

Vulnerability of white spruce tree growth in interior Alaska in response to climate variability: dendrochronological, demographic, and experimental perspectives¹

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Abstract: This paper integrates dendrochronological, demographic, and experimental perspectives to improve understanding of the response of white spruce (*Picea glauca* (Moench) Voss) tree growth to climatic variability in interior Alaska. The dendrochronological analyses indicate that climate warming has led to widespread declines in white spruce growth throughout interior Alaska that have become more prevalent during the 20th century. Similarly, demographic studies show that white spruce tree growth is substantially limited by soil moisture availability in both mid- and late-successional stands. Interannual variability in tree growth among stands within a landscape exhibits greater synchrony than does growth of trees that occupy different landscapes, which agrees with dendrochronological findings that the responses depend on landscape position and prevailing climate. In contrast, the results from 18 years of a summer moisture limitation experiment showed that growth in midsuccessional upland stands was unaffected by moisture limitation and that moisture limitation decreased white spruce growth in floodplain stands where it was expected that growth would be less vulnerable because of tree access to river water. Taken together, the evidence from the different perspectives analyzed in this study clearly indicates that white spruce tree growth in interior Alaska is vulnerable to the effects of warming on plant water balance.

Résumé : Cette étude intègre des perspectives dendrochronologique, démographique et expérimentale pour améliorer la compréhension des réactions de croissance de l'épinette blanche (*Picea glauca* (Moench) Voss) aux variations climatiques dans la partie intérieure de l'Alaska. Les analyses dendrochronologiques indiquent que le réchauffement climatique a entraîné le déclin de la croissance de l'épinette blanche partout dans la partie intérieure de l'Alaska, ce qui s'est accentué au cours du 20^e siècle. De même, les études démographiques montrent que la croissance de l'épinette blanche est substantiellement limitée par la disponibilité en eau du sol dans les peuplements de milieu et de fin de succession. La variation interannuelle de la croissance des arbres entre les peuplements d'un même territoire montre un synchronisme plus fort que celui de la croissance des arbres qui occupent des territoires différents, ce qui correspond aux résultats dendrochronologiques selon lesquels la réaction dépend de la position sur le territoire et du climat prédominant. À l'inverse, après 18 ans, les résultats d'une expérience visant à limiter la disponibilité estivale en eau montrent que la croissance de peuplements en milieu de succession et situés sur des hautes terres n'était pas influencée par la disponibilité en eau. Toutefois, la réduction de la disponibilité en eau diminuait la croissance de l'épinette blanche dans des peuplements situés sur des plaines inondables où nous anticipions une moins grande vulnérabilité parce que les arbres ont accès à l'eau des rivières. Globalement, les différentes perspectives analysées dans cette étude indiquent que la croissance de l'épinette blanche dans la partie intérieure de l'Alaska est vulnérable aux effets du réchauffement climatique par le biais du bilan hydrique des végétaux.

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Introduction

Over the past 50 years, mean annual temperature in Alaska has increased by 1.9 °C, with most of this warming

in the winter (3.5 °C) (Karl et al. 2009). The higher temperatures are already contributing to earlier spring snowmelt, later autumn freezeup, and permafrost warming throughout interior Alaska (ACIA 2004). Between 1970 and 2000, the

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snow-free season increased by approximately 10 days, primarily due to earlier snowmelt in the spring (Euskirchen et al. 2006, 2007). Summer water deficits have increased by 6.5 cm-decade⁻¹ in recent decades due to longer and warmer summers (0.5 °C-decade⁻¹; Oechel et al. 2000) and no change in precipitation (Hinzman et al. 2005).

While a longer warmer growing season has potential benefits for tree growth, there is a concern that increased water deficits in the summer could lead to declines in growth and cause widespread mortality of white spruce (*Picea glauca* (Moench) Voss) in interior Alaska (Juday et al. 2005). The projections for drastic declines in white spruce in interior Alaska are primarily based on dendrochronological studies showing that warming in interior Alaska during the 20th century has decreased the growth of white spruce because of warming-induced drought stress (Barber et al. 2000; Juday et al. 2005). Although white spruce tree growth appears to be sensitive to increasing summer water deficits, this response may vary according to landscape position (elevation, slope, aspect; uplands versus floodplains) and prevailing climate (Lloyd and Fastie 2002; Wilmking et al. 2004).

Ecosystem processes in interior Alaska are sensitive both to topographic variation in environment and to successional stage. Aboveground production, for example, which varies by more than an order of magnitude among forest types in interior Alaska (Van Cleve et al. 1983; Yarie and Van Cleve 2006), is greatest in midsuccessional stands on floodplains, where soil temperature and moisture are relatively high, and is constrained on south-facing slopes by drought and on north-facing slopes by soil temperature. Also, previous research in interior Alaska indicates that temperature constraints on tree production appear to be mediated largely by nitrogen supply, which varies substantially with topography (Yarie 1997; Yarie and Van Cleve 2006).

Vulnerability is the degree to which a system is likely to experience harm due to exposure and sensitivity to a specified hazard or stress and its adaptive capacity to respond to the stress (Turner et al. 2003). In this study, we evaluate the vulnerability of white spruce tree growth to continued warming in interior Alaska by synthesizing research of the Bonanza Creek Long Term Ecological Research (BNZ LTER) program, which has used several different approaches to understand the responses of white spruce tree growth to climatic variability. Dendrochronological approaches have documented decadal- to century-scale responses throughout interior Alaska (Barber et al. 2000; Lloyd and Fastie 2002; Wilmking et al. 2004). Long-term monitoring of climate, tree growth, and tree demography on permanent plots near Fairbanks, Alaska, have documented interannual to decadal-scale responses (Yarie and Van Cleve 2006). Finally, experimental manipulations of the environment on the long-term monitoring plots have documented decadal-scale responses and have allowed the study of underlying mechanisms responsible for the responses (Yarie 2008). Each of these approaches provides a unique perspective on the response of white spruce tree growth to climatic variability. In this paper, we compare the understanding developed from these perspectives with the goal of achieving a more synthetic understanding of the response of white spruce tree growth to climatic variability in interior Alaska.

