

# Recent changes in treeline forest distribution and structure in interior Alaska<sup>1</sup>

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**Abstract:** Although the forest-tundra boundary is likely to be sensitive to future climate warming, the degree to which treeline response may lag climate change and the extent to which sensitivity to climate may vary among sites remain largely unknown. We used tree-ring analysis to reconstruct white spruce (*Picea glauca*) density from 1800 to present at and beyond the current forest limit at seven altitudinal treeline sites in two regions of interior Alaska. Treeline advance was ubiquitous: cone-bearing spruce are present beyond the current forest limit at all but one site, and tree density has increased at and beyond the forest limit in recent decades at all sites. Increases in stand density were positively correlated with summer temperature at most, but not all, sites. The timing of inferred advances in treeline differed significantly between regions, beginning in the mid- to late 1800s in the White Mountains and in the mid-1900s in the Alaska Range. These differences in the timing of treeline advance may be caused by differences in the rate of forest response to climate or by differences in regional climate history, which remains poorly known. Despite the variation in timing of an advance of treeline, the similarities among sites in the pattern (if not the timing) of change at treeline suggest that recent shifts in the location of the forest-tundra border are a widespread response to recent warming in Alaska.

**Keywords:** Alaska, alpine treeline, boreal forest, climate change, *Picea glauca*, treeline advance.

**Résumé :** Bien qu'il soit fort probable que la limite de la toundra forestière soit sensible aux changements climatiques prévus, on connaît très peu de choses sur le temps de réponse de la limite aux variations du climat et sur la variabilité spatiale de cette réponse. Nous avons utilisé l'analyse des cernes de croissance pour déterminer la densité de l'épinette blanche (*Picea glauca*) de 1800 à nos jours à la limite actuelle de la forêt et au-delà de celle-ci. Nous avons choisi sept sites dans deux régions du centre de l'Alaska où on trouve une limite altitudinale des arbres. L'avancée récente de la limite des arbres est évidente : dans tous les sites, à une exception près, nous avons trouvé des épinettes portant des cônes au-delà de la limite de la forêt. De plus, au cours des dernières décennies, la densité des arbres s'est accrue à la limite de la forêt et au-delà de celle-ci dans tous les sites. Dans la plupart des cas, les augmentations de densité des peuplements sont corrélées de façon positive avec la température estivale. Des différences significatives ont été trouvées entre les régions en ce qui concerne le début de la progression altitudinale de la limite des arbres. Elle aurait commencé vers le milieu ou la fin du 19<sup>e</sup> siècle dans les White Mountains et vers le milieu du 20<sup>e</sup> siècle dans la chaîne de l'Alaska. Ces écarts pourraient être causés par une variation de l'amplitude de la réponse des forêts au climat ou par des différences régionales au niveau des changements climatiques, des caractéristiques qui sont encore peu connues. Malgré l'absence de synchronicité, les similitudes qui existent entre les sites sur la façon avec laquelle la limite des arbres progresse suggèrent que les récentes modifications de la position de la limite de la toundra forestière constituent une bonne indication de la réponse générale de la végétation aux changements climatiques en Alaska.

**Mots-clés :** Alaska, limite des arbres altitudinale, forêt boréale, changement climatique, *Picea glauca*, Avance de la limite des arbres.

**Nomenclature:** Hultén, 1968.

## Introduction

Treeline, the boundary between boreal forest and arctic or alpine tundra ecosystems, is widely expected to be affected by future warming: there is ample evidence that the distribution of trees is both physiologically limited by temperature (Sveinbjörnsson, 2000; Sveinbjörnsson, Hofgaard & Lloyd, 2002) and responsive to climate change on centennial to millennial time scales (Denton & Karlén, 1977; Kullman, 1987; Lloyd & Graumlich, 1997; MacDonald, Case & Szeicz, 1998; MacDonald *et al.*, 2000; Pellatt *et al.*, 2000). Furthermore, replacement of tundra by forested vegetation has the potential to generate measurable feedbacks on climate (Chapin *et al.*, 2000a; Chapin *et al.*,

2000b); thus, the response of treeline to warming has broader implications for high-latitude ecosystems.

Although an advance of treeline in response to warming seems likely, observations of the response of treeline to climate on decadal time scales are conflicting. Although observations of seedling establishment in tundra in the 20<sup>th</sup> century abound (Hopkins, 1972; Viereck, 1979; Morin & Payette, 1984; Cooper, 1986; Suarez, Binkley & Kaye, 1999), increased establishment of tree seedlings in tundra has not been a universal response to recent warming. In some cases, advances of the tree limit have been caused by changes in the growth form of the most marginal trees (*e.g.*, from krummholz to upright forms) rather than establishment of new seedlings (Lavoie & Payette, 1994; Lescop-Sinclair & Payette, 1995). In other sites, the forest limit has remained stable during the

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20<sup>th</sup> century, suggesting that treeline may not always respond immediately (or at all) to increasing temperature (Payette *et al.*, 1989; Szeicz & MacDonald, 1995a; MacDonald *et al.*, 1998).

Such variability in the response of treeline forests to recent warming may be an indication that variable and lagged responses to climate change are likely on decadal time scales. Lagged responses to warming are a common feature of models of treeline dynamics, which suggest that lags of at least 150 years are likely between the onset of warming and the development of forests beyond treeline (Chapin & Starfield, 1997; Lloyd *et al.*, in press). A range of processes at treeline may introduce such lags. For example, cold temperatures may limit the production of viable seed at treeline, in which case there may be insufficient seed in the early years following warming to support an increase in tree establishment (Lescop-Sinclair & Payette, 1995; MacDonald *et al.*, 1998). Lags may also arise if the effects of temperature are indirect: for example, in areas affected by permafrost, tree establishment may be delayed until rising air temperatures cause substantial change in active layer thickness (Lloyd *et al.*, in press). Finally, treeline response to warming may be slow if competitive interactions between trees and faster responding tundra plants limit successful establishment. In this case, treeline advance may be dependent upon the occurrence of a suitable disturbance. Thus, although treeline seems to fluctuate more or less synchronously with climate on long (multi-millennial) time scales, lagged and non-linear responses to climate may be likely on shorter (decadal) time scales.

