

Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska

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[1] Boreal tree species are expected to invade tundra ecosystems as climate warms. Because forested ecosystems differ from tundra ecosystems in a number of climatically relevant characteristics, this advance of the altitudinal and latitudinal tree limit may ultimately feedback on regional climate. We used tree rings to reconstruct the response of the treeline ecotone on the Seward Peninsula in northwestern Alaska to 20th century warming. We further explored the sensitivity of the treeline ecotone to climate change using the spatially explicit, frame-based model ALFRESCO. Our reconstructions of forest response to past warming indicate that in upland tundra spruce have successfully established progressively farther from the forest limit since the 1880s. Shrub tundra has thus been converted to low-density forest–tundra within a band extending approximately 10 km from the forest limit. In lowland sites, where soil thermal and hydrologic properties are the primary constraint on tree distribution, trees began establishing in tundra after 1920, and establishment was restricted to areas that had experienced thermokarst activity in the past. Modeling experiments suggested that changes in disturbance regime and spruce growth response to climate may introduce strongly nonlinear responses to climate change at treeline. Field data and model experiments thus both indicate that large and nearly instantaneous responses to warming are likely at the treeline ecotone but that sensitivity to warming is likely to vary substantially over space and time. *INDEX TERMS:*

1851 Hydrology: Plant ecology; 3322 Meteorology and Atmospheric Dynamics: Land/atmosphere interactions; 9315 Information Related to Geographic Region: Arctic region; *KEYWORDS:* Alaska, boreal forest, climate change, model, treeline, seed dispersal

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1. Introduction

[2] The position of treeline, which we define here as the latitudinal or elevational limit of upright trees, has changed in response to past climate changes, and advances of treeline are therefore widely expected to accompany future climate warming. A period of warm climate in the early Holocene (the Milankovitch maximum), for example, was associated with an expansion of treeline beyond its current limits in northern Eurasia [e.g., MacDonald *et al.*, 2000] and in central and western Canada [e.g., Spear, 1993]. Subsequent neoglacial cooling led to a retreat of treeline after 3500 years B.P. in eastern Canada [Payette and Gagnon, 1985; Gajewski *et al.*, 1993], western Canada [Moser and MacDonald, 1990; Macdonald *et al.*, 1993; Spear, 1993], northern Eurasia [MacDonald *et al.*, 2000],

and Alaska [Denton and Karlén, 1977]. In addition, there is evidence that the high-latitude warming trend that began in the early 1900s [e.g., Chapman and Walsh, 1993; Serreze *et al.*, 2000] has led to a renewed expansion of treeline tree species into adjacent tundra ecosystems at both arctic [e.g., Hopkins, 1972; Gorchakovskiy and Shiyatov, 1978; Morin and Payette, 1984; Cooper, 1986; Scott *et al.*, 1987; Lavoie and Payette, 1994; Suarez *et al.*, 1999] and alpine [e.g., Brink, 1959; Franklin *et al.*, 1971; Lloyd, 1998] treelines in North America and Eurasia.

[3] Expansion of trees into tundra in recent decades has been widespread, but not universal. MacDonald *et al.* [1998], for example, conclude from an analysis of dendrochronological and historical evidence that stand density increased at treeline but that the northern limit of treeline did not advance significantly in the 20th century. Similar observations have been made in eastern Canada, where apparent advances of treeline have either been due to changes in growth form rather than reproduction from seed [Lescop-Sinclair and Payette, 1995] or have been restricted to particular topographic contexts [Payette and Fillion, 1985]. In addition, recent studies have indicated that the response of boreal forest tree growth to temperature has changed in the 20th century throughout the boreal forest, suggesting that temperature-induced drought stress may

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become increasingly widespread in high-latitude forests [e.g., *Jacoby and D'Arrigo, 1995; Briffa et al., 1998; Barber et al., 2000; Lloyd and Fastie, 2002*]. The implications of such changes in tree growth response to climate for treeline dynamics remain unknown. The variability in individual and population-level responses to 20th century warming suggests that treeline responses to future warming may be similarly heterogeneous; the causal factors underlying variation in the sensitivity of treeline forests to climate change, however, remain largely unknown.

[4] Although there is conditional support from the paleoecological literature for the hypothesis that rising temperatures will lead eventually to an advance of treeline, the expected transient dynamics (e.g., the response on time-scales of years to decades) of treeline ecosystems remain highly uncertain. Regional variability (e.g., western versus eastern Canada) in response to recent warming, for example, may indicate that lagged responses to climate change may be common at treeline. *Chapin and Starfield [1997]* used a precursor of the frame-based model that we employ in this study to conclude that lags of 150–250 years may occur following the onset of warming before tundra ecosystems reach a threshold of 80% forestation. These lags resulted from limitations in seed input, combined with disturbances like fire and insect attack; forestation also occurred more rapidly in scenarios with more rapid warming.

[5] Lagged responses to climate change have particular significance at arctic treeline, where changes in the distribution of forested vegetation have the potential to feedback on climate. Compared to tundra ecosystems, forested ecosystems (and intermediate forest–tundra ecosystems) tend to have a lower albedo, higher sensible heat flux, and lower latent heat flux. These differences result primarily from differences in leaf color and canopy morphology, and have the effect of increasing the amount of atmospheric heating that occurs over forest vegetation relative to tundra vegetation [*Chapin et al., 2000*]. These differences in surface energy-exchange processes may lead to measurable feedbacks on regional or even global climate [*Bonan et al., 1992; Foley et al., 1994; Pielke and Vidale, 1995*]. The rate and spatial pattern of treeline forest response to changes in climate will influence the degree to which such feedbacks develop in the future.

[6] In this study, we examine the spatial and temporal dynamics of treeline response to climate change using both empirical data and a spatially explicit model of treeline dynamics [*Rupp et al., 2000a, 2000b, 2001*]. We use tree ring-based reconstructions of forest dynamics at the arctic treeline in western Alaska to explore the temporal relationship between treeline advance and recent warming, and to address the spatial dynamics of any advances that have occurred. Paleoclimate data suggest that annual temperatures in the arctic have risen by approximately 1.5°C since the mid-1800s [*D'Arrigo and Jacoby, 1993; Overpeck et al., 1997; Serreze et al., 2000*], an amount that is within the range of predicted warming in the arctic over the next several decades [*Houghton et al., 1996*]. The field data thus provide us with a relatively complete description of spruce population response to a magnitude of warming similar to what may be experienced over the next several decades. Because of the slow response time of the system,

however, we can not conduct the kinds of factorial experiments that would be necessary to determine the relative importance of different controls over treeline expansion or the interactions among those controls. We therefore used the model ALFRESCO to investigate the potential interactions among controls over treeline expansion under a variety of climate scenarios. The magnitude of warming used in the model experiments (2°–4°C) is probably slightly higher than that experienced in the last 100–150 years at our sites, but is still within the range of estimates of future warming in the arctic [*Houghton et al., 1996*]. In particular, we explored two questions. (1) How do temperature and precipitation, spatial structure of treeline, seed dispersal, and fire regime interact to influence the rate of treeline expansion? (2) What effect will changes in tree growth response to climate (e.g., decline in growth due to temperature-induced drought stress [*Barber et al., 2000; Lloyd and Fastie, 2002*]) have on the dynamics of treeline advance?

2. Methods

2.1. Description of Study Area

[7] Our study sites are located in the vicinity of Council, Alaska (64°54'N, 163°40'W), on the Niukluk River in the southeastern quarter of the Seward Peninsula (Figure 1). The Council area supports a diverse mosaic of tundra and forest vegetation types. Lichen-dominated tussock tundra dominates low-elevation surfaces with low relief, which tend to be heavily influenced by permafrost. A variety of shrub tundra and forest–tundra communities occur throughout the uplands around Council. Dense gallery forests of white spruce (*Picea glauca* (Moench) Voss) occur on well-drained soils along river floodplains.

[8] The area around Council is the approximate western limit of spruce forest in North America [*Viereck and Little, 1972*], and supports two distinct types of treeline ecotones. First, a diffuse treeline occurs in upland sites where relatively dense forests at low elevations gradually give way to shrub tundra at higher elevations. The forest–tundra ecotone in this situation can be several kilometers wide. Second, an abrupt treeline occurs along rivers, where dense gallery forests on well-drained floodplain soils abut tussock tundra on adjacent nonfloodplain surfaces. The forest–tundra ecotone in this case is <100 m wide.

