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Ecosystem responses to recent climate change and fire disturbance at northern high latitudes: observations and model results contrasting northern Eurasia and North America

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Abstract
Vegetation composition at high latitudes plays a critical role in the climate and, in turn, is strongly affected by the climate. The increased frequency of fires expected as a result of climate warming at high latitudes will feedback positively to further warming by releasing carbon to the atmosphere, but will also feedback negatively by increasing the surface albedo. The net effect is complex because the severity of fire affects the trajectory of both carbon stocks and albedo change following a fire, and these are likely to differ between high latitude ecosystems in North America and northern Eurasia. Here we use growth trajectories, productivity trends and regional carbon fluxes to characterize these fire- and climate-driven changes.

Keywords: albedo, climate, ecosystem, disturbance, energy budget, forcing, productivity, regrowth, response, feedbacks

1. Introduction
Temperature increases over the past few decades in the northern high latitudes, especially above 50°N (Hansen et al 2006), have led to a wide variety of ecosystem changes, including modification of plant productivity (Goetz et al 2005, Zhang et al 2007), latitudinal treeline advance (Lloyd et al 2005), increasing shrub density (Sturm et al 2001, Tape et al 2006), and a range of other documented responses (Hinzman et al 2005, Walker et al 2006). More favorable conditions for both insect and fire disturbance have resulted in well documented increases in the frequency, intensity, seasonality and extent of disturbance (e.g. Stocks et al 2002, Kasischke and Turetsky 2006, Werner et al 2006, Johnstone and Kasischke 2005, Soja et al 2007). These trends are likely to continue with warming and drying in continental interiors (Flannigan et al 2005).

Although increases in disturbance will lead to a net release of carbon in the short term and thus contribute to climate warming, the amount of carbon released is inseparably linked with changes in the age distribution and species composition of northern forests. Shifts in species composition, in turn, have the potential to influence the regional climate via a suite of biophysical mechanisms, including effects on spring and summer albedo and rates of surface conductance and evapotranspiration (Amiro et al 2006). Thus, an integrated analysis of carbon accumulation and surface energy fluxes over successional cycles is needed for understanding the role of northern forests in climate warming. Such an analysis is challenging because of the multiple pathways in which...
fires influence vegetation succession. A strong deciduous phase in the intermediate stage of succession, for example, may simultaneously increase the surface albedo and rates of biomass accumulation during the first few decades after a fire, both tending to act as negative feedbacks to climate warming. In contrast, in a conifer-dominated successional trajectory, the post-fire increase in the surface albedo may be smaller and carbon may accumulate at a slower rate. To the degree that burn severity regulates the establishment of conifer and deciduous tree species within burn perimeters (Johnstone and Kasischke 2005), it plays a critical role in determining the long-term impacts of high latitude fire regimes on the climate.

Here we examine how the coupled changes of fire disturbance and vegetation regrowth alter radiative forcing of the climate system at high latitudes. We first examine how the ecosystems of northern Eurasia and North America have responded to recent climate change, making use of satellite remote sensing and atmospheric transport models of net carbon exchange. We then explore how fire disturbance alters the vegetation composition and surface albedo, an important radiative forcing agent, also making use of remote sensing observations through time. Finally, we consider the links between the severity of disturbance and different pathways of vegetation recovery with time. The data and analyses suggest that the forests of northern Eurasia and North America, although both a part of the boreal forest biome, are responding differently to changes in climate and the disturbance regime. The different responses are, perhaps, not surprising. North America and northern Eurasia differ substantially in fire regime (figure 1) and the amount and type of vegetation cover, whether deciduous or evergreen, conifer or broadleaf and, as a result, have different successional trajectories, involving different patterns of albedo, productivity and carbon sequestration.

2. Observed ecosystem responses in northern Eurasia versus North America

Differences in ecosystem responses to climate change and associated disturbance in northern Eurasia versus North America have been noted at regional scales in satellite observations of gross productivity changes, and in models of net carbon exchange resolved from atmospheric transport models. We briefly summarize these findings before exploring some of the possible proximate causes for these observations.