Paleoclimatic data suggest that the most recent Little Ice Age minima were reached between 1700 and the early to mid-1800s in Alaska and the adjacent Yukon Territory and that temperatures have risen approximately 1.5–2.0°C since that time (D'Arrigo & Jacoby, 1993; Szeicz & MacDonald, 1995b; Serreze *et al.*, 2000; Hu *et al.*, 2001). In northwestern Canada, that warming was associated with an increase in the density of treeline forests, but no change in the forest limit (Szeicz & MacDonald, 1995a). In Alaska, there is indication from a limited number of sites that spruce began expanding into tundra sometime in the 1900s (Hopkins, 1972; Viereck, 1979; Cooper, 1986; Suarez, Binkley & Kaye, 1999; Lloyd *et al.*, in press). The goal of this research was to document temporal patterns of change at replicate alpine treeline sites in two geographically distinct regions of interior Alaska and, with those data, to investigate the degree of spatial variability in recent changes in treeline forests in Alaska.

## Methods

### STUDY AREAS

We investigated recent treeline dynamics at seven study sites in two mountain ranges in interior Alaska (Figure 1). The White Mountains are a low (1,500–1,800 m) mountain range between the Yukon and Tanana River drainages. Forests of black spruce (*Picea mariana*), white spruce (*Picea glauca*), and birch (*Betula papyrifera*) dominate lower elevations, but white spruce is the dominant tree-

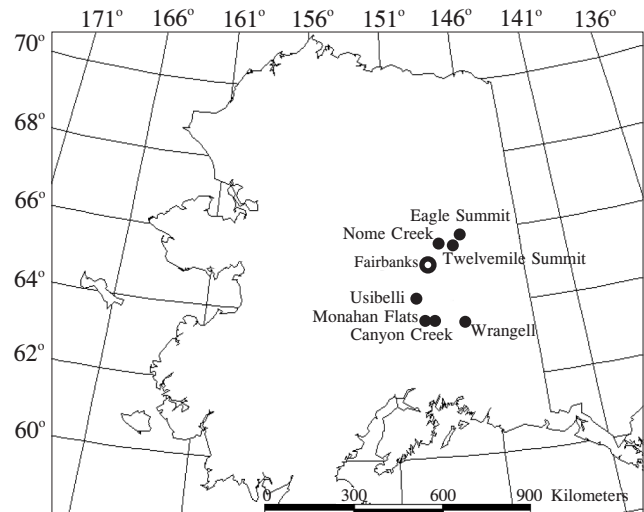


FIGURE 1. Location of study sites in interior Alaska. Solid circles indicate study sites, and open circles indicate the location of cities. The three northern study sites (Eagle Summit, Nome Creek, Twelvemile Summit) are in the White Mountains, and the four southern sites are in the Alaska Range.

line species. Alpine tundra in the White Mountains is typically low shrub/herb. The Alaska Range is a considerably higher system of mountains, with a number of peaks in excess of 6,000 m. Treeline forests are dominated by white spruce, and alpine tundra communities include herb and low to medium shrub ecosystems. The regions differ climatologically: the White Mountains are on the edge of the Yukon basin, which is the driest and most continental of Alaska's climate regions, while the Alaska Range, and particularly the southern flank of the range where three of our four sites are located, is considerably wetter (Hammond & Yarie, 1996).

### FIELD METHODS

We established a minimum of three permanently marked study plots at random points along two transects at each study site (Table I). The transects were systematically located at two elevations: lower transects were placed at the uppermost edge of forests of upright trees, and upper transects were placed immediately upslope in areas beyond the forest limit but within the range of spruce. Plots in the upper transects were no more than 200 m from the upper edge of the plots in the lower transects.

Within each study plot, we tagged each live tree and obtained an increment core that included the pith as close to the root crown as possible. The diameter of each tree was measured both at breast height and at the height from which increment cores were obtained, and the height of the core sample above the root crown was measured. Although cross-sections would likely produce a more accurate estimate of tree age, these are permanent study plots, and we thus needed to rely primarily on non-destructive methods for estimating tree age. Because the cores are all cross-dated to account for locally absent rings (which would be visible in a cross-section), the primary bias introduced by using increment cores instead of cross-sections to estimate age is the reduced ability to estimate the age at the root crown, and thus a likelihood

TABLE I. Description of study sites. Elevation (m) is the approximate elevation of the lower transect. Current live tree density (mean  $\pm$  SE) is based on the total number of live spruce of all age classes present in the site at the time of sampling.

Region Site	White Mountains			Alaska Range			
	Eagle Summit	Twelvemile Summit	Nome Creek	Usibelli	Monahan Flats	Canyon Creek	Wrangell View
Elevation (m)	945	945	880	760	885	875	895
Aspect	S	NW	SE	W	NE	N	S
# of study plots per transect	5	7 (lower) 6 (upper)	5	3	5	5	5
Area sampled per transect (m <sup>2</sup> )	2,000	4,200 (lower) 9,000 (upper)	2,500	1,200	2,500	2,500	2,500
Mean ( $\pm$ SE) live tree density (lower transect)	1,370 $\pm$ 456	312 $\pm$ 87	295 $\pm$ 128	3,108 $\pm$ 537	254 $\pm$ 101	628 $\pm$ 94	168 $\pm$ 47
Mean ( $\pm$ SE) live tree density (upper transect)	75 $\pm$ 36	86.7 $\pm$ 11.4	76 $\pm$ 18	2,633 $\pm$ 988	27 $\pm$ 13	20 $\pm$ 3	43 $\pm$ 23

of underestimating tree age. We have attempted to reduce this source of bias by adjusting tree ages for time to grow to core height (see below).

