

## ECOLOGICAL HISTORIES FROM ALASKAN TREE LINES PROVIDE INSIGHT INTO FUTURE CHANGE

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**Abstract.** Ecosystem responses to past climate change can provide insight into plausible scenarios of response to future change and can elucidate factors that may influence the overall predictability of such responses. I explore the utility of paleoecological studies for addressing questions about the predictability of ecosystem responses to climate change using Alaskan tree line ecosystems as a case study. Published studies were used to develop a regional analysis of patterns of recent tree line advance, and to estimate lags between recruitment onset and forest development beyond tree line. Tree line advance is ubiquitous, but asynchronous in time, occurring significantly earlier in the White Mountains in interior Alaska than in western Alaska or the Alaska Range. The mean lag between initiation of recruitment and forest development was estimated at approximately 200 years, similar to what modeling studies have found. Although continued advance of white spruce forests is the most likely scenario of future change, variability in the rate of forest response to warming may be likely due to limitation of spruce establishment in highly permafrost-affected sites, changes in seed dispersal and early establishment, and recent changes in the growth responses of individual trees to temperature. All of these factors may cause spruce populations to exhibit nonlinear responses to future warming, and uncritical extrapolation from recent trends is thus unwarranted.

**Key words:** *Alaska; alpine tree line; arctic tree line; boreal forest; climate change; lag; permafrost; Picea glauca; tree line advance; tundra.*

### INTRODUCTION

Analysis of ecological responses to past global changes forms a critical component of global change research (e.g., Davis 1989a, b). Indeed, paleoecological research has provided several fundamental insights to the question of how communities respond to change: that novel, “non-analog” communities are a persistent and recurring feature of the ecological history of most landscapes (e.g., Edwards et al. 2005); that lagged responses to climate may be common; that climate, disturbance, and vegetation can function as a tightly coupled system; and that simultaneous changes in multiple driving factors can produce highly unpredictable ecosystem responses (Davis 1989b). It is thus clear from a wealth of past studies that equilibrium approaches to predicting vegetation change are unlikely to capture the full complexity of responses, and that short-term (decadal scale) ecosystem responses to climate change may be particularly difficult to predict. In this paper, I will use the recent (e.g., last 150 years) ecological history of arctic and alpine tree lines in Alaska as a case study with which to explore the contribution paleoecological studies can make to questions about the predictability of ecosystem response to climate change.

Manuscript received 24 November 2003; revised 28 July 2004; accepted 20 September 2004. Corresponding Editor (ad hoc): L. J. Graumlich. For reprints of this Special feature, see footnote 1, p. 1667.

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Arctic and alpine tree lines mark the very limit of the boreal forest. This boundary has a number of advantages as a focal point for a discussion of the contribution of paleorecords to the goal of predicting future ecological change. First, it is a system where abiotic controls are relatively clear: the importance of temperature as a control over biological processes has been clearly demonstrated, despite considerable uncertainty about the exact mechanism of control (e.g., Körner 1998, Sveinbjörnsson 2000). Tree line has been shown to fluctuate in relative synchrony with climate over long time scales (e.g., Denton and Karlén 1977, Spear 1993, Lloyd and Graumlich 1997, MacDonald et al. 2000). The ultimate effects of future changes in climate should thus be relatively large in tree line ecosystems. Second, it is a system in which change is easily detected by the presence or absence of a single species that leaves a record with very high temporal precision (in the form of tree rings of living and dead trees) of its presence on the landscape. Third, recent tree line advance, resulting both from establishment of new seedlings and upward growth of existing krummholz, is common, although not ubiquitous (MacDonald et al. 1998b) throughout the North American boreal zone (Hopkins 1972, Viereck 1979, Cooper 1986, Scott et al. 1987, Lescop-Sinclair and Payette 1995, MacDonald et al. 1998b), indicating that tree line systems may already be responding to past warming.