Methods

Dendrochronology methods

We synthesized previously published analyses of white spruce growth–climate relationships from 25 sites around interior Alaska (Table 1) (Barber et al. 2000; Lloyd and Fastie 2002; Wilmking et al. 2004; Wilmking and Juday 2005; Lloyd and Bunn 2007). A minimum of 20 trees was sampled at each site. At all but one site (Barber et al. 2000), tree ring widths were detrended conservatively using a negative exponential curve or line of horizontal or negative slope to remove age-related growth trends. Ring widths were then compared with monthly climate data from Fairbanks, Alaska, or with the spatially interpolated Climate Research Unit data for the 0.5° × 0.5° grid cell within which the site was located (Climate Research Unit, CRU TS 2.10, available from www.cru.uea.ac.uk). Because conifers often exhibit lagged responses to climate, most studies used a climate window extending from the growing season of the prior year through the current growing season. Further details of analytical methods are provided in the original publications.

For this synthesis, we classified the response of growth at each site into one of three categories: positive (most correlations with temperature were positive), negative (most correlations with temperature were negative), or mixed (correlations with temperature were both positive and negative). In cases where climate responses were reported for multiple time periods, we used the last 50 years to classify climate response. Wilmking et al. (2004) and Wilmking and Juday (2005) analyzed climate response for individual trees, so for those sites, we classified the response of the entire site based on the most prevalent response among individual trees (e.g., a site with >50% of trees showing a positive response would be classified as positive). To test the hypothesis that negative responses to temperature were more prevalent in drier regions, we compared the mean annual precipitation (1902–2002, CRU TS 2.10) of sites with primarily positive responses to temperature and sites with primarily negative responses to temperature.

Demographic methods

Aboveground net primary productivity (ANPP) of white spruce was measured on long-term monitoring plots established by the BNZ LTER in the late 1980s to represent a chronosequence of forest development following sandbar formation in floodplain landscapes (primary succession) and fire in upland landscapes (secondary succession). Here, we present data from mid- and late-successional floodplain and upland stands over a 15-year period from 1993 to 2008. Midsuccessional floodplain stands (FPmid) are a mix of mature white spruce and balsam poplar (*Populus balsamifera* L.), while midsuccessional upland stands (UPmid) are a mix of white spruce, trembling aspen (*Populus tremuloides* Michx.), and Alaska paper birch (*Betula neoalaskana* Sarg.). Late-successional floodplain (FPlate) and upland (UPlate) stands are dominated by white spruce. Stands are replicated ($n = 3$ per successional stage) and plots range in size from 1200 to 3000 m². More detailed information concerning soil and vegetation characteristics of these stands can be found at <http://www.lter.uaf.edu/>.

Table 1. Response of white spruce (*Picea glauca*) ring widths to temperature and precipitation.

Region	Site	Latitude (°N)	Longitude (°W)	Temperature response	Months with significant correlations with temperature	Months with significant correlations with precipitation
Brooks Range	BRKG	68	161.5	Positive	February–July (+), prior July (–)	Not reported
Brooks Range	BRHF	67.8	152.4	Negative	Prior July (–), February–July (+)	
Brooks Range	BRCL	67.7	150.5	Positive	February–July (+), prior July (–)	
Brooks Range	BRNF	67.9	150.5	Negative	Prior July (–), February–July (+)	
Brooks Range	BRNC	67.9	149.8	Negative	Prior July (–), February–July (+)	
Brooks Range	BRSJ	68.5	143.8	Negative	Prior July (–), February–July (+)	
Brooks Range	BRFR	68.6	141.6	Negative	Prior July (–), February–July (+)	
Alaska Range	ARCC	63.6	150	Negative	Prior July (–), spring (+)	
Alaska Range	ARTL	63.4	149.2	Negative	Prior July (–), spring (+)	
Alaska Range	ARRC	63.7	149	Negative	Prior July (–), spring (+)	
Alaska Range	ARSC	63.5	148.8	Negative	Prior July (–), spring (+)	
Alaska Range	ARBC	63.4	146.4	Negative	Prior July (–), spring (+)	
Alaska Range	ARTK	63.3	143.3	Negative	Prior July (–), spring (+)	
Alaska Range	Usibelli	63.9	148.67	Mixed	Prior July (–), prior May (+)	None
Alaska Range	Canyon Creek	63.25	147.783	Positive	June, July (+)	Prior August and November (–)
Alaska Range	Monahan Flats	63.26	147.92	Positive	June, July (+)	None
Seward Peninsula	Bank	64.82	163.7	Negative	Prior July, current June (–)	April (+)
Seward Peninsula	Grasshopper Hill	64.92	163.67	Negative	Prior July, current June (–)	April (+)
White Mountains	Eagle Summit	65.5	145.33	Positive	Prior July (+)	None
White Mountains	Eagle Summit	65.5	145.33	Negative	Prior July (–)	August–September (+)
White Mountains	Twelvemile Summit	65.37	145.93	Negative	Prior July (–)	August–September (+)
White Mountains	Twelvemile Summit	65.37	145.93	Negative	Prior July (–), prior spring (–)	April (+)
White Mountains	Nome Creek	65.37	146.62	Negative	Prior April (–), June(–), July (–)	April (+)
White Mountains	Nome Creek	65.37	146.62	Negative	Prior April (–), June(–), July (–)	April (+)
Interior Alaska	BNZ and others	64.8	148	Negative	Prior/current May (–), July (–), August (–)	Growing season (+)

Note: Brooks Range sites are from Wilmking et al. (2005). Alaska Range sites are from Wilmking et al. (2004) (ARCC–ARTK) and Lloyd and Fastie (2002) (Usibelli, Canyon Creek, and Monahan Flats). White Mountains sites were originally published in Lloyd and Fastie (2002) and were reanalyzed in Lloyd and Bunn (2007). Interior Alaska sites are from Barber et al. (2000). Temperature response indicates the primary response to temperature at that site: positive (tree growth is positively correlated with temperature), negative (tree growth is negatively correlated with temperature), or mixed (tree growth responds positively to some months/seasons and negatively to others). Months in which tree growth was significantly correlated with temperature and precipitation are shown in the rightmost columns. The sign of the correlation is indicated parenthetically. At Wilmking's sites, positive and negative responding subpopulations were present within each site; the response of each is indicated with – (negative responders) or + (positive responders).

