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Expansion of forest stands into tundra in the Noatak National Preserve, northwest Alaska[1]

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Abstract: Temperatures across the northern regions of North America have been increasing for 150 years, and forests have responded to this increase. In the Noatak National Preserve in Alaska, white spruce (*Picea glauca* [Moench] Voss) forests reach their northern limit, occurring primarily on well-drained sites and as gallery forests along streams. Rolling plateaus of tundra separate the white spruce forests into disjunct stands. We examined patterns of tree age, tree growth, and tree encroachment into tundra ecosystems in six stands along the Agashashok River. Warming over the past 150 years appears to have increased tree growth and resulted in forest expansion into adjacent tundra ecosystems. The forest/tundra ecotone shifted by about 80 to 100 m into the tundra in the past 200 years, as evidenced by declining maximum tree age with distance towards the tundra. The decadal-scale pattern of tree establishment at the farthest extent of trees into the tundra (the tundra-forest ecotone) correlated with the detrended growth index for trees within the forests; climate conditions that led to higher tree growth appeared to foster tree establishment in the tundra. This recent forest expansion has occurred across topographic boundaries, from well-drained soils on slopes onto poorly drained, flatter areas of tundra. Further expansion of the forests may be limited by more severe wind exposure and poor drainage that make the majority of tundra less suitable for trees.
Keywords: *Picea glauca*, treeline, climate change.

Résumé : Au cours des derniers 150 ans, une augmentation de la température a été observée dans les régions nordiques de l'Amérique du Nord, augmentation à laquelle les forêts ont répondu. Dans la Réserve Nationale Noatak, en Alaska, les forêts d'épinette blanche (*Picea glauca* [Moench] Voss) atteignent leur limite septentrionale, se trouvant principalement sur les sites bien drainés et en bordure des cours d'eau. Des plateaux de toundra séparent ces forêts d'épinette en peuplements distincts. Les patrons d'âge et de croissance des arbres, ainsi que leur établissement dans les écosystèmes toundriques ont été étudiés dans six peuplements situés le long de la rivière Agashashok. Le réchauffement des derniers 150 ans semble avoir stimulé la croissance des arbres, résultant en une expansion des forêts dans la toundra adjacente. Un déplacement de 80 à 100 m de l'écotone forêt/toundra en direction nord au cours des derniers 200 ans se reflète par une diminution de l'âge maximum des arbres vers la toundra. Le patron décennal d'établissement des arbres est corrélé avec l'indice de croissance des arbres croissant en forêt. Les conditions climatiques ayant entraîné l'augmentation de la croissance des arbres semblent donc avoir prédisposé l'établissement des arbres dans la toundra. Cette expansion récente s'est manifestée à travers des frontières topographiques, à partir de sols sur pentes bien drainées vers les sites mal drainées de la toundra. Une nouvelle expansion des forêts pourrait être limitée par l'exposition à des vents plus violents et par le mauvais drainage, qui rendent la toundra moins favorable à la croissance des arbres.
Mots-clés : *Picea glauca*, limite des arbres, changement climatique.

Introduction

Treeline in Alaska falls between 66 and 68° N, with a mosaic of tundra and white spruce stands (Hultén, 1968). Forests of white spruce near treeline form disjunct stands, typically on well-drained slopes amid poorly drained plateaus of tundra. The boundaries between forest and tundra have been dynamic in this area on a time scale of centuries to thousands of years (Viereck & Dyrness, 1980; Pielou, 1991). Eighteen thousand years ago, tundra and bare ground characterized much of Alaska, with latitudinal tree line stands of white spruce (*Picea glauca* [Moench] Voss) near 35 to 40° N. White spruce reached the Beaufort Sea at the northern extreme of Alaska (70° N) during the hypsithermal period (9000 years ago) and then receded several hundred kilometers southward to the modern treeline on the southern side of the Brooks Range (Ritchie & MacDonald, 1986). The arctic and subarctic regions of North America have warmed substantially in the past 150 years (Maxwell, 1992; Deming, 1995; Overpeck *et al.*, 1997), and white spruce forests have expanded, as evidenced by dramatic increases in recruitment and local advances of treeline in Canada (Payette & Filion, 1985; Scott, Hansell & Fayle, 1987; Szeicz & MacDonald, 1995) and in the Brooks Range of Alaska (Garfinkel & Brubaker, 1980; Goldstein, 1981; Cooper, 1986; Rowland, 1996).