Patterns of future climate-induced vegetation change at this boundary between boreal and arctic vegetation

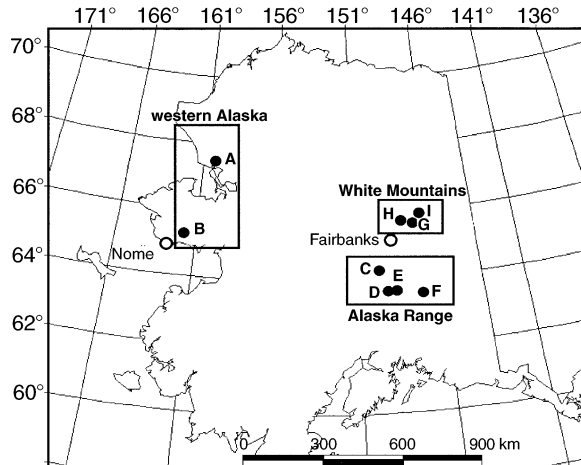


FIG. 1. Location of sites where paleoecological studies of tree line dynamics have been conducted. Site names are as follows: A, Noatak River (Suarez et al. 1999); B, Seward Peninsula (Lloyd et al. 2002); C, Usibelli; D, Monahan Flats; E, Canyon Creek; F, Wrangell View; G, Twelvemile Summit; H, Nome Creek; I, Eagle Summit (C–I in Lloyd and Fastie [2003]). Sites A and B are at arctic tree line, and sites C–I are at altitudinal tree line.

of key vegetation transitions such as those between non-woody and woody (shrub or forest) vegetation.

Paleoecological studies may improve predictions of future vegetation change in two primary ways. First, descriptions of ecosystem responses to recent climate change (e.g., tree line response to warming after 1850) can provide the basis from which to extrapolate responses over the next several decades. Second, analyses of ecological history can help elucidate the factors that may contribute to nonlinear and/or unpredictable system responses to climate change and thus provide a basis for assessing sources of uncertainty within a particular system. This paper will use the paleorecords of recent change in Alaskan tree line ecosystems to address two questions about the application of paleoecological approaches to predicting future vegetation change. First, what scenarios of future change at tree line are likely given the response of forests to recent warming? Second, what insights emerge from those paleorecords about the predictability of change at tree line, and what factors, if any, may be associated with nonlinear changes at tree line?

#### METHODS AND MATERIALS

##### *Field methods*

have broader implications for the arctic system, as changes in vegetation within this ecotone may be associated with changes in surface energy exchange (Bonan et al. 1992, Chapin et al. 2000) and carbon storage (Smith and Shugart 1993). For example, the advance of woody vegetation into herb and low shrub tundra may lead to feedbacks on climate that measurably influence local to regional-scale climates by altering surface albedo and roughness (Chapin et al. 2000) and patterns of snowpack depth (Liston et al. 2002). Our ability to predict the arctic system as a whole thus hinges, at least in part, on the predictability

The results described here represent the compilation of previously published reconstructions of tree line advance in Alaska (Fig. 1, Table 1). Studies were selected based on two primary criteria: availability of data and use of a sampling scheme appropriate to determine the timing of tree line advance and rate of population growth at tree line. Three regions are represented in this data set. The western Alaskan region (three sites) includes the Seward Peninsula (Lloyd et al. 2002) and the Noatak River valley (Suarez et al. 1999). These are arctic tree lines, associated with either the longitudinal (Seward Peninsula) or latitudinal (Noatak River) limits

TABLE 1. Study site characteristics and sources for original data.

Region and site	Source	Elevation (m)	Aspect	Mean temperature (°C)		Annual precipitation (cm)
				January	July	
Alaska Range				-20.2	13.2	36.7
Canyon Creek	Lloyd and Fastie (2003)	867	NE			
Monahan Flats	Lloyd and Fastie (2003)	901	N			
Usibelli	Lloyd and Fastie (2003)	762	W			
Wrangell View	Lloyd and Fastie (2003)	838	SW			
Western Alaska				-15.4	11.3	40.9
Noatak River	Suarez et al. (1999)	160	S			
Fox River	Lloyd et al. (2002)	46	E			
Bear Creek	Lloyd et al. (2002)	45	N			
White Mountains				-22.4	15.3	19.2
Eagle Summit	Lloyd and Fastie (2003)	945	S			
Nome Creek	Lloyd and Fastie (2003)	884	SE			
Twelvemile Summit	Lloyd and Fastie (2003)	945	NW			

*Notes:* Climate data are not available for individual study sites, so divisional data 30-year (1971–2000) climate normals are shown for each region. The divisions corresponding to each study region are Copper River Basin/Division 4 (Alaska Range), West Central/Division 7 (Western Alaska), and Interior/Division 8 (White Mountains). Divisional climate data were obtained from the Alaska Climate Research Center at the University of Alaska, Fairbanks, Alaska, USA.