At the beginning of the study, all trees >2.5 cm diameter at breast height (DBH) (1.37 m above the ground surface) were individually marked and DBH of all trees was remeasured every 3–4 years. Basal area (square metres per hectare) and density (trees per hectare) were calculated for each inventory date and a subset of trees from each plot was cored (at DBH) in 1993 to determine the age of diameter cohorts. It is important to recognize that the age of a tree at breast height is generally 10 or more years younger than the actual age of the tree. DBH was converted to biomass following equations established by Yarie et al. (2007) and ANPP of individual trees was computed as the incremental change in biomass between inventory dates. Average ANPP over the 15-year growth period was computed as the average of the four growth intervals (1993–1997, 1997–2000, 2000–2004, and 2004–2008) at the tree (kilograms biomass per tree per year for both size and age cohorts) and stand (kilograms biomass per hectare per year) levels. In midsuccessional stands, it is important to note that the estimate of white spruce ANPP at the stand level underestimates total stand tree production because white spruce constitutes less than half the stand basal area in these mixed stands.

To assess the sensitivity of individual tree growth to inter-annual climate variability, 10 trees across the range of diameter size classes within each plot were fitted with band dendrometers (0.3 mm × 12 mm) equipped with a vernier scale (Bormann and Kozlowski 1962), which were read annually in the fall. Changes in diameter were translated to ANPP as described above and related to current and previous year's climate using standard multiple regression methods (SAS Institute Inc. 2009). Monthly air and soil temperature data and precipitation data were obtained from the BNZ LTER climate monitoring program (www.lter.uaf.edu/data_b.cfm) and Tanana River gauge height data were obtained from waterdata.usgs.gov/ak/nwis/uv?15485500. The number of growing degree-days was determined by summing mean daily air temperatures >5 °C (determined from hourly data) over the summer months (June, July, and August). Palmer drought severity index (PDSI) data were obtained from greenleaf.unl.edu/greenleaf_project/faces/user/.

Moisture limitation experimental methods

The moisture limitation study was implemented at replicated upland and floodplain midsuccessional plots (UPmid and FPmid) by erecting a roof (10 m × 15 m) under the canopy to prevent summer rainfall recharging soil water during the growing season. Details of the cover design can be found in Yarie (2008). Plastic sheeting was installed vertically to a soil depth of 75 cm to prevent belowground lateral flow and root growth into and out of the plots. Ground water recharge from the water table was not a factor on the upland sites; however, on the floodplain, ground water was hypothesized to play a major role in tree moisture dynamics (Viereck et al. 1993). Daily precipitation was measured at climate stations within both upland and floodplain landscapes. Beginning in 1993, mineral soil moisture was measured by placing TDR probes horizontally at 5, 10, 20, and 50 cm below the organic matter – mineral soil interface at two locations within each plot. A combination of continuous recording, at one replicate site, and weekly readings from a

pair of sites in each landscape location was used to document soil moisture dynamics during the frost-free season.

A set of four ground water wells was used for weekly measurements of the depth to ground water (± 1 cm) on the FPmid sites. The surface elevation of the Tanana River was monitored at a downstream location from the FPmid sites. Ground water was not monitored in the upland site because it was well below the rooting zone and of no consequence to upland soil moisture relationships.

Measurement of tree growth on a selected set of white spruce trees across the diameter range on the plot was attained using dendrometer bands read on an annual basis at the end of the growing season. Periodic diameter measurements of all trees on each plot were also carried out in 1989, 1993, 1998, 2003, and 2008 using DBH tapes. A more detailed description of the experimental methods can be found in Yarie (2008).

The SAS MIXED procedure was used with a repeated ANOVA to calculate significant differences in the mean basal area growth using an estimate with an error type of AR(1) across individual species in each landscape location (floodplain or upland). The two data sets used were the annual dendrometer band readings on a subset of trees within each plot and the periodic 5-year measurement of all trees <5 cm DBH.

Results

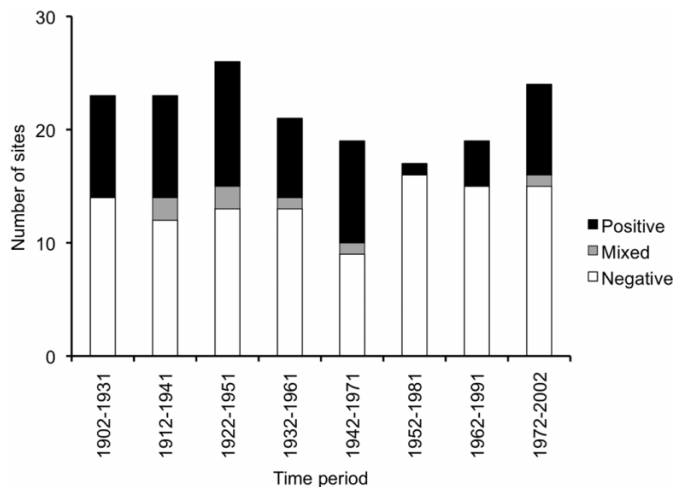
Dendrochronology results

Negative responses to temperature prevailed in all regions of Alaska (Table 1). Only five sites showed consistently positive responses to temperature: two in the western part of the Brooks Range, two in the southern Alaska Range, and one at the treeline in the White Mountains of interior Alaska. Growth at one site exhibited a mixed response to temperature, while the predominant response to temperature at the remaining 19 sites was negative. Contrary to our expectations, there was no significant difference ($t = -0.181$, $P = 0.858$, $df = 17$) in the annual precipitation of sites with a positive response (251 ± 44.4 mm·year⁻¹, $n = 5$ sites) and those with a negative response (242 ± 22.9 mm·year⁻¹, $n = 19$ sites). Tree growth studies supported a role for moisture limitations on tree growth as well. Tree growth was significantly correlated with precipitation at 12 of the study sites and growth was positively correlated with precipitation at all of the sites at which trees exhibited a negative response to temperature.

The seasonal pattern of response to temperature and, to a lesser extent, precipitation was strikingly consistent among sites. Growth at negatively responding sites was consistently highly correlated (negatively) with summer (specifically July) temperatures in the year prior to the growing season. Positive responses to temperature were more varied, with tree growth responding positively to prior summer, current spring, and current summer conditions. Tree growth was correlated with precipitation in the summer (interior Alaska; Barber et al. 2000) or in the spring and (or) late summer (Table 1).

