

MODELING THE IMPACT OF BLACK SPRUCE ON THE FIRE REGIME OF ALASKAN BOREAL FOREST

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Abstract. In the boreal biome, fire is the major disturbance agent affecting ecosystem change, and fire dynamics will likely change in response to climatic warming. We modified a spatially explicit model of Alaskan subarctic treeline dynamics (ALFRESCO) to simulate boreal vegetation dynamics in interior Alaska. The model is used to investigate the role of black spruce ecosystems in the fire regime of interior Alaska boreal forest. Model simulations revealed that vegetation shifts caused substantial changes to the fire regime. The number of fires and the total area burned increased as black spruce forest became an increasingly dominant component of the landscape. The most significant impact of adding black spruce to the model was an increase in the frequency and magnitude of large-scale burning events (i.e., time steps in which total area burned far exceeded the normal distribution of area burned). Early successional deciduous forest vegetation burned more frequently when black spruce was added to the model, considerably decreasing the fire return interval of deciduous vegetation. Ecosystem flammability accounted for the majority of the differences in the distribution of the average area burned. These simulated vegetation effects and fire regime dynamics have important implications for global models of vegetation dynamics and potential biotic feedbacks to regional climate.

1. Introduction

Understanding the response of terrestrial ecosystems to projected future climate change is difficult due to complex interactions among ecosystem structure and function, soil and permafrost processes, disturbance dynamics, and regional climate. Arctic and boreal ecosystems are expected to exhibit strong responses to directional changes in climate and play an important role in biospheric feedbacks to the climate system (Foley et al., 1994; Bonan et al., 1995; Betts et al., 1997; Claussen, 1998; Ganopolski et al., 1998; Levis et al., 1999; Kittel et al., 2000). Several different modeling approaches have indicated similar high-latitude vegetation response to climatic warming. Neilson et al. (1997) suggested a northward advance

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of boreal woodland and forest with an associated decrease in tundra. Rupp et al. (2000b, 2001) suggested a conversion of tundra to boreal forest and a conversion of conifer-dominated forest to a deciduous-dominated forest. Several dynamic global vegetation models (DGVMs) have suggested a similar northward movement of forest, with individual models differing in predictions of conifer versus deciduous dominance (Cramer et al., 1999). The application of ecological models to simulate realistic ecosystem response to climatic change provides some context, but further development is needed for accurate evaluation of the sensitivity of arctic and boreal vegetation to a changing climate (Kittel et al., 2000).

Changes in vegetation associated with climatic warming may have significant regional effects on landscape processes, including fire spread, seed dispersal and feedbacks to climate (Chapin et al., 2000; Rupp et al., 2000a,b, 2001). There is strong evidence that climate is warming at high latitudes (Beltrami and Mareschel, 1991; Chapman and Walsh, 1993; Kattenberg et al., 1996; Overpeck et al., 1997; Everett and Fitzharris, 1998), with warming being most pronounced in northwest North America and eastern Siberia (Serreze et al., 2000). It has been asserted that wildfire will increase generally with climatic warming (Overpeck et al., 1990), particularly in the boreal forest where predicted future increases in area burned exceed 40% (Van Wagner, 1988; Flannigan and Van Wagner, 1991). The average area burned in western Canada has doubled in the last 20 years (Kasischke et al., 1999). Increases in fire frequency and extent will likely cause a shift from conifer-dominated forest to deciduous-dominated forest (Rupp et al., 2000b, 2001). Such a fire-induced shift from conifer to deciduous forest would likely influence future feedbacks to the fire regime (Chapin et al., 2000). Past changes in boreal vegetation composition occurred rapidly (Ager, 1983; Anderson and Brubaker, 1994; Hu et al., 1993; Edwards and Barker, 1994) in response to a changing climate and were followed by significant changes in fire regime (Clark, 1988). In interior Alaska, fire frequency increased substantially with the arrival of black spruce (4000–6000 yr BP) to the landscape, despite the trend toward a cooler wetter climate, indicating strong vegetation effects on fire regime (J. Clark, unpublished data).

Fire disturbance in the boreal forest may become increasingly important to the global carbon budget because climate is changing in a region where carbon reserves are large and where fire disturbance dominates the distribution of plant and soil carbon (Harden et al., 2000). The projected increases in boreal forest area burned (Kasischke et al., 1999; Van Wagner, 1988; Flannigan and Van Wagner, 1991) and strong interactions to vegetation distribution (Clark, 1988; Baker, 1992) suggest significant feedbacks to the climate system and potentially large effects on the carbon budget. Disturbance and successional dynamics (i.e., species replacement) have been found to increase the seasonal amplitude of net carbon exchange at high latitudes (Zimov et al., 1999). Although boreal forests act as slight net sinks of C over decadal to century time periods severe fire activity may result in net sources of C (Harden et al., 2000). Alternatively, increases in fire frequency and extent that increase the proportion of deciduous forests would likely act as a negative

feedback to regional warming (Chapin et al., 2000). The impact of climate warming on the fire regime may yield significant and rapid changes in vegetation such that the change in fire regime has the potential to overshadow the direct impact of climate change on species migration, substitution and extinction (Weber and Flannigan, 1997). The uncertainty of future disturbance rates in the boreal forest and their effects on energy partitioning and carbon exchange (Chapin et al., 2000) demand ecological models that accurately portray transient ecosystem dynamics. In this paper a spatially explicit model of Alaskan subarctic treeline dynamics (ALFRESCO) is modified to simulate boreal vegetation dynamics in interior Alaska. ALFRESCO was originally developed to simulate the response of subarctic forest-tundra to climatic warming in northwest Alaska (Rupp et al., 2000a,b, 2001). The original treeline version of the model simulated recruitment and disturbance effects on four alternative states of upland vegetation (upland tundra, white spruce forest, deciduous forest, and dry grassland). In this paper we add a black spruce forest state and investigate the impacts of this vegetation type on landscape dynamics in interior Alaska.

2. Methods

2.1. STUDY LANDSCAPE

Simulations were performed using a 100×100 km region of typical boreal landscape in the Fairbanks region of interior Alaska (Figure 1). This region is the focal point for regional research of the Bonanza Creek Long-Term Ecological Research (LTER) program. The Fairbanks region is a mosaic of vegetation comprised mainly of late successional black and white spruce forest and early successional deciduous forest. In interior Alaska, late successional vegetation is strongly tied to topographic position and regional climate (Van Cleve et al., 1991, 1996). Black spruce forest is typically found on poorly drained lowlands and on cold northerly aspects. In contrast, white spruce forest inhabits the well-drained floodplains and on the warmer southerly aspects. Early successional deciduous shrubs and trees are associated with both spruce forest types and typically colonize following disturbance.

2.2. MODEL OVERVIEW

The boreal version of ALFRESCO was developed to explore the interactions and feedbacks between fire, climate, and vegetation in the boreal forest of interior Alaska. ALFRESCO is a state-and-transition model of successional dynamics. The model explicitly represents the spatial processes of fire and recruitment across the landscape (Rupp et al., 2000a). The boreal version of the model focuses on the dynamics of continuous successional change due to frequent fires and climate change. ALFRESCO is based on the idea that vegetation state can be explained