of trees. Alpine tree line dynamics were reconstructed in two regions in interior Alaska (Lloyd and Fastie 2003): the White Mountains (three sites), a low mountain range north of Fairbanks, and the Alaska Range (four sites), a range of high mountains cutting through central and south-central Alaska. The relatively wide spatial coverage of available data makes this an excellent case study with which to explore the contribution of paleoecological methods to predicting future vegetation change. White spruce (*Picea glauca*) is the dominant tree line species at all sites, although it occasionally mixes with black spruce (*Picea mariana*). Site characteristics are summarized in Table 1.

All of the studies shared a common sampling methodology, in which forest population history was reconstructed from tree core data obtained along transects that crossed tree line (Suarez et al. 1999, Lloyd et al. 2002, Lloyd and Fastie 2003). The relative age of stands at the current tree line (defined as the upper limit of adult, upright trees) and beyond tree line was then compared to determine whether tree line had advanced, and if so when the advance occurred. Tree-ring samples or cross-sections were collected from only live trees in the Noatak River (Suarez et al. 1999) and from both live and dead trees and seedlings at other sites (Lloyd et al. 2002, Lloyd and Fastie 2003).

#### *Laboratory methods*

Tree cores were mounted, sanded, and dated using standard dendrochronological methods that are described in detail elsewhere (Suarez et al. 1999, Lloyd et al. 2002, Lloyd and Fastie 2003). Estimated tree establishment dates were corrected for missing rings (by crossdating), for missed pith (from age–diameter regressions), and for years to grow to core height (from age–height regressions). Lloyd et al. (2002) and Lloyd and Fastie (2003) estimated death dates of dead trees by crossdating measured ring-widths.

#### *Statistical analysis*

Previous studies have used a variety of methods to identify the time at which tree line advanced (Suarez et al. 1999, Lloyd et al. 2002, Lloyd and Fastie 2003). In this paper, I defined the date of tree line advance as the date at which a newly establishing population reached a density of five adult trees/ha. The five-trees/ha threshold is arbitrary, and is meant simply to differentiate between the establishment of an isolated individual beyond tree line (an event that is relatively common) and a directional change in the limit at which populations of trees occur. I estimated the decade in which this threshold was passed for the Noatak River site from the published age structure (Suarez et al. 1999). For the other sites, I estimated the decade in which tree density (the number of trees per ha that were alive in a particular decade) surpassed five trees/ha from published reconstructions of tree density (Lloyd et al. 2002, Lloyd and Fastie 2003). Tree density was

estimated on a decadal time scale from the establishment and mortality dates of all sampled trees. I used a Kruskal-Wallis test to determine whether the median date of tree line advance differed significantly among the three regions. The sampling methodology was not designed to detect the maximum spread of spruce beyond the current tree line, but the data could be used to determine an estimate of the minimum amount of spatial displacement. Elevational changes in tree line were calculated for each site from published and unpublished data on the elevation of tree line and above tree line transects. The minimum distance that tree line advanced was calculated from the distance between transects.

In addition to inferring timing of tree line advance, for all sites except the Noatak River (where only live trees were cored and thus density could not be estimated for past decades) I also estimated the decade in which low-density spruce populations beyond the forest limit will attain densities equal to or greater than those observed at the current forest limit at the time of sampling. Models have concluded that lags of at least 150 years may occur between the onset of warming and the development of forest vegetation (e.g., Chapin and Starfield 1997, Bugmann and Pfister 2000), and this estimate will allow us to test those projections at a range of tree line sites. Rates of population increase for spruce beyond the current forest limit were determined at each site by fitting an exponential curve or a line to the reconstructed estimates of density at that site, from the time that density began to increase to present. The equation for that curve was then used to project population growth into the future and thus estimate the lag between onset of recruitment and development of forested vegetation. The lag was specifically calculated by subtracting the decade in which recruitment began from the decade in which density beyond the current forest limit equaled or exceeded current density at the forest limit. I compared mean lags among regions with a one-way ANOVA, and conducted pairwise comparisons using Tukey's honestly significant different post hoc test, which controls experimentwise error rate.