Although climate response of each site was stable over time at lowland sites (Barber et al. 2000), climate response at other sites was highly variable over time (Fig. 1). Sites at

Fig. 1. Number of white spruce (*Picea glauca*) sites in Alaska (expanded data set, total $n = 41$; see Lloyd and Bunn (2007) for details) exhibiting three different responses to mean, minimum, and annual monthly temperature from April of year $t - 1$ through October of year t : positive (greater than two thirds of significant correlations with temperature are positive), negative (greater than two thirds of significant correlations with temperature are negative), and mixed (one third to two thirds of significant correlations are positive). Sites in which growth was not significantly related to temperature are not shown on this figure. Figure modified from Lloyd and Bunn (2007).



which growth responded negatively to warming were more prevalent in the latter part of the 1900s than in the earlier part of the 1900s. These changes in response over time suggest that, particularly for treeline sites (which make up the vast majority of sites in the expanded data set shown in Fig. 1), the role of temperature as a limiting factor has changed in recent decades.

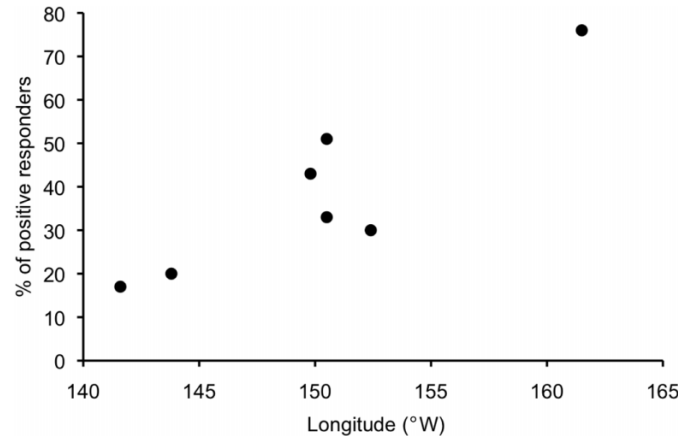
There is mounting evidence that climate response is variable within populations as well as among sites and over time. Wilmking et al. (2004, 2005) presented climate responses of individual trees and found that populations contained distinct subgroups that exhibited different climate response. Although both response types were present at all sites, the prevalence of negatively responding trees was significantly greater in warmer drier sites than in cooler moist sites (Fig. 2).

Demographic results

Stand structure and ANPP

Averaged across years and stand replicates, density of white spruce trees was greater in midsuccessional (1158 ± 271 trees·ha⁻¹) compared with late-successional stands (362 ± 13 trees·ha⁻¹) ($P < 0.01$), while basal area showed the opposite trend (10.8 ± 1.5 and 27.2 ± 0.6 m²·ha⁻¹, respectively) ($P < 0.001$). In late-successional stands, white spruce trees within a given size class were growing at statistically similar rates in floodplain and upland stands (Figs. 3c and 3d). However, when comparing growth of trees between successional stages, most size cohorts <30 cm diameter grew significantly faster in midsuccessional stands compared with late-successional stands. Examining average growth rate of

Fig. 2. The frequency of white spruce (*Picea glauca*) trees responding positively to temperature is significantly correlated with longitude ($r = 0.903$, $P = 0.005$). Precipitation rises along the longitudinal gradient from a low of 117 mm·year⁻¹ at the eastern end to a high of 257 mm·year⁻¹ at the western end. Data are from Wilmking et al. (2005).



known-age trees across successional stages and landscapes by age cohorts over the past 15 years confirms that midsuccessional trees of a given diameter size are substantially younger and growing much faster than late-successional trees of similar diameter sizes (Fig. 4). The inverse relationship between DBH and age and between growth and age (Fig. 4) for midsuccessional floodplain stands can be seen late in succession where younger trees are often larger in diameter than older trees. At the stand level, white spruce production was similar in midsuccessional (1769 ± 540 kg biomass·ha⁻¹·year⁻¹) and late-successional stands (1694 ± 107 kg biomass·ha⁻¹·year⁻¹), varying significantly between landscapes within midsuccessional but not within late-successional stands (Table 2).

Interannual variation in stand structure, tree growth, and stand-level ANPP

During the 1993–2008 growth period, late-successional upland and floodplain stands lost similar numbers of white spruce trees (–16% and –17%, respectively), mostly through net mortality (self-thinning) of the three intermediate diameter classes (10–20, 20–30, and 30–40 cm diameter) between 1993 and 1997. White spruce tree mortality translated to overall declines in basal area of 3.4% and 1.8% in late-successional floodplain and upland stands, respectively.

White spruce tree density declines in midsuccessional floodplain stands (–15%) over the 15-year period were due solely to net reductions in the numbers of 0–10 cm diameter trees, as net recruitment into all other existing size classes occurred. Approximately half of the 32% net decline in 0–10 cm diameter trees could be accounted for by recruitment into larger diameter size classes. White spruce density increased in midsuccessional upland stands from 1993 to 2008 (+56%) and nearly all of the net decline in 0–10 cm diameter trees (–26%) could be accounted for by net recruitment into larger size classes that accounted for 41% and 180% increases in basal area for floodplain and upland midsuccessional stands, respectively, over the growth period.

Fig. 3. Stand structure (density and basal area) and ANPP (expressed on a tree and stand basis) of white spruce (*Picea glauca*) growing in (a and c) floodplain and (b and d) upland late-successional stands grouped by DBH size classes (0 = 0–10 cm, 1 = 11–20 cm, 3 = 21–30 cm, 4 = 31–40, 5 = 51–60 cm, 6 = 61–70, and 7 = 71–80 cm diameter). Data are means ± SE from BNZ LTER inventory plots (n = 3 per landscape) remeasured every 3–4 years between 1993 and 2008.