Spruce stands appear to be expanding into the tundra in the mountainous region containing our study site in northwest Alaska (67° 28' N, 162° 14' W). Locally restricted white spruce forests grade into expanses of tundra, with a transition from pure forest, to forest mixed with common tundra plants, to tundra with substantial numbers of trees, to treeless tundra. We examined this sequence of ecosystems

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at several sites along the Agashashok River to determine whether the declining density and size of trees along forest-to-tundra ecotones represented a sequence of tree invasion, or simply a gradient of poorer growing conditions that restricted tree establishment and growth.

Material and methods

Our study area is along the Agashashok River, a tributary of the Noatak River, within the Noatak National Preserve. After reconnaissance from the air and on the ground, we chose five stands that showed the apparent expansion pattern, and another stand that showed an abrupt forest/tundra boundary (Figure 1). The major ecosystem types in this study area were described by Binkley *et al.* (1994). Understory vegetation in the forest was characterized by a thick carpet of *Hylocomium splendens* (Hedw.) B.S.G., abundant *Equisetum arvense* L. and *Boykinia richardsonii* (Hook.) Gray, and shrubs such as *Salix spp.* (primarily *Salix alexensis* [Anderss.] Cov. and *S. glauca* L.) and *Vaccinium uliginosum* L. The understories of forest-tundra, tundra-forest, and tundra were dominated by tussocks of *Eriophorum vaginatum* L., *Vaccinium uliginosum*, *Potentilla fruticosa* L., *Betula nana* L., and occasional *Salix reticulata* L. and *Arctostaphylos rubra* (Rehd. & Wilson) Fern.

A small western tributary of the Agashashok separates the relatively small stands (about 2 ha) of Fishgut North and Fishgut South (Figure 1). Both stands appear to expand downslope onto the poorly-drained toeslope adjacent to the stream. The Pygmy Creek stand (about10 ha) stretches along a broad slope, from a small eastern tributary of the Agashashok, to a high expanse of tussock tundra. The stand at Pygmy Creek appeared to expand both downslope (Pygmy Creek 1) and upslope (Pygmy Creek 2), with the greatest stand density and largest trees at mid-slope, tapering both upslope and downslope. The Aggie stand (about 10 ha) is on a sideslope of the main Agashashok drainage, with the forest apparently expanding upslope onto the flatter tundra above. The Mosquito stand (about 4 ha) has an abrupt boundary with the tundra, with no apparent invasion across the ecotone. The sharpness of this treeline was not observed anywhere else at our study area.

In each stand, we placed three transects perpendicular to the direction of apparent expansion. Transect 1 was adjacent to the forest, transect 2 was 40-50 m away within the forest-tundra portion of the ecotone, and transect 3 was an additional 40-50 m away within the boundary of tundra-forest and tundra. For the Mosquito stand that showed no apparent expansion, transect 1 was within the forest, transect 2 was on the abrupt stand boundary, and transect 3 was within the tundra. Three plot locations were chosen systematically along each transect at 50-m intervals, parallel to the ecotone.

Stand age structure was examined by sampling the five trees nearest each plot center that were greater than 20 mm dbh (diameter at 1.4 m height). In transect 3, trees were commonly less than 20 mm dbh, so we sampled the nearest five trees of the dominant height class. The distance from plot center to the farthest tree in the plot determined the radius of our variable-area plots.

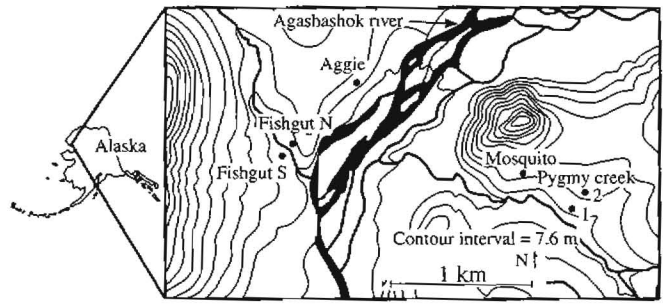

FIGURE 1. Agashashok River study areas.

