\textsubscript{4} is hence an indication of how reduced the soil environment is. An increasingly reduced soil environment (i.e. higher CH\textsubscript{4}/CO\textsubscript{2} ratio) also leads to slower overall decomposition rates as the anaerobic decomposition is less efficient in absolute C terms compared to aerobic decomposition. This is what generally leads to a build up of stored organic carbon in wet tundra soils as the net primary production is not normally limited by wet soil conditions to the same extent as the respiration.

The net CH\textsubscript{4}/CO\textsubscript{2} ratio of the total respiration is also a function of the amount of CH\textsubscript{4} that is oxidized in the aerobic soil layers above a given anaerobic zone of production and even the possible atmospheric CH\textsubscript{4} uptake that takes place in some dry tundra soil environments. The CH\textsubscript{4}/CO\textsubscript{2} ratio or the % contribution of CH\textsubscript{4} to the total respired carbon varies from < 1\% in dry ecosystems to > 20\% in extreme cases in wet tundra ecosystems. Typical annual average contributions of CH\textsubscript{4} to the total C flux lies in the range 2–10\% for wet tundra and northern wetlands (e.g. 39–43).

It is very important in a climate change context to note that the relative contribution of CH\textsubscript{4} as a greenhouse gas to the total radiative forcing is much stronger on a per molecule basis than CO\textsubscript{2} (44). The so-called global warming potential (GWP) indicates how many times stronger a given greenhouse gas is to CO\textsubscript{2} on a per molecule basis and this is dependent on a particular time horizon. For example over a 100 year time horizon, the GWP of CH\textsubscript{4} is 23 and with a 20 year horizon it is 63 (44).

From a global warming perspective it is, hence, not very informative only to look at the carbon balance of any ecosystem if this exchanges CH\textsubscript{4} or other greenhouse gases such as N\textsubscript{2}O (45). Calculations have shown that ecosystems such as the huge western Siberian lowlands, despite being strong sinks for carbon, are sources of radiative forcing due to the considerable CH\textsubscript{4} emissions (46). Data are, however, scarce when it comes to full annual budgets of both CO\textsubscript{2} and CH\textsubscript{4} fluxes from tundra regions. Figure 1 shows calculations based on accumulated continuous eddy correlation measurements of CO\textsubscript{2} and CH\textsubscript{4} fluxes in the Zackenberg valley during 1997 (12, 47). The figure illustrates that a net carbon accumulation (“minus” in the accumulated budget) during the season is completely cancelled out in effect if CH\textsubscript{4} is calculated and added as CO\textsubscript{2} equivalents using the 20-yr time horizon. Using the 100-yr time horizon the ecosystem is still a small sink of CO\textsubscript{2} equivalents at the end of the growing season. However, given the autumn and winter fluxes which are entirely sources but are not in the figure, the annual total will probably add up to a source as well.

\begin{figure}[h]
\centering
\includegraphics[width=0.5\textwidth]{figure1.png}
\caption{Accumulated carbon and greenhouse warming potential from CO\textsubscript{2} and CH\textsubscript{4} exchanges calculated as CO\textsubscript{2} equivalents throughout the summer of 1997 at Zackenberg, Northeast Greenland (data from Søgaard et al. (12) and Friborg et al. (47)).}
\end{figure}

In general, due to the predominantly wet soil conditions in the most productive tundra areas, there are significant CH\textsubscript{4} emissions there. It is most likely that, at the landscape, regional and global scales, the tundra represents a source of radiative forcing due to CH\textsubscript{4} emissions being the most important greenhouse gas driving the ecosystem influence on atmospheric radiative forcing.

\section*{CURRENT CIRCUM-ARCTIC WATER AND ENERGY BALANCES}

Arctic ecosystems exhibit the largest seasonal changes in energy exchange of any terrestrial ecosystem because of the large changes in albedo from late winter, when snow reflects most incoming radiation (albedo about 0.7), to summer when the ecosystem absorbs most incoming radiation (albedo about 0.15). This change in albedo combined with the greater incoming solar radiation in summer than in winter causes much greater energy...
absorption in summer than in winter. About 90% of the energy absorbed during summer is transferred to the atmosphere, with the rest transferred to the soil in summer and released to the atmosphere in winter (48). Also, snow within shrub canopies is deeper and less dense, which reduces heat transfer through the snowpack and increases winter soil temperatures by 2°C relative to adjacent shrub-free tundra. Consequently, Arctic ecosystems have a strong warming effect on the atmosphere during the snow-free season, and any increase in the duration of snow-free conditions results in a strong positive feedback to regional climate warming (49, 50).