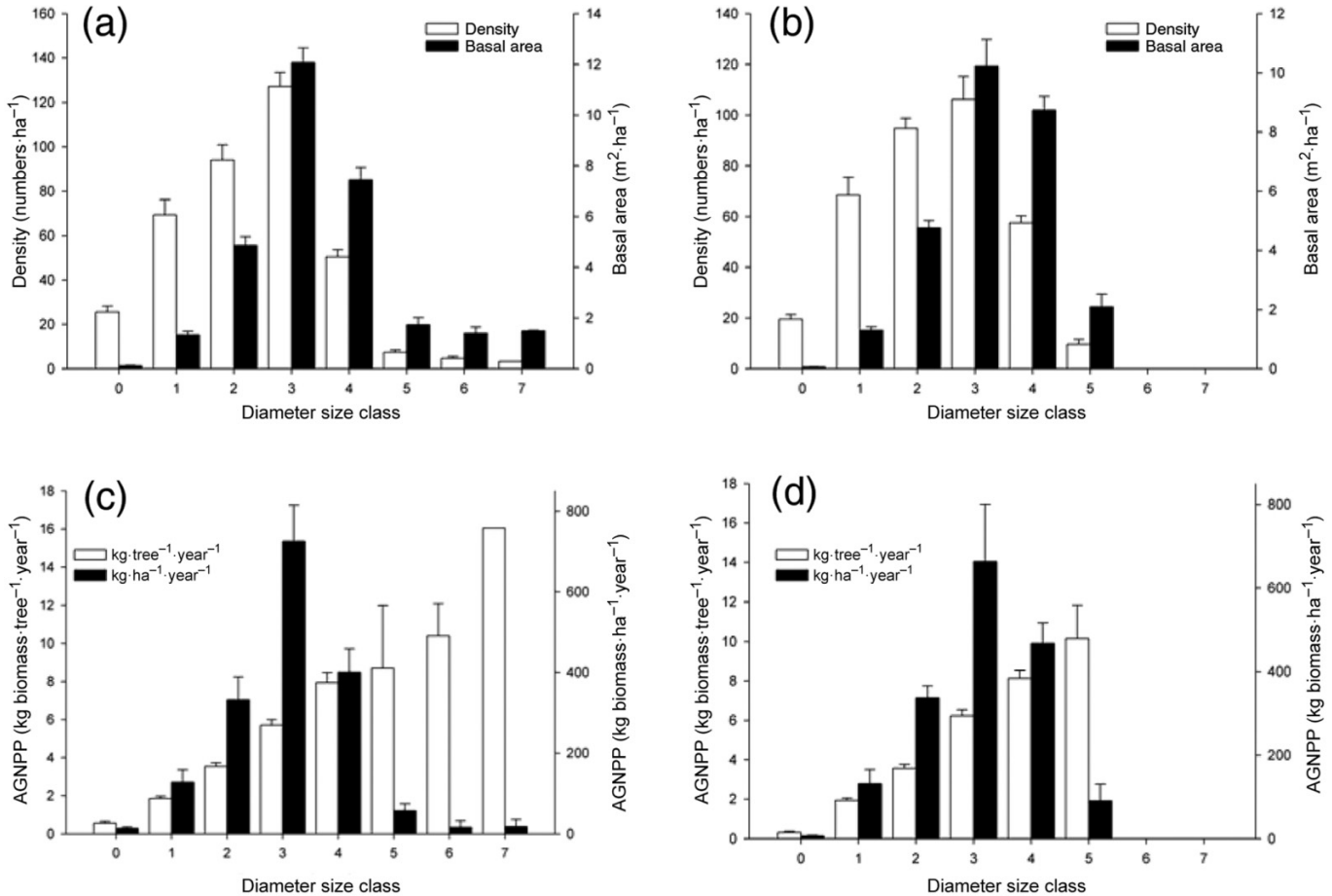
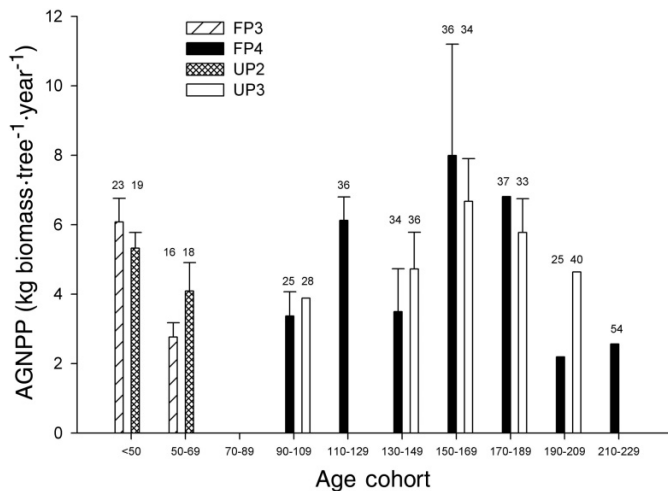


Fig. 4. ANPP of known-aged white spruce (*Picea glauca*) trees from BNZ LTER inventory plots growing in mid- and late-successional floodplain (FP3 and FP4, respectively) and upland stands (UP2 and UP3, respectively) averaged (mean ± SE) by age cohorts. Data are from stand inventories of all trees measured every 3–4 years between 1993 and 2008. Numbers above bars correspond to average diameters (DBH) of a given age cohort.



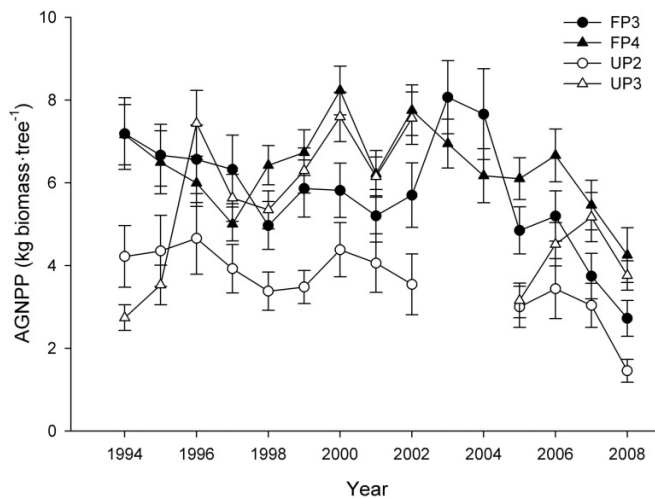
Coefficients of variation in average white spruce tree production over the 15-year measurement period ranged from 16% for late-successional floodplain trees to 32% for late-successional upland trees and were intermediate for midsuccessional floodplain and upland trees (25% and 23%, respectively) (Fig. 5). Average rates of tree growth were positively correlated among replicate stands across years for mid- and late-successional floodplain stands (average r^2 across three stands = 0.47 and 0.34, respectively) and for mid- and late-successional upland stands ($r^2 = 0.41$ and 0.61, respectively). When averaged across replicate stands within a stand type, rates of tree growth were strongly correlated for upland and floodplain midsuccessional stands among years ($r^2 = 0.77$, $P < 0.0001$) but not for late-successional stands between the two landscapes ($r^2 = 0.05$, not significant). Moreover, inter-annual patterns of average tree growth were not correlated between mid- and late-successional upland stands ($r^2 = 0.05$, not significant) and only marginally correlated between mid- and late-successional floodplain stands ($r^2 = 0.17$, $P = 0.07$).