For each of the five sample trees per plot, we measured dbh, height, and age. Cores were taken at 0.2 m above ground on the uphill side of the tree. A ground-level cross-section was taken from one tree per plot to determine the difference between age-at-0.2 m and age-at-ground-level. We converted all measured ages at 0.2 m to total estimated age and year of establishment. Cores were mounted, sanded, and ages counted with a binocular 40x dissecting scope. The number of years to reach 0.2 m averaged 13 (standard deviation = 11, n = 51).

Thirty-five cores from trees in transect 1 (the oldest portion of the stands) were also measured for annual increment. Raw ring width data were checked for accuracy with COFECHA (Holmes, 1983), a program that compares ring width measurements of each core against the remainder of the data set to determine the accuracy of cross-dating. Inter-series correlation and year-to-year sensitivity of ring width data are also computed in COFECHA to determine the quality of the data set. To determine whether tree growth increased during the period of apparent tree invasion of the tundra, we applied a best-fit, detrending linear regression model to ring width data from each core, and computed ring-width indices. For each year from each core, a ring width index was computed as:

$$I_t = W_t / Y_t \qquad [1]$$

where the ring width index for each year (I_t) equals the ring width measurement (W_t) divided by the expected growth (Y_t) as determined by the linear model. Ring-width indices from each core for each year were then averaged to compute composited ring width indices for the data set. and then combined into decadal intervals to characterize broad patterns in tree growth through time.

For each five-tree plot we also recorded, by size class, the number of seedlings (trees less than 20 mm dbh, or trees of subordinate height class in the tundra plots with small trees). We aged a subsample of five to ten seedlings from each transect in each stand. We also tallied dead trees and seedlings in each plot, to determine if episodes of mortality appeared important in the overall expansion of the stands. Slow decomposition in this area appeared to preserve even very small (< 0.1 m height) dead seedlings.

For descriptive purposes, we measured the texture of the 0-50 mm depth soil (by the hydrometer method, Gee & Bauder, 1986).

We analyzed the age structures along the three transects at each of the five sites that showed apparent expansion. The age structure at the non-expanding Mosquito stand was examined separately. For the expanding sites we examined the mean tree age at each transect, and also the age of the oldest of the five trees in each plot. The mean establishment time of the entire stand at a given distance into the tundra, and the oldest age represents the initial time of tree establishment.

We used a two-way ANOVA to test for differences in average tree age and maximum tree age among transect positions (forest, forest/tundra, and tundra/forest). Transect was a fixed main effect because the orientation of the three transects was consistent across all stands. Stand was used as a random main effect. We used Tukey's HSD Multiple Comparison to determine which transects differed.

Results

Patterns of tree size and stand basal area (Table 1) supported our description of stand expansion as moving from a dense old stand through an increasingly sparse young stand in the ecotone. The transect effect (representing distance beyond the edge of the closed stand) was highly significant for both mean and maximum age ($p < 0.001$). The pattern was consistent across all five sites, as the average and maximum ages for each transect position did not differ among sites ($p > 0.2$). The mean age declined from 161 years at the edge of the forest, to 99 years at the forest/tundra ecotone, to 65 years in the tundra/forest end of the ecotone. The maximum tree age at the edge of the forest averaged 222 years, compared with 132 years at the forest/tundra area, and 103 years at the tundra/forest end of the ecotone. The maximum age at the forest edge was significantly older than in the ecotone areas which did not differ significantly from each other ($p = 0.2$). The living trees indicate that initial stand expansion occurred about 1770 at what is now the forest edge. It is possible that a forest was present on this site earlier, but no woody debris remains (in this cold, low decomposition environment) to support this possibility. The first trees were established beyond this edge in the period around 1860-1890. Increases in tree density over space and time corroborate the pattern of stand expansion at our sites (Figure 2).

The absence of older trees with distance along the ecotone into the tundra (Figure 2) resulted from recent invasion rather than recent death of old trees. In the forest, the number of dead stems in our plots averaged about 18% of the number of live trees, whereas no dead trees occurred in the tundra-forest plots. The numbers of dead seedlings equaled about 5% of the number of live seedlings across all transects. The high density (Figure 2) and low mortality of seedlings across forest-tundra and tundra-forest boundaries indicates that the present extent of our stands will likely persist and may expand in the future unless more severe climate conditions return.

