

MODELING THE INFLUENCE OF TOPOGRAPHIC BARRIERS ON TREELINE ADVANCE AT THE FOREST-TUNDRA ECOTONE IN NORTHWESTERN ALASKA

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Abstract. The response of terrestrial ecosystems to climate warming has important implications to potential feedbacks to climate. The interactions between topography, climate, and disturbance could alter recruitment patterns to reduce or offset current predicted positive feedbacks to warming at high latitudes. In northern Alaska the Brooks Range poses a complex environmental and ecological barrier to species migration. We use a spatially explicit model (ALFRESCO) to simulate the transient response of subarctic vegetation to climatic warming in the Kobuk/Noatak River Valley (200 × 400 km) in northwest Alaska. The model simulations showed that a significantly warmer (+6 °C) summer climate would cause expansion of forest through the Brooks Range onto the currently treeless North Slope only after a period of 3000–4000 yr. Substantial forest establishment on the North Slope did not occur until temperatures warmed 9 °C, and only following a 2000 yr time lag. The long time lags between change in climate and change in vegetation indicate current global change predictions greatly over-estimate the response of vegetation to a warming climate in Alaska. In all the simulations warming caused a steady increase in the proportion of early successional deciduous forest. This would reduce the magnitude of the predicted decrease in regional albedo and the positive feedback to climate warming. Simulation of spruce forest refugia on the North Slope showed forest could survive with only a 4 °C warming and would greatly reduce the time lag of forest expansion under warmer climates. Planting of spruce on the North Slope by humans could increase the likelihood of large-scale colonization of currently treeless tundra. Together, the long time lag and deciduous forest dominance would delay the predicted positive regional feedback of vegetation change to climatic warming. These simulated changes indicate the Brooks Range would significantly constrain regional forest expansion under a warming climate, with similar implications for other regions possessing major east-west oriented mountain ranges.

1. Introduction

In the past decade there has been renewed interest in modeling vegetation response to climatic change because the potential changes in vegetation strongly influence both climate (Overpeck et al., 1991; Bonan et al., 1992, 1995; Foley et al., 1994) and the ecosystem characteristics that are important to people. Typically, large-scale biogeochemistry models of ecosystem change have assumed that vegetation

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type does not change (VEMAP members, 1995; McGuire et al., 2000) or, as with older biogeographic models, that vegetation remains in equilibrium with climate (Prentice et al., 1992). A new generation of Dynamic Global Vegetation Models (DGVM) are being developed that simulate transient changes in vegetation based on plant responses to climate and climate-induced changes in water and nutrient availability (Woodward et al., 1995; Foley et al., 1996; Neilson and Running, 1996, Kittel et al., 2000). However, these physiologically based models currently ignore spatial processes such as fire spread and plant migration which can strongly influence rates and patterns of vegetation change (Rupp et al., 2000a, b). One critical test of the importance of these spatial processes is to consider situations where there are large geographic barriers to fire and/or migration.

Topography exerts a strong influence on vegetation distribution and successional trajectory at northern latitudes, through its effects on regional climate (Van Cleve et al., 1991, 1996) and seed dispersal (Hadley, 1994; Malanson and Cairns, 1997). Barriers to seed dispersal can slow the rate of forest migration or halt migration completely (Rupp et al., 2000a). Colder growing-season temperatures at higher elevations reduce potential forest expansion by limiting tree establishment and survival (Stevens and Fox, 1991; Körner, 1998). Therefore, high-mountain climates may act as a strong environmental barrier to forest migration even under a substantially warmer climate.

Disturbance, particularly wildfire, is an important driver of ecosystem change at landscape and regional levels. Climate-disturbance interactions influence the rate and pattern of changes in vegetation (Neilson, 1993; Noble, 1993) and disturbance (Gardner et al., 1996) through effects on fire probability and spread (Gardner et al., 1999) and pattern of colonization (Turner et al., 1997; Rupp et al., 2000b). Increases in fire frequency and annual area burned, as observed under current warming trends (Kasischke et al., 1999), will likely result in an increasingly early successional deciduous-dominated landscape (Rupp et al., 2000b). Deciduous forest would reduce energy absorption and increase evapotranspiration (Baldocchi et al., in press), offsetting the predicted positive feedback to warming at high latitudes (Chapin et al., 2000).

White spruce expanded rapidly from Canada into interior Alaska approximately 9000 BP (Brubaker et al., 1995). Spruce reached the southern reaches of the Brooks Range at this time, but did not cross over the mountains to the North Slope. The fact that white spruce did not migrate north of its current limit in Alaska has suggested to many that the Brooks Range (and its environment) act as a major barrier to migration. Understanding the factors that control the rate of forest expansion is critical in evaluating the potential feedbacks to climate from the future response of boreal forest to warming. Here, we use a spatially explicit model (ALFRESCO) that simulates the response of subarctic vegetation to climatic warming (Rupp et al., 2000a, b) to investigate the limitations to forest establishment on the North Slope of Alaska.