Because all diameter classes of trees were not represented in our band dendrometer data set, we were only able to estimate annual rates of the white spruce component of stand-level ANPP for late-successional stands. These estimates are restricted to five diameter classes of trees (10–60 cm di-

Table 2. Density, basal area, and ANPP of white spruce (*Picea glauca*) growing in mid- and late-successional upland and floodplain forests.

Stand	Density (numbers·ha ⁻¹)	Basal area (m ² ·ha ⁻¹)	ANPP (kg biomass·ha ⁻¹ ·year ⁻¹)
Upland			
Midsuccessional	576±93b	3.6±0.6c	842±338
Late successional	354±22b	26.8±0.8a	1696±144
Floodplain			
Midsuccessional	1684±503a	17.6±1.6b	2696±694
Late successional	370±21b	27.7±1.0a	1692±191

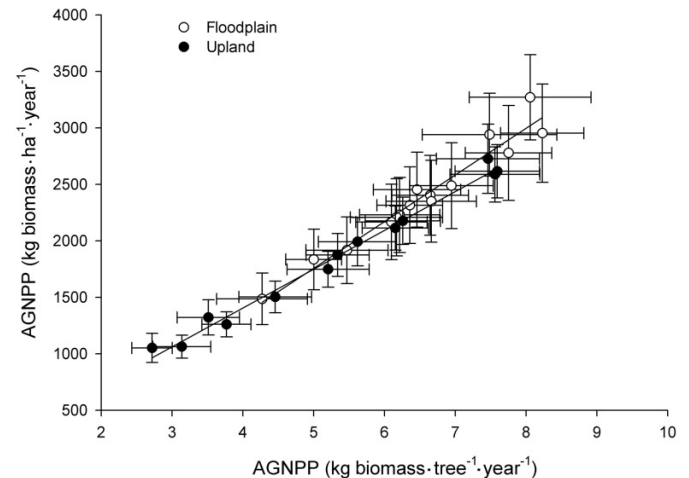
Note: Data averaged (mean ± SE) across four consecutive periods between 1993 and 2008. The letters a, b, and c indicate significant differences among stand types within a column.

Fig. 5. ANPP of white spruce (*Picea glauca*) trees determined from band dendrometers from BNZ LTER inventory plots in mid- and late-successional floodplain (FP3 and FP4, respectively) and upland stands (UP2 and UP3, respectively). Data are means ± SE across all banded trees and replicate stands within a given successional stage and landscape.

ameter), which constitute approximately 98% of ANPP as indicated by the inventory data (data not shown). Analyses show that variation in the white spruce component of stand-level ANPP over the 15-year period was controlled primarily by interannual variation in individual tree growth rather than changes in stand demography (Fig. 6).

Climate sensitivity of white spruce ANPP

Climate parameters explained, on average, 40%, 65%, 77%, and 84% of the interannual variation in ANPP (kilograms biomass per tree per year) using one-, two-, three-, and four-factor stepwise linear regression models, respectively (Table 3). Given that the additional variation explained in the three- and four-factor models is minimal compared with the variation explained by the one- and two-factor models, we primarily focus on the results of the one- and two-factor models. Negative relationships to June soil temperature were found in late-successional forests but not in midsuccessional forests. This suggests that white spruce tree ANPP is limited by soil moisture conditions, given that soil moisture and temperature during May, June, and July

Fig. 6. Relationship between stand-level and tree-level ANPP for white spruce (*Picea glauca*) growing in late-successional upland ($r^2 = 0.99$, $P < 0.0001$) and floodplain stands ($r^2 = 0.93$, $P < 0.0001$). Tree-level ANPP was calculated from biomass changes derived from band dendrometers, and multiplied by annual density data from inventory plots to estimate stand-level production. Data points represent means ± SE calculated across three replicate BNZ LTER inventory plots for each year between 1993 and 2008. Upland stand data for 2003–2004 are missing and not included in the figure.

tended to be negatively correlated for all stand types (data not shown). Gauge height of the Tanana River was an important predictor of ANPP for both floodplain stands and upland stands, suggesting that it is a useful climate index beyond the role of providing hyporheic water to floodplain vegetation (Nossov 2008). Interestingly, June gauge height entered as the most important variable in the one-factor model for the late-successional floodplain stands but did not enter until the two-factor model for the midsuccessional floodplain stands, suggesting that the ANPP in late-successional floodplain stands is more tightly coupled to hyporheic water. ANPP in the midsuccessional floodplain stands was positively related to the previous year's August PDSI in the one-factor model, which suggests that late-summer drought of the previous year has an important effect on wood production in the current year for this stand type. In contrast, ANPP values in the upland midsuccessional stands were most sensitive to the current year's July precipitation, which suggests that the current year's drought sensitivity affects production. Alternatively, light availability may limit growth in these stands in years with rainy July climate.

Table 3. Results from stepwise multiple linear regression models predicting white spruce (*Picea glauca*) ANPP (kg biomass-tree⁻¹·year⁻¹) from the current and previous year's climate variables listing parameters, regression coefficients, and *r*² values for best one-, two-, three-, and four-factor models (**P* < 0.05, ***P* < 0.01, and****P* < 0.001) for trees growing in floodplain midsuccessional (FPmid), floodplain late-successional (FPlate), upland midsuccessional (UPmid), and upland late-successional (UPlate) stands.