We collected cores or cross-sections of all dead trees. Trees that were too small to core (defined as height < 1.3 m and basal diameter < 2.5 cm) were classified as seedlings. Seedling height was measured, and ages were estimated from counts of annual stem internodes. The accuracy of stem internode counts was assessed in the field by comparing internode counts with ring counts from basal sections on a limited number of harvested seedlings. We detected no systematic bias in internode counts, which were thus considered to be acceptable estimates of seedling age within the decadal-scale resolution of the study. Seedling measurements were completed for both live and dead seedlings.

The presence of cones was also noted for each live tree. Although the presence of cones can provide an index of the existence of potentially reproductive individuals, it is subject to two sources of bias as an estimate of reproductive potential within a population. First, white spruce exhibit high interannual variability in cone production (Zasada & Viereck, 1970), and single-year estimates of reproductive status are thus likely to provide poor estimates of long-term reproductive potential. Second, the presence of cones may provide no information on the presence of viable seeds, which is the true measure of reproductive output. We use our estimate of the abundance of cone-bearing spruce at each site, therefore, as a crude index of the potential for *in situ* reproduction at a particular location. The density of cone-bearing spruce was compared between transects using a paired samples *t*-test ( $n=7$  sites).

#### LABORATORY METHODS

All cores were mounted on wooden strips and sanded until individual xylem cells were visible. Each core was measured to a precision of 0.001 mm on a Velmex sliding-stage micrometer (Velmex, Inc., Bloomfield, New York, U.S.A.). Cores were cross-dated using both visual and statistical cross-dating methods (Stokes & Smiley, 1996; Holmes, 2000); cross-dating allowed us to correct for missing rings and to determine the establishment and death dates of dead trees. Cross-dated inner ring dates were corrected for two errors: (1) missed pith and (2) time to grow to core height. Distance to missed pith was

estimated either from the curvature of the inner ring or from the tree's radius at core height. The number of rings in that distance was estimated from regressions of age on radius for those trees in which the pith was obtained. The time to grow to core height was estimated by regressing seedling age on seedling height. Age-radius and age-height regressions were estimated separately for each study site, but separate regressions were not calculated for different transects within a site because of inadequate sample size.

Estimated establishment and death dates were thus obtained for each tree (live and dead) within each study plot. These data were used to estimate the density of live trees for each decade of the record. Dendrochronological reconstructions of stand history are limited in temporal extent because of the decomposition of dead seedlings and trees. The decomposition of dead trees is likely to lead to systematic underestimates of tree density as time-since-present increases. Based on the distribution of death dates of dead trees, we expect that our estimates of adult tree density are likely to be severely biased by the fading record prior to the mid-1800s. Although recent decades are likely to include a relatively complete history of adult trees, the history of dead seedlings is impossible to reconstruct. Seedlings decompose relatively rapidly after death and thus fail to persist on the landscape for the length of time that an adult tree does, and seedlings are generally difficult to cross-date even before they decompose. The record of dead seedlings is therefore unlikely to extend more than a decade back in time, and our understanding of the temporal dynamics of the seedling portion of the population is necessarily limited. Our estimates of tree density for decades prior to approximately 1970 should therefore be interpreted as estimates of the density of live trees that survived to adulthood.

Because of the fading record of dead seedlings, high densities of seedlings observed in recent decades may be explained by two competing hypotheses. First, the high density of seedlings may be evidence of high levels of recruitment and thus further increases in stand density. Second, the high density of seedlings relative to adult trees may simply indicate high mortality of young age classes and thus not be evidence of further increases in stand density. Although these alternative explanations are not fully testable given the absence of a long-term record of seedling death, we can evaluate them qualitatively by

analyzing the abundance of dead seedlings at the time of sampling. The abundance of dead seedlings (as a proportion of the total seedling population) provides at least a crude estimate of instantaneous mortality rates and can thus provide some insight into the plausibility of the second hypothesis. We compared the abundance of dead seedlings in upper and lower transects using a paired samples *t*-test ( $n=7$  sites).

Reconstructions of stand density provide information on changes in forest structure at a particular elevation and also provide the basis for inferences about changes in treeline position. An advance in treeline should be indicated by a more recent onset of spruce establishment in the upper transect compared to the lower transect at each site. We used three methods to identify changes in the position of treeline. First, we simply determined the decade in which spruce began recruiting within each transect in a particular site. Although this method is likely to be strongly influenced by the presence of isolated individuals above treeline, it is nonetheless an important description of forest history. Second, we determined the earliest recruitment date of a live or dead spruce in each replicate study plot within each transect, calculated a mean earliest recruitment date for each transect, and conducted a paired-samples *t*-test ( $n=7$  sites) to test the hypothesis that mean maximum tree age would be significantly less above than at treeline. Finally, we determined the decades in which a population density threshold of 5 and 15 trees  $\text{ha}^{-1}$  was reached at each elevation. These represent arbitrary thresholds and are meant simply to describe the timing of establishment of a population of spruce within a particular transect. Differences between regions in the date at which these thresholds were passed were tested using a Mann-Whitney *U*-test. A non-parametric test was chosen for this comparison because of relatively low replication ( $n=3$  or 4 sites) within each region.

The relationship between stand density and climate was quantified by comparing the proportional change in stand density in each decade with estimates of summer temperature obtained from two long climate reconstructions: the northernmost gridpoint ( $65^\circ \text{N}$ ,  $150^\circ \text{W}$ ) in a reconstruction of April-September temperatures from 1750-1982 (Briffa, Jones & Schweingruber, 1992) and a reconstruction of June-July temperature from 1638-1988 for northwestern Canada (Szeicz & MacDonald, 1995b). Temperatures were averaged over 10-year time periods corresponding to the years included in each decadal estimate of stand density (1741-1750, 1751-1760, etc.). Net recruitment may also respond to climate in the decades immediately following establishment, so changes in stand density were also compared to average temperature in 20-year and 50-year windows following the decade of recruitment (Szeicz & MacDonald, 1995a).