2. Methods

2.1. STUDY SITE

Model simulations were conducted in northwest Alaska in the Kobuk and Noatak River valleys (the simulation landscape measured 400×200 km) (Figure 1). The landscape includes a climate/vegetation gradient from upland tundra north of the Range to a treeline ecotone south of the Range. The area was selected because it is bisected by the east-west oriented Brooks Range and, therefore, might not respond as expected to a warming climate. Elevation ranges from sea level along the coast to 1700 m in the Brooks Range, with much of the Range being above 600 m. Fires are infrequent, due to the low density of lightning strikes (Reap, 1991) and burn primarily at the tundra-treeline ecotone.

Initial landscape conditions were generated from GIS raster coverages (ESRI, 1994) of Alaskan data sets of current growing-season temperature and precipitation (Hammond and Yarie, 1996), current vegetation (Fleming, 1997), current fire regime (Kasischke and French, 1997), and topography (USGS, 1990). ASCII input files were generated from the spatial data sets and read into the initialization routine of ALFRESCO.

2.2. MODEL OVERVIEW

The simulation model (ALFRESCO), described in detail by Rupp et al. (in press-a, b; <http://www.lter.alaska.edu/pubs/ALFRESCO.html>), simulates the response of subarctic vegetation to transient climatic change in Alaska. The model assumptions reflect our hypothesis 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).

ALFRESCO operates at a 10-yr time step, the average frequency of severe fire years in the North American boreal forest (Flannigan and Harrington, 1988) and calculates vegetation change in a landscape composed of 2×2 km pixels, a scale appropriate for interfacing with mesoscale climate models (Starfield and Chapin, 1996).

The model simulates four major subarctic ecosystem types: upland tundra, white spruce forest, deciduous forest, and grassland-steppe. Grassland-steppe represents a novel ecosystem that is uncommon under present climate but was a major component of the Alaskan landscape during the drier late-Pleistocene climate (Hopkins et al., 1982). The ecosystem types represent a generalized classification of the complex vegetation mosaic characteristic of the circumpolar arctic and boreal zones of Alaska (Solomon, 1992; Starfield and Chapin, 1996; Rupp et al., 2000a).

ALFRESCO is a frame-based model (Starfield et al., 1993) that uses rules to simulate the changes in ecosystem types and disturbance regimes to a changing cli-