2.2. Field Methods

[9] We reconstructed forest dynamics across the forest–tundra ecotone at two study sites near Council, Alaska. The first study site, along the Fox River, is an example of the diffuse upland forest–tundra ecotone described previously. At that site, we sampled trees in four to six replicate plots at four locations along the forest–tundra ecotone (Table 1). The sampling locations extended from open spruce forests at 46 m asl to low shrub tundra communities with scattered small spruce at 168 m asl. Plot size varied according to tree density, and ranged from 0.25 to 1.0 ha. The second study site, along Bear Creek, is an example of an abrupt floodplain forest–tundra ecotone. At that site, we sampled trees in four replicate 0.1 ha study plots: two each on floodplain and adjacent nonfloodplain surfaces (Table 1). The area immediately adjacent to the active river floodplain along Bear Creek was previously affected by thermokarst activity,

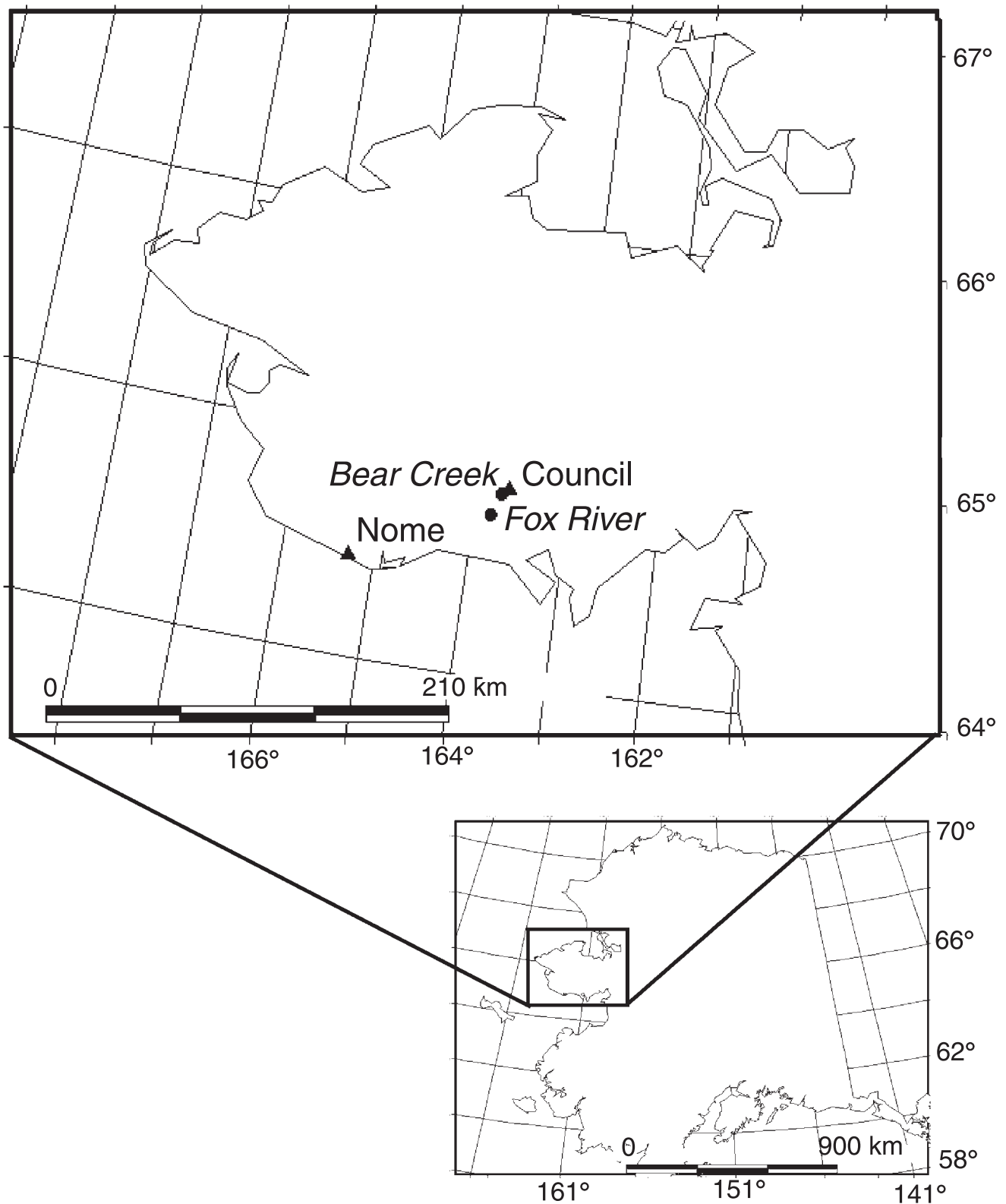


Figure 1. Location of study sites on the Seward Peninsula. The sites are at the approximate western limit of spruce: areas at comparable elevations and latitudes west of our sites are treeless.

and each of our replicate plots on the nonfloodplain surface extends from highly disturbed areas closest to the floodplain to less disturbed areas far from the floodplain (K. Yoshikawa and L. Hinzman, personal communication, 2001).

[10] All trees and saplings in each study plot were mapped and tagged with numbered aluminum tags. We obtained an increment core through the pith (or as close as possible to the pith) of each tree (live or dead) with a

Table 1. Description of Study Sites in the Vicinity of Council, Alaska^a

Site	Elevation, m	Latitude, °N	Longitude, °W	Number of Plots	Area Sampled, ha	Tree Density, (Mean ± 1 SE)
A. Fox River sites						
Forest	46	64°49′	163°45′	4	1	190 ± 116
Lower forest–tundra	61	64°48′	163°46′	6	2.5	30.6 ± 9.2
Middle forest–tundra	100	64°44′	163°53′	5	5	21.4 ± 4.8
Upper forest–tundra	168	64°43′	163°58′	5	5	18 ± 4.5
B. Bear Creek sites						
Floodplain	45	64°52′	163°45′	2	0.2	7216.6 ± 683.5
Nonfloodplain	45	64°52′	163°45′	2	0.2	13,998.3 ± 1180.8

^a The Fox River study sites are arrayed along an elevational gradient from low-elevation sites with open spruce forests to high-elevation low tundra sites with scattered spruce. The Bear Creek sites include dense gallery forests on the floodplain of Bear Creek and nonforested tussock tundra areas immediately adjacent to the active river floodplain.

basal diameter >2.5 cm. Trees were cored as close to the root crown as possible. Height above root crown and basal diameter were recorded for each cored tree. For trees that were too small to core, the number of stem internodes was counted and the total height and basal diameter were measured. Because seedling density was extremely high at Bear Creek, we subsampled seedlings in three replicate 25 m² plots within each of the replicate permanent plots.

2.3. Laboratory Methods

[11] Increment cores were mounted in wooden strips and sanded to 400 grit. Cores were measured on a sliding bench micrometer (Velmex, Inc.) to a precision of 0.001 mm. Measured rings were crossdated using the computer program Cofecha [Holmes, 2000] and using visual crossdating [Stokes and Smiley, 1968]. Tree germination dates were estimated by correcting the crossdated inner ring dates for years to pith (in cases where the core missed the tree's pith) and for the time required for the tree to grow to the height at which it was cored. The number of years to core height was estimated from age–height regression equations established for all seedlings at each sampling location. A unique age–height regression was estimated for each sampling location to account for site-specific differences in tree growth rate. Age and height were significantly related to each other with either a linear or logarithmic relationship at all sites ($R^2 > 0.4$, $P < 0.001$). In cores lacking the pith, the distance to the center of the tree was estimated by fitting a circle template to the innermost curved ring or, if no ring curvature was present, by subtracting the core length from the measured radius at core height. The number of years to the center of the tree was then estimated from an equation relating age to diameter, which was established from all seedlings and trees with pith. Age and diameter were significantly related at all sites ($R^2 > 0.4$, $P < 0.001$). An average (± 1 standard error) of 16.04 ± 0.9 years was added to each core at the Fox River sites, and an average of 15.7 ± 0.55 years was added to each core at the Bear Creek sites. Tree germination dates estimated using these methods were compiled into 10-year time classes to describe the recruitment history for each site.