2.1. Satellite observations of trends in high latitude productivity

Analyses of productivity indices from satellite image observations at high latitudes indicate that past evidence for ubiquitous ‘greening’ trends (Myneni et al 1997, Nemani et al 2003) have not remained consistent through time or uniform in space (Goetz et al 2005, Bunn and Goetz 2006). Tundra vegetation in both northern Eurasia and North America experienced an increase in both peak productivity and growing season length between 1982 and 2005 (figure 2), a finding supported by a wide and increasing range of local field measurements characterizing elevated net CO₂ uptake, greater depths of seasonal thaw, changes in the composition and density of herbaceous vegetation, and increased woody encroachment in the tundra areas of North America (see discussion in Goetz et al 2005). In contrast, and surprisingly, many (more than 25%) forested areas of North America not recently disturbed by fire experienced a decline in productivity and showed no systematic change in growing season length, particularly in recent years (post 2000). Very
few (less than 4%) undisturbed forest areas showed positive trends in productivity. Climatic warming occurred across the entire circumpolar region, but the change in the forest response indicated that neither the intensity nor the length of the growing season changed in a way that reflected a simple relationship with increasing temperature or CO₂. The productivity trends in forested areas were most evident in the latter part of the growing season, indicating impacts of late summer drought (vapor pressure deficit, VPD) on stomatal control and photosynthesis. Moreover, more densely forested areas were significantly more likely to show strongly negative productivity trends (Bunn and Goetz 2006), particularly those areas with a greater density of larch in northern Eurasia and in black spruce forests of North America (figure 3). These observations are supported by other recent work comparing anomalies in modeled net productivity to those in gridded climate data (Zhang et al 2007).

Further, an extensive analysis of the tree ring record (Lloyd and Bunn 2007) shows that the Picea species which dominate North America (particularly Picea mariana) respond negatively to temperature increases (i.e., browning), particularly in recent decades. Although the onset of photosynthesis by Picea mariana is advanced during warm springs, eddy flux measurements provide evidence that, integrated over the growing season, gross primary production does not substantially increase, possibly as a result of greater mid-summer drought stress (Welp et al 2007). Larix species common to northern Eurasia (particularly Larix sibirica) were significantly less likely to exhibit a browning response, but higher than expected frequency of browning occurred in dry continental interiors, indicating a response to moisture stress associated with increased evapotranspirative demands at higher temperatures (Bunn et al 2007). In forested areas that were impacted by fire, regrowth trajectories and productivity recovery times appear to differ between northern Eurasia (Balzter et al 2005) and North America (Goetz et al 2006).

In the latter, a database of large fire disturbances was used to document recovery times (for vegetation indices to return to pre-burn levels) that averaged about 6 years, which was shorter than previous estimates of 9 years (Amiro et al 2000, Hicke et al 2003). The reasons for the difference in recovery times is likely due to the way that spatial variability within burned areas was accounted for in the remote sensing analysis (e.g., sampling the most impacted areas or instead using values more indicative of average burn severity within given fire boundaries). Both of these approaches provide insight into the recovery of vegetation following different intensities of fire disturbance. We note, however, that structural attributes of vegetation (e.g., biomass) take much longer to recover after fire disturbance than functional attributes (e.g., leaf area or canopy light harvesting), particularly in stand-replacing fires. Spectral vegetation indices from optical remote sensing are primarily (albeit not exclusively) sensitive to the functional attributes of vegetation (Goetz 2002).

In northern Eurasia, specifically central Russia, recent results using moderate resolution imaging spectroradiometer (MODIS) observations across a broad range of stand-replacing burned areas suggest recovery times on the order of 13 years for areas that were previously evergreen conifer or deciduous broadleaf cover (Cuevas et al 2008). In this analysis specific fires were not tracked through time; rather time since the fire was used to effectively trade space for time, and a series of burns thus provided a chronosequence (comparable to earlier analyses in North America by Amiro et al 2000). The longer recovery times may be related to the tendency for more intense stand-replacing fires in northern Eurasia.

The results of studies in both northern Eurasia and North America further indicate that the variability within fires can be as great as between them, partly because not all fires are contained within forested areas, but cross into grassland, peat bogs, fens and other land-cover types (Soja et al 2007). Assuming that these land-cover types burn at different levels of severity associated with surface conditions and fuel loads, and also that they recover differently from fire disturbance, recovery times reflect the integrated ecosystem response to the heterogeneity of fire behavior and must be considered when conducting comparisons between regions.