This approach assumes that the time series of reconstructed stand density can be interpreted as an exponentially growing population. Forest stand reconstructions are problematic because of the "fading record": decomposition of dead individuals causes systematic underestimates in density, and the magnitude of those underestimates becomes progressively longer back through time. Few of the populations beyond the current forest limit pre-date 1850, and because decomposition occurs relatively slowly in these cold tree line environments (and thus long-dead trees can be sampled), estimates of the density of trees that survived to be adults are probably reasonably accurate. However, seedlings decompose too rapidly (probably within a decade) to leave an interpretable record, and thus the

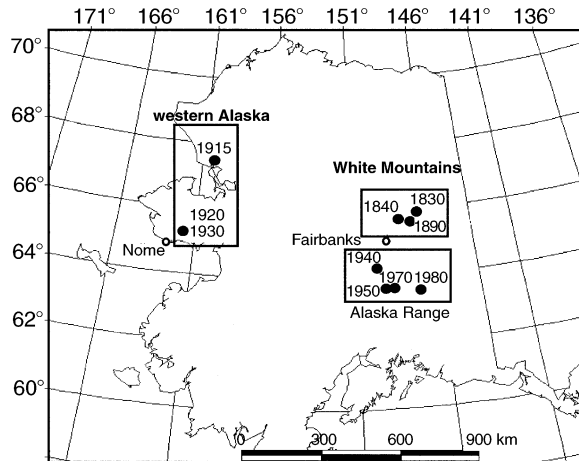


FIG. 2. Decade in which the population of  $\geq 5$  trees/ha was established at eight sites in Alaska. Site names and references are as indicated in Fig. 1.

estimates of stand density for recent decades can be difficult to compare with estimates from earlier decades. Lloyd and Fastie (2003) presented evidence that mortality of seedlings in sites beyond the current forest limit was relatively low, and thus that the apparent increase in density since 1950 most likely represents a real increase in stand density, and is not simply a methodological artifact. The assumption that changes in stand density represent an exponentially growing population is therefore not unreasonable at these sites.

## RESULTS

### *Regional variability in tree line advance*

The date at which populations of at least five trees/ha established in tundra was generally consistent within a region (Fig. 2), but the median date of the advance differed significantly among regions ( $H = 8.018$ ,  $P =$

0.018,  $df = 2$ ), with the earliest median advance (1840) occurring in the White Mountains, and the most recent median advance (1950) occurring in the Alaska Range. Although tree line advance was detected at all eight locations, the timing of the advance thus varied by more than a century among regions. The spatial scale of the advance varied among sites as well (Table 2). At alpine tree lines in the interior, the average minimum change in the position of tree line was relatively small ( $25.7 \pm 3.1$  m elevation;  $200 \pm 28$  m distance [all measurements, mean  $\pm$  SE]), and varied little among sites. The spatial scale of the advance was larger and more variable at arctic tree lines. At the two sites situated on level terrain along river drainages (Bear Creek and Noatak River), tree line moved very little (80–100 m). At the upland arctic tree line site (Fox River), in contrast, spruce advanced more than 10 km from the current forest limit into tundra, an advance that involved an elevational change of 122 m.

### *Rate of conversion from forest to tundra*

Estimates of the time lag between the onset of spruce establishment beyond the forest limit and the development of forests equal in density to those at the current forest limit varied widely among sites, even within a region (60–450 years; Table 3). The mean across all sites was  $207 \pm 44$  years. The mean lag time differed significantly among regions ( $F = 8.103$ ,  $P = 0.020$ ,  $df = 2$ ), with significantly shorter lags occurring on the Seward Peninsula and the Alaska Range, and the longest lags occurring in the White Mountains (Table 3).

## DISCUSSION

### *Summary of recent change at tree line in Alaska*

Four conclusions emerge from the analysis of paleorecords of recent change at tree line in Alaska. First, tree line advance was ubiquitous, occurring throughout three widely separated regions of Alaska (Suarez et al.

TABLE 2. Minimum extent of tree line advance in Alaska.

Region and site	Minimum change in tree line elevation (m a.s.l.)	Minimum distance advanced (m)
Alaska Range		
Canyon Creek	20	<100
Monahan Flats	29	<100
Wrangell View	14	<100
Western Alaska		
Fox River	122	>10
Bear Creek	0	<100
Noatak River	0	80
White Mountains		
Eagle Summit	~30	<100
Nome Creek	~30	<100
Twelvemile Summit	30	<100

*Notes:* Elevational change was determined either from GPS measurements of plot locations or (at sites where elevational change is preceded by '~') from topographic maps. Sampling methods were not designed to detect the maximum distance that spruce have spread into tundra, so these estimates should be interpreted as minima.