[12] Changes in live tree density over time were estimated by calculating the number of trees alive at each site during each 10-year time period. Estimates of past stand density are subject to the fading record (decomposition of dead trees), which will cause systematic underestimates of stand density. Analysis of the death dates of crossdated dead trees suggests that trees sapling-sized and larger will persist on the landscape for several decades, so our stand density estimates

provide a robust estimate for those size classes for at least the 20th century. Because smaller seedlings are likely to decompose rapidly, we do not have good estimates of how seedling density has changed through time, and our density estimates prior to 1970 should thus be interpreted as the density of sapling-sized or larger trees.

[13] Changes in live tree density were used to reconstruct treeline advance. Because isolated trees frequently establish beyond the limit of forest, we used two different criteria to estimate the date at which a tundra site converted to forest–tundra. First, we set an arbitrary density criterion of 5 trees/ha as an indication that viable spruce populations had established at a particular site. Second, we determined the decade at which successful spruce recruitment became continuous (i.e., at least 1 tree/decade established).

2.4. Modeling Experiments

[14] The landscape-fire-succession model (ALFRESCO), described in detail by Rupp *et al.* [2000a, 2000b, 2001], simulates the response of subarctic vegetation to transient climatic change in Alaska. The model assumptions reflect the 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 [Van Cleve *et al.*, 1991; Starfield and Chapin, 1996]. ALFRESCO operates on a 10-year 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].

[15] 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 climate. Each ecosystem type (i.e., frame) constitutes an independent submodel. Within a given submodel those mechanisms and processes that might cause a switch to a new ecosystem type are simulated. Parameter values are compared 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, a tundra pixel may

Table 2. Summary of Model Experiments Run With ALFRESCO^a

Factor	Levels
Climate regime	6.5°–9.5°C growing season temperatures 9.5°–12.5°C growing season temperatures
Landscape spatial structure	Abrupt Patchy
Dispersal curve	Seeds fall within 4 km radius “Fat tail” distribution
Tundra fire regime	250 years between fires 500 years between fires no tundra fire
Forest fire regime	40 years between fires 50 years between fires 100 years between fires 150 years between fires 200 years between fires 500 years between fires no forest fire

^aThe experiments were run as a full $2 \times 2 \times 2 \times 3 \times 7$ factorial experiment in which all levels of each factor were run with all levels of each other factor.

switch to spruce forest when tree canopy cover exceeds 50% or switch to grassland following a fire and two consecutive hot, dry decades. Tree canopy cover increases as a function of temperature and seed rain and decreases as a function of insect attack (causes a 25% reduction in canopy cover) and fire (causes a removal of all spruce trees). The seed rain variable accounts for both in filling (seed input from established trees on the site) and dispersal from surrounding seed sources (spruce forest within 4 km of tundra). Fire and insect attack are stochastic functions of climate and tree canopy cover.

[16] The successional dynamics of ALFRESCO, described by *Rupp et al.* [2000a, 2000b, 2001], were modified to match observed vegetation patterns on the Seward Peninsula. In particular, spruce forest replaces itself after fire (instead of going through an early successional deciduous phase), and reproductive maturity of trees is set at 40 years. In association with extremes in climate, however, fire may cause a switch to grassland-steppe (e.g., hot and dry climate) or a switch to upland tundra (e.g., cold climate).

[17] We conducted two sets of experiments with the model (Table 2). In the first experiment, we assessed the relative importance of four potential controls over spruce migration: magnitude of warming, spatial structure of tree-line, dispersal curve, and fire regime. This experiment used a hypothetical landscape composed of actual vegetation types found on the Seward Peninsula. We compared two general climate regimes: growing season temperatures between 6.5°C and 9.5°C (the moderate scenario; representing a 2°C warming), or growing season temperatures between 9.5°C and 12.5°C (the extreme scenario; representing a 4°C warming). To assess the effect of treeline spatial structure, we compared spruce migration rate between a patchy treeline boundary, in which outlying populations of spruce were established in tundra away from the forest edge, and an abrupt boundary, in which all cells were either tundra or forest. The effects of our assumptions about spruce dispersal were assessed by comparing a standard scenario, in which the maximum dispersal distance was set at 4 km, to a “fat tail” scenario [Clark *et al.*, 1998] in which rare, long-

distance dispersal events occurred at some fixed probability. Finally, we estimated the effects of fire by running the model with three different tundra fire frequencies (250 years between fires, 500 years, and no fire) and seven forest fire frequencies (40 years between fires, 50 years, 100 years, 150 years, 200 years, 500 years, and no forest fires).

[18] The model was run as a full factorial experiment, in which all levels of each main effect (climate, spatial structure, dispersal curve, tundra fire, and forest fire) were run with all levels of each other factor. Each model run lasted for 15,000 years, and we ran five replicate model runs for each combination of factor levels. Treeline expansion rate was estimated by monitoring a strip of 100 4 km² cells 10 km from treeline (in the case of the abrupt boundary) or 20 km from treeline (in the case of the patchy boundary) and determining the number of years required for the cell to convert to >50% cover of spruce.

[19] Results were analyzed using a one-way analysis of variance with a full factorial design. Different levels of main effects with more than two levels were compared using Tukey’s HSD test, which controls the experimentwise error rate.

[20] In the second experiment, we examined the effect on treeline migration of changes in the growth response of spruce to temperature. Recent tree ring studies suggest that spruce growth has declined despite increasing temperature at both low elevation [Barber *et al.*, 2000] and high elevation [Lloyd and Fastie, in review] sites in Alaska, indicating that a change in the growth response of spruce to climate may be likely if temperatures increase in Alaska in the future. We compared a standard scenario, in which treeline spruce respond favorably to increased temperature, to a drought-stress scenario, in which spruce growth was positively correlated with both temperature and precipitation. In this scenario, spruce growth was fastest in warm/wet conditions, and climate scenarios that incorporated cold and/or drought produced slower growth. The two scenarios were repeated for four different climate scenarios involving two levels of temperature increase (+2°C and +4°C instantaneous increases) and two levels of precipitation change (30% increase, 30% decrease). The model was run as a full factorial experiment. Each model run lasted 1000 years, and each of the eight scenarios was replicated ten times. The model was run on an actual vegetation map of the Seward Peninsula, which allowed us to tally the areal extent of major vegetation types (spruce forest, tundra, grassland) at the end of the simulation. The significance of effects of temperature, precipitation, and spruce climate response on vegetation and fire regime was determined using a one-way analysis of variance.

3. Results

3.1. Forest Dynamics Along the Fox River

[21] Spruce populations at higher elevations along the Fox River are younger than those at lower elevations (Figure 2). The oldest spruce sampled in the forested sites established prior to 1750 (Figure 2A). At the lower and middle forest–tundra sites the oldest spruce established in the 1880s (Figures 2B and 2C). At the uppermost forest–tundra site, the oldest spruce established in the 1920s (Figure 2D). At the lower and middle forest–tundra sites,