2.2. Atmospheric transport model simulations of net carbon exchange

The interannual variability of atmospheric CO₂ fluxes suggests that the high latitudes of North America and northern Eurasia also differ in their relationship between net carbon exchange and climate variability. The results presented here represent the mean of 13 participating modeling groups in the Transcom 3 inversion experiment, and reflect CO₂ observations spanning the 1980 to 2006 time period (Gurney et al 2003). The inclusion of a number of different transport models allows for some assessment of uncertainty due to transport within the inversion approach and makes it possible to examine a mean inversion result (Gurney et al 2002). The inversion results have been deseasonalized, detrended, normalized to zero mean, and standardized in order to focus on interannual variability.
Figure 4. (Left) Lagged correlation (two-, one-, zero-month lags) between the inverse-estimated spring (MAM) boreal North America net carbon exchange anomalies and spatially explicit spring temperature anomalies. (Right) Same as for left panels but for precipitation rather than temperature. Lags and leads of one month, not shown here, were also significant. The anomalies have been deseasonalized, detrended and standardized. Only correlations that achieved 95% statistical significance are shown.

It is important to note that these results contain no carbon cycle mechanisms. The inversion methodology simply distributes net carbon exchange in space and time to obtain consistency with the atmospheric CO₂ observations and the atmospheric transport algorithms.

Regional aggregated temperature and precipitation time series for the time period 1980–2006 (Kalnay et al 1996) were directly related to the net carbon fluxes in the two regions, and revealed distinct seasonal relationships. Fall (SON) northern Eurasia carbon exchange anomalies (the sign convention is that a positive flux anomaly is out of the land surface) were positively correlated with warm ($r = 0.65; p < 0.02$) and wet ($r = 0.64; p < 0.02$) conditions. In contrast, spring (MAM) boreal North America carbon exchange anomalies were negatively correlated with warm ($r = -0.67; p < 0.02$) and wet ($r = -0.72; p < 0.02$) conditions (i.e., warmer and wetter springs caused more ecosystem uptake). These observations in North America are consistent with earlier findings of Randerson et al (1999) documenting strong negative correlations between inversion-estimated fluxes and warmer spring temperatures.

These results were explored further by considering the spatial patterns of carbon exchange anomalies as related to gridded time series information for temperature and precipitation (Kalnay et al 1996). Figure 4 shows the monthly mean patterns that emerge for spring boreal North American carbon exchange and global gridded spring temperature anomalies, starting with a two-month lag (temperature anomaly followed two months later by carbon anomaly). Only correlations achieving 95% statistical significance are included, and temporal autocorrelations are accounted for through a reduction in the degrees of freedom (after Bretherton et al 1999). As in the aggregate analysis, negative spring boreal North America carbon exchange anomalies (net exchange from atmosphere to land) were negatively correlated with temperature anomalies. These correlated temperature anomalies began in winter in the tropical Pacific and migrated to the western portion of boreal North America, then moved eastward before losing significance.

A similar relationship was noted for precipitation (figure 4). In this case, the net carbon exchange anomalies were related to precipitation anomalies primarily within the boreal North American region, with some significant correlation to tropical Pacific anomalies at a zero lag. In contrast, the fall northern Eurasian net carbon exchange was positively correlated (net exchange from land to atmosphere) with warm and wet conditions in the fall months (figure 5). These correlations were widespread in northern Eurasia and coincident in both space and time. Recent analyses indicate the temperature variability in central Eurasia may be associated with the arctic oscillation and the precipitation variability in eastern Eurasia may be coincident with El Nino/Southern Oscillation (ENSO) (Balzter et al 2007).