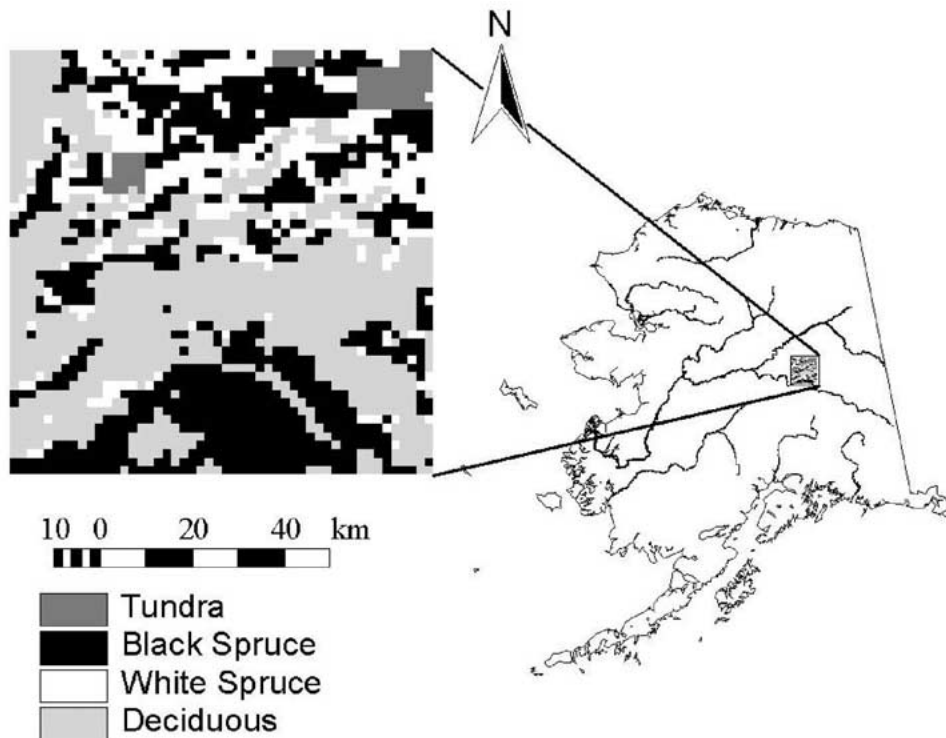


Figure 1. Map showing the Fairbanks study area (100 × 100 km) in interior Alaska.

using probabilistic rules, which respond to the model drivers of disturbance and climate. The model assumptions reflect our supposition that fire regime and climate are the primary drivers of landscape-level changes in the distribution of vegetation in the circumpolar arctic/boreal zone (Payette, 1983; Van Cleve et al., 1991; Bliss and Matveyeva, 1992; Holling, 1992; Starfield and Chapin, 1996).

Fluvial processes and insect outbreaks also serve as important disturbance agents in the Alaskan boreal forest. Flooding events drive successional trajectories along river floodplains throughout Alaska (Van Cleve et al., 1991, 1996). However, relative to the model resolution and the extent of the interior Alaskan landscape, these events and their effects are localized. Therefore, in this boreal version of ALFRESCO fluvial processes are masked out by the 2×2 km pixel resolution. In contrast, insects play a major role in the Alaskan landscape as evidenced by the severe bark beetle outbreaks observed over the past 30 years in the Copper River Basin and on the Kenai Peninsula of southcentral Alaska (Holsten, 1990). However, north of the Alaska Range in interior Alaska, insect outbreaks (specifically spruce budworm and bark beetle) so far play only a localized role in forest structure and function (Werner, 1986); so we do not currently include insect outbreaks in our model.

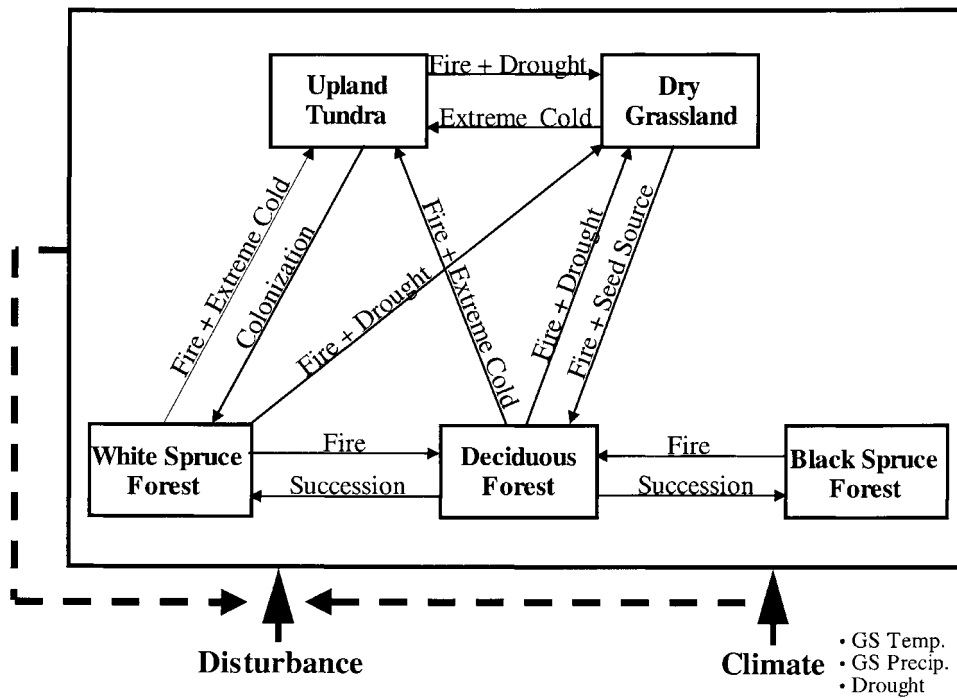


Figure 2. Model structure showing ecosystem types (boxes) and the potential switches (arrows) that occur among ecosystems. Disturbance and climate are the driving variables of change in the model, and dynamically interact with one another and the landscape.

ALFRESCO is a frame-based model (Starfield et al., 1993), where each ecosystem type (i.e., frame) constitutes an independent submodel (Figure 2). Each submodel calculates and monitors factors and processes that could cause a switch to another ecosystem type. Switching rules establish whether a switch from one frame to another occurs, deactivating the current submodel and activating the submodel representing the new ecosystem type. This approach emphasizes processes causing vegetation change, not variables controlling productivity or species composition within a vegetation type, as developed in gap-dynamics models (Shugart and West, 1980; Pastor and Post, 1986; Starfield and Chapin, 1996). The ecosystem types were chosen as the simplest possible representation of the complex vegetation mosaic occupying uplands in the circumpolar arctic and boreal zones (Solomon, 1992) and ignore the substantial variation in species composition within these and other intermediate vegetation types (Payette, 1992; Starfield and Chapin, 1996).

The model operates on a 10-yr time step and a spatial scale of 2 × 2 km grid cells; each cell has eight immediate neighbors (Rupp et al., 2000a). This time step approximates the average frequency of severe fire years in the North American boreal forest (Flannigan and Harrington, 1988) and easily accommodates replicated modeling of vegetation change over time scales of decades to centuries (NRC,

1994; Starfield and Chapin, 1996). The spatial scale is appropriate for interfacing with mesoscale climate models (Starfield and Chapin, 1996).

Model input data were generated from GIS raster data, within the GRID environment of ARC/INFO (ESRI, 1994). The data originated from Alaskan data sets of current growing-season (May–Sept.) temperature and precipitation (Hammond and Yarie, 1996), current vegetation (Fleming, 1997), topography (USGS, 1990), and current fire regime (Kasischke and French, 1997). The fire regime data originate from a statewide firescar database maintained by the Alaska Fire Service that identifies fires >400 hectares since 1950. The firescar database was not used as model input, but rather was used to calibrate the fire routine. The current model version was calibrated to provide realistic values of the number of fires and area burned in the Fairbanks region under currently observed vegetation and climatic conditions (Rupp et al., 2000b, 2001).

The current vegetation data set was derived by reclassifying the original 22-class statewide AVHRR-derived land-surface map (Fleming, 1997) into the 5 vegetation classes represented in ALFRESCO. Currently, the dry grassland ecosystem type represented in ALFRESCO occurs only locally (Yurtsev, 1982; Lloyd et al., 1994), and at a scale masked by the model's 2×2 km pixel resolution. Differences among tundra vegetation types recognized in the original 22-class vegetation map were ignored, and all tundra types were lumped together as a single tundra class. Tundra types that identified some level of spruce canopy on site were indicated. The actual spruce-canopy level (level 1 = 1–20% or level 2 = 21–50%) was determined using growing-season climate thresholds. Remotely sensed satellite data is currently unable to distinguish species-level differences between black and white spruce. We therefore stratified spruce forest using deterministic rules related to topography (i.e., aspect, slope position, and elevation) and growing-season climate. Aspect and slope were used to identify 'typical' black spruce forest sites (i.e., poorly drained and northerly aspects) throughout the study region. Growing-season climate and elevation were used primarily to distinguish treeline white spruce forest. In addition, we used growing-season climate thresholds to distinguish young deciduous forest stands from tall shrub tundra. These deterministic rules were also used to denote the climax vegetation state (i.e., black or white spruce forest) for each deciduous pixel. In other words, the rules were used to predetermine the successional trajectory of each deciduous pixel. In this manner, we were able to develop an input vegetation data set that best related the original AVHRR classified data into the five vegetation types represented by ALFRESCO, based on a sensible ecological foundation.