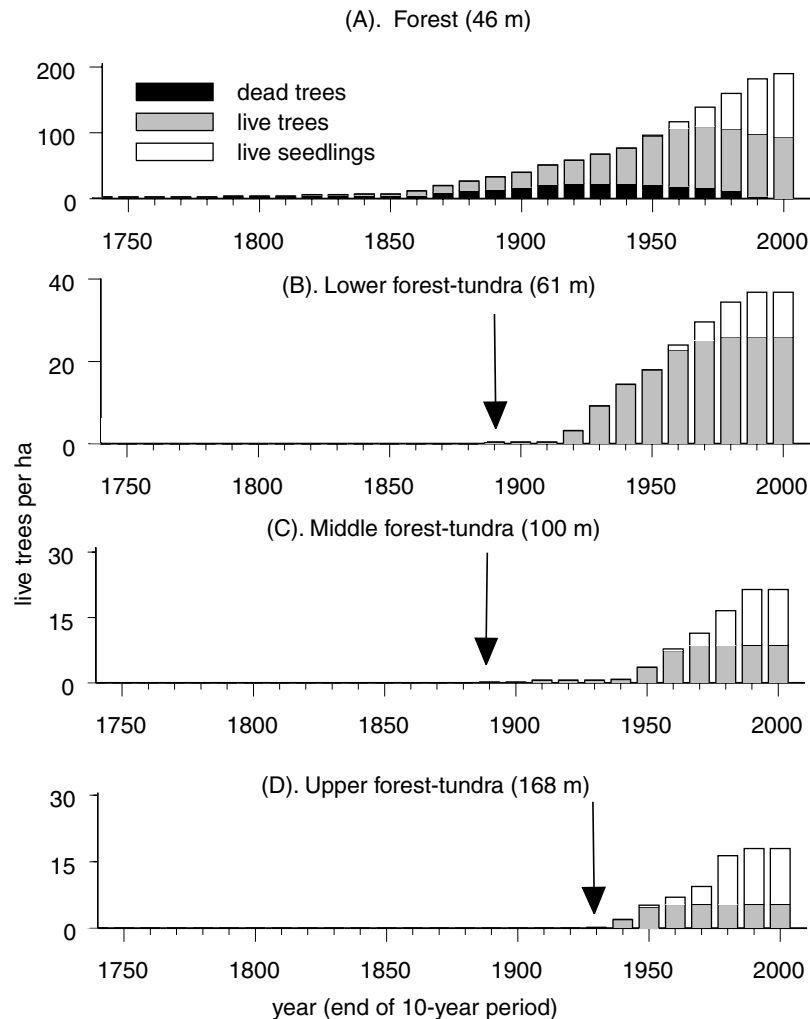


Figure 2. Density of live spruce trees (trees/ha) for each decade from 1740 to 2000 at Fox River, Alaska. Year on the x axis indicates the end year of the decade. The status of trees at the time they were sampled is indicated by the bar color: dead trees were dead at the time of sampling, live trees were alive and large enough to core at the time of sampling, and seedlings were alive but too small to core at the time of sampling. Arrows indicate the date at which the first tree established at each site; absence of an arrow indicates that establishment began prior to 1740.

recruitment was sporadic for the first several decades after the oldest spruce established, but became constant beginning in the 1910s (lower forest-tundra) or 1930s (middle forest-tundra). Recruitment at the uppermost site was continuous from its onset in the 1920s. Few seedlings <10 years old were found at any site, but this probably reflects the difficulty of finding very small seedlings in dense tundra vegetation rather than a decline in recruitment. Dead trees were found only at the lowermost site, and crossdated outer ring dates ranged from 1913 to 1998. The mean diameter of live and dead cored trees did not differ significantly ($P > 0.05$).

[22] The density of live trees at all sites has increased since the middle of the 20th century (Figure 2). Although the absolute size of the per decade increase in density after 1950 has been greatest at the lower elevation sites (Figures 2A and 2B), the relative increase (as a % of previous density) has been greatest at the upper elevation sites (Figures 2C and 2D).

[23] The density of spruce exceeded 5 trees/ha, the threshold beyond which we consider a site to have converted from tundra to forest-tundra, more recently at higher elevations than at lower elevations (Figures 2A–2D). The reconstruction of treeline advance indicates that the lowermost site has probably been forested for at least 200–250 years. At the lower forest-tundra site spruce exceeded the critical density of 5 trees/ha in the 1920s. At the middle forest-tundra site, that density was exceeded in the 1950s, and at the upper forest-tundra site that density was exceeded in the 1940s.

3.2. Forest Dynamics Along Bear Creek

[24] Spruce populations on the floodplain of Bear Creek were older than those on the nonfloodplain surface. The oldest spruce on the floodplain established in the 1730s (Figure 3A), while the oldest spruce on the nonfloodplain surface established in the 1920s (Figure 3B). We found dead trees only in the floodplain surface, and crossdated outer

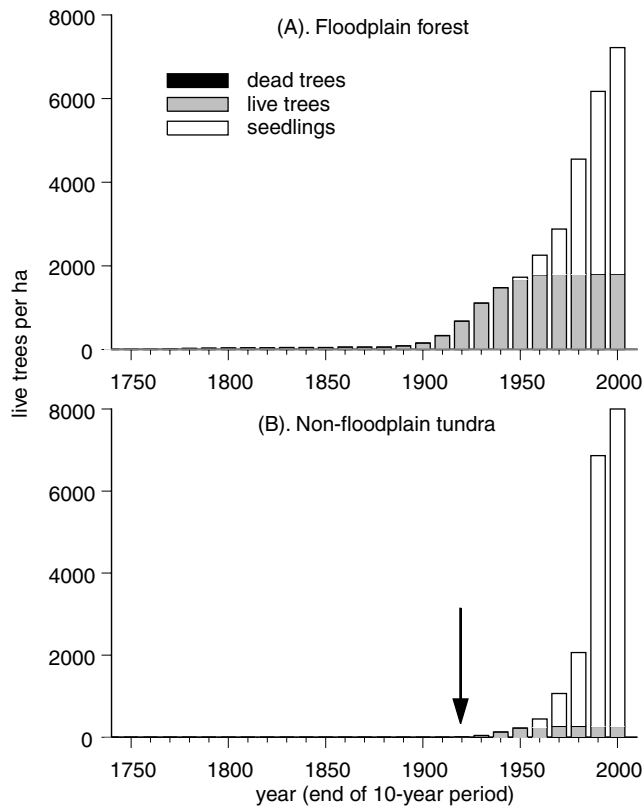


Figure 3. Density of live spruce trees (trees/ha) for each decade from 1740 to 2000 at Bear Creek, Alaska. See Figure 2 caption for description of significance of bar color and arrows.

ring dates ranged from 1942 to 1998. The mean diameter of live and dead cored trees did not differ significantly ($P > 0.05$).

[25] Large increases in the density of live spruce have occurred in the past several decades at each site (Figure 3). The rate of increase in density (in both absolute and relative terms) has been highest on the nonfloodplain surface, where very high densities of seedlings have established in recent decades.

[26] Spruce have exceeded the density criterion of 5 trees/ha for the duration of the tree ring record (<1740) on the active floodplain surface. Spruce exceeded the density criterion of 5 trees/ha in the 1920s on the nonfloodplain surface.

3.3. Modeling Experiments

3.3.1. Influences on Rate of Treeline Advance

[27] The magnitude of warming had the largest effect on the rate of treeline advance: migration rate was 16 times greater in the extreme warming scenario than in the moderate warming scenario ($F = 445,868.81$, $P < 0.001$) (Figure 4A). Spruce migration rate was significantly higher in patchy than abrupt landscapes ($F = 21,091.87$, $P < 0.001$) (Figure 4B). Not surprisingly, the incorporation of long-distance dispersal events (the “fat tailed distribution” scenario) significantly increased the rate of treeline migration ($F = 10,356.49$, $P < 0.001$) (Figure 4C). Increases in the interval between tundra ($F = 620.97$, $P < 0.001$) and forest ($F = 78.64$,

$P < 0.001$) fires significantly increased treeline migration rate (Figures 4D and 4E).

[28] There were a number of significant interactions among the five main effects. A significant interaction between warming and treeline spatial structure ($F = 20,662.74$, $P < 0.001$) indicated that warming had a greater effect on treeline migration in patchy landscapes, and that conversely landscape spatial structure had little influence on migration in the moderate warming scenario (Figure 5A). A significant interaction between treeline spatial structure and dispersal curve ($F = 1768.83$, $P < 0.001$) indicated that the effects of long-distance dispersal events are more important at patchy treelines than at abrupt treelines (Figure 5B). The effects of long-distance dispersal events were also more pronounced in the extreme climate scenarios ($F = 10,335.5$, $P < 0.001$) (Figure 5C).

3.3.2. Effects of Spruce Climate Response on Treeline Dynamics

[29] Increases in temperature ($F = 516.9$, $P < 0.001$) (Figure 6A) and precipitation ($F = 9766.4$, $P < 0.001$) (Figure 6B) were associated overall with greater abundance of spruce and reduced abundance of tundra. Spruce was also significantly more widespread overall in the scenarios that assumed temperature limitation only than in those that assumed spruce would be both precipitation and temperature limited ($F = 465.5$, $P < 0.001$) (Figure 6C).