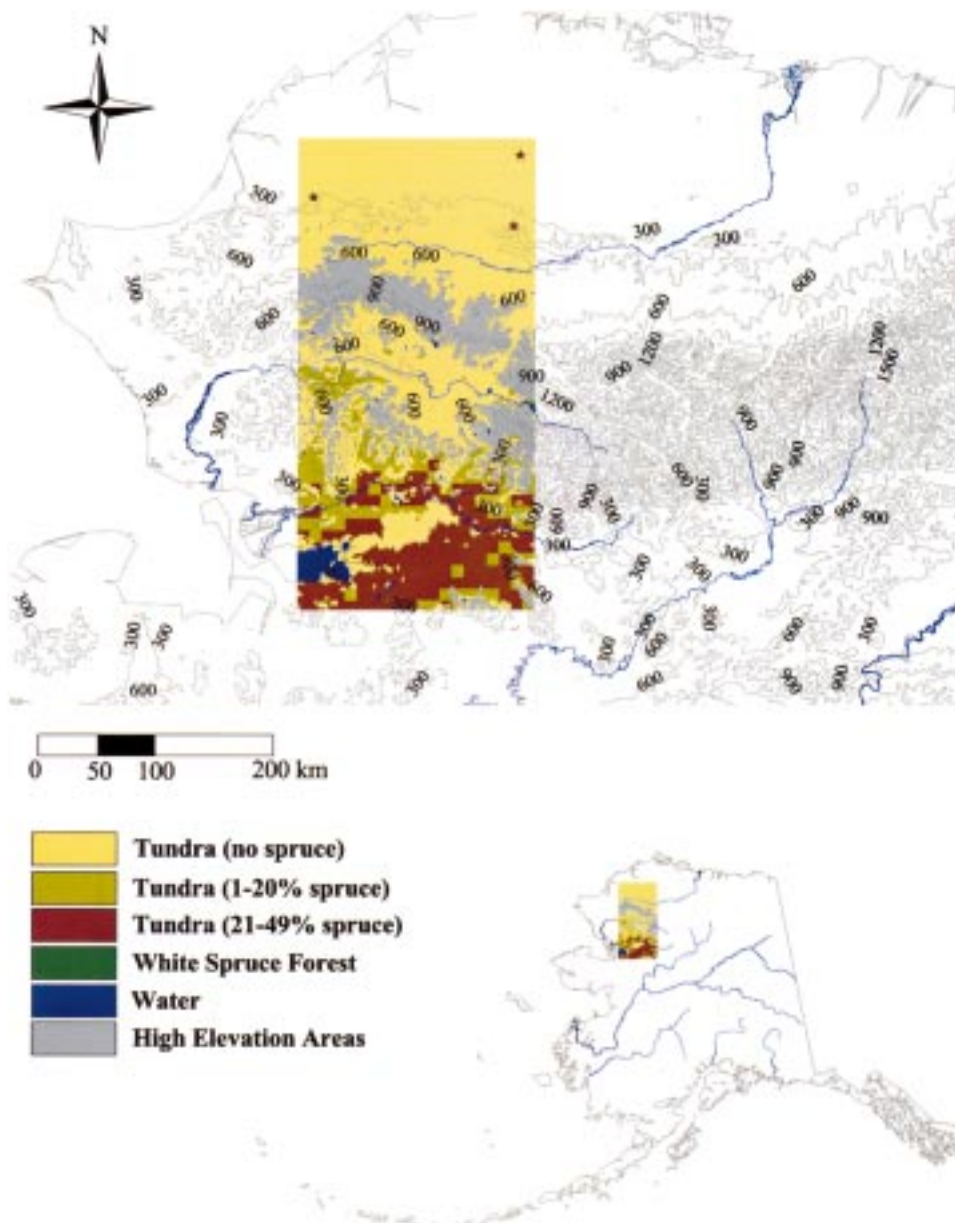


Figure 1. Map of the Kobuk/Noatak Rivers study area showing the current vegetation. The tundra vegetation type was stratified into 3 classes determined by the level of white spruce tree canopy cover (treeless, 1–20%, and 21–49% cover). The landscape is 200 × 400 km. Barriers (dark gray) to seed dispersal under current climate occur where elevation is greater than 600 m. Contour intervals are 300 m. Red stars indicate the location of white spruce forest stands (16 km²) used in the refugia experiment.

mate. Each ecosystem type (i.e., frame) constitutes an independent submodel that calculates and monitors factors and processes that could cause a switch to another 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).

2.3. CLIMATE

ALFRESCO generates climate stochastically based upon observed (1960–1990) 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 differ in the magnitude of temperature and precipitation. The temperature maps range from -2°C colder to $+12^{\circ}\text{C}$ warmer than current climate. Precipitation maps were derived from projections of future Alaskan climate by four GCM's (Maxwell, 1992; Chapin and Starfield, 1997). From these projections, precipitation maps were uniformly increased (or decreased for colder temperature maps) by 15% for each 1°C change from the observed current average temperature.

First, a user defined climate scenario is chosen (e.g., current climate or $+2^{\circ}\text{C}$ instantaneous change) at the start of the simulation. Then, for each climate scenario there is an associated probability distribution of choosing a particular map of temperature and of precipitation for a given time step. These frequency distributions (around growing-season mean values) of both current temperature and precipitation were developed from climate records for a tundra site (Kotzebue), a treeline site (Haugen, 1982), and a boreal forest site (Fairbanks) (Starfield and Chapin, 1996; Chapin and Starfield, 1997). Precipitation and temperature maps are chosen independently at a given time step. It follows that a 1°C temperature increase does not necessarily result in a 15% increase in precipitation for any particular decade, but on average warmer climates will be associated with higher precipitation. For example, under the current climate scenario, the map that represents the currently observed average growing-season temperature (1960–1990) has a 60% chance of being chosen (in any given time step), while the observed precipitation regime has only a 40% chance of being chosen. The temperature and precipitation in each pixel of the map is then converted to temperature and precipitation classes (1, 2, 3 or 4) that have defined effects on vegetation (Starfield and Chapin, 1996; Rupp et al., 2000a). In this way we define coherent scenarios of climatic change (e.g., instantaneous or gradual climatic warming), allow stochastic variation in temperature and precipitation at each time step for a climate scenario, and provide geographic patterns of climate that are consistent with topography and synoptic climatology.

2.4. DISTURBANCE

Fire regime is simulated stochastically and is driven by climate, vegetation type, canopy cover, and time since last fire. ALFRESCO employs a cellular automaton approach, where an ignited pixel may spread to any of the eight surrounding pixels. Fire spread depends on the flammability of the receptor pixel and the effect of natural fire breaks including topographic barriers (which are assumed to contain little or no fuels) and large water bodies (i.e., lakes and river systems comprising the majority of a 2×2 km pixel). A 'fire' implies that more than 50% of the area burned with an intensity that killed a majority of trees. In all ecosystem types flammability is assumed to be a function of an 'effective drought' index (Trigg, 1971; Clark, 1988), which decreases (i.e., more severe drought conditions) as climate becomes warmer and dryer (Thorntwaite and Mather, 1957; Starfield and Chapin, 1996). Fire probability differs among ecosystem types due to differences in fuel build-up (e.g., vegetation type, time since last disturbance, and canopy cover) (Rupp et al., 2000a). In this manner, we can simulate the dynamic interactions between fire, climate, and vegetation change.

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), others explicitly. Thus the model assumes that there are scattered deciduous species present in spruce forest, so seed is available when conditions are right for establishment.

An increase in 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. ALFRESCO uses elevation data to identify barriers to migration (i.e., inhibit the dispersal of seed) (Rupp et al., 2000a, b). Under currently observed climate the model interprets cells higher than 600 m as barriers to seed dispersal. As the climate warms, the model determines the new elevational threshold of barrier cells by using the observed adiabatic lapse rate of 0.63 °C per 100 m for Alaskan treeline (Haugen et al., 1971; Viereck, 1979). For example, if growing-season temperature increases 1 °C from current temperature the barrier threshold increases from 600 m (i.e., the current climate threshold) to 767 m (i.e., 167 m per 1 °C increase). We assume seed dispersed (when not inhibited by a barrier cell) from a seed source has a dispersal distance maximum threshold of 4 km (beyond which no seed travels). 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 canopy cover (Rupp et al., 2000a, b). Thus, following a change in the barrier threshold the migration lag rate is a function of seed source strength (i.e., propagule availability) and growing-season climate (i.e., temperature limitations to canopy cover growth).