Climate influences the partitioning of energy between sensible and latent flux. Cold moist air from coastal oceans, for example, minimizes latent heat flux (evapotranspiration), as does extremely warm dry air, which can induce stomatal closure (48, 51); evapotranspiration is therefore greatest at intermediate temperatures. Conversely, sensible heat flux is a larger proportion of the energy transfer to the atmosphere when air is cold and moist or when drought limits stomatal conductance under dry conditions. Heat that is conducted into the ground during summer is released to the atmosphere in winter, with any seasonal imbalance causing changes in permafrost temperature and probability of thermokarst (52).

There are large regional differences among Arctic ecosystems in energy exchange and partitioning. Albedo during the period of snow cover is extremely high in tundra and declines with increasing development of a plant canopy above the snow from tundra to shrub tundra, to forest tundra to deciduous forest to evergreen forest (53). These differences in albedo are an important feedback to climate during spring, when the ground is snow-covered, and incoming radiation is high. As a result of differences in albedo and sensible heat flux, forests at the Arctic treeline transfer about 5 W m⁻² more energy to the atmosphere than does adjacent tundra (54). This vegetation difference in energy transfer to the atmosphere is an order of magnitude less than the heating contrast which had been hypothesized to be required for treeline to regulate the position of the Arctic Front (55). Thus, the location of the Arctic front is more likely to govern the position of treeline than the other way around (56).

LARGE-SCALE PROCESSES AFFECTING FUTURE BALANCES OF CARBON, WATER AND ENERGY

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

Permafrost Degradation

Soil carbon storage is greatest where the drainage is slight and the limited precipitation is held near the surface by permafrost and modest topography. This results in ponds, wetlands, and moist tundra with a saturated seasonal active layer that limits microbial activity. Increases in the active layer can cause subsidence at the surface, a lowering of the soil watertable (57), and, potentially, thermokarst erosion (58). This can drain surrounding areas, often increasing the decomposition rate of soil organic matter which accelerates the loss of belowground carbon stores (59, 60) and results in a change in plant communities and their abilities to sequester atmospheric CO₂. Initially, increased soil decomposition rate can increase mineralization rates (61) and result in increased net primary productivity (1). However, continued thawing of permafrost and increased drainage of surface water in areas with low precipitation could lead to a drying process, a decrease in NPP and even desertification (see below).

Full permafrost disintegration in subarctic discontinuous permafrost regions may in some cases show a rather different response. Monitoring of changes in permafrost distribution in sub-Arctic Sweden as part of the Circumpolar Active Layer Monitoring Program (CALM: 62), shows that permafrost loss causes mires to shift from ombrotrophic moss and shrub-dominated systems to minerotrophic wet vascular plant-dominated systems (43, 63). This, in turn, leads to a significant lowering of soil redox potentials, an increase in anaerobic decomposition, and increased methane emissions. Wet minerotrophic soils and vegetation are in general associated with the highest methane emissions in subarctic and Arctic tundra environments. Discontinuous permafrost regions are considered some of the most vulnerable to climate warming, so with the predicted warming over the next 100 yrs effects such as the one listed above are expected to be strong.

Permafrost degradation and disintegration will therefore, have major effects on ecosystem C balances and methane emissions. The rate of permafrost thawing, the amount of ground surface subsidence and the response of the hydrologic regime to permafrost degradation all depend on numerous site characteristics. Changes in hydrological regime will also alter the soil thermal regime. In areas of significant topographic variations, flowing water can carry heat into drainage channels causing increased soil temperatures and increased active layer thickness (64, 65).

In regions with minor topographic variations, subtle differences in elevation can create cooler, saturated wetlands (as mentioned above) or markedly drier, warmer uplands (66).

Changes in Circumpolar Vegetation Zones

While climate-driven changes in the structure and the distribution of plant communities affect trace gas fluxes and water and energy at the landscape scale (1), changes in the location and extent of broad vegetation zones is a long-term integrative process that is likely to potentially lead to regional and even global impacts on feedbacks to the climate system (67–70). Such vegetation zone changes will probably also affect permafrost dynamics (Chapter 6 in ref. 3), biodiversity (71, 72) and ecosystem services (73). Past climate-driven changes in vegetation zones such as forest and tundra (2, 74) lead us to expect that future climate-warming will result in vegetation and ecosystem change, but predicting future changes is complex and relies on modeling.