Significant variance in age for the entire dataset was attributed to the transect x stand interaction and the among-plots-within-transect component ($p = 0.012$ and 0.001, respectively), which indicates a heterogenous distribution of age in the ecotone that was independent of distance towards the tundra. Whereas younger trees tended to occur farther towards the tundra at our sites, they also tended to occur in association with older trees (Figure 2). Payette & Filion (1985) termed the latter tendency a "contagious distribution," which, when significant, gives spatial dimension to the variance in an all-aged stand. Possible processes underlying the contagious distribution of ages in our stands are variable seed production, seed dispersal (Zasada, 1986), and shade

TABLE I. Descriptive measurements of expanding stands (means, with standard errors in parentheses)

Stand description	Fishgut North	Fishgut South	Pygmy Creek 1	Pygmy Creek 2	Aggie
Aspect (°)	240	50	180	180	150
Elevation (m)	100	100	160	170	130
Slope (%)					
Forest	10	5	15	15	33
Forest-tundra	5	5	10	15	5
Tundra-forest	5	5	5	15	5
Soil texture (0-50 mm) %sand/%silt/%clay					
Forest	17/72/11	62/27/11	14/68/18	14/68/18	43/49/8
Forest-tundra	28/60/12	24/63/13	7/70/23	15/71/14	35/54/11
Tundra-forest	*n*/a	13/71/16	25/68/7	28/57/15	3/78/19
Tree height (m)					
Forest	4.9 (0.5)	4.0 (0.3)	5.8 (0.7)	5.8 (0.7)	5.7 (0.4)
Forest-tundra	2.6 (1.3)	2.9 (0.3	3.9 (0.4)	3.3 (0.3)	3.4 (0.3)
Tundra-forest	1.4 (0.1)	1.2 (0.1	2.7 (0.2	2.7 (0.4)	1.1 (0.1)
Tree diameter (mm)					
Forest	91 (12)	67 (6)	105 (18)	105 (18)	95 (10)
Forest-tundra	29 (2)	37 (4)	53 (8)	38 (5)	49 (6)
Tundra-forest	0 (0)	0 (0)	25 (6)	29 (9)	0 (0)
Basal area (m^2/ha)					
Forest	8.1 (1.7)	4.1 (0.2)	18.9 (1.9)	18.9 (1.9)	23.4 (3.7)
Forest-tundra	0.9 (0.2)	0.8 (0.1)	2.5 (0.4)	1.3 (0.2)	2.4 (0.2)
Tundra-forest	0 (0)	0 (0)	0.7 (0.3)	0.3 (0.1)	0 (0)