## Results

### ABUNDANCE OF DEAD SEEDLINGS

The relative abundance of seedlings that were dead at the time of sampling ranged from 0 to 22% (Figure 2). The relative abundance of dead seedlings did not differ between transects ( $t=1.57$ ,  $P=0.167$ ,  $n=7$  sites per transect).

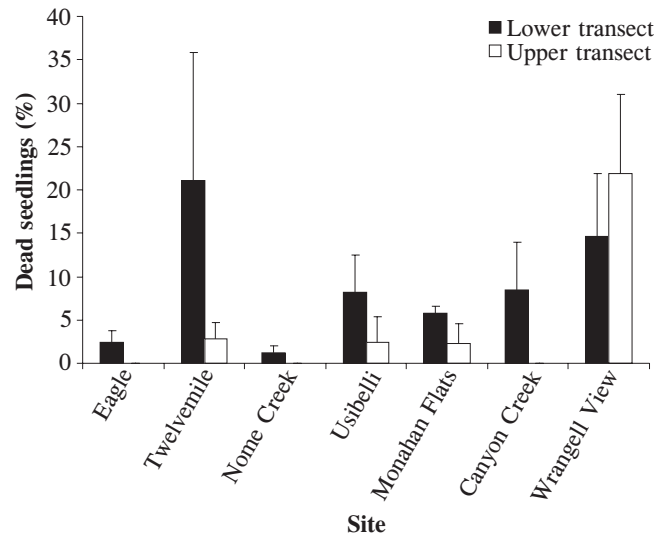


FIGURE 2. Relative abundance of dead spruce seedlings in lower and upper transects at each study site. Relative abundance is the percentage of all seedlings that were dead at the time of sampling. Values are mean  $\pm$  SE (see Table I for sample sizes).

### RELATIVE AGE OF SPRUCE POPULATIONS

Recruitment of spruce populations began significantly earlier in the lower transects than in the upper transects. With the exception of the Eagle Summit site, where the earliest establishment date was identical in both transects, the oldest tree (live or dead) present in the lower transect established earlier than the oldest tree present in the upper transect (Table II). Furthermore, the mean earliest establishment date was significantly **earlier** in the upper than the lower transects: the mean difference in this date between populations in upper and lower transects was  $160.7 \pm 48.3$  years ( $t=-3.59$ , one-tailed  $P=0.005$ ; Figure 3). However, the difference in mean earliest establishment date between the two transects was significantly less ( $t=5.199$ ,  $P=0.003$ ) in the White Mountains ( $45.6 \pm 29$  years;  $n=3$  sites) than in the Alaska Range ( $247.1 \pm 35.3$  years;  $n=4$  sites), reflecting the presence of low densities of old, krummholz spruce beyond the forest limit in the White Mountains.

### TEMPORAL CHANGES IN TREE DENSITY

In the White Mountains, spruce density in both upper and lower transects has increased since the 1800s. Spruce were present in low densities ( $<15$  trees  $\text{ha}^{-1}$ ) in the upper transects as early as the mid-1700s (Figure 4). In all cases, trees  $>100$  years old in the upper transect were stunted krummholz trees with a largely prostrate growth form. At all three sites, spruce density increased in the upper transects throughout the 1900s, but by 2000 mean spruce density in these upper transects was still less than one third the mean density in the lower transects (Table I). Relatively old spruce were common in the lower transects in the White Mountains, except at Eagle Summit, where a modern radiocarbon date on soil charcoal indicates the occurrence of a fire within the last 300 years. The density of live spruce in the lower transects increased slowly throughout the 1800s and more rapidly beginning in the early 1900s (Figure 4).

Shouldn't this say later?

TABLE II. Earliest recruitment date of white spruce (living or dead) in upper and lower transects at the 7 study sites. The difference in earliest establishment date was calculated by subtracting the date in the lower transect from that in the upper transect; positive numbers indicate that the earliest establishment date in the upper transect is more recent than that in the lower transect.

Site	Earliest recruitment date upper transect	Earliest recruitment date lower transect	Difference (upper - lower)
Eagle Summit	1822	1822	0
Twelvemile Summit	1728	1628	100
Nome Creek	1764	1652	112
Usibelli	1939	1742	197
Monahan Flats	1697	1444	253
Canyon Creek	1691	1426	265
Wrangell View	1953	1575	378

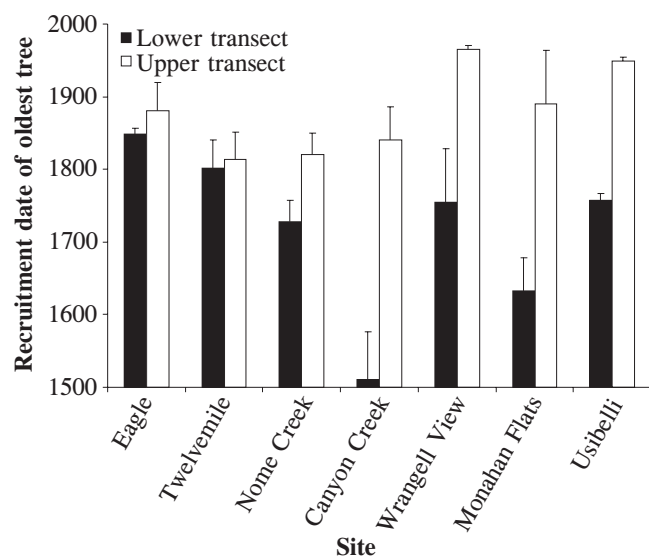


FIGURE 3. Average recruitment date of the oldest white spruce (mean + SE of  $n=3$  to 7 plots; see Table I for sample sizes) at seven study sites. The difference in recruitment date is significant ( $P < 0.05$ ).

In the Alaska Range, the establishment of spruce within the upper transects is a more recent phenomenon (Figure 5). Very low densities ( $< 5$  trees  $\text{ha}^{-1}$ ) of spruce were present in the upper transects at Canyon Creek and Monahan Flats prior to 1900, but at Usibelli and Wrangell View there is no evidence of spruce in the upper transects until after 1950. The density of spruce in the upper transects increased significantly after 1950 at all sites. Increases in the density of live trees in the lower transects were seen at all sites; at two sites these increases were coincident with establishment beyond the forest limit, and at two sites these increases predated establishment beyond the forest limit (Figure 5).