[30] The model suggested that grassland communities, which are not now present on the Seward Peninsula, could become more widespread under conditions of extreme warmth ($F = 114.7$, $P < 0.001$) (Figure 6A) and reduced precipitation ($F = 161.5$, $P < 0.001$) (Figure 6B). Grassland communities were significantly more abundant in scenarios in which spruce were precipitation limited than in those in which spruce were just temperature limited ($F = 62.16$, $P < 0.001$) (Figure 6C).

[31] There was a significant interaction between warming and spruce climate response ($F = 2231.4$, $P < 0.001$). Following a 2°C rise in temperature, spruce were significantly more widespread when their growth was limited by temperature and precipitation (6240.5 ± 134.4 cells, mean \pm standard error) than when their growth was limited only by temperature (4579.2 ± 136.8 cells). In contrast, after 4°C warming, spruce were significantly less widespread when they were limited simultaneously by temperature and precipitation (4654.3 ± 176.2 cells) than when they were limited only by temperature (9109.1 ± 246.5 cells). Addition of precipitation limitation thus created nonlinear responses to climate.

[32] Fire regimes were also affected by changes in the growth response of spruce to climate; changes in fire regime mirrored the vegetation response in that scenarios with more spruce were more fire prone (Table 3). Significantly more fires occurred during the 1000-year model run after 4°C warming than after 2°C warming ($F = 479.3$, $P < 0.001$), and the size of fires was significantly greater after 4°C warming than after 2°C warming ($F = 743.5$, $P < 0.001$). Fires were also significantly more frequent ($F = 351.9$, $P < 0.001$) but smaller ($F = 23.11$, $P < 0.001$) in the dry scenario than in the wet scenario. Although there was no difference in number of fires between the two scenarios of spruce climate response ($F = 1.75$, $P = 0.189$), fires were significantly larger under the assumption of temperature limitation

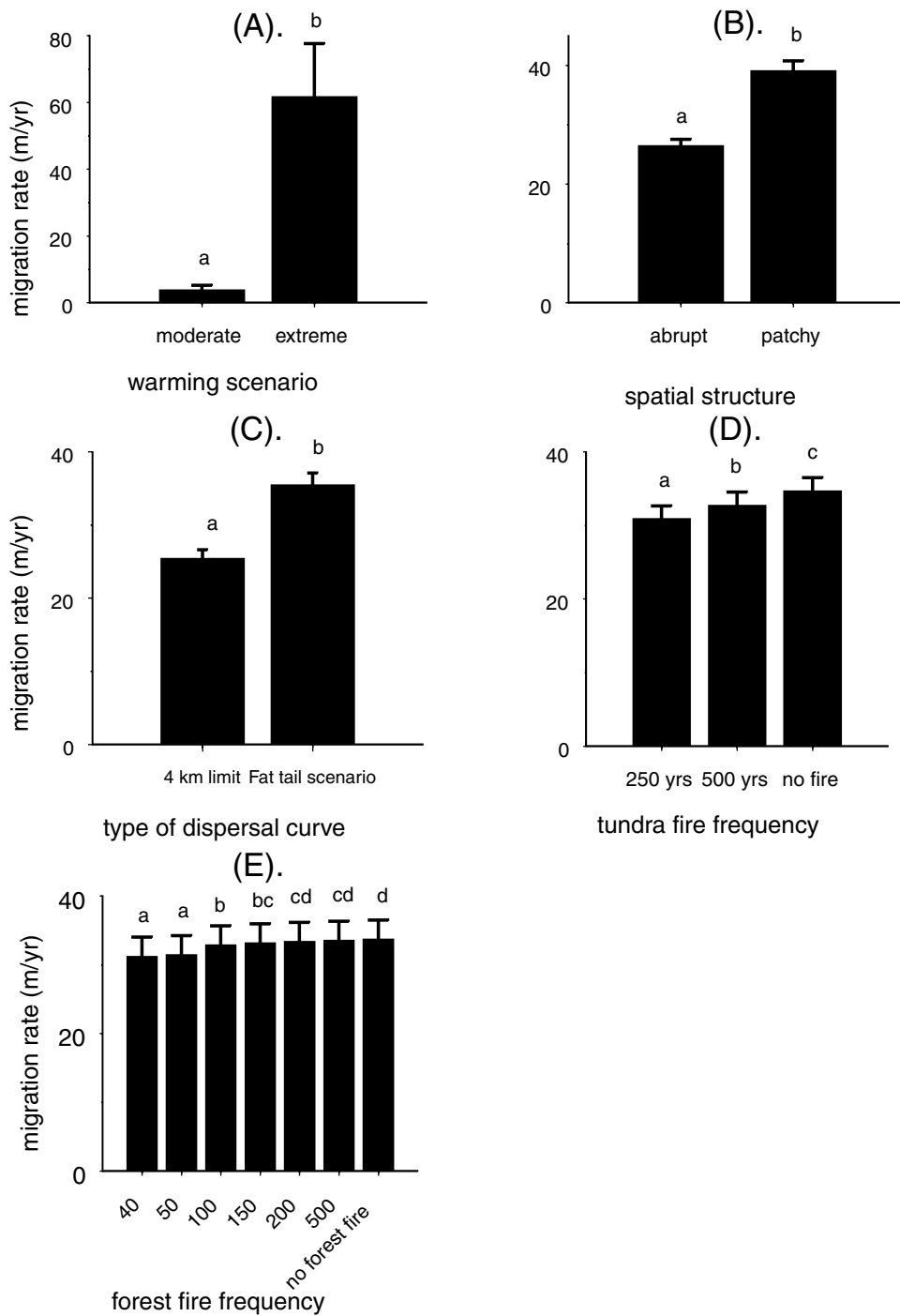


Figure 4. Mean (± 1 standard error) migration rate of spruce in different levels of the five main factors investigated in the first set of modeling experiments (see section 2). Means are the average of five replicate model runs. Means with different letters are significantly different ($P < 0.05$). See Table 2 for a complete description of the levels of each of the five main effects shown here.

than under the assumption of temperature and precipitation limitation ($F = 362.4, P < 0.001$).

[33] There were significant interactions between climate response, temperature, and precipitation that indicate that changes in spruce growth response have a varying effect on fire regime depending on the nature of climate change. After a 2°C warming, increases in precipitation had the effect of decreasing the frequency of fires for both assumptions about

climate response, and had the effect of either decreasing fire size (temperature limitation scenario) or not affecting it (temperature and precipitation limitation) (Figures 7A and 7B). After a 4°C warming, we found evidence for a tradeoff between fire size and fire frequency. Under the temperature limitation scenario, an increase in precipitation was associated with a decrease in fire frequency but a significant increase in fire size. Under the assumption that spruce are