2.3. CLIMATE

ALFRESCO generates climate stochastically based upon observed (1961–1990) growing season (May–Sept.) climate in Alaska (Hammond and Yarie, 1996). Climate is input to the model as a series of alternative maps of growing-season

temperature and precipitation. These maps have a geographic pattern of climate that is logically consistent with topography and latitude (e.g., colder in mountains and to the north) and with observed synoptic climatology. The climate maps preserve these basic geographic patterns of climate, but uniformly differ in the magnitude of temperature and precipitation (Rupp et al., 2000b, 2001).

First, a user-defined climate scenario is chosen (e.g., current climate) at the start of the simulation. Then, for each climate scenario there is an associated probability of choosing a particular map of temperature and of precipitation for a given time step. Temperature and precipitation maps are independently chosen at a given time step. The probability of choosing a particular map is obtained from a discrete probability distribution for the variable of interest (i.e., temperature or precipitation). The frequency distributions of both current temperature and precipitation were developed from climate records (around growing-season mean values) for the Fairbanks study landscape (Starfield and Chapin, 1996; Chapin and Starfield, 1997). The temperature and precipitation in each pixel of the map are then converted to temperature and precipitation classes that have defined effects on vegetation (Starfield and Chapin, 1996; Rupp et al., 2000a). In this way coherent scenarios of climate are represented, stochastic variation in temperature and precipitation at each time step is provided for a climate scenario, and geographic patterns of climate that are consistent with topography and synoptic climatology are utilized.

An 'effective drought' index (Trigg, 1971; Clark, 1988) provides a measure of drought severity and is utilized in determining vegetation growth, and vegetation flammability (Rupp et al., 2000a,b). The database for probability distributions of temperature and precipitation for different climate scenarios and the relationships of climate to vegetation growth and composition, and flammability, are presented in Starfield and Chapin (1996) and Rupp et al. (2000a,b).

It is important to reiterate that in this particular study each time step of the climate series was randomly drawn. Growing-season temperature and precipitation were chosen independently of one another. Although climate models predict increases in precipitation in response to the enhanced temperature response of the Arctic (Kattenberg et al., 1996), the climate series developed for this study reflects currently observed climate and not a climate change scenario. Additionally, the coarse temporal resolution of ALFRESCO eliminates any short-term temporal (i.e., inter-annual) auto-correlation issue. We used the same climate series for each of the 100 replicate simulations. By fixing a sequence of stochastically generated climate maps for each of the 100 replicate simulations, we eliminated the contribution of climate variability to any differences exhibited between vegetation scenarios.

2.4. FIRE IGNITION AND SPREAD

Climate, vegetation type, and time since last disturbance drive disturbance events. Fire spread across the landscape is simulated using a cellular automaton approach, where an ignited grid cell may spread to any of its eight neighboring cells (Rupp et

al., 2000a,b). Fire ignition within a cell is determined stochastically with a random number generator as a function of the flammability of the cell. The flammability of the receptor cell and the effects of topographic barriers determine the probability of a fire spreading from one cell to another. In all ecosystem types, fire probability (the probability of a fire that kills the majority of trees in a cell) is assumed to be proportional to the drought index (Trigg, 1971; Clark, 1988) since the drought index increases with increasing temperature and decreasing precipitation (Thornwaite and Mather, 1957; Starfield and Chapin, 1996). The relationship between fire probability and the drought index is assumed to be the same among ecosystem types (based on data from boreal forests), but actual probabilities differ among vegetation types, due to factors that are specific to each ecosystem, as described in Rupp et al. (2000a,b). For example, white spruce and deciduous forest differ in fire probability, but fire probability in these two forest types shows the same response to changes in the drought index.

2.5. SEED DISPERSAL

ALFRESCO models some forms of seed dispersal implicitly (because the sources are too small to be seen at a 2×2 km resolution), and others explicitly. Thus the model assumes that small patches of grassland are present in pixels classified as tundra, deciduous forest, and spruce forest, so seed is available when conditions are right for grasses to out-compete other species. Similarly, scattered deciduous species are assumed to be present in spruce forest and vice-versa.

An increase in white spruce canopy cover in tundra occurs in two ways: seed inputs from trees already present on the site (in-filling) are modeled implicitly while dispersal from outside the site is simulated in a manner similar to the fire-spread routine. Black spruce is typically not associated with treeline in Alaska (Viereck, 1979) and has limited dispersal abilities. We assume that white spruce seed dispersed from a seed source has a dispersal distance threshold of 4 km (beyond which no seed travels). Black spruce seed input is limited to in-filling. Mountains and large water bodies physically inhibit the spread of white spruce seed. The number of neighboring seed sources determines the amount of seed available (from outside) to a given pixel, which along with climate and in-filling determines increases in white spruce canopy cover (Rupp et al., 2000a,b).

2.6. ECOSYSTEM DYNAMICS

The individual submodels (ecosystem types) used in ALFRESCO (a detailed description can be found at – <http://www.lter.alaska.edu/pubs/ALFRESCO.html>) are identical to those described by Starfield and Chapin (1996) and Rupp et al. (2000a,b). We therefore provide only a description of the new black spruce ecosystem type.

Black spruce is one of the most abundant forest types in the North American boreal forest and occupies 44% of interior Alaska (Viereck et al., 1986). Black

spruce most commonly grows as pure stands on organic soils and as mixed stands on mineral soil sites, and with an almost continuous ground cover of feather-mosses and sphagnum mosses (and lichen on mesic sites) (Viereck and Johnston, 1990). In interior Alaska, black spruce dominates poorly drained lowland sites and cold north-facing upland sites, and is typically associated with the presence of permafrost.

The combination of mosses, lichens, and ericaceous shrubs in the understory, along with the low stature and persistent branches (i.e., fuel ladders) of black spruce make this vegetation type particularly volatile and susceptible to burning (Rouse, 1976). The fire return interval for black spruce forest types in Alaska ranges from 40–100 years (Dyrness et al., 1986; Kasischke et al., 1995). The semi-serotinous character of black spruce cones, which provides a continuous seed bank, is well suited for immediate re-occupation of the site. This canopy seed bank has significant quantities of seed available for on-site dispersal (without delay) following fire (Zasada et al., 1992). The capacity to regenerate within large disturbances offers a considerable advantage to black spruce (Greene et al., 1999). Revegetation by black spruce following fire is therefore rapid. There is an initial post-disturbance deciduous-shrub phase of 40–60 yr followed by dense black spruce and rapid development of feathermosses in the understory (Van Cleve and Viereck, 1981).

In ALFRESCO the black spruce frame differs from the white spruce frame in three ways. First, following fire in both the white and black spruce frames, early successional deciduous vegetation normally colonizes the site. However, the deciduous residence time on black spruce sites is considerably shorter (40–60 yr) than on white spruce sites (80–100 yr). Second, the black spruce vegetation type is 50% more flammable than white spruce. Third, black spruce has limited dispersal capabilities (i.e., in-filling) and does not colonize tundra.