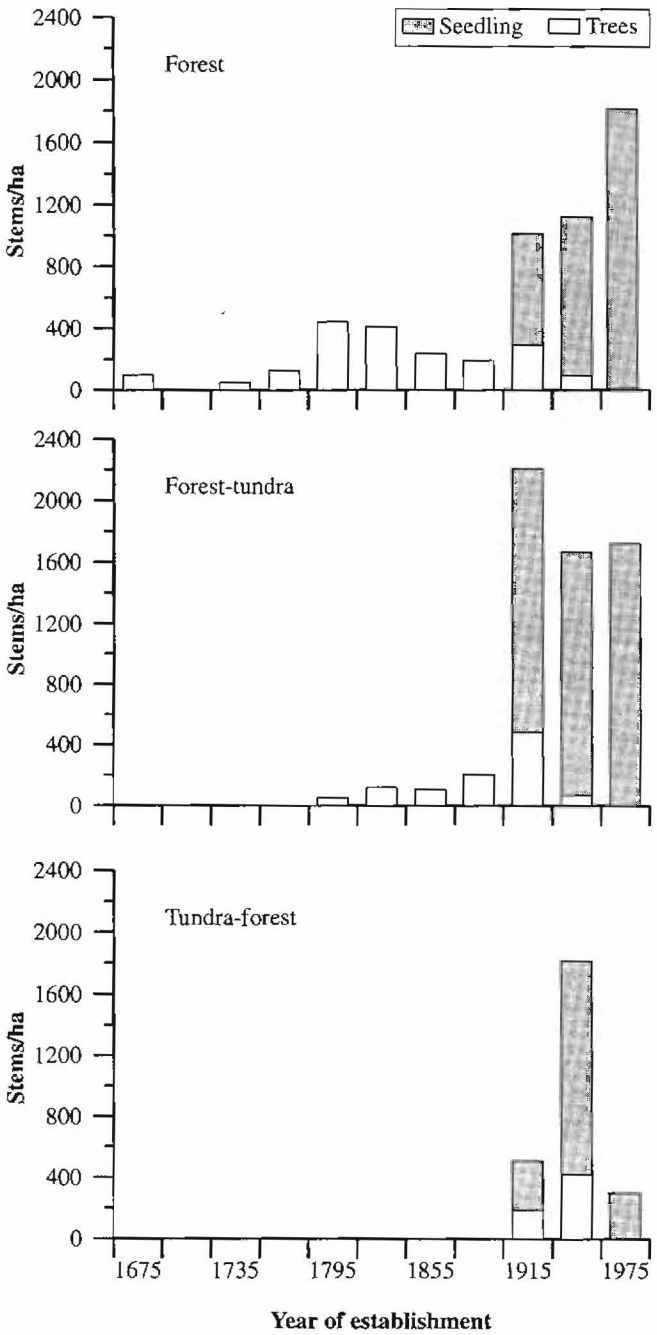

FIGURE 2. Density of trees by 30-year age classes across five expanding stands.

tolerance (Fowles, 1965) of white spruce, and the lack of disturbance at our sites. We found no consistent pattern of change in soil texture along the invasion sequence (Table I). Human impacts at our study area were absent, and we found no evidence of fire.

The unique, sharp boundary of the forest at the Mosquito stand involved old trees (mean age of about 90 years) at transect 2 (the stand boundary) and virtually no trees or seedlings in the adjacent tundra. Although soil texture did not change dramatically along the ecotone (% clay changed from 10% to 12%), the micromorphology of the upper soil changed abruptly across the stand boundary. Soil profiles in the forest and at the forest edge consisted of a friable, dark mineral soil, frozen at about 0.2 m depth. In the tundra, the soil consisted of about 0.20 m of saturated peat overlying a mottled, gray and tan mineral soil, frozen at a depth of about 0.05 m. The forest and forest edge locations also had small microtopographic variations including small areas (1 to 8 m^2) raised 0.2 to 0.5 m above the surrounding soil surface. The trees (and shrubs) established preferentially on these raised sites. This variation in microtopography of the soil surface stopped abruptly at the forest/tundra boundary. In cross-section, a vegetation mat covered the mound of mineral soil, and permafrost rose and fell with the convexity of the mound, maintaining a uniform depth from the surface.

The growth of trees in the forest (transect position 1) generally increased from 1800 onwards (we had too few cores for reliable trends prior to 1800), with notable negative trends in the early part of the twentieth century, and from 1950 into the 1970s (Figure 3). These broad trends are consistent with patterns from across northern Alaska and northwestern Canada (Jacoby, Cook & Ulan, 1985). The trends in tree growth and establishment were both positive over the period of 150 years. At a decadal scale, the proportion of trees in the tundra-forest ecotone (transect position 3) related moderately well to the growth index for trees in the forest (transect position 1, r^2 of 0.28, $p = 0.02$).

Forest expansion required roughly a century to move about 80 to 100 m from the edge of the forest to the farthest expanse of trees into the tundra. "Local advances" and a similar spatial and temporal scale were documented for white spruce near latitudinal treeline east of Hudson Bay (Payette & Filion, 1985), and for white spruce north of our study site at the Kelly and Kugururok Rivers (Rowland, 1996).