The spatial pattern of the relationship between the spring boreal North American anomalous fluxes and temperature at a lag of one to two months suggests a relationship with ENSO.
activity due to widespread correlation with eastern tropical Pacific temperature variations. Other studies have suggested a relationship between extratropical carbon exchange and ENSO, but generally at a global or hemispheric scale. Analyses have focused primarily on productivity or atmospheric CO₂ rather than the net exchange of carbon (Fraeney et al. 1995, Keeling et al. 1995, Jones et al. 2000, Dargaville et al. 2002, Schaefer et al. 2002, Buermann et al. 2003, Potter et al. 2003). Direct correlation to the ENSO time series shows significant values ($r = -0.5; p < 0.02$) between the spring boreal North America carbon anomalies and the spring ENSO index (MEI index: Wolter and Timlin 1993, 1998). This correlation suggests that negative carbon flux anomalies are associated with the peak warm phase of the ENSO index in eastern tropical Pacific. The results presented here indicate a much more spatially specific, teleconnected relationship between ENSO and carbon exchange in the boreal North American region.

It is not yet clear how these broad-scale patterns of net carbon exchange are influenced by climate related disturbance regimes or regrowth trajectories (described below). The observed differences between northern Eurasia and North America indicate an important area of research. Moreover, although inversions cannot separate photosynthetic responses from respiration, the timing of the fall northern Eurasia responses, with strong correlations well after the peak of photosynthetic activity, suggest a dominant influence of soil heterotrophic respiration. In contrast, warm and wet spring conditions in boreal North America may be associated with an earlier onset of the growing season and a dominance of photosynthesis over heterotrophic respiration, which may be delayed by snowmelt. As discussed further below, the timing of snowmelt also strongly influences the albedo and related climate forcings.

3. Albedo and radiative forcing changes with composition and disturbance

Surface reflectivity, and hence the albedo, in high latitude ecosystems is determined by the spectral properties of elements such as leaves, soils, and vegetation structure. Tundra and forested regions differ substantially in this regard, although systematic changes in both biomes have recently been highlighted (Chapin et al. 2005, Randerson et al. 2006). In tundra, albedo changes are largely associated with changes in vegetation composition, notably the reduced albedo associated with increased shrub cover. Shrub canopies impact the surface energy balance of the arctic landscape by increasing sensible heat exchange with the atmosphere, and also strongly affect the soil heat balance, effectively warming the soil in winter due to trapping of insulating snow and cooling the soil in summer by intercepting radiation in the canopy before it heats the soil (Shaver and Chapin 1991, Sturm et al. 2005, Chapin et al. 2006).

In forested regions, the surface albedo is strongly determined by vegetation type and density, and disturbance. Fire destroys vegetation and blackens the surface, significantly influencing the albedo and other components of the energy budget (e.g. sensible versus latent heat flux). As noted earlier, wildfires in the boreal forest are often stand replacing (Larsen 1997), and a stand can take multiple successional pathways (trajectories) following fire, depending on burn severity, topography, permafrost and factors that affect plant survival and recruitment (Viereck et al. 1986). Differences in the mean albedo at different times of the year in areas recently disturbed by fire are, therefore, critical to monitor through time across a range of conditions.

Using MODIS satellite imagery and a fire boundary database for Alaska, albedo changes were recently assessed for areas that burned between 1950 and 2004. The seasonality of changes in the albedo were pronounced, with changes in early season values being more clearly discriminated than during the snow-free summer months. In spring under snow conditions, the broadband albedo of burned areas in Alaska increased by 21% in the first year after fire relative to the average of unburned areas. The albedo continued to increase during the first decade, remained elevated and mostly constant in 10–30 year stands, and then decreased to pre-burn levels after approximately 50 years (figure 6). The broadband albedo in summer (during snow-free periods) initially decreased by 22% during the first year after a fire, but was immediately followed by a rapid increase to levels that substantially exceeded pre-fire controls. The albedo remained elevated for 10–35 year stands, and eventually returned to pre-burn levels after 50 years. Both the spring and the summer broadband albedo reached maximum values around 20–25 years following a
The broadband albedo as a function of time since a fire in interior Alaska for (top) spring (February, March, April) and (bottom) summer (June, July, August). Albedos were derived from MODIS satellite images sampled within the perimeter of fire scars of varying ages. These observations are the same as those shown in figure 2 of Randerson et al. (2006). No fires of sufficient size for analysis with the MODIS data were available for the period 1965–1968 (years 37–40 since a fire). The solid lines indicates the mean of evergreen conifer forests.

Figure 6.