2.7. MODEL SIMULATIONS

Previous modeling experiments show that vegetation pattern and distribution affect both the frequency and extent of fire across the landscape (Rupp et al., 2000a,b, 2001). We therefore expected that the addition of the new black spruce ecosystem type to the landscape would result in a different fire regime (i.e., frequency and extent) than that obtained from a landscape without black spruce. We used the Fairbanks region to test the impacts of different vegetation distributions on the overall dynamics of the model system. We did this by comparing three different vegetation distributions (a) the currently observed mix of vegetation (i.e., a mosaic of late successional white and black spruce forest, and early successional deciduous forest) in the Fairbanks landscape (Figure 1), (b) a hypothetical vegetation distribution in which all spruce sites were reclassified as white spruce, and (c) a hypothetical vegetation distribution in which all spruce sites were reclassified as black spruce. As described, the deterministic rules used to develop the input vegetation map denote the climax vegetation state (i.e., black or white spruce forest) for each deciduous

pixel. In the absence of fire each deciduous cell will eventually switch to its pre-determined climax spruce forest type. Therefore, the two hypothetical vegetation scenarios represent extremes in landscape vegetation distributions in which only one (either black or white spruce forest) climax vegetation state functions. These three vegetation distributions were used to measure the impacts and consequences of differences in vegetation on the fire regime and successional dynamics of the regional system.

The primary goal of the simulations is to assess whether the addition of the black spruce vegetation alters the regional fire regime. In order to simplify the interpretation of the results, the three scenarios used in the simulations differed only in the initial vegetation distribution. In the initial vegetation distribution, the spatial location of deciduous vegetation was identical for each of the vegetation scenarios. The only difference among the vegetation scenarios lies in the initial classification of conifer forest as either black spruce, white spruce or a mix of the two.

The spatial locations of fire ignitions depend on vegetation-determined patterns of a flammability index. Within stands with the same flammability index, fires are probabilistically ignited. Each vegetation scenario was replicated 100 times, using the same climate regime for each replicate simulation of the three scenarios. Using the identical climate for each replicate eliminates any stochastic climate effects on the observed differences in fire regimes. Each replicate was run for 100 decadal timesteps (i.e., 1000 years).

Additionally, we performed simple sensitivity analyses to assess the respective influences of vegetation flammability and successional time course on system dynamics. We did this by separately altering the flammability and successional parameters for the two vegetation types (black and white spruce). We compared three different scenarios of the all black spruce landscape where the black spruce frame structure was set to: (a) black spruce flammability and successional time course, (b) white spruce flammability and black spruce successional time course, and (c) black spruce flammability and white spruce successional time course. The same current climate regime was used for each replicate ($n = 100$) in each scenario, again removing stochastic climate effects from the transient system dynamics.

3. Results

Vegetation scenarios that differed in the proportion of black and white spruce on the landscape had strikingly different fire regimes in terms of both the numbers of fires and the total area burned. The median number of fires was greatest in the scenario where all spruce forest was classified as black spruce (Figure 3). The white spruce scenario had the smallest median number of fires, and the current-mix scenario (where black spruce accounted for 67% of the spruce forest and white spruce accounted for 33%) was intermediate. Likewise, we found the me-

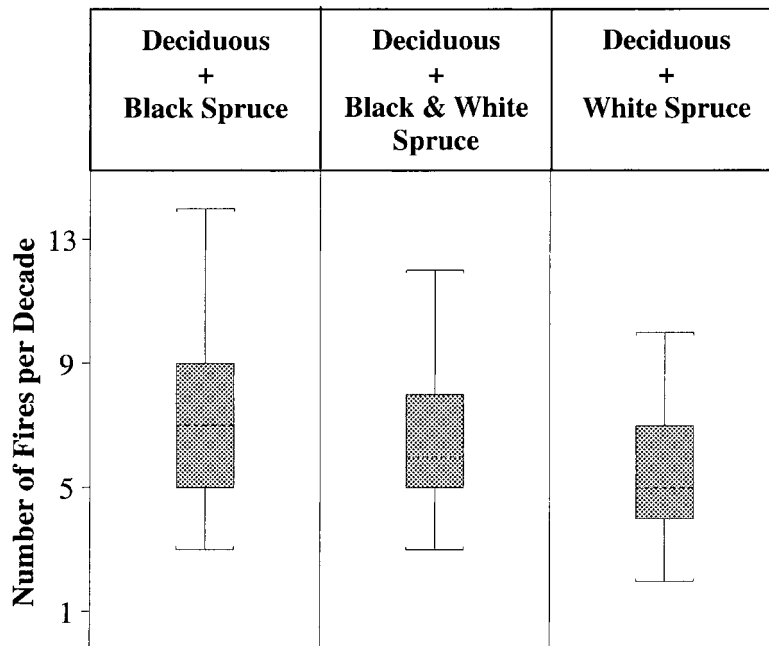


Figure 3. Boxplots of the number of fires per decade for three vegetation simulations that differed in the initial proportion of black and white spruce. The black spruce landscape was composed of 44% deciduous forest and 56% black spruce forest. The current mix landscape was composed of 44% deciduous forest, 37% black spruce, and 19% white spruce forest. The white spruce landscape was composed of 44% deciduous forest and 56% white spruce forest. The dashed line represents the median. The shaded box around the median represents the Inner Quartile Range (IQR), which identifies the region between the 25th and 75th percentiles. The whiskers extending from the IQR represent the largest/smallest value that is still within the median $\pm 1.5 \times$ IQR. Results are from 100 replicates of 1000 years.

dian total area burned was greatest in the black spruce scenario (Figure 4). The white spruce scenario had the smallest median total area burned, and the current-mix scenario was intermediate. The distribution of total area burned for each of the vegetation scenarios was skewed (Figure 4). The black spruce scenario revealed more ($n = 11$) decades in which greater than 10% of the total landscape burned (see 'outliers' in Figure 4), compared to less than half ($n = 5$) such decades for the current-vegetation mix and none for the white spruce scenario. These results suggest that landscapes dominated by black spruce forest experience more fires that burn a greater proportion of the landscape, and differences in vegetation (i.e., black vs. white spruce forest) have a considerable impact on the fire regime. Furthermore, black spruce-dominated landscapes experience episodic large-scale fire events (i.e., time steps or decades) that burn substantial proportions of the landscape. Large-scale fire events have the potential to significantly alter the distribution of vegetation and to switch ecosystem dominance across the landscape.

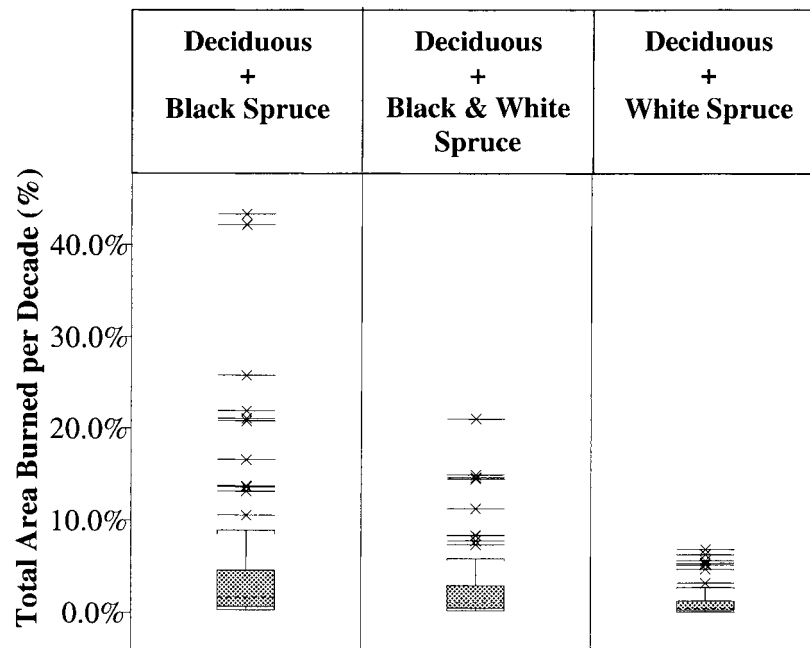


Figure 4. Boxplots of the total area burned per decade (expressed as a percentage of the total landscape) for three vegetation simulations that differed in the initial proportion of black and white spruce. The black spruce landscape was composed of 44% deciduous forest and 56% black spruce forest. The current mix landscape was composed of 44% deciduous forest, 37% black spruce, and 19% white spruce forest. The white spruce landscape was composed of 44% deciduous forest and 56% white spruce forest. The dashed line represents the median. The shaded box around the median represents the Inner Quartile Range (IQR), which identifies the region between the 25th and 75th percentiles. The whiskers extending from the IQR represent the largest/smallest value that is still within the median $\pm 1.5 * IQR$. Any value beyond the median $\pm 1.5 * IQR$ is subjectively considered to be an outlier, and as such is marked with an 'x'. Results are from 100 replicates of 1000 years.