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

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

The treeline stretches for more than 13 000 km around the Northern Hemisphere and through areas that are experiencing different types of environmental change for example, cooling, warming, marginal temperature change and increasing compared with decreasing land use. However, climate is only one of a suite of environmental factors that are now changing and a critically important challenge is to determine how human impacts on the ecotone will modify the zone’s expected response to climate (73).

The lack of standardization of terminology and the wide variation in methodology applied to locate, characterize, and observe changes in the boundary have resulted in a rather poor understanding of even the current location and characteristics of the boundary. Particular areas of uncertainty include the Lena Delta of Siberia (75) and forests in Iceland that have been subjected to major environmental and land-use changes since colonization by people from 1100 years ago. One of the major problems in the current studies of the latitudinal “treeline” is the concept of “line” inappropiately applied to the transition from forest, through an area dominated by forest in which patches of tundra occur, to tundra in which patches of forest occur, and then eventually to tundra without trees. Often there are East-West gradients related to the
presence of a river valley, bogs, mires, uplands, etc. which also confound the concept of a linear boundary.

**Dynamics of the boundary**

Current and projected changes in the location of the tundra-taiga boundary should be seen in the context of the longer term past cooling trend during which the treeline has been at its lowest locations for several thousands of years (2). Examples of recent treeline advance include upward displacements of the sub-Arctic treeline of 40 m during the 20th century in northern Sweden (76–79), an increase in shrub growth in Alaska (80), and an increase in shrubbiness and larch advance in the Northeast Russian European Arctic (Katenin, unpubl.). In contrast, other studies show a surprising displacement to the South of the tundra-taiga boundary (73, 81, 82). Part of this is a counter-intuitive response to warming in which increasing oceanicity together with permafrost thawing and water-logging have led to paludification and the death of tree line trees (83). Part is associated with human activities including mining, farming, forestry, that have led to ecosystem degradation in the forest tundra zone and the movement of its northern boundary southwards in some locations (73). In the Archangelsk region and the Komi Republic, the southern border of the forest tundra zone now lies 40 to 100 km further south than when previously surveyed. One report claims that human-derived tundra now covers about 470 – 500 000 km² of the forest tundra stretching from Archangelsk to Chukotka (73), although it is likely that this estimate includes deforestation in some of the northern boreal forest zone.

Although records of recent changes in the location of the latitudinal treeline are surprisingly rare, there is good evidence of increased growth of current northern forests. Comparisons of the greenness index (NDVI) from satellite images show that May to September values for the Northern Hemisphere between 55 and 75°N increased by 12.5 to 9.3%, respectively (84; Fig. 3 in ref. 71). The increases were larger in North America than in Eurasia. The increased greenness was associated with an increase in growing season length of 4.3 to 3.8 days for the circumpolar area mainly due to an earlier start of the growing season.

**Predicting Future Changes in the Tundra-Taiga Boundary**

In order to model changes in the location of the tundra-taiga ecotone and to estimate future areas of tundra to the north and taiga to the south, it is necessary to understand the causes of the treeline. Opinions on the mechanisms controlling the location of the treeline vary greatly. Some researchers see the limit of tree growth as a universal mechanism related to a specific process such as sink limitation (85, 86) or carbon limitation (87). Others see a range of possible mechanisms that operate in different places and at different times (88). These mechanisms are in turn affected by environmental factors such as incident radiation, temperature, wind, moisture and soil nutrients, which exert their impacts on tree reproduction, seedling establishment and the growth and physiology of mature trees. Extreme conditions such as ice crystal abrasion and soil movement also directly damage tree tissues such as conifer needles and displace individuals. Diseases, pests, fires and human activities all exert some control on the treeline at certain places and at certain times (Chapter 14 in Callaghan et al. (3)).

Models of vegetation redistribution resulting from global change operate on more general mechanisms such as biogeography and biogeochemistry. Most current global vegetation models and regional models suggest that a major part of the tundra (between 11 and 50% according to location) will be displaced by an advance of the boreal forest over the period in which atmospheric CO₂ will double (67, 83, 89; Table 1; Table 1 in ref. 90). Treeline is predicted to advance in all sectors of the Arctic, and even in Greenland and Chukotka where only fragments of forest exist today (89). However, this rate, or type, of forest response has been recorded less than would be expected even though temperature has already risen dramatically in some areas.