Spruce populations of  $> 15$  trees  $\text{ha}^{-1}$  successfully established in the upper transects at each of our 7 study sites in the 20<sup>th</sup> century (Table III), although the date that that threshold was passed varies widely among sites. Sites in the White Mountains, where old krummholz trees were common in the upper transects, began accumulating spruce in the upper transects relatively early (mid-1800s), while in the Alaska Range the establishment of moderate

densities of spruce in the upper transects did not generally begin until the late 1800s or early 1900s. The date at which populations in the upper transect reached densities of 5 trees  $\text{ha}^{-1}$  differed significantly between the White Mountains and the Alaska Range ( $U=0$ ,  $P=0.034$ ,  $n=7$ ). The date at which the threshold of 15 trees  $\text{ha}^{-1}$  was passed exhibited the same trend between regions, but was not significant ( $U=1$ ,  $P=0.074$ ,  $n=7$ ).

#### REPRODUCTIVE STATUS OF TREES AT AND BEYOND THE FOREST LIMIT

Cone-bearing spruce were present in both transects at six of the seven sites. No cone-bearing spruce were found within the study plots in the upper transect at Usibelli (Figure 6). The density of cone-bearing spruce was significantly greater at each site in lower transect plots than in upper transect plots ( $t=3.54$ ,  $P=0.006$ ).

#### CORRELATION BETWEEN CHANGES IN STAND DENSITY AND CLIMATE

Significant positive correlations between changes in stand density and summer temperature were found at all of the Alaska Range sites, with the exception of the upper transect at Usibelli, where sample size was insufficient for analysis due to the youth of the stand (Table IV). In the White Mountains, significant positive relationships between change in stand density and climate were found in the upper transects at Twelvemile Summit and Eagle Summit, but changes in stand density at treeline in those sites were uncorrelated with reconstructed temperature. At Nome Creek, changes in stand density in both transects were inversely correlated with reconstructed temperature (Table IV).

## Discussion

The advance of spruce upslope from the current forest limit will generate a pattern of declining stand age with increasing elevation; in our sampling design, therefore, such an advance would be expressed as younger spruce populations beyond the current forest limit (*i.e.*, in upper transects) than at the current forest limit (*i.e.*, in lower transects). We found such evidence for an advance at all of our study sites, both in the White Mountains and in the Alaska Range. Both absolute and mean earliest tree establishment dates were more recent in populations beyond the forest limit (upper transect plots) than in populations at the forest limit (lower transect plots). Furthermore, establishment of spruce beyond the forest limit was not restricted to isolated trees: population densities have exceeded 15 trees  $\text{ha}^{-1}$  at all sites in recent decades. The potential exists for reproduction within the most marginal populations, as cone-bearing spruce were present in densities  $> 1$  tree  $\text{ha}^{-1}$  at all but one site (where the advance began so recently that no sufficiently old trees exist above treeline). Because the proportion of viable seeds and the total seed rain often decrease towards treeline (Molau & Larsson, 2000; Sirois, 2000), the presence of cones is simply indicative of a potential for reproduction within these stands and does not provide an estimate of the quantity of viable seed (if any) produced.

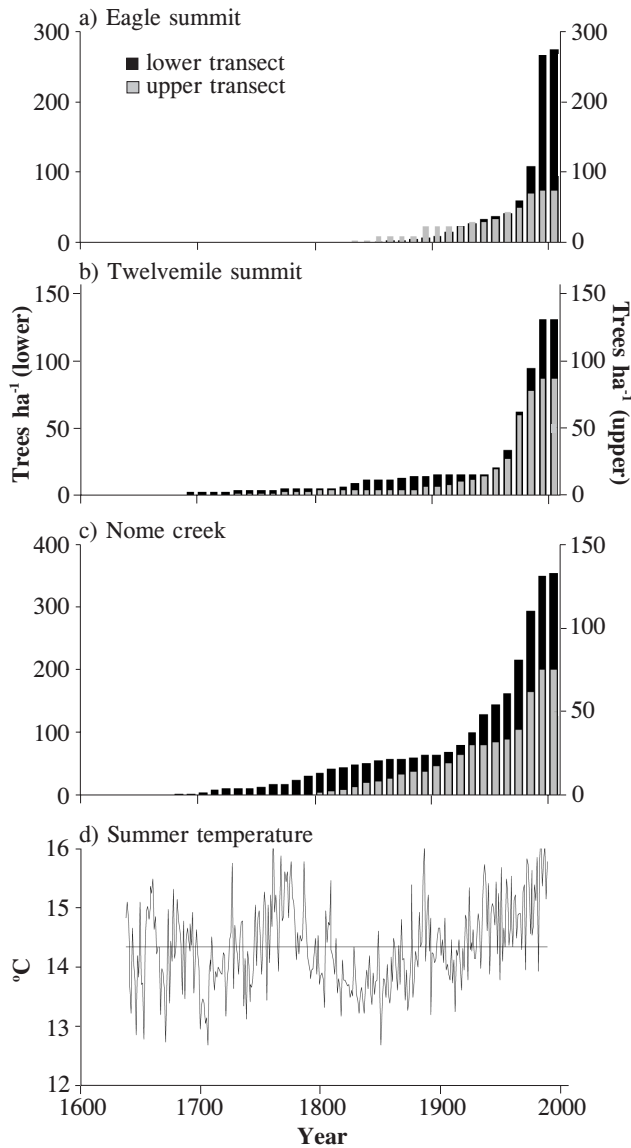


FIGURE 4. (a-c) Reconstructed density of white spruce in lower transects (solid bars; left axis) and upper transects (hatched bars; right axis) at three sites in the White Mountains. Bar height indicates the density of live spruce present in the study plots during the decade indicated (year is the last year of the decade), as estimated from cross-dated establishment dates of live and dead trees. d) June-July temperature in north-western Canada (Szeicz & MacDonald, 1995b).