TABLE 3. Estimated number of years required for spruce populations beyond the current forest limit to reach the density of populations at the forest limit at the time of sampling.

Region and site	No. years	Regional estimate (no. years)
Alaska Range		160 <sup>a</sup> ± 67
Canyon Creek	300	
Monahan Flats	210	
Usibelli	70	
Wrangell View	60	
Western Alaska		118 <sup>a</sup> ± 32
Noatak River	NA	
Fox River	133	
Bear Creek	70	
White Mountains		390 <sup>b</sup> ± 37
Eagle Summit	450	
Nome Creek	350	
Twelvemile Summit	370	

Notes: Estimates are based on exponential curves fit to the density reconstruction at each site. At the Fox River site, the value is the mean for three transects at the site. Estimates for each region (mean ± SE) are also provided. Superscripts following the means indicate which pairs of means differed significantly ( $P < 0.05$ ) in a Turkey's post hoc test: means with different letters differ significantly.

1999, Lloyd et al. 2002, Lloyd and Fastie 2003). The sole exception was at a highly permafrost-affected site on the Noatak River, where Suarez et al. (1999) did not find evidence for recent spruce establishment in tundra. Second, despite the near unanimity of tree line advance, the timing of the advance varied significantly among regions, occurring earliest in the White Mountains and most recently on the Seward Peninsula and in the Alaska Range (Lloyd and Fastie 2003). Estimates of lags between the onset of recruitment and the development of forests were similarly variable among sites. Lags were longest in the White Mountains and shortest on the Seward Peninsula (in western Alaska; Noatak River sites were not included in this analysis) and in the Alaska Range. However, the mean time lag closely matched that projected by modeling studies (Chapin and Starfield 1997, Bugmann and Pfister 2000).

Two distinct patterns of response at tree line thus emerge from this retrospective analysis. In the White Mountains, where stunted, krummholz trees are common beyond the forest limit, tree line advanced earliest but tree density increased relatively slowly, leading to long projected time lags between the onset of establishment and the development of forests. In contrast, advances began much later but are occurring more rapidly in the remaining two regions, which generally lack a well-developed krummholz zone. The two distinct patterns of response (early/slow and late/fast) may be attributed to three possible causes. First, the reconstructed early onset of tree line advance in the White Mountains is driven at least in part by the methodology with which an advance of tree line was detected. Lloyd and Fastie (2003) used three methods to detect an ad-

vance of tree line, and with all three the estimate of the date at which tree line advances would be strongly influenced by the presence of old krummholz above tree line. There may, however, also be a causal relationship between the relatively slow rate of population growth in the White Mountains and the abundance of krummholz above tree line. Krummholz trees may be more common in highly wind-affected sites, where the most exposed trees are subject to tissue injury and apical bud death (Lindsay 1971, Hadley and Smith 1986, 1987). These same factors may cause slow growth rates and high mortality of young trees establishing beyond tree line, and thus reduce the rate at which populations expand. Climatic differences are a third possible explanation for the regional differences: the White Mountains are in the most continental region in Alaska, experiencing the greatest temperature extremes and the most pronounced summer drought (Table 2; Hammond and Yarie 1996).

The third conclusion to emerge from this analysis of recent tree line history is that the spatial scale of the advance also varied widely among sites. Changes at alpine tree line were consistently small, with a mean minimum elevational change of <30 m, compared with >100 m elevation change at one of the arctic tree lines sampled. In addition, the two types of tree line that are common in the arctic exhibited very different patterns of response. Abrupt forest boundaries occur along the floodplains of arctic rivers, where trees occupy relatively well-drained, often permafrost-free floodplain soils, and low tussock tundra occupies poorly drained, permafrost-affected sites adjacent to the floodplain. Much more gradual boundaries occur in the uplands, where low density spruce forests gradually give way to shrub and dry herb tundra. Abrupt arctic tree lines seem to have experienced relatively less spatial displacement than the more gradual tree lines that characterize uplands in the arctic. Suarez et al. (1999) report that in the Noatak River valley the forest edge advanced 80–100 m into tundra within a century, a figure similar to that reported by Lloyd et al. (2002) on the Bear Creek floodplain on the Seward Peninsula. In contrast, Lloyd et al. (2002) report that in upland sites on the Seward Peninsula the limit of spruce advanced more than 10 km into tundra in the 1900s. The explanation for this difference remains unknown, but relatively shallow permafrost and the resulting poor drainage may have limited the spatial extent of spruce invasion of tundra at those abrupt tree lines (Lloyd et al. 2002, 2003). Predictions of tree line response might therefore be improved by grouping tree line sites into a few geographically similar types (e.g., interior alpine, arctic upland, permafrost-affected arctic lowland).