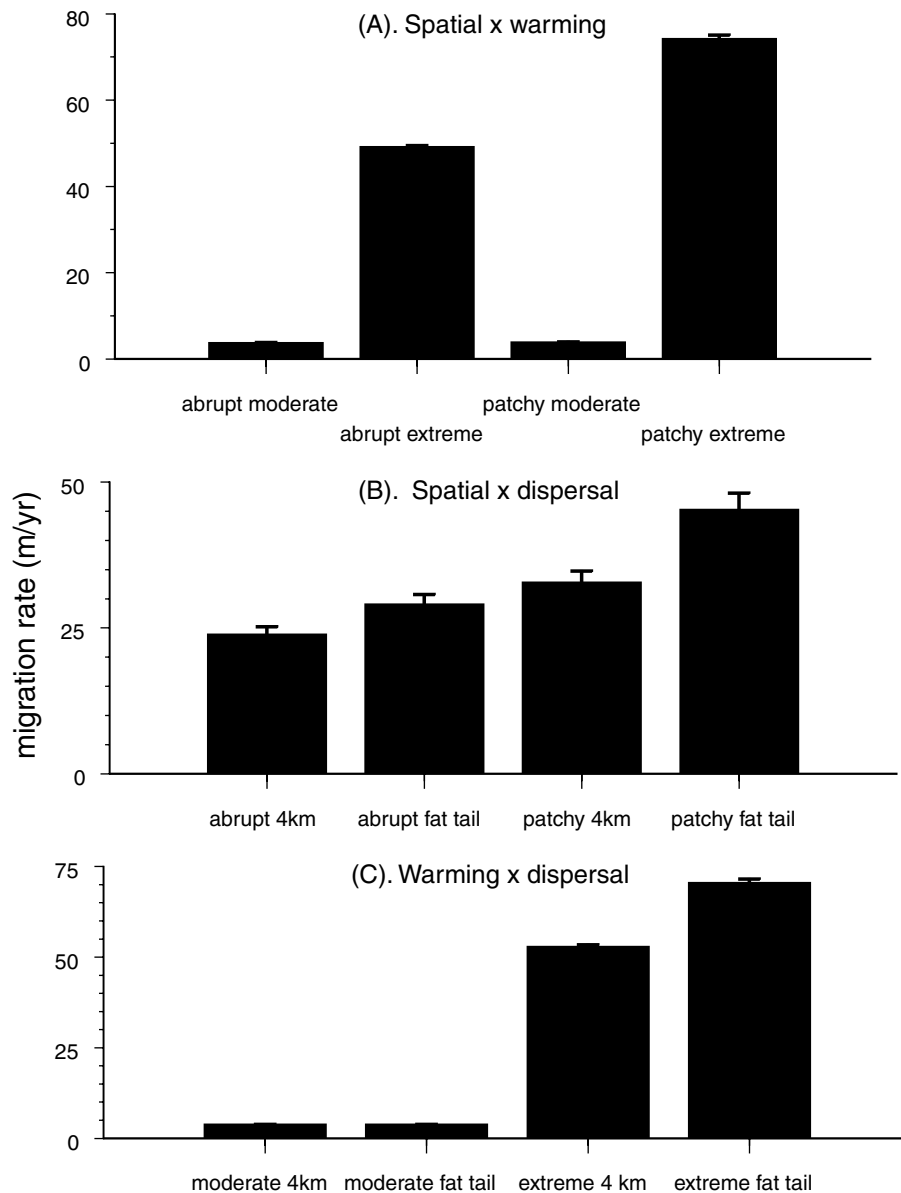


Figure 5. Mean (± 1 standard error) migration rate of spruce in different levels of three significant two-way interactions in the first set of modeling experiments (see section 2). Means are the average of five replicate model runs. See Table 2 for a complete description of the levels of each of the effects shown here.

both temperature and precipitation limited, in contrast, an increase in precipitation led to a decline in fire frequency and a slight decrease in area burned (Figures 7A and 7B).

4. Discussion

4.1. Timing and Rate of Treeline Advance on the Seward Peninsula

[34] Age structures of spruce populations at treeline on the Seward Peninsula are consistent with the hypothesis that warming during the 20th century has led to an expansion of boreal forest vegetation at treeline. We found that spruce were progressively younger along transects from established forest into tundra. Such a pattern could result from two processes. First, a gradual expansion of spruce from warmer

sites into cooler sites would lead to a gradient of forest stand age like the one we observed. Second, such a gradient in stand ages could arise if life span is shorter and thus population turnover is more rapid in harsher, high-elevation sites. Because we based our age structures on both live and dead trees, we are able to reject this second explanation for the observed gradients in tree age. Along the Fox River, we found dead trees only at the lowest elevation site (Sandy Bridge). Although dead seedlings almost certainly decompose (or become buried) relatively rapidly and may thus be lost from the paleoecological record, dead saplings and adult trees persist on the landscape for decades (based on crossdated death dates; A. Lloyd and C. Fastie unpublished data). If the relative youth of spruce populations at higher elevations reflects shorter lifespan, we would expect to find

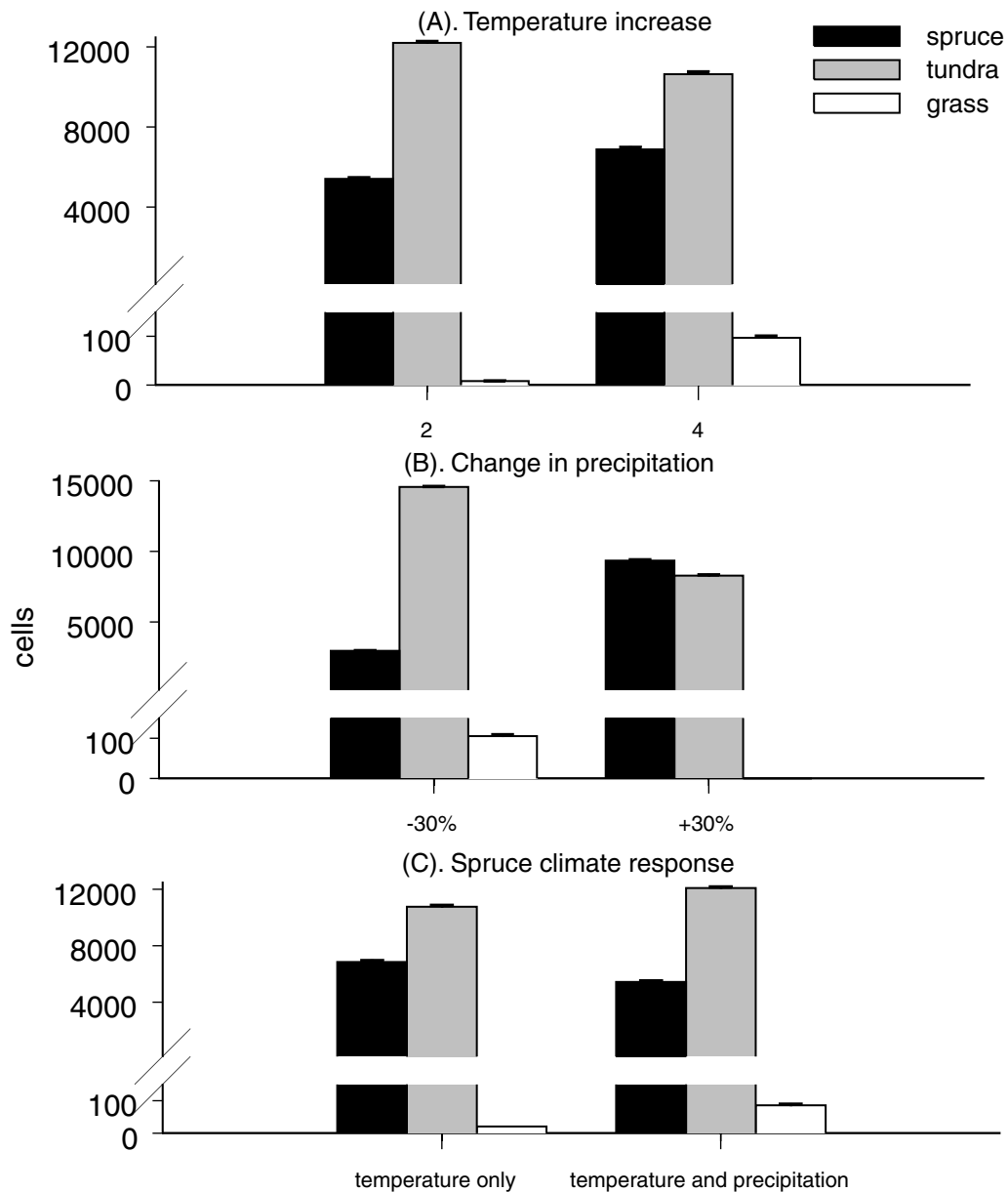


Figure 6. Mean (± 1 standard error) number of cells (2×2 km) in each of three vegetation types after 1000 years of model simulation for three main effects. Means are the average of 10 replicate model runs.

dead trees in the age range of the oldest living spruce at those sites. The complete absence of dead saplings and adults in those sites (and their presence at the lower elevation sites) suggests that differences in spruce lifespan can not explain the differences in population age observed among our sites, and that a recent expansion of spruce into tundra is the probable explanation.