Treeline advance is only one possible explanation for a pattern of relatively young spruce beyond the forest limit, however: the same pattern would occur if mortality was higher beyond the forest limit, resulting in a population with very high turnover and thus few or no old trees. If higher mortality is the explanation for the relative youth of spruce populations beyond the forest limit, then dead trees and seedlings should be common in these sites, particularly as colder temperatures (and perhaps reduced risk of fire) should create a better preservational environment for dead wood. We found no such evidence. Indeed, although the abundance of dead seedlings did not differ significantly between upper and lower transects, there was a trend towards greater relative abundance of dead seedlings in lower transects. We thus conclude that higher

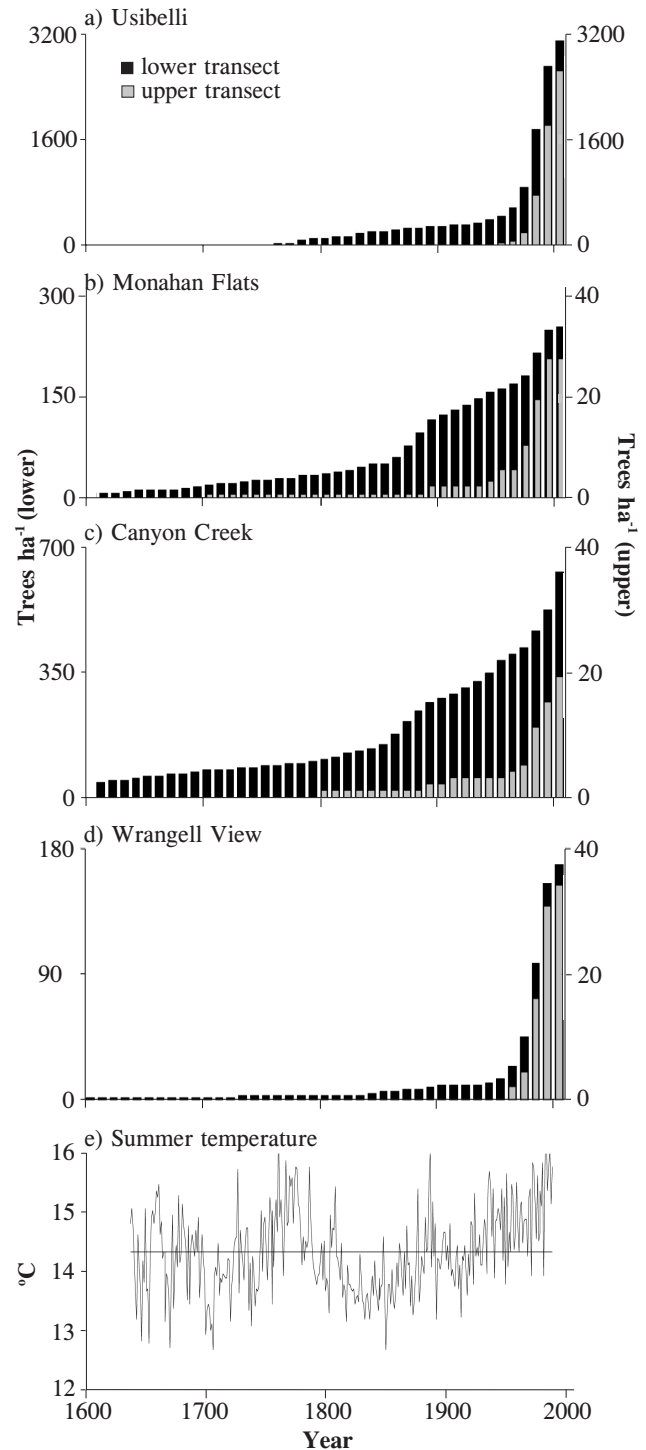


FIGURE 5. (a-d) Reconstructed density of white spruce in lower transects (solid bars; left axis) and upper transects (hatched bars; right axis) at three sites in the Alaska Range. Bar height indicates the density of live spruce present in the study plots during the decade indicated (year is the last year of the decade), as estimated from cross-dated establishment dates of live and dead trees. (e) June-July temperature in north-western Canada (Szeicz & MacDonald, 1995b).

mortality is an unlikely explanation for the youth of spruce beyond treeline. The alternative hypothesis, then, is that the more recent establishment of spruce beyond the forest limit is the result of an upward shift of treeline. The high densities of live seedlings, positive trends in

Should say four?

TABLE III. Decade in which the density of live white spruce in the upper transects reached thresholds of 5 and 15 trees ha<sup>-1</sup>. The year is the end year of the decade (so 1830 is the decade from 1821-1830).

Region	Site	5 trees ha <sup>-1</sup>	15 trees ha <sup>-1</sup>
White Mountains	Eagle Summit	1830	1890
	Twelvemile Summit	1890	1950
	Nome Creek	1840	1900
Alaska Range	Usibelli	1940	1940
	Monahan Flats	1950	1990
	Canyon Creek	1970	1990
	Wrangell View	1980	1980

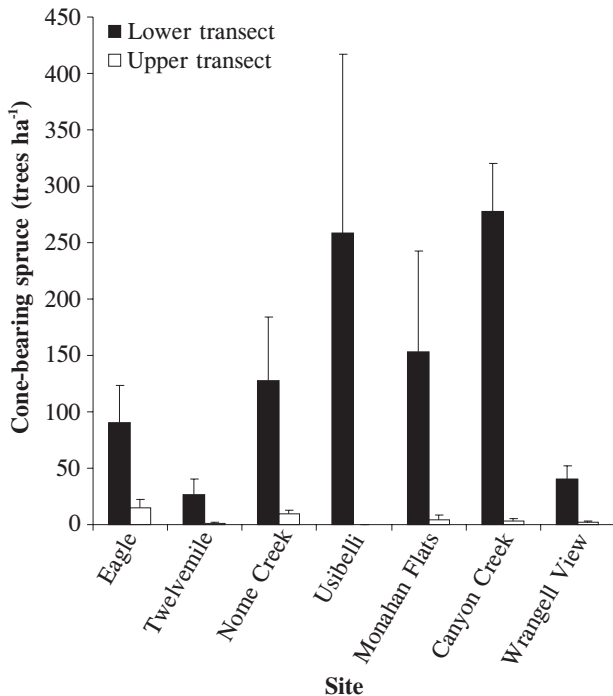


FIGURE 6. Density of cone-bearing white spruce trees in upper and lower transects at each study site. Values are mean + SE of n=3 to 7 plots (see table I for sample sizes).

density of adult trees over time, and low densities of dead seedlings in the upper transects argue strongly for this explanation for the observed patterns in spruce establishment history.