The total amount of deciduous forest that burned increased with increasing black spruce forest in the landscape (Figure 5). The white spruce scenario showed almost no deciduous forest burning and little variability over time, whereas the black spruce scenario revealed the largest amount of deciduous forest burned and showed the most variability over time. Although the total area burned was small (relative to the entire study landscape), there were several extreme fire decades where greater than 1% of deciduous forest in the landscape burned. The black spruce scenario revealed a very dynamic system with numerous deciduous forest stands burning at a relatively young age (i.e., 10–40 yr), compared to either the current mix or white spruce scenarios (Figure 6).

Our model simulations identified major differences in system dynamics between landscapes with and without black spruce forest. The two essential differences between the white spruce and black spruce model frames were the greater flammability and shorter early successional deciduous shrub/tree stage in black

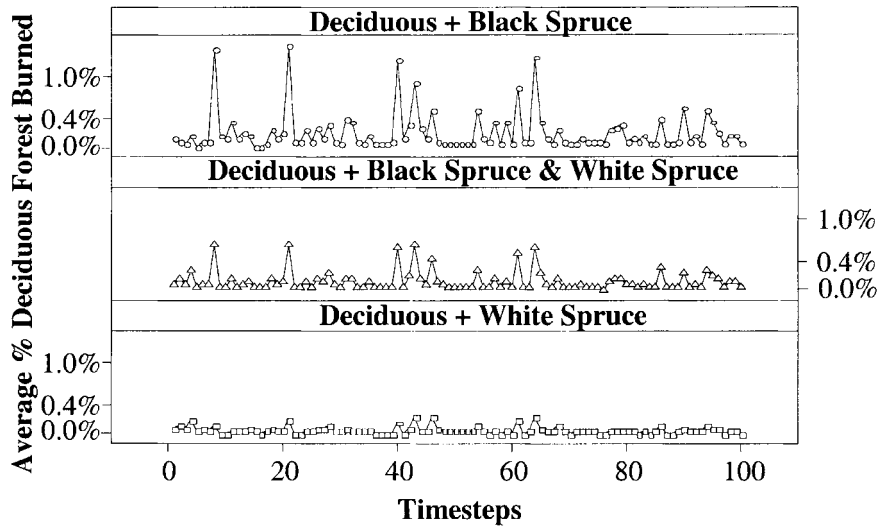


Figure 5. Differences in the average % deciduous area burned for 100 replicates of three vegetation scenarios that differed in the initial proportion of black and white spruce. The black spruce landscape was composed of 44% deciduous forest and 56% black spruce forest. The current mix landscape was composed of 44% deciduous forest, 37% black spruce, and 19% white spruce forest. The white spruce landscape was composed of 44% deciduous forest and 56% white spruce forest.

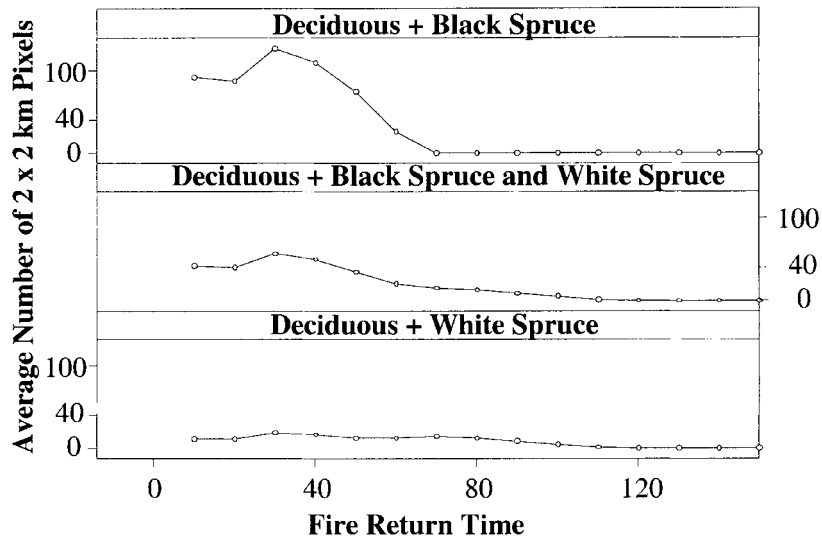


Figure 6. Differences in the deciduous average fire return intervals for 100 replicates of three vegetation scenarios that differed in the initial proportion of black and white spruce. The black spruce landscape was composed of 44% deciduous forest and 56% black spruce forest. The current mix landscape was composed of 44% deciduous forest, 37% black spruce, and 19% white spruce forest. The white spruce landscape was composed of 44% deciduous forest and 56% white spruce forest. Fire intervals were calculated across all pixels in the 100 × 100 km study area.

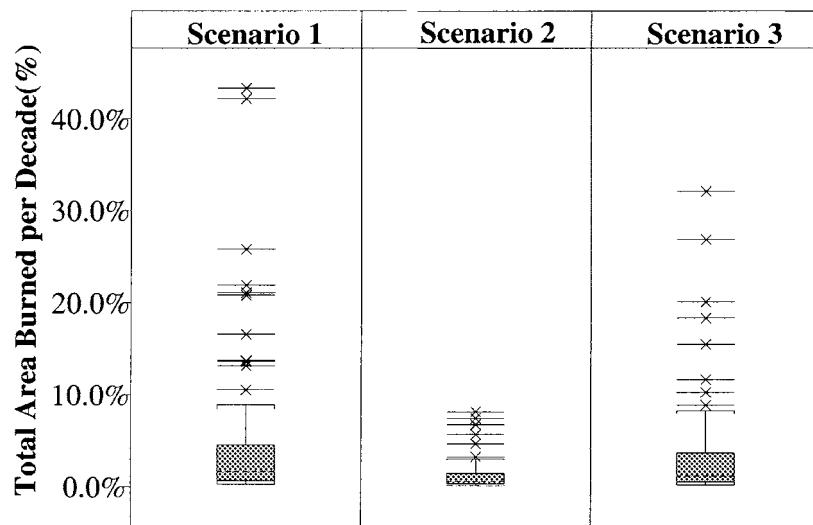


Figure 7. Boxplots of the total area burned per decade (expressed as a percentage of the total landscape) for the sensitivity analyses of black and white spruce flammability and successional time course. Scenario 1 represents black spruce flammability and successional time course. Scenario 2 represents white spruce flammability and black spruce successional time course. Scenario 3 represents black spruce flammability and white spruce successional time course. The dashed line represents the median. The shaded box around the median represents the Inner Quartile Range (IQR), which identifies the region between the 25th and 75th percentiles. The whiskers extending from the IQR represent the largest/smallest value that is still within the median $\pm 1.5 * IQR$. Any value beyond the median $\pm 1.5 * IQR$ is subjectively considered to be an outlier, and as such is marked with an 'x'. Results are from 100 replicates of 1000 years.

compared to white spruce. Sensitivity analyses showed that total area burned was more sensitive to vegetation flammability than to the length of the deciduous forest phase. Differences in the distribution of average area burned, for different flammabilities but identical successional trajectories, were large (Figure 7). In contrast, there were only small differences in area burned when only the length of successional trajectories was altered. The same analyses were performed in the all-white-spruce scenario with similar results (not shown), identifying vegetation flammability as the more sensitive parameter. These results indicate that differences in the flammability of vegetation can significantly impact system dynamics.