[35] The inferred expansion of spruce began in the early 1880s in upland tundra sites along the Fox River, and in the 1920s in our lowland tundra site along Bear Creek. Spruce establishment in tundra has continued through the present at both study sites. Our results suggest that there were probably not substantial lags between the onset of recent warming and the advance of treeline spruce into tundra. Temperatures began rising in Alaska (and, indeed, in much of the Northern Hemisphere) beginning in the mid to late

1800s. In a reconstruction of circumarctic temperatures, *D'Arrigo and Jacoby* [1993] identified a Little Ice Age temperature minimum at approximately 1830, and find evidence for rapid warming beginning at approximately 1900. In Alaska, several paleoclimatic reconstructions indicate that temperature minima were reached at approximately 1830 and again between 1870 and 1890, and that warming occurred rapidly after 1880 or 1890 [*Garfinkel and Brubaker*, 1980; *Jacoby et al.*, 1985; *Jacoby and D'Arrigo*, 1995]. In the absence of localized climate reconstructions, we can not determine with any confidence the exact lag between onset of warming and treeline advance, but based on regional and circumarctic reconstructions we can conclude that there is no evidence that lags of more than a few decades occurred between the onset of warming and the successful establishment of spruce in tundra.

Table 3. Modeled Effects of Changing Climate and Climate Response on the Number and Size of Fires^a

Factor	Total Number of Fires	Average Fire Size (Cells)
Temperature increase		
+2°C	1343 ± 30.9	68.2 ± 2.4
+4°C	1858 ± 55.7	118.2 ± 10.1
Precipitation change		
-30%	1821 ± 58.7	75.7 ± 3.5
+30%	1380 ± 38.9	110.6 ± 10.6
Climate response		
Temperature limitation only	1616 ± 68.6	114.9 ± 10.5
Temperature and precipitation limitation	1584 ± 52.2	71.5 ± 2.4

^aThe number of fires was calculated as the total number of fires that occurred during the 1000-year model run. Fire size was calculated by dividing the number of fires per year by the total area burned per year and averaging over all 1000 years of the model run. Area units are number of 4 km² cells. All values are mean ± 1 SE.

[36] We identified distinct spatial patterns of spread of spruce at each of our two study sites. At the Fox River sites, where spruce expanded rapidly into upland shrub tundra communities with relatively well-drained soils, expansion was rapid but patchy and occurred at relatively low densities. Since the late 1800s, spruce moved approximately 120 m upwards in elevation and a distance of >10 km. This migration rate, approximately 100 m/yr, is less than the maximum dispersal rates observed in other empirical studies: *Fastie* [1995] documented spruce migration rates into newly deglaciated terrain in Glacier Bay, Alaska, of 300–400 m/yr, and paleoecological studies have documented postglacial range expansions in North America and Eurasia of >100 m/yr [*Huntley and Webb*, 1989]. This suggests that spruce expansion at our sites was not limited by dispersal ability per se but was instead limited by climate or by interactions with tundra vegetation.

[37] Despite the relative rapidity with which spruce expanded into upland tundra, the expansion occurred at very low densities. Although spruce are common in our upper forest–tundra sites (168 m asl), tundra shrubs still comprise the majority of the plant canopy. Conversion of tundra into closed-canopy spruce forest is thus likely to be a relatively slow process in these sites. *Chapin and Starfield* [1997], similarly, suggested based on model results that tree cover would increase slowly in tundra. Slow forestation rates in their model of treeline advance resulted both from limited seed input and periodic mortality from disturbances like fire and insects. There is no evidence that mortality-causing disturbances like fire and insect outbreaks have affected tree population growth since spruce began establishing in tundra in the 1900s, suggesting that at these sites factors influencing regeneration (seed input, competition with tundra vegetation) may be more important in limiting the rate at which forests develop.

[38] A very different mode of spruce expansion was observed at the Bear Creek sites, where the range of spruce appears to be restricted more by the presence and absence of permafrost than by air temperature. At these sites, we found that spruce seedlings have established in densities that are two orders of magnitude greater than those observed in upland tundra, but that spruce have invaded only a very small area extending approximately 100–200 m away from the forest edge. This suggests that although rapid conver-

sion of tussock tundra into spruce forest is possible in these sites once spruce begin to establish, the rate at which spruce advance into tundra has been considerably slower than the migration rates observed in upland sites. Abrupt treelines (such as those at Bear Creek), which tend to be maintained by soil thermal properties (e.g., presence and absence of permafrost) or other geomorphic features, may thus exhibit fundamentally different responses to warming than the gradual treelines (such as those along the Fox River) that occur in areas where air temperature is the primary limitation on spruce distribution.

[39] The observed rate of spruce migration (approximately 100 m/yr) on the Seward Peninsula exceeded the modeled rate of spruce migration in virtually all model experiments. Model experiments that used a “fat tail” distribution [*Clark et al.*, 1998] achieved migration rates that were relatively close to observed rates, suggesting that long-distance dispersal events may be an important feature of spruce dispersal. Spruce migration rate at treeline was strongly influenced in the modeling experiments by the magnitude of warming, the spatial structure of the treeline ecotone, and assumptions about dispersal. The more rapid migration rates in warmer climates were not surprising, given that the model assumes that the production of viable seed is temperature limited at treeline. Large increases in temperature therefore increase the reproductive output of the most marginal trees, thus increasing seed rain and migration rate. Temperature limitation on seed production has been demonstrated at other arctic treeline locations [e.g., *Black and Bliss*, 1980], and is therefore plausible at treeline in western Alaska.

[40] Model experiments confirmed the empirical result that spruce expansion proceeded more rapidly at patchy (e.g., Fox River) than at abrupt (e.g., Bear Creek) boundaries. The mechanisms, however, probably differ. In the model experiments, rapid migration at patchy treelines is a consequence of the fact that outlying spruce can function as a seed source, and thus expansion can occur by the coalescence of isolated, outlying populations rather than as the advance of a single “front” of spruce. This mechanism probably differs from the one underlying the observed difference in spread at a patchy (Fox River) and abrupt (Bear Creek) boundary on the Seward Peninsula. In that case, the relatively slow expansion at the abrupt boundary may have reflected the presence of continued constraints on spruce growth rather than a limit on migration rate per se. Nevertheless, both model and field results suggest that the migration rate of spruce at treeline may exhibit high variability depending on the spatial structure of the treeline ecotone.

4.2. Effects of Disturbance on Treeline Response to Warming

[41] Although our results suggest that if warming continues spruce will likely continue to invade tundra communities, both field data and model experiments suggest that the occurrence of disturbances that alter conditions for spruce establishment may have a large influence on future trajectories of change at treeline. Two types of disturbance are particularly likely to affect treeline areas: thermokarst, which can expose areas of mineral soil, increase soil temperature, and alter soil drainage [*Osterkamp and Romanovsky*, 1999; *Osterkamp et al.*, 2000;