These results are consistent with previously published studies and suggest that treeline advance has become a nearly ubiquitous phenomenon at both arctic and alpine treelines in Alaska. Observations of seedlings establishing in tundra have been made since the early 1970s in Alaska (Hopkins, 1972), but interpreting isolated reports of seedlings in tundra is difficult. Seedlings may routinely establish beyond the forest limit, for example, but fail to survive to adulthood, in which case such observations can not be taken as evidence of directional change in the position of the ecotone. Evidence that such observations are indicative of directional change in the treeline ecotone has begun to mount in recent years, however. Suarez, Binkley, and Kaye (1999) published age structures of spruce populations at and beyond the forest limit at arctic treeline in northwestern Alaska, and their data suggested that not only had seedlings established in tundra, but at least some of those seedlings had survived to adulthood. **Lloyd et al. (in press)** concluded from reconstructions of stand density that treeline was advancing at two sites on the Seward Peninsula. Treeline advances may thus be widespread at arctic treelines in Alaska, and the data presented here indicate that treeline advance also occurred within the same time frame at alpine treeline sites throughout Alaska. Evidence for treeline advance in Alaska now exists at ten study sites in three regions, encompassing a range of current climates (Hammond & Yarie, 1996) and a range of treeline types (alpine, upland arctic, lowland arctic).

Reconstructions of temporal trends in population density at the current forest limit suggest that the advance of spruce into tundra (*i.e.*, recent establishment in upper transects) is part of a wholesale shift in the forest-tundra ecotone, in which low-density stands at the current forest limit have increased in density and low-density populations have established beyond the current forest limit. Previous studies have suggested that asynchronies may occur between the population-level response to climate at

TABLE IV. Correlations between climate and changes in stand density at and above treeline at each of the 7 study sites. Results show the highest correlation coefficient, based on comparisons between decadal-scale changes in stand density and six possible climate variables (see Methods). At two sites (Wrangell View and Usibelli) the above treeline stands were so young that sample size was inadequate to conduct the analysis. Significance is indicated following the correlation coefficient as \*\*\*( $P < 0.001$ ) or \*\*( $P < 0.05$ ). The sample size ( $n$ ) varies according to the age of the stands at each site.

Site	Transect	Climate variable	$r$	$n$
Canyon Creek	Treeline	summer temperature Briffa, Jones & Schweingruber, 1992), 50-year mean	0.802***	19
	Above treeline	summer temperature (Szeicz & MacDonald, 1995b), 10-year mean	0.563**	19
Monahan Flats	Treeline	summer temperature (Briffa, Jones & Schweingruber, 1992), 50-year mean	0.646**	19
	Above treeline	summer temperature (Szeicz & MacDonald, 1995b), 10-year mean	0.455**	23
Wrangell View	Treeline	summer temperature (Briffa, Jones & Schweingruber, 1992), 50-year mean	0.551**	19
	Above treeline			
Usibelli	Treeline	summer temperature (Szeicz & MacDonald, 1995b), 10-year mean	0.605**	24
	Above treeline			
Nome Creek	Treeline	summer temperature (Briffa, Jones & Schweingruber, 1992), 50-year mean	-0.515**	19
	Above treeline	summer temperature (Szeicz & MacDonald, 1995b), 50-year mean	-0.651**	15
Twelvemile Summit	Treeline	no significant correlations		
	Above treeline	summer temperature (Szeicz & MacDonald, 1995b), 20-year mean	0.553**	25
Eagle Summit	Treeline	no significant correlations		
	Above treeline	summer temperature (Briffa, Jones & Schweingruber, 1992), 20-year mean	0.537**	14

1995b correct?

the forest limit (*i.e.*, an increase in density) and a directional shift in the ecotone (*i.e.*, an advance of treeline) (Szeicz & MacDonald, 1995a). An increase in the density of forests at the current forest limit (lower transect plots) was approximately coincident with an increase in establishment beyond the forest limit at some sites (Usibelli, Wrangell View, Twelvemile Summit, Eagle Summit) but not at others (Nome Creek, Canyon Creek, Monahan Flats). These differences in the synchrony of population change at treeline and above treeline suggest that the inertia of the treeline ecotone (Szeicz & MacDonald, 1995a) may vary among sites, for reasons that remain unknown.

A climatic basis for the changes in stand density and treeline position is likely for a number of reasons. First, with the exception of extremely arid sites where population growth appears to be simultaneously limited by moisture and temperature (Lloyd & Graumlich, 1997), temperature seems to be the most important factor limiting spruce recruitment at treeline (Kullman, 1987; Scott, Hansell & Fayle, 1987; Sveinbjörnsson, Hofgaard & Lloyd, 2002). On purely mechanistic grounds, it is thus likely that the increased recruitment at and beyond treeline described here is a response to the  $> 1.5^{\circ}\text{C}$  rise in temperature that has occurred in Alaska since the mid-1800s (D'Arrigo & Jacoby, 1993; Overpeck *et al.*, 1997; Suarez, Binkley & Kaye, 2000; Hu *et al.*, 2001). Second, similar patterns of change in treeline forest structure were identified at replicate sites spread across two large regions, suggesting that small-scale environmental factors (*e.g.*, disturbance) are an unlikely explanation.