	One-factor model	Two-factor model	Three-factor model	Four-factor model
FPmid	+0.119 × PREVPDSIAUG	+0.118 × PREVPDSIAUG +0.793 × RIVERJUL	+0.103 × PREVPDSIAUG +0.870 × RIVERJUL +0.063 × PREVAIRSPRING	+0.079 × PREVPDSIAUG +0.672 × RIVERJUL +0.078 × PREVAIRSPRING −0.097 × PREVSOILJUL
Intercept	1.640	−3.833	−4.428	−1.774
<i>r</i> ²	0.26*	0.46*	0.58*	0.67**
FPlate	+0.563 × RIVERJUN	+0.840 × RIVERJUN −0.096 × SOILTEMPJUN	+0.883 × RIVERJUN −0.091 × SOILTEMPJUN +0.232 × PREVRIVERMAY	+0.904 × RIVERJUN −0.064 × SOILTEMPJUN 0.028 × PREVPDSIAUG −0.001 × GDD
Intercept	−1.937	−2.701	−4.366	−2.055
<i>r</i> ²	0.38*	0.70***	0.81***	0.87***
UPmid	−0.007 × PPTJUL	−0.007 × PPTJUL +0.376 × RIVERJUN	+0.273 × PDSIJUN −0.330 × PDSIJUL +0.419 × PREVRIVERJUN	+0.380 × PDSIJUN −0.439 × PDSIJUL +0.563 × PREVRIVERJUN −0.043 × PREVAIRSPRING
Intercept	1.358	−0.992	−1.824	−2.704
<i>r</i> ²	0.43**	0.66**	0.83**	0.94***
UPlate	−0.115 × SOILTEMPMAY	−0.292 × SOILTEMPJUN +1.239 × RIVERJUL	−0.301 × SOILTEMPJUN +1.211 × RIVERJUL −0.061 × PREVAIRSPRING	−0.230 × SOILTEMPJUN −0.064 × SOILTEMPMAY +1.170 × RIVERJUL −0.053 × PREVAIRSPRING
Intercept	1.830	−4.218	−3.888	−4.079
<i>r</i> ²	0.54**	0.76***	0.85***	0.88***

Note: Current year's climate: GDD, growing degree-days; PDSIJUN and PDSIJUL, PDSI June and July; PPTJUL, July precipitation (mm); RIVERJUN and RIVERJUL, Tanana River gauge height (ft) for June and July; SOILTEMPMAY and SOILTEMPJUN, average soil temperature (°C at 5 cm depth) for May and June. Previous year's climate: PREVAIRSPRING, average air temperatures for previous April and May; PREVPDSIAUG, previous PDSI August; PREVRIVERMAY and PREVRIVERJUN, Tanana River gauge height (ft) for previous May and June; PREVSOILJUL, average soil temperature (°C at 5 cm depth) for previous July.

Experimental results

The hypothesis that launched the moisture limitation study was that within an area experiencing a similar temperature regime, summer rainfall is the primary environmental factor controlling growth of upland forests, while forest growth on the floodplain is controlled by a combination of growing season river levels through their effect on soil water supply from shallow ground water and seasonal precipitation. In contrast with the hypothesis, the results from 18 years of the summer moisture limitation experiment showed that white spruce growth in midsuccessional upland stands was unaffected by moisture limitation and that moisture limitation decreased white spruce growth in floodplain stands. Based on results from 18 years of the summer moisture limitation study, reverse trends were found in midsuccessional upland and floodplain stands. In comparison with control plots, white spruce trees in midsuccessional upland stands showed no change in basal area growth resulting from summer throughfall limitation (Fig. 7). In contrast, the growth of midsuccessional floodplain white spruce trees was significantly reduced by summer throughfall limitation (Fig. 7).

Discussion

Dendrochronology perspective

According to the dendrochronological analysis, negative relationships between growth and warming prevail at the vast majority of sites in Alaska, including both warm, dry sites in the interior (Barber et al. 2000) and relatively cool treeline locations in three mountain ranges (Brooks Range: Wilmking and Juday 2005; Alaska Range: Lloyd and Fastie 2002; Wilmking et al. 2004; White Mountains: Lloyd and Fastie 2002). This finding is consistent with the expectation that an increase in temperature may, in the absence of a simultaneous increase in moisture, change effective moisture availability and increase physiological drought stress. At sites in interior Alaska, the negative relationship between growth and temperature has prevailed consistently throughout the period covered by the instrumental record. At many treeline locations, however, negative responses to temperature are more recent in origin. At these sites, temperature, perhaps exacerbated by increasing moisture deficits, has exceeded some negative sensitivity threshold in recent decades.

Although there is no consistent relationship between the precipitation received at a site and the temperature response of trees growing there, several lines of evidence point to temperature-induced drought stress as a likely cause of negative correlations between growth and climate. First, sites with positive responses to temperature are most prevalent in the cooler, moister regions; 80% of the sites with positive responses to temperature were found in the coolest, moistest regions of two major mountain ranges (Brooks Range and Alaska Range). Second, Wilmking and Juday (2005) have shown that the prevalence of positively responding trees within a population is positively correlated with precipitation of the site, suggesting that variation in water balance within a region is a predictor of negative responses to temperature, despite the absence of a relationship across regions. Third, for those sites for which correlations with both

temperature and precipitation were reported, sites that responded negatively to temperature universally exhibited positive growth responses to precipitation. It thus seems likely that NPP of white spruce stands has the potential to be moisture limited at a wide range of sites, including both warm, dry sites in interior Alaska and comparatively cool and moist treeline sites.