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 Chapin and Starfield (1996) and Rupp et al. (2000a). We provide only a general overview.

Within a given submodel we simulate those mechanisms and processes that might cause a switch to a new ecosystem type. We then compare values of these parameters to thresholds defined in switching rules to determine if a switch from one ecosystem to another occurs. If a switch occurs, the ‘old’ submodel is terminated and the ‘new’ submodel is activated. For example, upland tundra will switch to spruce forest if tree canopy cover exceeds 50% or switch to grassland following fire and two decades of hot and dry climate. Following conversion of tundra to white spruce forest there is no change until a fire occurs. A fire will normally cause a switch to deciduous forest, but fire in conjunction with extremes in climate may cause a switch to grassland-steppe (two decades hot and dry climate) or switch back to tundra (two cold decades). Deciduous forest is maintained by fire, but following a fire-free period of 90–120 yr deciduous forest switches back to white spruce forest. Following a fire in grassland-steppe, a switch to deciduous forest or tundra may occur, or the system may remain grassland, depending on temperature and seed availability.

2.7. MODEL SIMULATIONS

The model was first calibrated with the goal of producing simulation results that, under current climate, best matched the observed fire records between 1950 and 1997 (Kasischke and French, 1997). We further assumed that the current vegetation observed for the simulation landscape (Fleming, 1997) is in equilibrium with the current environment (i.e., observed climate and disturbance regime). Under these assumptions there was a single parameter set that accurately simulated fire size, fire number, and vegetation composition. We used this parameter set for the remaining simulations.

Under current climate ALFRESCO simulated an average of 9.4 fires per decade that burned a total of 120,848 hectares compared to 9.2 fires per decade that burned 121,248 ha, as observed from fire records. The model also simulated a steady-state equilibrium vegetation distribution that closely matched current vegetation composition, with average total forest remaining at less than 1% of the landscape after 500 yr (replicated 100 times). This vegetation stability is consistent with the assumption that current vegetation is in equilibrium with the current climate and fire regime for the study area. To further test the appropriateness of the model we simulated the response of the landscape to a colder (instantaneous decrease of 2 °C) climate. As expected, under a colder climate, new tree establishment and survival was prevented. Furthermore, when spruce forest in a pixel was destroyed by fire, the cold climate prevented trees from recolonizing and so the pixel remained tundra

through the remainder of the simulation period. These results suggest ALFRESCO offers a plausible representation of current vegetation dynamics.

We next performed a suite of warming experiments to explore the interactions between topography, climate and disturbance on the rate and pattern of spruce forest migration through the Brooks Range to the North Slope of Alaska. We simulated several instantaneous climate change scenarios (ranging from 2 °C to 12 °C warmer than current climate), run for 5000 yr. To gain insight into the species migration potentials and distributions without the constraints (i.e., physical and environmental) imposed by the Brooks Range, we then repeated the simulations, but with three spruce forest refugia (each 16 km²) established north of the Brooks Range (Figure 1). Expansion of the spruce refugia was measured and compared to the simulations with no refugia present.

3. Results

We first simulated (for 500 yr, replicated 100 times) instantaneous warming scenarios of 2 °C and 4 °C. These same warming scenarios caused substantial increases in forest cover in a neighboring landscape on the Seward Peninsula (Rupp et al., 2000b). However, the results from the Kobuk/Noatak landscape showed considerably less response by the vegetation to climatic warming. Forest increased only 9% when climate warmed 2 °C and increased 28% when warmed 4 °C, compared to 15% and 65% on the Seward Peninsula for 2 °C and 4 °C increases, respectively. A major difference between the two landscapes is topographic relief. Although both landscapes are currently dominated by tundra, the coastal landscape of the Seward Peninsula is relatively flat with few high mountains. These differences lend support to the hypothesis that topography constrains forest migration rates through highly mountainous regions.

To investigate the influence of the Brooks Range on the rate and extent of forest migration in the Kobuk/Noatak landscape we simulated additional instantaneous warming scenarios to identify at what climate (i.e., growing-season temperature and precipitation) forest would successfully migrate to the North Slope. Considerable warming was necessary before forest migrated through the Brooks Range (Figure 2). In fact, boreal forest did not reach the north side of the range until climate was warmed 6 °C and then only after a period of 3000–4000 yr. Substantial colonization did not occur until average growing-season temperatures reached 9 °C warmer than current climate (Figure 3). Even at climates substantially warmer than today a 2000–3000 yr time lag occurred before large portions of the landscape north of the range became forested. Future growing-season temperatures of this magnitude eliminate virtually all barriers to seed dispersal that are currently present on the landscape. Therefore, the time lags are a result of climate constraints on forest establishment and growth in the Brooks Range, where growing-season climate is considerably colder than in low-elevation portions of the landscape. This