The observations of the latitudinal treeline noted above that show a recent southern displacement of the treeline suggest that there will very probably not be a general northwards displacement of the latitudinal treeline throughout the circumpolar region as the models suggest. In addition to possibilities of paludification (81) and local human activities displacing treelines southwards, permafrost thawing, surface-water drainage and drying of soils in areas of low precipitation are likely to lead to the formation of tundra steppe-like vegetation (91). Increased disturbance such as pest outbreaks, thermokarst, and fire are likely to also locally affect the direction of treeline response. In addition, some tree species show reduced responsiveness to increases in temperature with increasing continentality of their location and decreased precipitation (92; Chapter 14 in Callaghan et al. (3)): this suggests that increased temperatures in combination with no comparable increase in precipitation will probably lead to reduced tree growth and/or change in species and lack of treeline advance. Even in areas expected to undergo warming with none of the moderating factors listed above, it is uncertain if the rate of tree migration can keep up with the rate of increases in expected warming. Past tree migration rates were generally in the order of 0.2 to 0.4 km yr⁻¹ but could reach 4.0 km yr⁻¹ (2, 74). Such rates would suggest that those areas of the Arctic that have warmed substantially in the last 30 years should have already seen an advance of treeline of about 6 to 120 km. Such observations have not been recorded in the Arctic, although Parmesan and Yohe (93) claim to have identified a poleward displacement of species ranges of 6.1 km per 10 years globally.

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

Projections of changes in vegetation in the northern areas of the Arctic have been made by the LPJ model (24; Table 1 in Callaghan et al. (90)) for the ACIA process. Although the results and interpretations are preliminary, model runs for B2 scenarios of the CCC, GFDL, HadCM3 and ECHAM4 GCMs are consistent in showing a decrease in the area of polar desert that will be replaced by northward moving tundra (Table 1). Compared with a starting date of 1960, the area of the Arctic covered by polar desert is predicted to decrease by 17.6% (range 14 to 23%) by 2080. In this model, the two vegetation zones were defined by plant functional types: woody species for the tundra, and absence of woody species for the polar desert. In the BIOME model simulations by Kaplan et al. (89), and driven by the HadCM2-SUL GCM using the IS92a greenhouse gas scenario, 5 tundra biomes were constructed (Table 1 in ref. 71). The most significant changes appear to be a significant northward advance of the cold evergreen needleleaf forest that is particularly dramatic in the region of Arctic Russia between Chukotka and the Taymyr peninsula. This greatly reduces the area of tundra. However, low and high shrub tundra in the Canadian Arctic Islands remains as a wide zone and displaces prostrate dwarf shrub tundra (Fig. 2) (See also Fig 2 in Callaghan et al. (4)). Earlier modeling by White et al. (23) predicted that the area of tundra would be halved by forest expansion by 2100.

PROJECTIONS OF FUTURE BALANCES OF CARBON, WATER AND ENERGY EXCHANGE

Because the Arctic contains huge stores of carbon in the soil and permafrost (1), and because the Arctic has capacity for unlimited additional storage or significant loss (94, 95), it can be a major positive or negative feedback on increasing trace gas concentrations in the atmosphere and on global warming. Loss of CO2 from Arctic ecosystems could lead to enormous positive feedbacks on global warming by release to the atmosphere of the estimated 250 GtC from the large Arctic soil pool (6–8, 94, 96, 97, 98). In addition, an increasing snow-free period (99, 100), increasing shrub cover (80, 101, 102), and the northerly migration of treeline (103) would act to decrease Arctic albedo and further increase regional warming (49, 68, 104–107). Below, we assess likely changes in balances of carbon, water and energy exchange in relation to vegetation change.

Projected Changes in Carbon Balance

Using the vegetation distribution model, BIOME 3, for current and 2 x CO2 scenarios, changes in extent of the Scandinavian, central northern Siberian and Eurasian tundra areas were calculated as between 10% and 35% as a result of displacement by taiga (67). This process was calculated to significantly increase CO2 drawdown and to significantly reduce CH4 emissions with a net result in favor of carbon sequestration in the biosphere of a magnitude that would alter the radiative forcing of the Earth. Using another model, McGuire et al. (21) estimate circumpolar mean carbon uptake to increase from a current 12 g C m2 yr–1 to 22 g C m2 yr–1 by the end of the period (2100) because NPP is increasing more than respiration throughout the period (21). It should be noted, however, that throughout the 200-year model run, the standard deviation always crosses the zero line (21). White et al. (23) produced comparable results from their Hybrid v4.1 model, predicting that high latitude terrestrial ecosystems would remain a sink for carbon.