Finally, temporal patterns of change in stand density at all of the Alaska Range sites and some of the White Mountains sites were positively correlated to reconstructed summer temperature, thus confirming a relationship between decadal-scale variation in recruitment and regional climate. At those sites, large increases in stand density corresponded to warming in the late 1800s and latter half of the 1900s (D'Arrigo & Jacoby, 1993; Szeicz & MacDonald, 1995b; Jacoby & D'Arrigo, 1997; Figures 4d and 5d). The dates of treeline advance (Table III) are similarly coincident with periods of warming in the mid- to late 1800s and the late 1900s, and the isolated spruce that established beyond the forest limit prior to that advance seem in many cases to have established during a period of relatively warm temperatures in the late 1700s.

Although the majority of sites do, therefore, exhibit the expected relationship between temperature and recruitment, it is by no means universal: the relationship between climate and spruce recruitment at treeline in the White Mountains is highly variable within and among sites. Warming began in the 1840s-1850s in that region (D'Arrigo & Jacoby, 1993; Jacoby & D'Arrigo, 1997), roughly coincident with the initiation of treeline advance, but correlations between stand density and reconstructed summer temperature were highly variable in magnitude and direction. This may reflect a difference in climate history between the White Mountains and northwestern Canada, but strong positive correlations between tree-ring chronologies from the White Mountains (Lloyd & Fastie, 2002) and reconstructed summer temperature in northwestern Canada argue against this explanation (Table V).

Alternatively, treeline spruce populations in the White Mountains may have an intrinsically different response to or sensitivity to climate than populations in other regions. This hypothesis is supported to some extent by analyses of the relationship between tree growth and climate. Lloyd and Fastie (2002) found that tree growth in the Alaska Range was uniformly positively related to temperature, whereas tree growth in the White Mountains was either unrelated to temperature (at treeline at Twelvemile Summit) or inversely related to temperature (at and below treeline at Nome Creek, below treeline at Twelvemile Summit and Eagle Summit). Regional and site-specific differences in tree growth response to climate thus mirror differences in population-level response to climate, suggesting that the nature of climatic controls over population processes may differ among sites, for reasons that remain unknown.

Regional differences also occurred in the date of treeline advance: treeline began to advance significantly earlier in the White Mountains than in the Alaska Range. Two general hypotheses may explain the differences between regions. First, the two regions may have experienced different patterns of post-Little Ice Age warming. An earlier advance of treeline would be expected in the White Mountains, for example, if warming began earlier there than in the Alaska Range. Unfortunately, the climate histories of the two regions remain incompletely known, and this hypothesis is thus difficult to test conclusively.

The second hypothesis to explain regional differences in the timing of treeline advance is that treeline forests in the two regions may exhibit different response times to climate change. In other words, even if the two regions experienced identical patterns of post-Little Ice Age warming, the rate at which forests respond to that warming may differ because of ecological or environmental differences between regions. Some support for this hypothesis is found in the reconstructions presented here. In two of the Alaska Range sites (Canyon Creek and Monahan Flats), the density of trees at treeline began to increase in the late 1800s, decades before spruce establishment increased beyond the forest limit at each site. Assuming that climate is the primary cause of changes in tree density at treeline, these data would seem to suggest that warming had, indeed, begun by the mid- to late 1800s in the Alaska Range and thus that at least part of the difference between the two regions may be a result of system-

TABLE V. Correlations between tree growth in the White Mountains and reconstructed summer temperature in northwestern Canada. Tree-ring chronologies, developed from old trees at treeline, for each of the study sites in the White Mountains are described in Lloyd and Fastie (2002). Chronologies were compared to reconstructed summer temperature from northwestern Canada (Szeicz & MacDonald, 1995b) for the period 1800-present. Significant correlations ( $P < 0.05$ ) are indicated with an asterisk (\*).

Site	Correlation with northwestern Canada summer temperature
Eagle Summit	0.468*
Twelvemile Summit	0.453*
Nome Creek	0.524*

atic differences between the two regions in the dynamics of seedling establishment beyond the forest limit.

One possible explanation for more rapid seedling establishment beyond treeline in the White Mountains than in the Alaska Range may be found in structural differences in treeline in the two regions: old krummholz trees were common above the forest limit in the White Mountains, whereas such trees were rare in the Alaska Range. Krummholz trees beyond the current forest limit may function as islands from which spruce may be able to rapidly spread. Isolated krummholz above the current forest limit may enhance seed availability and may also moderate microclimatic conditions sufficiently to enhance seedling survival rates (Scott, Hansell & Fayle, 1987; Wilson & Agnew, 1992; MacDonald *et al.*, 1998). Seedling establishment above treeline at sites lacking such individuals may thus be limited by an absence of suitable microsites (Szeicz & MacDonald, 1995a). Such a mechanism might explain the relatively early onset of seedling establishment in tundra in the White Mountains, where old krummholz trees are common beyond the forest limit, but further research is needed to test this and other possible explanations for differences in the rate of seedling establishment beyond the forest limit between the two regions.

In conclusion, we have presented evidence for an upward shift in the forest-tundra ecotone within the last 150 years at seven sites in the Alaska Range and White Mountains in interior Alaska. High spruce recruitment at and beyond the current forest limit was associated with periods of warm summer temperatures at most, but not all, sites. These results are consistent with previous observations of treeline advance in Alaska (Hopkins, 1972; Viereck, 1979; Cooper, 1986; Suarez, Binkley & Kaye, 1999; Lloyd *et al.*, *in press*), and indicate that change is widespread at both arctic and alpine treeline in Alaska. The inertia of the treeline ecotone, however, may be highly variable among sites: treeline advance in the White Mountains occurred within a few decades of the onset of post-Little Ice Age warming, suggesting a rapid response of treeline in that region, whereas treeline advance lagged substantially behind increases in treeline population density in the Alaska Range and in northwestern Canada, where density increased with no substantial change in the position of treeline (Szeicz & MacDonald, 1995a).

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