4. Discussion

Our simulations suggest that vegetation effects can cause significant changes in the fire regime in interior Alaska. Landscapes with a black spruce component had more fires and more area burned than did landscapes with no black spruce component. Black spruce landscapes also experienced numerous burning events that consumed extensive portions (more than 40%) of the landscape. These results

agree with observations in the Canadian boreal forest where 2% of the fires account for 98% of the total area burned (Stocks, 1991). Large-scale fire events need to be realistically represented in ecosystem models because they strongly influence ecosystem processes at landscape and regional scales (McKenzie et al., 1996; Alvarado et al., 1998). These results have strong implications for global scale models of terrestrial ecosystems. Currently, these models consider only plant functional types distinguished by their physiological (C_3 versus C_4), phenological (deciduous versus evergreen), and physiognomic (grass versus tree) attributes (Smith et al., 1997). Our results suggest finer resolution vegetation structure and composition related to flammability may be needed to simulate accurately the dynamics of the fire regime in interior Alaska and to understand the implications for ecosystem processes at multiple scales.

Fire regime plays an important role in determining the relative abundance of ecosystem types and may cause qualitatively different patterns across the landscape (Rupp et al., 2000b, 2001). Our simulation results revealed increases in the total amount of deciduous forest that burned in the two landscapes with a black spruce component. The results indicated a much shorter fire return interval for deciduous forest in a landscape dominated by black spruce with return times similar to those observed by Yarie (1981) for deciduous forest in interior Alaska. Landscape-level changes in the fire return interval of specific fuel types is an important effect of spatial contagion that currently cannot be addressed by statistical formulation within a global vegetation model. Although there is an excellent quantitative understanding of fire behavior as a function of climate and vegetation at the scale of hours and meters (Johnson, 1992), the dynamic simulation of fire effects at landscape or regional scales remains rudimentary (Gardner et al., 1999). A long-term potential consequence is that fire-induced changes in vegetation may lead to a more homogenous landscape dominated by early successional deciduous forest (Rupp et al., 2000b, 2001). This has strong implications for the regional carbon budget and feedbacks to climate. Changes in landscape-level vegetation pattern would influence disturbance dynamics, which feedback to regional carbon dynamics (Kasischke et al., 1995). Deciduous forest dominance would have a negative feedback to climate warming due to changes in albedo and energy partitioning (Chapin et al., 2000).

It is estimated that 40% of the world's reactive soil carbon is contained in high-latitude ecosystems (McGuire et al., 1995, 2000; Mellilo et al., 1995). A substantial amount of this carbon could be released in response to climatic warming (Nadelhoffer et al., 1992; Oechel et al., 1993, 1995), which may have consequences for the rate and magnitude of climatic change (McGuire et al., 2000). Future interactions between climate, fire disturbance, and vegetation composition and distribution will likely result in changes in forest structure and carbon exchange. Our simulations suggest vegetation composition and distribution strongly influence the fire regime (both fire numbers and areal extent). Forecasted increases in fire disturbance, including extreme fire events, will likely lead to increases in fire emissions. It is important to recognize that carbon may respond very differently to the episodic

nature of fire in the boreal forest, relative to gradual changes in temperature and decomposition (Harden et al., 2000).

We have presented a dynamic spatial model of boreal forest dynamics and performed some simple experiments that cannot be readily explored in the real world. These experiments highlight the important role of black spruce ecosystems in the fire regime of interior Alaska boreal forests. The most compelling result from the model simulations was the importance of a black spruce landscape component to the frequency and magnitude of large-scale burning events (i.e., time steps with total area burned far exceeding the normal distribution of total area burned). It is critical to understand the controls that drive these events and to show how they may change under predicted increases in global temperatures. The current version of ALFRESCO simulates fire ignition and spread using coarse-scale rules relating ignition and fire-spread hazard to climate, vegetation type, and stand age. Future model development will focus on improving the precision of fire hazard-fuel load relationships developed from survival analysis of the major boreal forest fuel types in Alaska. This will result in a more accurate simulation of fire regimes. In addition, a climatic gradient study will provide empirical data for improved representation of fire hazard-climate relationships within and among the major fuel types.

An on-going challenge to the global-change modeling community is to understand how disturbance-generated landscape patterns influence the spatial dynamics of ecosystem processes. We suggest that spatially explicit models of succession (like ALFRESCO) provide the ability to identify landscape-level processes, interactions, and feedbacks that drive long-term system dynamics, and serve as a useful tool for assessing the potential impacts and changes to the system in response to a changing climate and disturbance regime at the regional and global scales. Interactions between climate, vegetation, and disturbance are complex, and ecological models provide a means for gaining an improved understanding of biospheric feedbacks and the implications to carbon dynamics.

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References

- Ager, A. T.: 1983, 'Holocene Vegetational History of Alaska', in Wright, H. E. Jr. (eds.), *Late Quaternary Environments of the United States. Vol. 2. The Holocene*, University of Minnesota Press, Minneapolis, pp. 138–140.
- Alverado, E., Sandberg, D. V., and Pickford, S. G.: 1998, 'Modeling Large Forest Fires as Extreme Events', *Northwest Science* **72**, 66–75.
- Anderson, P. M. and Brubaker, L. B.: 1994, 'Vegetation History of Northcentral Alaska: A Mapped Summary of Late-Quaternary Pollen Data', *Quat. Sci. Rev.* **13**, 71–92.
- Baker, W. L.: 1992, 'Effects of Settlement and Fire Suppression on Landscape Structure', *Ecology* **73**, 1879–1887.
- Beltrami, H. and Mareschal, J. C.: 1991, 'Recent Warming in Eastern Canada Inferred from Geothermal Measurements', *Geophys. Res. Lett.* **18**, 605–608.
- Betts, R. A., Cox, P. M., Lee S. E., and Woodward, F. I.: 1997, 'Contrasting Physiological and Structural Vegetation Feedbacks in Climate Change Simulations', *Nature* **387**, 796–799.
- Bliss, L. C. and Matveyeva, N. V.: 1992, 'Circumpolar Arctic Vegetation', in Chapin, III, F. S., Jefferies, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*, Academic Press, San Diego, pp. 59–89.
- Bonan, G. B., Chapin, III, F. S., and Thompson, S. L.: 1995, 'Boreal Forest and Tundra Ecosystems as Components of the Climate System', *Clim. Change* **29**, 145–167.
- Chapin, III, F. S., McGuire, A. D., Randerson, J., Pielke, R., Baldocchi, D., Hobbie, S. E., Roulet, N., Eugster, W., Kasischke, E., Rastetter, E. B., Zimov, S. A., and Running, S. W.: 2000, 'Feedbacks from Arctic and Boreal Ecosystems to Climate', *Global Change Biol.* **6** (Suppl. 1), 211–223.
- Chapin, III, F. S. and Starfield, A. M.: 1997, 'Time Lags and Novel Ecosystems in Response to Transient Climatic Change in Arctic Alaska', *Clim. Change* **35**, 449–461.
- Chapman, W. L. and Walsh, J. E.: 1993, 'Recent Variations of Sea Ice and Air Temperatures in High Latitudes', *Bull. Amer. Meteorol. Soc.* **74**, 33–47.
- Clark, J. S.: 1988, 'Effect of Climate Change on Fire Regimes in Northwestern Minnesota', *Nature* **334**, 233–235.
- Claussen, M.: 1998, 'On Multiple Solutions of the Atmosphere-Vegetation System in Present-Day Climate', *Global Change Biol.* **4**, 549–559.
- Cramer, W., Shugart, H. H., and Noble, I. R. et al.: 1999, 'Ecosystem Composition and Structure', in Walker, B. H. (ed.), *The Terrestrial Biosphere and Global Change: Implications for Natural and Managed Ecosystems*, Cambridge University Press, Cambridge, pp. 190–228.
- Dyrness, C. T., Viereck, L. A., and Van Cleve, K.: 1986, 'Fire in Taiga Communities of Interior Alaska', in Van Cleve, K., Chapin, III, F. S., Flanagan, P. W., Viereck, L. A., and Dyrness, C. T. (eds.), *Forest Ecosystems in the Alaskan Taiga*, Springer-Verlag, New York, pp. 74–86.
- Edwards, M. E., Anderson, P. M., Garfinkel, H. L., and Brubaker, L. B.: 1985, 'Late Wisconsin and Holocene Vegetational History of the Upper Koyukuk Region, Brooks Range, AK', *Can. J. Bot.* **63**, 616–626.
- ESRI: 1994, *ArcDoc version 7.0: On-line Documentation for ARC/INFO Geographic Information Software*, Environmental Systems Research Institute, Inc, Redlands, California.
- Everett J. T. and Fitzharris, B. B.: 1998, 'The Arctic and the Antarctic', in Watson, R. T., Zinyowera, M. C., Moss, R. H., and Dokken, D. J. (eds.), *The Regional Impacts of Climate Change: An Assessment of Vulnerability*, Cambridge University Press, New York, pp. 85–103.
- Flannigan, M. D. and Harrington, J. B.: 1988, 'A Study of the Relation of Meteorological Variables to Monthly Provincial Area Burned by Wildfire in Canada (1935–80)', *J. Appl. Meteorol.* **27**, 441–452.
- Flannigan, M. D. and Van Wagner, C. E.: 1991, 'Climate Change and Wildfire in Canada', *Can. J. Forest Res.* **21**, 66–72.