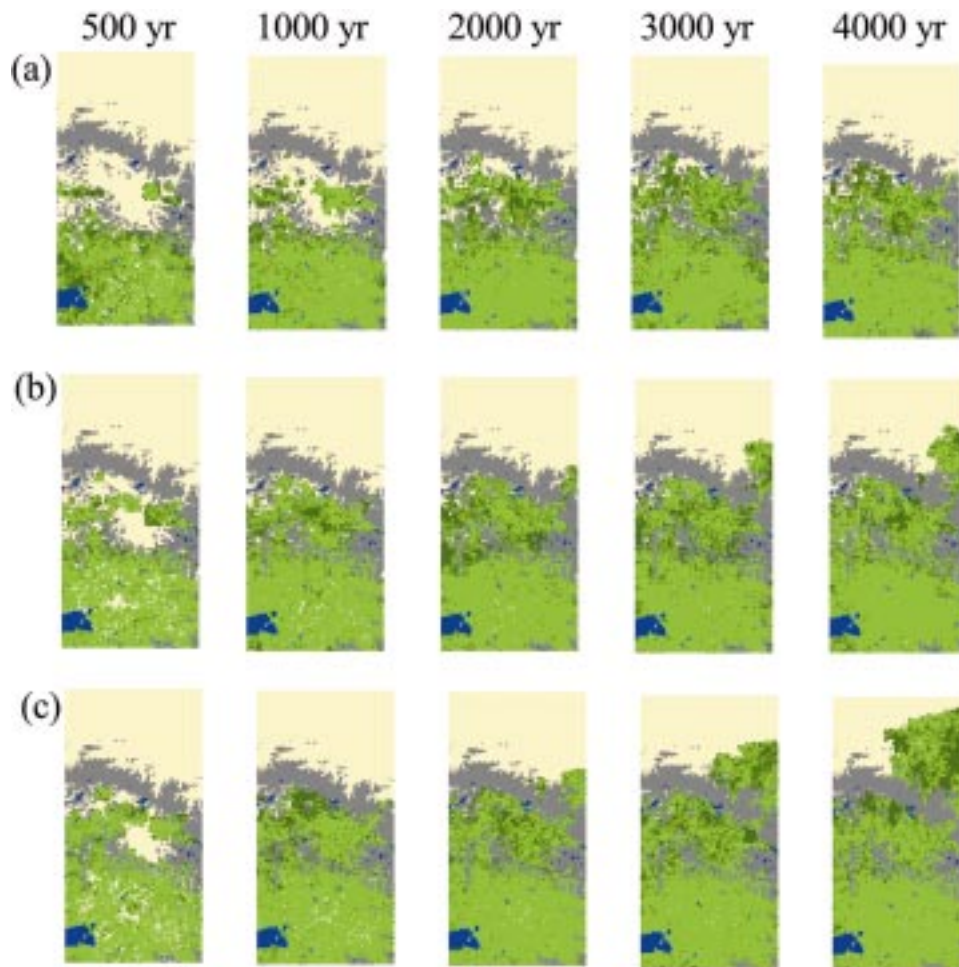


Figure 2. Simulated response of the Kobuk/Noatak landscape to instantaneous warming scenarios of (a) +6°C, (b) +7°C and (c) +8°C from current climate. The maps show changes in tundra (beige), spruce forest (dark green), and deciduous forest (light green) distribution at 500–4000 yr. Superimposed seed dispersal barriers (elevation >600 m) for currently observed climate are indicated in dark gray. These may or may not be barriers under warmer temperatures (see Methods).

results in a complete halt of forest expansion (at temperatures less than 6°C warmer than current climate) or substantial forest conversion periods (for temperatures between 6°C and 9°C) before forest successfully migrates through the Brooks Range (Figure 4).

Using maps of currently observed growing-season temperature in Alaska (Hammond and Yarie, 1996) and 6.5°C as the environmental threshold (i.e., climate limitation for forest establishment), we found that there are no areas within or north of the Brooks Range capable of supporting boreal forest. We performed the same analysis for climate 8°C warmer than current climate and found the Range would