The Dynamic Global Vegetation Model (DGVM) LPJ (24) was used to produce ACIA-exclusive estimates for future changes in Arctic carbon storage and fluxes based on four different GCM outputs. The results and analyses are preliminary but indicate a consistent net further sink of the Arctic in 2080 compared to 2000 with global Arctic C storages varying between +12 Gt C and +31 Gt C depending on the climate scenario used. Figure 3 shows the predicted carbon storage anomalies as predicted by LPJ and Table 1 in Callaghan et al. (90) shows further details of the regional subdivision of these outputs.
There are great uncertainties associated with these estimates due to the complex differential response of NPP and respiration to the climate drivers (temperature, precipitation), which themselves are highly spatially variable and interact. But the general response of the model seems to be as follows. In areas with no or little vegetation (e.g., polar desert), increasing CO2 and temperature (e.g., increasing growing season), lead to increased vegetation growth and northward plant migration, leading to an increase in future productivity throughout the Arctic, all else being equal (see NPP predictions in Table 1). However, increased temperature leads also to increased heterotrophic (soil microorganisms) respiration. Therefore, areas, which at present contain large soil carbon stocks will release larger amounts of carbon from the soil as the respiration is responding to a warmer climate. Whether these areas are net sources or sinks depends on the balance between increased productivity (hence increased biomass and litterfall), due to increased CO2, longer growing seasons, and temperature enhanced respiration. When LPJ is forced with the climate prediction of ECHAM4 which produces very large temperature increases, respiration is enhanced more than productivity. Over the entire Arctic, carbon storage is balanced, due to northward migration of plants, etc, with carbon loss in areas which experience large temperature changes and have large stocks of soil carbon. On the whole the result is that all runs with the model agree on an increased carbon gain. The "warmest" GCM, ECHAM4, predicts overall the lowest carbon gain, and the "coldest" CCC the highest carbon gain.

| Table 1. Average and ranges of the drivers and responses of a leading Dynamic Global Vegetation Model, the LPJ model (24) to the forcing of outputs from four different climate models (CCC, GFDL, HadCM3, Echam4) run for the Arctic (i.e. terrestrial > 60° N). |
|---|---|---|
| Temperature change (°C) | Average | Range |
| 2100–2000 | 5.0 | 4.7–5.7 |
| 2100–2000 | 42.9 | 9.04–78.0 |
| Precipitation change (mm yr⁻¹) | | |
| 2050–1960 | 7.4 | 4.7–5.19 |
| % change | 72.4 | 60.9–87.4 |
| Change in C storage (Pg C) | | |
| 2080–1960 | 5.73 | 3.59–7.65 |
| Vegetation C | | |
| 1960s | 2.83 | 2.77–2.88 |
| 2080s | 4.87 | 4.57–5.19 |
| Soil C | 6.98 | 1.6–15.6 |
| Litter C | 5.6 | 3.4–9.6 |
| Total C | 18.3 | 12.2–91.3 |
| Percent areal vegetation change* | | |
| Taiga v tundra† | | |
| 2020–1960 | 4.4 | 3.1–5.3 |
| 2050–1960 | 7.4 | 6.4–8.4 |
| 2080–1960 | 11.3 | 9.8–14.4 |
| Polar desert v tundra‡ | | |
| 2020–1960 | -7.5 | -13.3–4.2 |
| 2050–1960 | -13.2 | -18.5–10.6 |
| 2080–1960 | -17.6 | -23.0–14.2 |

* Only a proxy as the change is derived from functional characteristics of the vegetation produced by the model rather than predictions of specific vegetation composition per se. For a proper vegetation distribution estimate it would be more appropriate to use a dedicated biogeographical model such as BIOME4.
† Based on percentage increase in woody plants produced by LPJ.
‡ Based on the percentage reduction in bare-ground produced by LPJ.