Spectral vegetation indices, in contrast, showed gradual increases through time (not shown), reflecting the influence of increasing vegetation cover. These albedo changes can have climate effects that are comparable to biogeochemical effects of changing fire regime. A detailed analysis of a single boreal forest fire by Randerson et al. (2006), for example, showed a net effect of decreased radiative forcing ($-2.3 \pm 2.2 \text{ W m}^{-2}$), mainly from sustained multi-decadal increases in the surface albedo exceeding warming effects from fire-emitted greenhouse gases.

We hypothesize that fire severity is likely to play a key role shaping post-fire changes in surface albedo changes during both spring and summer (figure 7). Sites which burn more severely lose more canopy cover and soil organic matter, and this may cause greater snow exposure and higher values of albedo over the first decade after fire. Greater exposure of mineral soil after high severity fires may also allow for increased recruitment and growth of broadleaf deciduous trees (Johnstone et al. 2004). Increased abundance of these trees during intermediate stages of succession, in turn, may cause the albedo to remain at values that substantially exceed those in low burn severity sites during both spring and summer. As a consequence, in North America, if the fire severity increases, it may produce a negative feedback to the climate system even if the burned area remains unchanged. Related implications of the severity of fire disturbance and vegetation composition at different stages of regrowth are discussed more generally below, in the context of successional pathways or regrowth trajectories.

4. Links between disturbance severity and pathways of forest recovery

The radiative forcing trade-offs between carbon and surface energy fluxes are likely to vary during at least three different periods of post-fire succession: (1) immediately following a fire (years 1–10 after the fire), (2) at intermediate stand ages (20–40 years after the fire), (3) older stands (more than 60 years after the fire). In North America, boreal forests are typified by a single-cohort stand structure where substrate conditions, demographic processes and community interactions 1–10 years after a fire determine relative species abundance and density...
throughout succession (see figure 7). In this system, increases in fire severity reduce the net primary production during the first few years after a fire, but may substantially increase it over a period of decades because of greater recruitment of broadleaf deciduous trees (Kasischke and Johnstone 2005). The relative abundance of deciduous broadleaf and evergreen conifer plant functional types in canopy cover (deciduous/evergreen ratio) in intermediate stand ages is thus a particularly important stand attribute for characterizing regrowth trajectories, or pathways of succession, in boreal ecosystems. After ~60 years deciduous tree species tend to senesce and decrease in abundance relative to spruce (Viereck et al 1986) but may leave legacy effects in low spruce density (Mack et al 2008), coarse woody debris pools, and reduced soil organic carbon storage (Harden et al 2006).

The net result of these patterns is that, in North America, increased fire severity results in regrowth with a high deciduous component which, over the first 40 years of succession, has higher rates of net production and biomass carbon accumulation (e.g. Goetz and Prince 1996, Kasischke and Johnstone 2005) and a longer sustained interval of high albedo values during spring than burned areas dominated by conifers (Randerson et al 2006). As these stands mature they have lower productivity, reduced carbon storage, and higher albedo due to legacy effects of deciduous trees on the ecosystem structure and function. In less severely burned areas dominated by conifer stands, higher soil organic carbon accumulation and carbon storage result in more mature stands with lower albedo throughout succession. The combined effect of these processes, when compared using the concept of radiative forcing (e.g., Randerson et al 2006), may be a net cooling effect of boreal forest fire. That is, an increase in fire severity, when integrated over a full successional cycle, can lead to climate cooling via the longer-term trade-offs between carbon accumulation and the radiative forcing of albedo changes. This net negative effect is likely to be exacerbated when high severity burning causes vegetation to shift from conifer dominance to a broadleaf–conifer mix, since the latter is unlikely to accumulate carbon stocks over succession that replace those lost in fire.

Over multiple fire and successional cycles, the sign of atmospheric forcing from increased fire severity is less clear because of the potential for negative feedbacks between deciduous broadleaf plant functional types and the fire regime. Deciduous broadleaf forest stands tend to be less flammable than evergreen conifer stands due to lower accumulation of fine ground fuels and inherently less flammable tree biomass (Dynergy et al 1986, Chapin et al 2006). A severity-driven increase in the abundance of deciduous stands across the landscape, then, could feedback negatively by decreasing the frequency, magnitude and severity of large scale burning events (Rupp et al 2002), increasing the landscape-integrated fire return interval and shifting the regional disturbance regime. Alternatively, fire severity may be more strongly driven by factors such as regional or global climate (Johnson et al 2001, Duffy et al 2005), topographic complexity (Duffy et al 2007) and fire management (Kasischke and Stocks 2000, Bridge et al 2005) than by vegetation composition or age, reducing the importance of feedbacks between vegetation composition and fire regime.