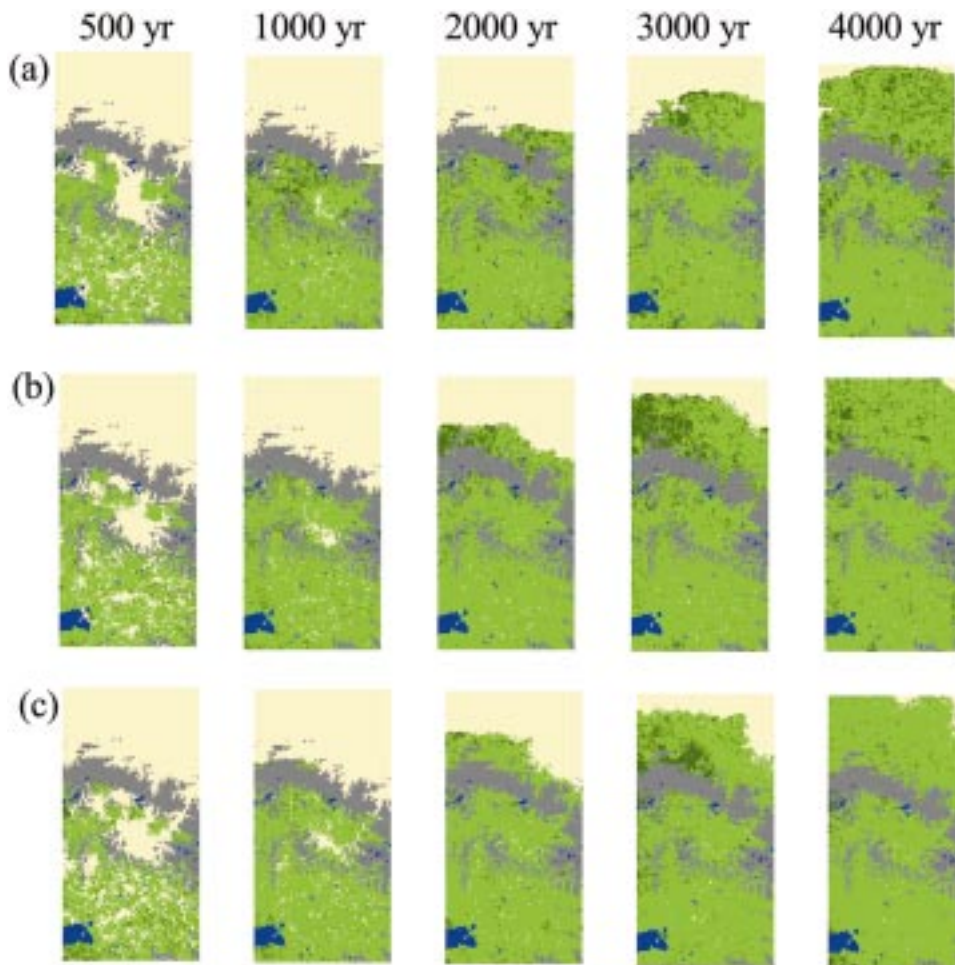


Figure 3. Simulated response of the Kobuk/Noatak landscape to instantaneous warming scenarios of (a) +9 °C, (b) +10 °C and (c) +11 °C from current climate. The maps show changes in tundra (beige), spruce forest (dark green), and deciduous forest (light green) distribution at 500–4000 yr. Superimposed seed dispersal barriers (elevation >600 m) for currently observed climate are indicated in dark gray. These may or may not be barriers under warmer temperatures (see Methods).

still restrict spruce forest expansion from the south to most of northern Alaska, except in a few mountain passes (Figure 5).

Disturbance reduced both the rate and extent of forest migration across the landscape. We compared simulated runs with a fire regime and without (i.e., suppression of all fires), and measured forest conversion rate across the landscape (Table I). The model simulations without fire showed an increase in the rate of forest conversion, where tundra switched to forest as much as 650 yr earlier than simulations with an unsuppressed fire regime. The increased time required for forest to move across the landscape highlights the negative impact fire has on

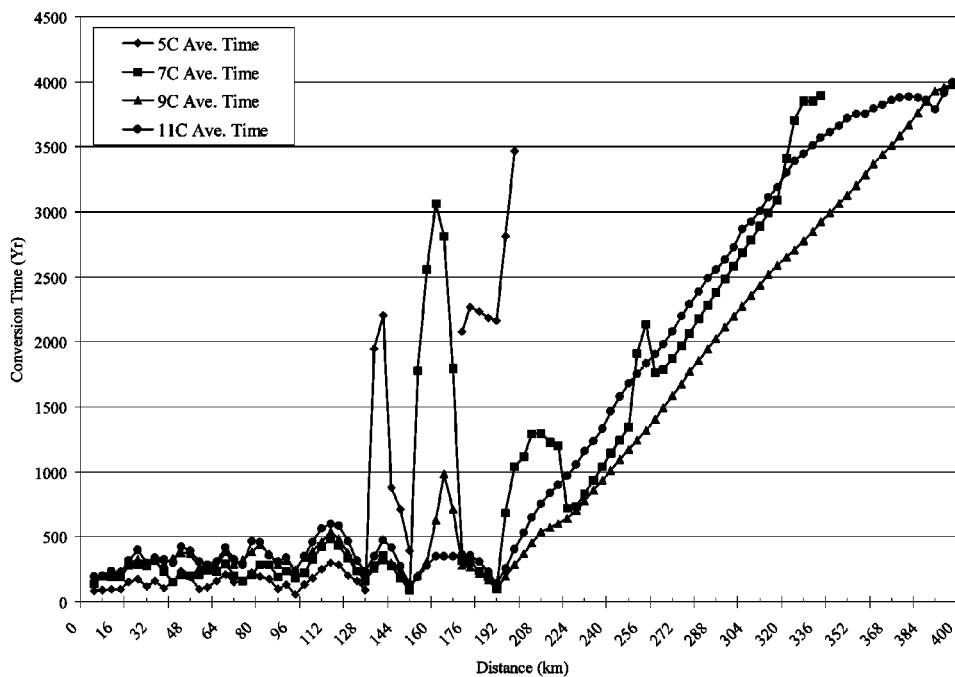


Figure 4. Average rate of forest conversion of upland tundra, with disturbance, along a south-north transect under instantaneous warming scenarios of 5 °C (diamonds), 7 °C (squares), 9 °C (triangles), and 11 °C (circles) warmer than current growing-season (May–Sept.) temperatures. The spikes in forest conversion time show the effect of the Brooks Range on regional climate and its control over forest establishment and expansion rates. Simulation results are averages from 100 replicates.