Finally, there is good evidence that the advance has a climatic basis. The importance of temperature as a control over aspects of the growth, reproduction, and survival of trees at tree line is well established, both in Alaska and elsewhere, despite ongoing debate about

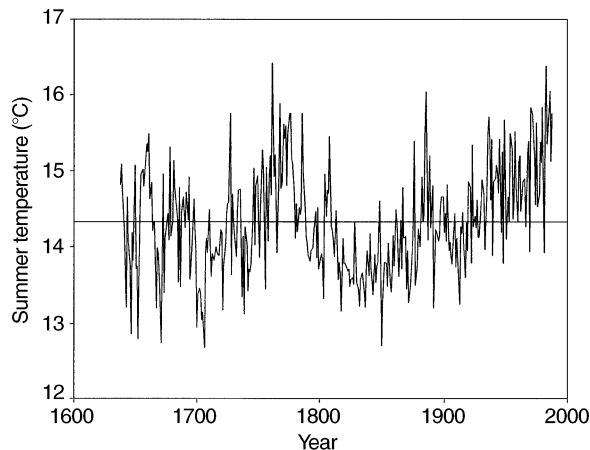


FIG. 3. Mean summer temperature in northwestern Canada, 1638–1988, reconstructed from ring widths of white spruce (Szeicz and MacDonald 1995).

the precise mechanism by which temperature limits tree growth (Körner 1998, Sveinbjörnsson 2000, Sveinbjörnsson et al. 2002). A change in this important limiting factor is thus the most plausible explanation for an advance of tree line. The consistency within regions in the timing of the expansion suggests that local changes in environmental conditions are an unlikely explanation. Non-climatic factors (disturbances, changes in permafrost depth) may certainly be sufficient to cause spruce to advance into tundra in particular locations, but such factors are unlikely to cause the region-wide initiation of spruce establishment in tundra, nor the synchrony within regions that I describe here. The timing of the advance of tree line is also roughly coincident (within several decades) with the onset of recent warming: paleoclimatic data from Alaska suggest that temperature minima were reached in the early to mid 1800s, and that warming occurred relatively rapidly after that point (Jacoby et al. 1985, Jacoby and D'Arrigo 1995, Szeicz and MacDonald 1995, Overpeck et al. 1997, Serreze et al. 2000; Fig. 3).

#### *Scenarios of future change*

What scenarios of future change can be derived from the recent history of tree line expansion? The near universality of tree line advance in these studies and its approximate synchrony with warming climate suggests that it is highly probable that spruce will continue to establish in tundra sites as climate warms in the future. Lags between warming and the onset of establishment of spruce in tundra were, from these data, negligible at most sites: with the exception of highly permafrost-affected sites (Suarez et al. 1999, Lloyd et al. 2002, 2003), there is no evidence that the initiation of spruce establishment in tundra is dependent upon disturbance. The large spatial displacement of tree line in upland sites on the Seward Peninsula furthermore suggests that

long-distance dispersal of spruce seeds may be sufficiently common to allow spruce to continue to spread over long distances.