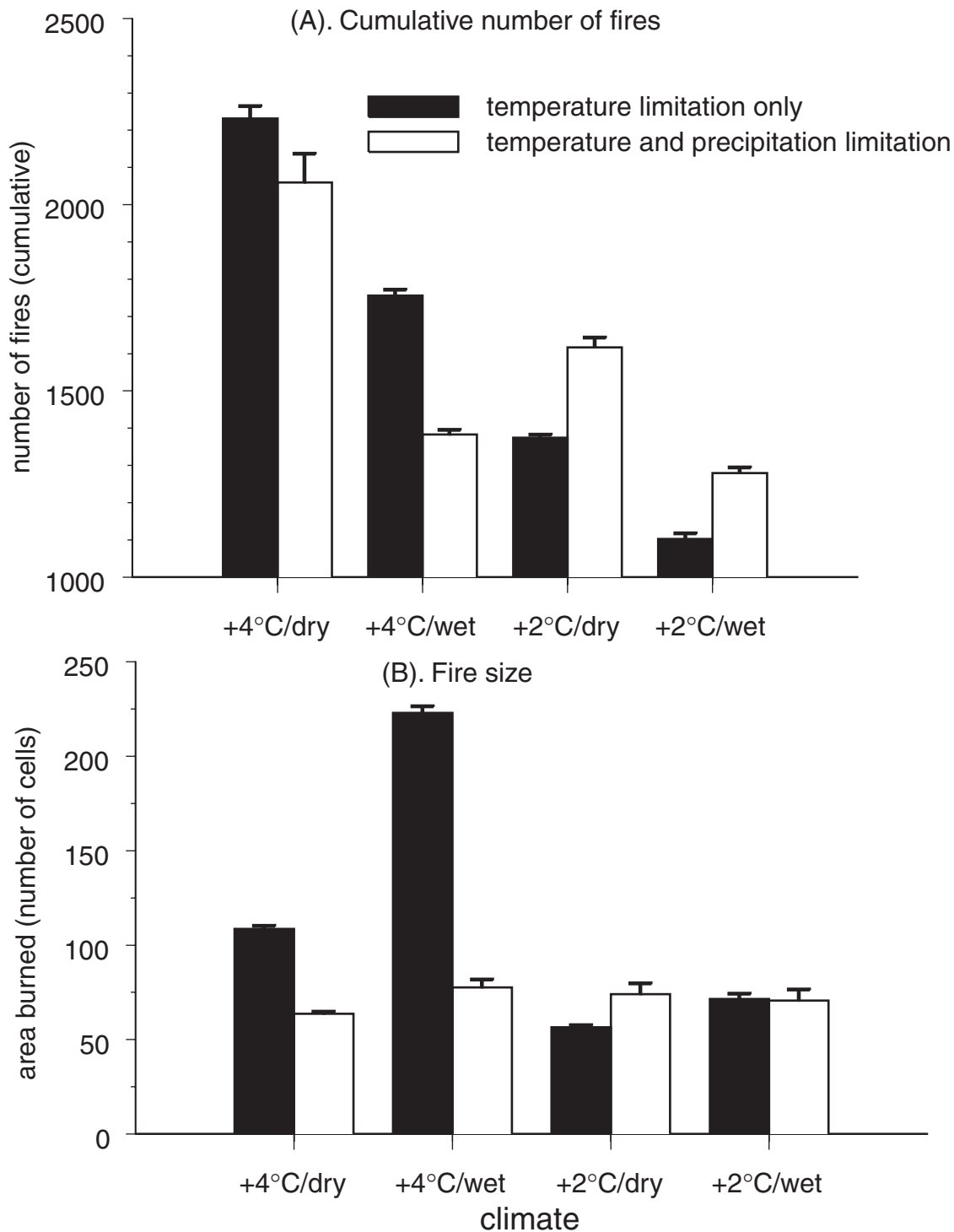


Figure 7. Cumulative number of fires and cumulative area burned during 1000 years of model simulation for four different climate scenarios. Values are means (± 1 standard error) of 10 replicate model runs. Black bars show means for scenarios that assume that spruce are only limited by temperature. White bars show means for scenarios that assume that spruce are limited by both temperature and precipitation.

Jorgenson et al., 2001] and fires, which kill some or all trees and alter the seedbed. These disturbances may affect the rate of change at treeline in two ways. First, disturbances may increase the rate at which spruce successfully establish in tundra by reducing competition with tundra plants and creating more favorable seedbeds through

mechanical disturbance (thermokarst) or charring (fire). In extreme cases, invasion could be entirely dependent on the prior occurrence of a suitable disturbance to modify site conditions sufficiently to promote establishment, in which case significant lags in response to climate change could be introduced.

[42] The time-transgressive nature of spruce expansion along the Fox River, combined with the absence of any evidence of widespread disturbance (e.g., soil charcoal, fire scars, charred wood), suggests that spruce expanded into upland tundra along the Fox River in the absence of disturbance and thus that in upland sites spruce expansion is unlikely to be contingent upon the occurrence of disturbance. In contrast, spruce expansion into lowland tundra along Bear Creek was limited in extent to areas that had been previously disturbed by thermokarst (L. Hinzman and K. Yoshikawa, personal communication, 2001). This spatial association between spruce invasion and tundra highly disturbed by thermokarst suggests that at sites where treeline corresponds to an abrupt gradient in soil conditions (e.g., the presence and absence of permafrost), spruce expansion may be contingent upon the prior occurrence of a disturbance, like thermokarst, that is associated with a change in soil properties. The mechanism of this apparent association between spruce invasion and disturbance remains unknown, however, and could reflect the direct effects of changes in soil temperature or drainage, or the indirect effects of thermokarst on the tundra vegetation. The apparent importance of changes in permafrost conditions to spruce expansion at Bear Creek suggests that future iterations of the ALFRESCO model should incorporate the effects of climate on permafrost, particularly at low-elevation arctic treelines where spruce distribution may be highly constrained by the presence of shallow permafrost.

[43] Second, disturbances like fire that kill mature trees may reduce the rate at which spruce successfully establish in tundra by reducing the seed source available for colonization. Modeling experiments indicated that treeline dynamics are highly sensitive to changes in fire regime, and thus suggest that changes in fire regime that accompany climatic change and shifts in vegetation cover may modify observed trajectories of change at arctic treeline. Feedbacks of vegetation on fire arose in some model experiments, and these may contribute to nonlinear changes in both fire regime and vegetation. The model assumes that the probability of a fire occurring (given a randomly occurring ignition source) is dependent on both climate (based on a drought index that incorporates effects of temperature and precipitation) and vegetation (based on the assumption that spruce is more flammable than tundra). Given the model's parameterization, it is not surprising that increases in temperature and decreases in precipitation were associated with an increase in fire frequency and area burned, and that increases in spruce cover were similarly associated with a more fire-prone landscape. However, we found evidence for "switches" in fire regime when vegetation change exceeded particular thresholds. For example, in the climate response experiments we found that in the 4°C warming scenarios an increase in precipitation was associated with a decrease in the cumulative area burned during the 1000-year model run if spruce were relatively uncommon (as in the temperature and precipitation limitation scenario) and an increase in the cumulative area burned if spruce were relatively abundant (as in the temperature limitation scenario). The increase in spruce cover thus led to a major shift in the response of fire regime to changing climate. This result

suggests that three-way interactions among vegetation, fire regime, and climate may create highly nonlinear system dynamics.

[44] The absence of recent fires at our sites prevents us from evaluating empirically the model result that fire (and, presumably, other disturbances that kill mature trees) may reduce the rate of treeline expansion, although that conclusion is supported by empirical data from treeline sites in Canada [Payette and Gagnon, 1979; Payette and Gagnon, 1985; Landhäusser and Wein, 1993].

4.3. Effects of Increasing Drought Stress on Treeline Response to Warming

[45] Future trajectories of change at treeline may also be modified by the potential for the growth response of spruce to climate to change as climate continues to warm. Lloyd and Fastie [2002] present evidence that old spruce trees on the Seward Peninsula (at sites within 20 km of the sites described here) began to experience reduced growth in the last half of the 20th century despite continued increases in temperature. Warming in the 20th century thus seems to be associated, at least on the Seward Peninsula, with an expansion of young spruce populations at the forest margin but a decline in the growth of old spruce at and near the forest margin [Lloyd and Fastie, 2002]. The potential certainly exists for population-level treeline dynamics to be affected if growth declines become more widespread at treeline in the future.

[46] In the model, increasing drought stress had a negative effect on seed production, and thus decreased spruce migration rates. However, the model also suggested that the effects of an increase in sensitivity to precipitation may be highly dependent on the particular combination of climatic conditions that occurs. Spruce migration rates were actually enhanced under a moderate (+2°C) warming scenario when drought sensitivity was included in the model because spruce in some parts of the landscape experienced somewhat wetter conditions, which then enhanced growth and seed production despite the relatively small amount of warming. Model results thus suggest that the kind of complex growth responses to climate that have been documented in older trees at treeline near those sites [Lloyd and Fastie, 2002] may translate eventually into more complex, nonlinear population-level climate responses at treeline.

5. Summary and Conclusions

[47] Spruce have successfully established in both upland shrub tundra and lowland tussock tundra on the Seward Peninsula since the late 1800s. The timing of spruce expansion was roughly coincident with the onset of post-Little Ice Age warming, thus rejecting the idea that long lags in spruce forest response to warming are likely. Spruce expansion was more rapid, but occurred at a significantly lower density, in upland sites than in lowland sites. In lowland sites, there was some indication that spruce invasion of tundra may be dependent on thermokarst. Modeling experiments suggest that disturbance may modify observed trajectories of change, and that complex feedbacks among vegetation, climate and disturbance are likely. The model experiments also suggest that changes in the growth

response of spruce to climate may eventually lead to more complex population-level responses to climate. Inferences about future forest dynamics from observed rates of response to past climate change must therefore incorporate a more complete understanding of the effects of disturbance on treeline forests and of the potential for changes in the response of individual spruce trees to climate.

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