treeline seed sources in ALFRESCO. Furthermore, fire number and area burned increased substantially as climatic warming increased. Although growing-season precipitation increased with warmer temperatures, the relative increase in temperature compared to precipitation caused an overall increase in the drought index (i.e., resulted in dryer fuels). Changes in area burned occurred due to climate-induced increases in the flammability of all vegetation types, which influenced the number of fire ignitions and the extent of spread. These disturbance regime changes resulted in large proportions of deciduous forest establishment across the landscape (Table II). There appears to be a tradeoff where a warming climate produces more favorable growing conditions for spruce forest establishment but also a more hostile environment (i.e., more and larger fires) for long-term spruce survival (Rupp et al., 2000b).

We further tested the mountain barrier hypothesis by establishing spruce forest refugia on the north side of the Brooks Range (Figure 1) and then simulating the same instantaneous warming scenarios. At both current climate and a 2 °C warming the refugia did not colonize neighboring treeless tundra cells and eventually were killed by fire and replaced by tundra, due to growing-season temperatures

TABLE I

Summary of the average conversion time (yr) to forest of grid cells along a south-north transect, under increasingly warmer climate scenarios. Each simulation was run for 4000 yr (replicated 100 times) with and without a fire regime

Distance ^a	+5 °C	+6 °C	+7 °C	+8 °C	+9 °C	+10 °C	+11 °C	+12 °C
	No fire/fire	No fire/fire	No fire/fire	No fire/fire	No fire/fire	No fire/fire	No fire/fire	No fire/fire
50	49/104	47/159	49/212	50/269	50/302	47/309	47/284	49/309
100	109/130	109/163	109/222	110/295	110/340	109/334	109/351	109/321
150	1988/3270	483/1297	393/1071	223/413	108/120	89/105	90/117	89/122
200	3023/-	1816/3262	748/1113	380/437	337/373	335/412	336/532	335/591
250	-/-	3532/3955	1430/1592	1109/1189	1074/1199	1074/1398	1073/1724	1074/1782
300	-/-	-/-	2543/2683	2095/2199	2059/2276	1948/2486	1923/2867	1923/2976
350	-/-	-/-	3983/-	3156/3309	2887/3168	2738/3344	2697/3731	2678/3838
400	-/-	-/-	-/-	-/-	3824/-	3245/3908	3115/-	3080/-

^a Kilometers from the southernmost grid cell in the landscape.

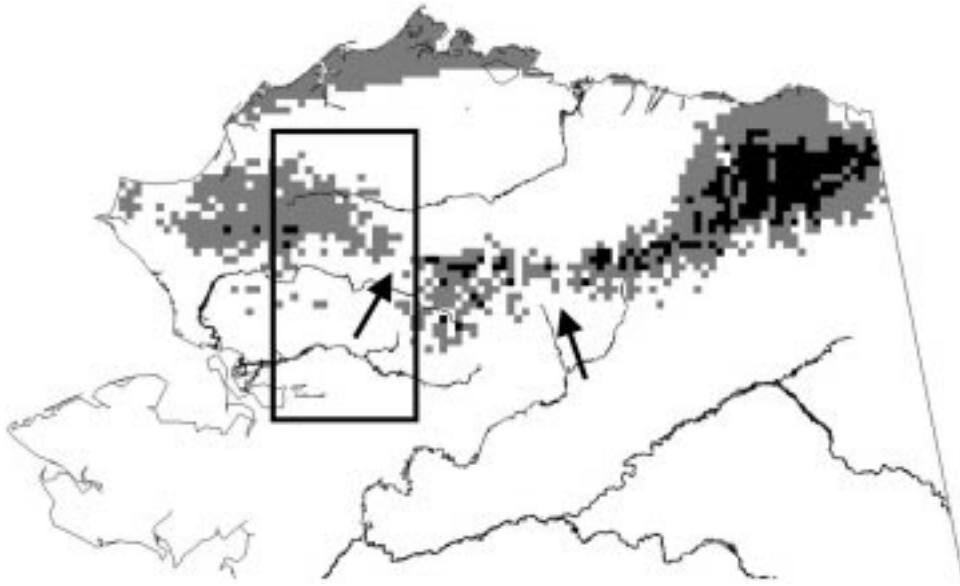


Figure 5. Speculated influence of Brooks Range climate on the potential for forest migration under climate 8 °C warmer than current climate. Shaded regions identify areas where climate substantially slows forest migration (gray) or halts migration completely (black). The arrows indicate the two areas in northern Alaska most likely to support forest migration to the North Slope. The box shows extent of study area.