The current estimated circumpolar emissions of CH4 are in the range 20–60 Tg CH4 yr⁻¹. These have a significant potential for feedback to a changing climate. Large-scale CH4 flux models are currently not as advanced as general carbon cycling models and few allow for climate change scenario-based projections of changes in the future. Early attempts to assess and model tundra CH4 emissions driven by climate change all indicated a potential increase in emissions (109–111), but more recent improved mechanistic models (112, 113) have not yet been followed up by full coupling to GCM predictions to assess the circumpolar CH4 emissions in the future. A critical factor is not only the mechanistic responses of soil processes but also the geographical extent of wetlands and how these may change in the future. There is, however, little doubt that with climate scenarios of warming and wetting of the Arctic soils, there will undoubtedly be increases in CH4 emissions while with warming and drying there will be few changes or a decline of emissions relative to the current scale. Lakes and streams cover large portions of many Arctic landscapes and, due to low evapotranspiration, runoff is a major component of Arctic water budgets. These surface freshwaters contain large amounts of dissolved organic and inorganic C that is carried into them by soil and groundwater flow from the terrestrial portions of their watersheds (114, 115). The inorganic C is largely CO2 produced by soil and root respiration. Organic C concentrations in soil-water, groundwater, and surface waters are typically several times greater than inorganic C concentrations and are a major source of respiratory CO2 produced in lakes and streams, thus adding to their already high dissolved inorganic C content. Because the dissolved CO2 in surface waters is typically supersaturated with respect to the atmosphere, and the surface area and flow of freshwater is large, surface waters of Arctic landscapes lose large amounts of CO2 to the atmosphere (116; Chapter 8 in ref. 3). Estimates of CO2 emissions from surface waters are as large as 20–25% of gross landscape CO2 fixation and thus may be a major component of landscape C balance that is not accounted for in studies that include terrestrial CO2 fluxes only. Similar large CO2 losses also occur in freshwaters of boreal, temperate, and tropical landscapes (117), but they are generally not considered in landscape-level C budgets. At present, little is known of controls over these CO2 losses or how they might change with changes in climate or water balance. Attempts to measure the losses directly have yielded inconsistent results (118).

Projected Changes in Exchanges of Energy and Water

Many of the likely changes in water and energy exchange that occur in response to projected future warming will likely act as a positive feedback to warming. Earlier disappearance of snow from the tundra will lead to a decline in albedo and an increase in regional warming (104, 105). Similarly, an expansion of forest will lead to a reduction in albedo, because trees mask a snow-covered surface. In areas where forest expansion occurs, this will lead to significant heating of the lower atmosphere (1). Paleoclimate modeling experiments have shown that the northward movement of treeline 6000 yr BP accounted for half of the climatic warming that occurred at that time (49). Although the current Arctic treeline appears relatively stable or to be retreating in some areas of human impact (73, 75), any future northward advance of treeline will likely contribute to regional warming or treeline retreat would contribute to regional cooling, particularly in late spring due to the large differences in albedo between snow-covered tundra and adjacent forest.

A positive feedback (leading to increased warming) of displacement of tundra by trees and shrubs will tend to offset the negative feedback (leading to cooling) due to increased carbon sequestration at the local level (67), but the climate forcing by energy and water exchange operates primarily at the regional scale, where the energy exchange occurs, whereas the negative feedback due to atmospheric carbon sequestration will likely vary between regions and will contribute to warming through changes in the globally mixed pool of atmospheric CO2. Models suggest that forests in the eastern Canadian Arctic would show a net negative feedback through sequestration of carbon whereas forests in Arctic Russia would have a net positive feedback to climate through decreased albedo (53, 69). This complex balance between opposing feedbacks indicates that encouraging forest to displace tundra as an appropriate mitigation strategy against global climate change should take into account the local feedback.
An important contributing factor to the effect of vegetation change on albedo is the characteristics of the plant canopy in terms of canopy height relative to snow height, leaf duration, and leaf optical properties. The greatest changes in albedo will occur in terms of canopy height relative to snow height, leaf duration, and change on albedo is the characteristics of the plant canopy in

the active layer in the soil and in vegetation, and not that trapped in permafrost and methane hydrates.

CONCLUSIONS

Biological and physical processes and phenomena in the Arctic system such as exchanges of energy, water and greenhouse gases between biosphere and atmosphere have impacted large-scale feedbacks and interactions with the earth system in the past. These processes are sensitive to changes in climate and future warming has the potential to alter biological systems and processes in such a way as to profoundly modify local and regional climate. However, complex interactions between processes contributing to feedbacks, variability over time and space in these processes, and insufficient data have generated considerable uncertainties in estimating the net effects of climate change on terrestrial feedbacks to the climate system. This uncertainty applies to magnitude, and even direction of the feedbacks. Because of the great potential importance of the feedbacks, it is necessary to analyze the uncertainties and to recommend research and monitoring that will reduce them (120).

References and Notes