Discussion

Changes in latitudinal treeline have been slight over the past few centuries in Canada (Payette & Filion, 1985) and Alaska (Brubaker, Garfinkel & Edwards, 1983), but white spruce stands may have increased in density. Recruitment of white spruce near treeline increased dramatically at our sites (Figure 1), in the Brooks Range (Goldstein, 1981; Rowland, 1996), and across Canada (Payette & Filion, 1985; Scott, Hansell & Fayle, 1987; Szeicz & MacDonald, 1995). Tree encroachment into the tundra at our site included the initial establishment of a few trees and later increases in stand density as additional trees filled in among the original colonizers. Rowland (1996) also documented "in-filling" of existing spruce stands north of our locations on the north side of the Noatak River. This pattern of stand expansion is a small-scale version of the model described by MacDonald & Cwynar (1991): low densities are quickly established over a large area but later increases in density are patchy in both space and time.

In general, the relation of white spruce growth and warmer climate in the arctic is strongly positive (Jacoby, Cook & Ulan, 1985). However, precipitation has also been significantly correlated with white spruce growth in the Yukon (Jacoby & D'Arrigo, 1995) and in the Central Brooks Range (Garfinkel & Brubaker, 1980). Our sites actually showed increasing growth rates from 1970 onward, which is

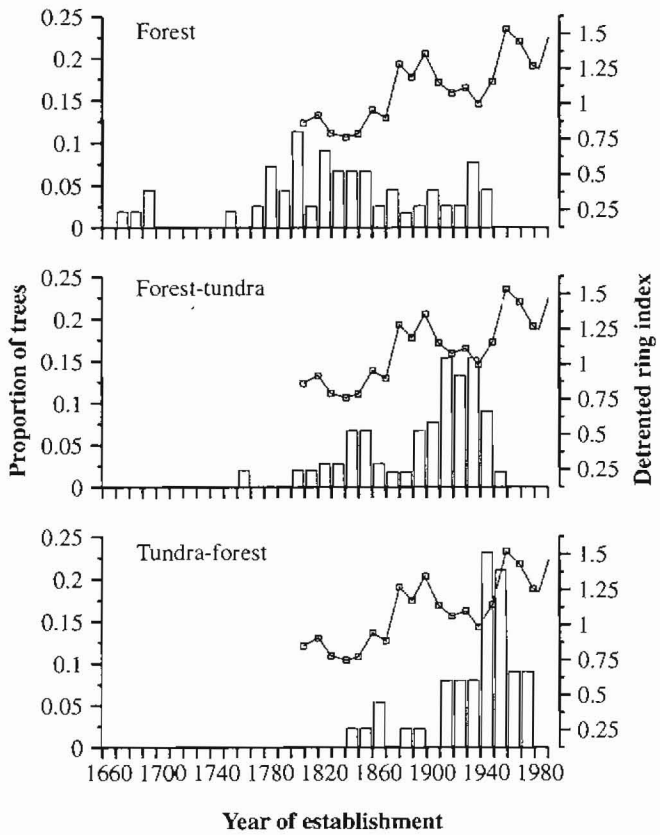

FIGURE 3. Relative frequency histograms with 10-year age classes across five expanding stands (45 sampled trees/stand), and detrended tree ring growth index (35 trees across all stands).

consistent with white spruce at some wet treeline sites (Jacoby & D'Arrigo, 1995). Continued warming may also prove beneficial for trees at some extreme sites, since white spruce seedlings have been recently observed above treeline at several locations in the Brooks Range (Cooper, 1986).

Stand expansion in our study largely represents relatively minor forest encroachment into vast areas dominated by tundra vegetation. Previous rates of encroachment may not be maintained into the core of tundra landscapes where conditions are less favorable for trees. Stand expansion has occurred in our study site on a limited portion of the landscape, where the landscape is characterized by moderate slope and poor (but not very poor) drainage. We expect that this topographic boundary may vacillate readily between tundra and forest. Forest expansion beyond this topographic boundary onto the broad expanses of tundra may require a substantially larger change in climatic conditions than that which has occurred in the past 150 years. Experimental studies by Hobbie & Chapin (1998) have documented that germination and establishment of white spruce seedlings in Alaska is favored by warming temperatures, reduced competition from other vegetation, and perhaps increased nutrient availability. More work is needed (such as that of Rowland, 1996) to document the gradient in environmental conditions across these ecotones (and into the tundra), and to document the extent of these gradients across the landscapes of northern Alaska.

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