- Fleming, M. D.: 1997, *Alaska Vegetation/Land Cover Classes*, U.S. Geological Survey Global Change Program, Land Data Systems – Arctic Land Process Studies, <http://agdc.usgs.gov/data/projects/hlct/hlct.html>.
- Foley, J. A., Kutzbach, J. E., Coe, M. T., and Levis, S.: 1994, 'Feedbacks between Climate and Boreal Forests during the Holocene Epoch', *Nature* **371**, 52–54.
- Ganopolski, A., Kubatzki, C., Claussen, M., Brovkin, V., and Petoukhov, V.: 1998, 'The Influence of Vegetation-Atmosphere-Ocean Interaction on Climate during the Mid-Holocene', *Science* **280**, 1916–1919.
- Gardner, R. H., Romme, W. H., and Turner, M. G.: 1999, 'Predicting Forest Fire Effects at Landscape Scales', in Mladenoff, D. J. and Baker, W. L. (eds.), *Spatial Modelling of Forest Landscapes: Approaches and Applications*, Cambridge University Press, Cambridge, pp. 163–185.
- Greene, D. F., Zasada, J. C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., and Simard, M.-J.: 1999, 'A Review of the Regeneration Dynamics of North American Boreal Forest Tree Species', *Can. J. Forest Res.* **29**, 824–839.
- Hammond, T. and Yarie, J.: 1996, 'Spatial Prediction of Climatic State Factor Regions in Alaska', *Ecoscience* **3**, 490–501.
- Harden, J. W., Trumbore, S. E., Stocks, B. J., Hirsch, A., Gower, S. T., O'Neill, K. P., and Kasischke, E. S.: 2000, 'The Role of Fire in the Boreal Carbon Budget', *Global Change Biol.* **6** (Suppl. 1), 174–184.
- Holling, C. S.: 1992, 'The Role of Forest Insects in Structuring the Boreal Landscape', in Shugart, H. H., Leemans, R., and Bonan, G. B. (eds.), *A Systems Analysis of the Global Boreal Forest*, Cambridge University Press, Cambridge, pp. 170–191.
- Holsten, E. H.: 1990, *Spruce Beetle Activity in Alaska: 1920–1989*, USDA Forest Service, Alaska Region, Anchorage, U.S.A.
- Hu, F. S., Brubaker, L. B., and Anderson, P. M.: 1993, 'A 12000 Year Record of Vegetation Change and Soil Development from Wien Lake, Central Alaska', *Can. J. Bot.* **71**, 1133–1142.
- Johnson, E. A.: 1992, *Fire and Vegetation Dynamics: Studies from the North American Boreal Forest*, Cambridge University Press, Cambridge.
- Kasischke, E. S., Bergen, K., Fennimore, R., Sotelo, F., Stephens, G., Janetos, A., and Shugart, H. H.: 1999, 'Satellite Imagery Gives a Clear Picture of Russia's Boreal Forest Fires', *EOS – Trans. Amer. Geophys. Union* **80**, 141–147.
- Kasischke, E. S., Christensen, N. L., and Stocks, B. J.: 1995, 'Fire, Global Warming, and the Carbon Balance of Boreal Forests', *Ecol. Appl.* **5**, 437–451.
- Kasischke, E. S. and French, N. H. F.: 1997, 'Constraints on Using AVHRR Composite Index Imagery to Study Patterns of Vegetation Cover in Boreal Forests', *Int. J. of Remote Sens.* **18**, 2403–2426.
- Kattenberg, A., Giorgi, F., Grassl, H., Meehl, G. A., Mitchell, J. F. B., Stouffer, R. J., Tokioka, T., Weaver, A. J., and Wigley, T. M. L.: 1996, 'Climate Models – Projections of Future Climate', in Houghton, J. T., Meira Filho, L. G., Callander, B. A., Harris, N., Kattenberg, A., Maskell, K. (eds.), *Climate Change 1995. The Science of Climate Change*, Cambridge University Press, Cambridge, pp. 285–357.
- Kittel, T. G. F., Steffen, W. L., and Chapin, III, F. S.: 2000, 'Global and Regional Modelling of Arctic-Boreal Vegetation Distribution and its Sensitivity to Altered Forcing', *Global Change Biol.* **6** (Suppl. 1), 1–18.
- Levis, S., Foley, J. A., and Pollard, D.: 1999, 'Potential High-Latitude Vegetation Feedbacks on CO₂-Induced Climate Change', *Geophys. Res. Lett.* **26**, 747–750.
- Lloyd, A. H., Armbruster, W. S., and Edwards, M. E.: 1994, 'Ecology of a Steppe-Tundra Gradient in Interior Alaska', *Journal of Vegetation Science* **5**, 897–912.
- McGuire, A. D., Melillo, J. M., Kicklighter, D. W., and Joyce, L. A.: 1995, 'Equilibrium Responses of Soil Carbon to Climate Change: Empirical and Process-Based Estimates', *J. Biogeogr.* **22**, 785–796.