In northern Eurasia, the response of the post-fire albedo to burn severity may be quite different from that in North America. As a result of high severity fires, post-fire recruitment of the larch (Larix species) contributes to a higher stand density during intermediate stages of regrowth (Gower and Richards 1990). Denser forests have reduced snow exposure during spring, causing more sunlight to be absorbed by the deciduous larch canopy overstory (Peregon et al 2008). The net climate impact of an increase in burned area and severity may thus be more closely linked with changes in carbon stocks than changes in surface biophysics in these systems because of the absence of an evergreen conifer plant functional type.

Contrasts in plant life history, such as those of the larch in northern Eurasia and the black spruce in North America, may also contribute to differences in feedbacks between fire severity and vegetation composition. Black spruce are generally killed by fire, but carry a multi-year bank of cones in their canopies that release seeds when heated, ensuring the presence of propagules after fire. As a result, successional trajectories appear to be relatively deterministic in low severity burns where residual organic soil remains after fire. Black spruce seedlings establish readily on burned organic substrates, but the establishment of deciduous species is limited by moisture stress (Johnstone et al 2004). In contrast, successional trajectories in high severity burns of black spruce may be more dependent upon stochastic factors such as the availability of deciduous tree propagules, which must disperse from outside the burned area, or the outcome of competitive interactions between deciduous and spruce seedlings (Johnstone and Kasischke 2005). Siberian larch species, in contrast to black spruce, release seeds annually. Their seeds do not appear to survive fire and thus post-fire recruitment is dependent upon relatively stochastic factors such as the proximity of a seed source to a newly burned area and annual variability in seed crop. Larch recruitment failure has been observed in areas that burned during low seed crop years, leading to low larch densities and retrogression of forest into tundra (Zimov 2007).

As noted, North American and northern Eurasia differ substantially in the amount and type of vegetation cover, whether deciduous or evergreen, conifer or broadleaf. As a result, they have different successional trajectories and different trade-offs associated with biophysical versus biogeochemical climate effects of a changing fire regime. Similarly, forest and tundra ecosystems have very different ecosystem composition and structural properties, and also differ quite substantially in their responses to warming and drying (section 2.1).

5. Conclusions

We have summarized work from a series of approaches, ranging from field measurements to satellite remote sensing and inverse modeling, which point to distinct differences in the responses of high latitude systems to the well documented changes in climate taking place. It is not yet
clear how these recent changes in high latitude ecosystems will ultimately modify the regional and global climate, but we have presented likely scenarios, based on observations, that indicate substantially different responses in northern Eurasia and North America. The relative impacts of the different effects associated with the composition changes noted above can inform climate policy discussions, yet better understanding of the likely trade-offs between various forcing agents is a particularly critical area of research, and requires improved representation in coupled climate–carbon-cycle models (see Balshi et al. 2007). In particular, more work is needed to understand how these changes may mitigate additional warming via negative feedbacks to the climate system (e.g. greater carbon sequestration via increased productivity, and reduced radiative forcing via the greater albedo in forest succession following fire disturbance), or exacerbate further warming via positive feedback mechanisms (e.g. greater carbon emissions via increased fire disturbance, and greater microbial respiration via deeper thaw and mobilization of frozen carbon pools).

Further resolution of these research questions is relevant to the North America Carbon Program and the northern Eurasia Earth Science Partnership Initiative, which both require better integration of field data, models and satellite observations to characterize and quantify the effects of vegetation disturbance and recovery patterns in high latitude ecosystems. More focused assessments and better understanding of the controlling factors would also benefit International Polar Year activities, including simulations of the changes taking place across circumpolar ecosystems, which cover more than 20% of the global land surface and have strongly coupled feedbacks to the climate system.

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