TABLE II

Summary of the fire regime (average # fires and area burned per decade) and the proportion of deciduous and spruce forest on the landscape (after 4000 yr) under increasingly warmer climate scenarios. Simulation results are averages from 100 replicates

	+5 °C	+6 °C	+7 °C	+8 °C	+9 °C	+10 °C	+11 °C	+12 °C
# Fires	12.0	13.2	14.1	14.6	15.2	16.3	17.2	17.6
Area burned ^a	908	1478	1904	2235	2650	3259	3808	4060
% Spruce	12.2	12.8	14.2	15.9	16.5	10.8	5.2	3.8
Deciduous	29.9	40.2	49.1	62.3	76.6	86.6	90.3	90.1

^a Average # of 2 × 2 km cells burned per decade.

too limiting (i.e., cold) to support forest trees. The refugia survived up to 500 yr with a 4 °C increase (data not presented) and increased total forest cover with a 5 °C instantaneous warming in the first 500 yr (Table III). Total forest increased by as much as 27% relative to the simulations with no refugia present. In fact after 2000 yr, with climate 9 °C warmer than present, over 95% of the landscape was forested. This conversion of a tundra landscape to boreal forest occurred twice as fast (2000 vs. 4000 yr) as when refugia were not present on the North Slope.

TABLE III

Summary of the effect on the landscape of spruce forest refugia. The table shows the increase in the percent of total landscape that is forested if refugia are present. Simulation results are averages from 100 replicates

Time	+5 °C	+6 °C	+7 °C	+8 °C	+9 °C	+10 °C	+11 °C	+12 °C
1000	0.3	1.4	4.9	11.9	15.8	15.2	12.3	10.8
2000	0.7	2.7	10.6	22.7	27.0	21.2	19.9	19.6
3000	1.0	4.2	12.9	20.0	18.6	8.5	11.1	13.1
4000	1.3	5.9	14.9	13.7	4.1	0.4	2.4	3.9

4. Discussion

Our simulations suggest that, under a warmer climate, forest expansion in northern Alaska would be substantially constrained by the Brooks Range and its environment. In the Kobuk/Noatak region of northwestern Alaska, white spruce forest migrated to the North Slope only 3000–4000 yr after the simulated climate had warmed 6 °C. A lack of evidence of spruce forest establishment on the North Slope over the past 9000 yr (including periods considerably warmer than today) (Hopkins, 1972; Brubaker et al., 1983; Edwards et al., 1985; Anderson, 1985) supports these results. Field experiments indicate that both conifer and deciduous trees can establish and grow in tundra north of the Brooks Range (Hobbie and Chapin, 1998). Regardless of the degree of warming, there was at least a 1000 yr time lag for forest to expand from its current limits to the north side of the Brooks Range (Figure 4). These results have important implications for the predicted positive feedback of forest expansion to regional warming (Chapin et al., 2000). Inaccurate projections of the rate of boreal forest expansion and the associated change in albedo and energy partitioning would likely result in an over-estimate of the rate of high-latitude climate warming. Our results indicate that topography and its affect on regional climate play a major role in constraining the expansion of forest into currently treeless areas, in response to a warming climate, and may cause migration patterns to differ across regions of the circumpolar north that contain major east-west oriented mountain ranges.

Although there are few landscapes where mountains act as an absolute physical barrier to seed dispersal, the altitudinal influence on climate in high mountain ranges can produce extensive areas that are too cold to support forest development under predicted climatic warming scenarios and, therefore, fail to disperse seeds beyond the mountains. For example, assuming boreal forest cannot survive at average growing-season temperatures less than 6.5 °C and can grow only marginally at temperatures less than 9.5 °C (Starfield and Chapin, 1996; Chapin and Starfield,

1997; Rupp et al., 2000a), the Brooks Range acts as a major environmental barrier to northward forest expansion.

The large increase in proportion of deciduous forest in response to warmer climate is consistent with the dominance of poplars during the Holocene 9000 yr BP (Brubaker et al., 1995), which contrasts with spruce dominance during cooler periods. Our results suggest that the higher albedo deciduous forest dominance will reduce spring energy absorption and may offset the current spring warming trend (Chapin et al., 2000; Keyser et al., 2000).

One important reason for investigating the rate of treeline advance northward is to predict positive feedbacks to climate as a result of substantial changes in regional albedo. Such predictions are currently based on the assumption that treeline will indeed advance northward, probably rapidly, in response to climatic warming (Chapin et al., 2000). Our results suggest that topography-climate-disturbance interactions dictate the rate and pattern of vegetation colonization in Alaska in response to climatic warming. Furthermore, topographically mediated climate poses a strong environmental barrier (i.e., the Brooks Range) to species migration, causing a pronounced time lag in forest expansion, or even preventing expansion altogether if temperature increases are less than 6 °C. Migration corridors (i.e., low mountain passes and river valleys) or human introduction of trees will be particularly critical for successful northward movement of forest through the Brooks Range in northern Alaska. Presence of major east-west oriented mountain ranges in other regions of the circumpolar north, for instance certain regions of Siberia, could experience similar responses to climatic warming. We suggest that any simulations of vegetation feedback to climate must take into account the overriding controls of topography, both explicit and implicit, on species response to climatic warming.

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