- McGuire, A. D., Melillo, J. M., Randerson, J. T., Parton, W. J., Heimann, M., Meier, R. A., Clein, J. S., Kicklighter, D. W., and Sauf, W.: 2000, 'Modeling the Effects of Snowpack on Heterotrophic Respiration Across Northern Temperate and High Latitude Regions: Comparison with Measurements of Atmospheric Carbon Dioxide in High Latitudes', *Biogeochemistry* **48**, 91–114.
- McKenzie, D., Peterson, D. L., and Alvarado, E.: 1996, *Predicting the Effect of Fire on Large-Scale Vegetation Patterns in North America*, USDA Forest Service, Pacific NW Research Station, U.S.A.
- Melillo, J. M., Kicklighter, D. W., McGuire, A. D., Peterjohn, W. T., and Newkirk, K. M.: 1995, 'Global Change and its Effects on Soil Organic Carbon Stocks', in Zepp, R. G. and Sontag, C. H. (eds.), *Role of Nonliving Organic Matter in the Earth's Carbon Cycle*, John Wiley and Sons, New York, pp. 175–189.
- Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., and Linkins, A. E.: 1992, 'Microbial Processes and Plant Nutrient Availability in Arctic Soils', in Chapin, III, F. S. (ed.), *Physiological Ecology of Arctic Plants: Implications for Climate Change*, Academic Press, New York, pp. 281–300.
- Nielson, R. P., Prentice, I. C., Smith, B., Kittel, T., and Viner, D.: 1997, 'Simulated Changes in Vegetation Distribution under Global Warming', in Watson, R. T. (ed.), *The Regional Impacts of Climate Change. An Assessment of Vulnerability*, Cambridge University Press, New York, pp. 439–456.
- NRC (National Research Council): 1994, *The Role of Terrestrial Ecosystems in Global Change: A Plan for Action*, National Academy Press, Washington, D.C.
- Oechel, W. C., Hastings, S. J., Vourlitis, G. L., Jenkins, M. A., Reichers, G., and Grulke, N.: 1993, 'Recent Changes in Arctic Tundra Ecosystems from a Carbon Sink to a Source', *Nature* **361**, 520–523.
- Oechel, W. C., Vourlitis, G. L., Hastings, S. J., and Bochkarev, S. A.: 1995, 'Change in Arctic CO₂ Flux over Two Decades: Effects of Climate Change at Barrow, Alaska', *Ecol. Appl.* **5**, 846–855.
- Overpeck, J. T., Bartlein, P. J., and Webb, III, T.: 1991, 'Potential Magnitude of Future Vegetation Change in Eastern North America: Comparisons with the Past', *Science* **254**, 692–695.
- Overpeck, J., Hughen, K., Hardy, D., Bradley, R., Case, R., Douglas, M., Finney, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonald, G., Moore, J., Retelle, M., Smith, S., Wolfe, A., and Zielinski, G.: 1997, 'Arctic Environmental Change of the Last Four Centuries', *Science* **278**, 1251–1256.
- Pastor, J. and Post, W. M.: 1986 'Influence of Climate, Soil Moisture, and Succession of Forest Carbon and Nitrogen Cycles', *Biogeochemistry* **2**, 3–27.
- Payette, S.: 1983, 'The Forest Tundra and Present Tree-Lines of the Northern Quebec-Labrador Peninsula', in Morisset, P. and Payette, S. (eds.), *Tree-Line Ecology*, Proceedings of the Northern Quebec Tree-Line Conference, pp. 3–23.
- Payette, S.: 1992, 'Fire as a Controlling Process in the North American Boreal Forest', in Shugart, H. H., Leemans, R., and Bonan, G. B. (eds.), *A Systems Analysis of the Global Boreal Forest*, Cambridge University Press, Cambridge, pp. 144–169.
- Rouse, W. R.: 1976, 'Microclimatic Changes Accompanying Burning in Subarctic Lichen Woodland', *Arc. Alp. Res.* **8**, 357–376.
- Rupp, T. S., Chapin, III, F. S., and Starfield, A. M.: 2000b, 'Response of Subarctic Vegetation to Transient Climatic Change on the Seward Peninsula in Northwest Alaska', *Global Change Biol.* **6**, 541–555.
- Rupp, T. S., Chapin, III, F. S., and Starfield, A. M.: 2001, 'Modeling the Influence of Topographic Barriers on Treeline Advance of the Forest-Tundra Ecotone in Northwestern Alaska', *Clim. Change* **48**, 399–416.
- Rupp, T. S., Starfield, A. M., and Chapin, III, F. S.: 2000a, 'A Frame-Based Spatially Explicit Model of Subarctic Vegetation Response to Climatic Change: Comparison with a Point Model', *Landsc. Ecol.* **15**, 383–400.

- Serreze, M. C., Walsh, J. E., Chapin, III, F. S., Osterkamp, T., Dyrgerov, M., and Romanovsky, V.: 2000, 'Observational Evidence of Recent Change in the Northern High-Latitude Environment', *Clim. Change* **46**, 159–207.
- Shugart, H. H. and West, D. C.: 1980, 'Forest Succession Models', *BioScience* **30**, 308–313.
- Smith, T., Shugart, H. H., and Woodward, F. I.: 1997, *Plant Functional Types*, Cambridge University Press, Cambridge.
- Solomon, A. M.: 1992, 'The Nature and Distribution of Past, Present and Future Boreal Forests: Lessons for a Research and Modeling Agenda', in Shugart, H. H., Leemans, R., and Bonan, G. B. (eds.), *A Systems Analysis of the Global Boreal Forest*, Cambridge University Press, Cambridge, pp. 170–191.
- Starfield, A. M. and Chapin, III, F. S.: 1996, 'Model of Transient Changes in Arctic and Boreal Vegetation in Response to Climate and Land Use Change', *Ecol. Appl.* **6**, 842–864.
- Starfield, A. M., Cummings, D. H. M., Taylor, R. D., and Quadling, M. S.: 1993, 'A Frame-Based Paradigm for Dynamic Ecosystem Models', *A I Applic.* **7**, 1–13.
- Stocks, B. J.: 1991, 'The Extent and Impact of Forest Fires in Northern Circumpolar Countries', in Levine, J. S. (ed.), *Global Biomass Burning: Atmospheric, Climatic and Biospheric Implications*, MIT Press, Cambridge, MA, pp. 197–202.
- Thornwaite, C. W. and Mather, J. R.: 1957, 'Instructions and Tables for Computing Potential Evaporation and the Water Balance', *Publications in Climatology* **10**, 183–311.
- Trigg, W. M.: 1971, *Fire Season Climatic Zones of Mainland Alaska*, U.S. Department of Agriculture, Portland, U.S.A.
- USGS: 1990, *Digital Elevation Models: Data Users Guide 5*, U.S. Department of the Interior, U.S. Geological Survey, Reston, Virginia.
- Van Cleve, K., Chapin, III, F. S., Dyrness, C. T., and Viereck, L. A.: 1991, 'Element Cycling in Taiga Forests: State-Factor Control', *BioScience* **41**, 78–88.
- Van Cleve, K. and Viereck, L. A.: 1981, 'Forest Succession in Relation to Nutrient Cycling in the Boreal Forest of Alaska', in West, D. C., Shugart, H. H., and Botkin, D. B. (eds.), *Forest Succession Concepts and Applications*, Springer-Verlag, New York, pp. 185–211.
- Van Cleve, K., Viereck, L. A., and Dyrness, C. T.: 1996, 'State Factor Control of Soils and Forest Succession along the Tanana River in Interior Alaska, U.S.A.', *Arc. Alp. Res.* **28**, 388–400.
- Van Wagner, C. E.: 1988, 'The Historical Pattern of Annual Burned Area in Canada', *Forestry Chronicle* **64**, 182–185.
- Viereck, L. A. and Johnston, W. F.: 1990, '*Picea mariana* (Mill.) B.S.P. – Black Spruce', in Burns, R. M. and Honkala, B. H. (eds.), *Silvics of North America. Vol. 1. Conifers*, USDA Forest Service, Agric. Handb. 654.
- Viereck, L. A., Van Cleve, K., and Dyrness, C. T.: 1986, 'Forest Ecosystem Distribution in the Taiga Environment', in Van Cleve, K., Chapin, III, F. S., Flanagan, P. W., Viereck, L. A., and Dyrness, C. T. (eds.), *Forest Ecosystems in the Alaskan Taiga*, Springer-Verlag, New York, pp. 22–43.
- Weber, M. G. and Flannigan, M. D.: 1997, 'Canadian Boreal Forest Ecosystem Structure and Function in a Changing Climate: Impact on Fire Regimes', *Environmental Reviews* **5**, 145–166.
- Werner, R. A.: 1986, 'Association of Plants and Phytophagous Insects in Taiga Forest Ecosystems', in Van Cleve, K., Chapin, III, F. S., Flanagan, P. W., Viereck, L. A., and Dyrness, C. T. (eds.), *Forest Ecosystems in the Alaskan Taiga*, Springer-Verlag, New York, pp. 203–212.
- Yarie, J.: 1981, 'Forest Fire Cycles and Life Tables: A Case Study from Interior Alaska', *Can. J. Forest Res.* **11**, 554–562.
- Yurtsev, B. A.: 1982, 'Relics of the Xerophyte Vegetation of Beringia in Northeastern Asia', in Hopkins, D. M., Matthews, J. V., Schweger, C. E., and Young, S. B. (eds.), *Paleoecology of Beringia*, Academic Press, New York, pp. 157–177.
- Zasada, J. C., Sharik, T. L., and Nygren, M.: 1992, 'The Reproductive Process in Boreal Forest Trees', in Shugart, H. H., Leemans, R., and Bonan, G. B. (eds.), *A Systems Analysis of the Global Boreal Forest*, Cambridge University Press, Cambridge, pp. 85–125.

Zimov, S. A., Davidov, S. P., Zimova, G. M., Davidova, A. I., Chapin, III, F. S., Chapin, M. C., and Reynolds, J. F.: 1999, 'Contribution of Disturbance to Increasing Seasonal Amplitude of Atmospheric CO₂', *Science* **284**, 1973–1976.

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