The recent history of tree line also allows more specific inferences to be drawn about the most plausible future scenarios of change. Although spruce began establishing in tundra approximately synchronously with the onset of a change in climate, fairly long lags between the initiation of establishment and the development of forest vegetation are still projected. The results reported here confirm the prediction of tree line models that lags of >150 years are likely between the onset of warming and the development of vegetation that is functionally a forest (Chapin and Starfield 1997, Rupp et al. 2000a, b). Our analyses suggest a mean lag (i.e., time from the onset of establishment to the development of forests) of slightly over 200 years, but the variability around that mean is high, and the range of estimates among the seven sites analyzed is 60–450 years. The cause of this variation remains unknown, and further investigation into the variability is warranted. The confirmation of these long lags is an important result of this analysis, as lagged responses have implications for the rate at which feedbacks between vegetation and climate will develop, and thus on predictions about the future state of the climate system. For example, the increased radiative forcing associated with an advance of woody vegetation (Chapin et al. 2000) becomes substantially less important as a driver of local climates if lags of 200 years or more will occur between the onset of spruce establishment and the transformation of the landscape to a state that is functionally forested.

Although it is tempting, given the nearly ubiquitous advance of tree line in Alaska over the last 150 years, to conclude that tree line will continue to advance inexorably, the site-to-site variability revealed in the paleoecological record argues against uncritical extrapolation into the future. The variability in the rate and timing of tree line advance observed within Alaska occurs at a broader scale as well. Advances of tree line similar to those reported here have been observed in the Polar Urals (Gorchakovskiy and Shiyatov 1978), but not farther east in Siberia, where the failure of tree line to advance during the period of recent warming was attributed to absence of suitable soil (MacDonald et al. 1998a). In eastern Canada, Payette and Fillion (1985) found small increases in the elevation of altitudinal tree line (on the order of what was observed in the data presented here), but their work and subsequent authors have found no displacement of latitudinal tree line in eastern Canada, the position of which has shifted only as a result of changes in tree growth form (from krummholz to upright tree) and not as a result of new recruitment from seed (Lavoie and Payette 1994, Lescop-Sinclair and Payette 1995). On multiple spatial scales, therefore, it is clear that the recent history of tree line is marked by enormous site to site variability. Two

general categories of explanation exist for this variability. First, it may simply reflect regional differences in the pattern of warming. Indeed, low recruitment at tree line in central Canada in recent decades has been attributed in part to cool climates in the 1960s and 1970s (MacDonald et al. 1998b). The climate history of the regions on which this study focused is not sufficiently well known to test this hypothesis, but as the consensus is that warming has occurred throughout Alaska over the last several decades (Serreze et al. 2000), it seems unlikely that differences in the timing of warming would be of a sufficient magnitude to account for the 100-plus-year difference among sites in the timing of tree line advance that was observed. Second, high variability among sites may reflect different rates of response to climate. If this is the case, then disentangling the causes of site to site variability may point to controls over the rate at which ecosystems respond to climate, and thus improve the accuracy of predictions about future changes. The data presented here point to three factors which may be important modulators of forest response to climate change.

Permafrost emerges as one clear correlate of site-to-site variability in Alaska. Data from arctic tree lines in western Alaska (Suarez et al. 1999, Lloyd et al. 2002) suggest that at highly permafrost-affected tree line sites, the invasion of tundra by spruce may be contingent upon a disturbance to the permafrost. Suarez et al. (1999), for example, failed to find evidence of tree line advance at a site in which the tundra was underlain by a very shallow active layer (0.5 m thaw at the time of sampling, compared to 2.0 m thaw in adjacent forested sites). Lloyd et al. (2002) found that although spruce had invaded tundra areas adjacent to the Bear Creek floodplain in high densities, they had done so only in areas that were affected by thermokarst (i.e., permafrost melting), which creates well-drained microsites on which spruce (and woody shrubs) can successfully establish (Lloyd et al. 2003). Tree lines adjacent to highly permafrost-affected tundra may thus be dependent on melting of that permafrost, in which case strongly nonlinear responses (e.g., long periods of stasis followed by rapid change) are likely.

Second, long lags between the onset of establishment and the development of dense forests suggest that early establishment may act as a bottleneck, limiting the rate of population response to climate. The relatively long lags between the onset of tree line advance and the development of relatively dense populations of spruce are consistent with the conclusions of modeling studies (Chapin and Starfield 1997, Rupp et al. 2000a, b, Lloyd et al. 2002) which attribute long lags to low seed input, slow growth, and periodic mortality due to disturbance. The studies on which our analysis is based find no evidence for episodic mortality due to disturbance at tree line, and thus suggest that slow rates of forestation are likely due to limits on seed availability, seed germination, or very early seedling survival. If slow rates

of forestation are limited by seed availability, then the rate of spruce expansion may decrease in the future as the distance between the advancing front and dense populations of spruce increases. In contrast, if slow rates of forestation are limited by post-dispersal life stages, then rates of forestation might be expected to increase as trees establish beyond tree line. Isolated spruce establishing far beyond the forest limit may promote further establishment by serving as an in situ seed source and by ameliorating environmental conditions and thus enhancing survival of establishing seedlings (e.g., Wilson and Agnew 1992, MacDonald et al. 1998b). A slow initial start to establishment might thus be followed by increasingly rapid rates of vegetation change as initial colonists facilitate subsequent establishment. In either scenario, the rate of tree line advance would be expected to vary over time and/or among sites, depending on how conditions for dispersal and early establishment vary.

Finally, changes in physiological responses to warming, although not apparent in the data presented here, may ultimately affect population responses to warming, and there is some indication that such changes are occurring in Alaska. The population responses shown here, in which spruce recruitment in tundra increased during a period of warming, are at odds with studies of the growth of mature trees at tree line at these (and other) sites. A number of published studies have found that older trees at tree line commonly exhibit nonlinear responses to warming, and that, by the late 20th century, warmth had ceased to benefit tree line trees. For example, Lloyd and Fastie (2002) found that white spruce growth in two of the regions (White Mountains, Seward Peninsula) began to decline after 1950, and correlations between tree growth and climate changed from positive, in which warm years were associated with increased growth, to negative, in which warm years were associated with decreased growth. These results were consistent with previous tree-ring research, which had suggested that at both tree line (Jacoby and D'Arrigo 1997) and non-tree line (Barber et al. 2000) locations, there may be thresholds of warmth beyond which the response of white spruce to climate changes. Moisture stress has been proposed as the most likely explanation for changes in tree growth response to temperature (e.g., Barber et al. 2000).

Tree lines that are simultaneously limited by temperature and moisture have been described elsewhere (e.g., Lloyd and Graumlich 1997 in the Sierra Nevada), but moisture limitation has not generally been considered a major control over tree line in the boreal forest. There is at present no evidence that increased warmth during the 20th century has negatively affected the reproduction of trees, and thus at this point the response of growth (of old trees) to climate seems to be uncoupled from the population-level response described here. Nevertheless, the apparent complexity of the effects of climate on the growth of individual trees serves as a

caution that there may be thresholds of warmth beyond which spruce populations become moisture-limited and thus cease to expand into tundra. Moisture limitation may also favor deciduous species over spruce, and thus produce the type of broad-leaved deciduous forest described by Edwards et al. (2005).

Decadal-scale records of ecological change thus contribute much to our understanding of future ecological change. Paleorecords can clearly help to define plausible scenarios of future change. At tree line in Alaska, an examination of recent patterns of change indicates that further advance of tree line is highly likely at all but the most permafrost-affected sites. These data also help to define the sites in which change will be most pronounced: they suggest that the largest advances are likely at arctic tree lines in upland locations, and that future advances at more abrupt alpine tree lines and arctic tree lines associated with river floodplains are likely to be much smaller in extent. On the other hand, paleorecords of recent change at tree line also indicate that our understanding of these systems is at present incomplete, and point to factors that may cause the rate of change at tree line to vary over time, with the potential for variation in both the magnitude and the direction of change. The effects of permafrost, the degree to which viable seed limits population growth, and the causes of regional variability in the timing of tree line advance all emerge as important unanswered questions that may substantially influence the development of scenarios of future change. Paleorecords of recent change are thus valuable not only for their ability to provide insight into possible pathways of future change, but for their ability to highlight the key uncertainties that limit our ability to generate reasonable predictions about future system states.

#### ACKNOWLEDGMENTS

I am grateful to the Bureau of Land Management for providing permission for us to conduct research in the White Mountains and Alaska Range, to the Council Village Native Council for providing us access to the study sites on the Seward Peninsula, and to Bering Land Bridge National Park for assistance with the early stages of site selection on the Seward Peninsula. The field and laboratory work were completed with the able assistance of legions of undergraduates from Middlebury College and the University of Wyoming. This research was supported by a National Science Foundation grant (OPP-9731717), by the Bonanza Creek LTER (DEB-0080609), by the USDA Forest Service PNW Station, and by Middlebury College. This manuscript was greatly improved by comments from Chris Fastie and two anonymous reviewers.

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