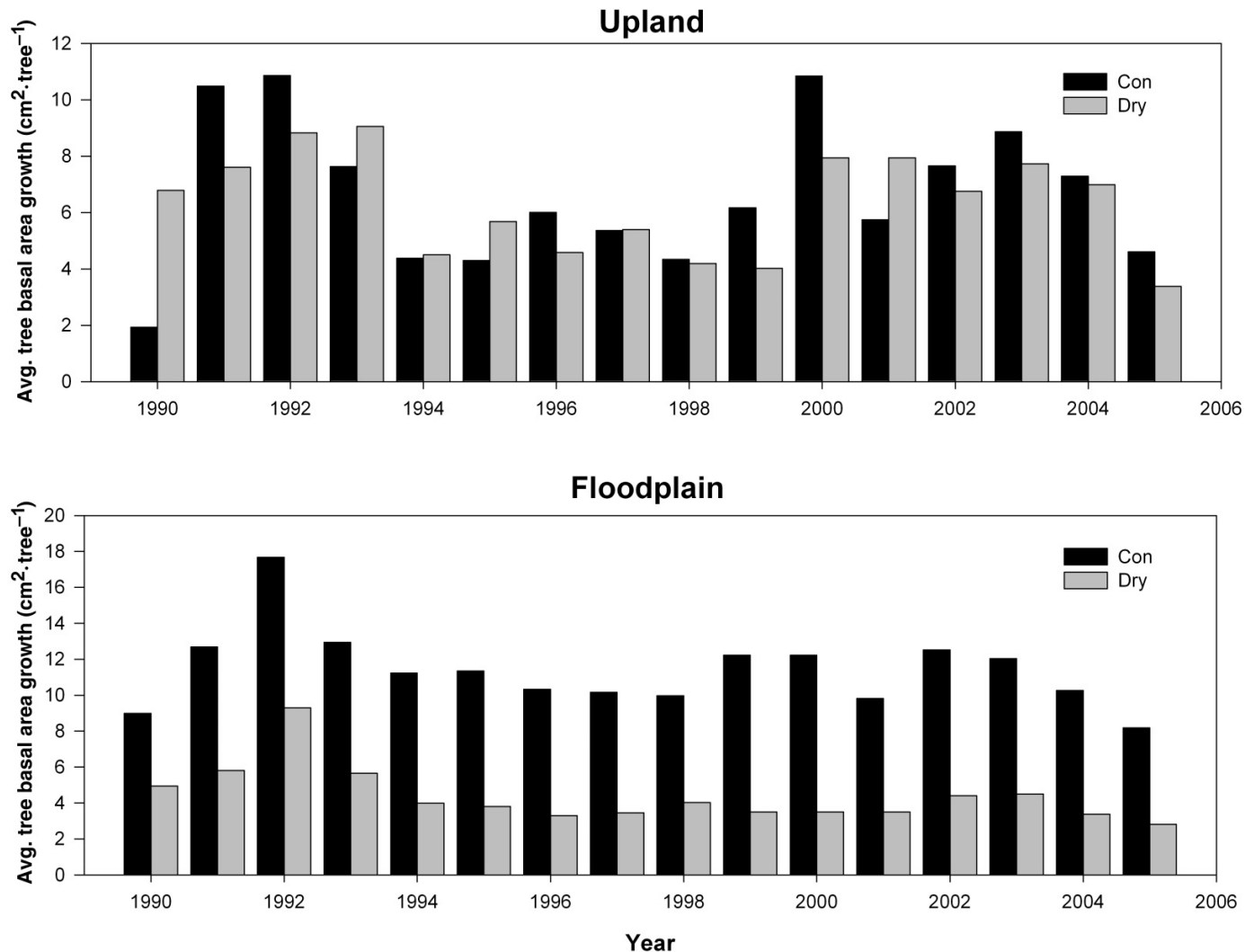
The variability in climate response over time suggests that nonlinear, threshold responses to climate are likely in the boreal forest. Although climate response is consistent over time at stands in the warm and dry interior of Alaska, climate response varied over time at all other locations reported here. Efforts to extrapolate NPP into the future should therefore take into account the likelihood for responses to be nonlinear over even fairly small ranges of temperature.

Demographic perspective

In assessing the climatic sensitivity of white spruce stand-level production, it is important to determine the degree to which responses of stand-level production are associated with tree productivity versus changes in stand demography as the stand continues to grow. We had predicted that in late succession, a progressive increase in mortality of older trees would prevent the detection of climate sensitivity in white spruce ANPP at the stand level, despite an acute sensitivity of individual trees to interannual variation in climate drivers. Our analysis indicated that mortality in late-successional stands was 16%–17% over a 15-year period and was concentrated in intermediate diameter classes, which we interpret as the “self-thinning” phenomenon often observed in maturing forests. Nevertheless, the strong relationship between white spruce stand-level and tree ANPP indicates that growth sensitivity rather than stand demographics is driving stand-level ANPP in these late-successional floodplain and upland stands. Both tree-level and stand-level ANPP are greater for white spruce growing in midsuccessional stands compared with late-successional stands. In midsuccessional stands, younger trees are both bigger and growing faster than older trees and are likely contributing more to stand-level production. In late-successional stands, intermediate size classes are most abundant and contribute the most to stand-level ANPP; however, tree ages of this size cohort may vary by up to 100 years. Tree growth increases linearly with diameter in both mid- and late-successional stands, but data from a limited set of known-aged trees indicate that growth declines in trees >170 years old. We were not able to statistically establish this linkage between stand and tree production for midsuccessional stands because of sample size issues, but the relationship is strong because no mortality was detected for intermediate- to larger-sized trees. Thus, although recruitment history plays a strong role in shaping stand structure and demography in late-successional stands, temporal patterns of white spruce tree and stand-level ANPP in both midsuccessional and late-successional stands in uplands and floodplains were closely linked within the time frame of this study.

Our analyses show that interannual variability of white spruce tree ANPP is significantly correlated among the three replicate stands of the midsuccessional and late-successional stages in both floodplains and uplands, despite replicate

Fig. 7. Comparison of white spruce (*Picea glauca*) tree growth between control (Con) and summer moisture exclusion (Dry) plots in upland and floodplain midsuccessional forest stands at the Bonanza Creek Experimental Forest between 1990 and 2005.



stands being separated by up to several kilometres distance. Furthermore, interannual variability of white spruce tree ANPP is significantly correlated between midsuccessional floodplain and upland stands but not between late-successional floodplain and upland stands. Moreover, there is no synchrony of white spruce ANPP interannual variability between either midsuccessional and late-successional trees within either floodplain or upland landscapes. This suggests that white spruce ANPP in mid- and late-successional stands has different sensitivities to climate that may be related to differences in overstory shading between mid- and late-successional stands.

Overall, our stepwise regression analysis found substantial evidence that white spruce tree ANPP is sensitive to interannual and probably interseasonal variation in soil moisture availability. However, the degree of synchrony among stand types appears to be driven by different sensitivities to climate drivers. ANPP of white spruce in late-successional floodplain stands appears to be most sensitive to the availability of hyporheic water and therefore river gauge height, while late-successional upland ANPP appears to be most sensitive to soil moisture as indicated by the negative rela-

tionship of ANPP with June soil temperature. This is consistent with the asynchrony in ANPP between late-successional floodplain and upland stands. In contrast with the pattern of synchrony found in the ANPP of midsuccessional floodplain and upland stands, our stepwise regression analysis indicates that floodplain stands are primarily sensitive to drought conditions in the previous August, while upland stands are primarily sensitive to current July precipitation. However, July and June river gauge height does explain an additional 20% of the variation in ANPP of midsuccessional floodplain and upland stands, respectively, and may be the factor behind the pattern of synchrony if river gauge height is a useful index of both hyporheic and atmospheric water availability.

Experimental perspective

In midsuccessional upland stands, the melting snowpack recharges surface soil to field capacity prior to tree growth. This timing depends on the size of the winter snowpack, the melt characteristics during the spring, and the water-holding properties of the soil. Most tree diameter growth occurs early in the growing season (Downing 1960; Gregory and Wilson 1968). Both the drought and control sites in the up-

lands displayed a significant soil moisture reduction during the early part of the growing season (May and June). The growth limitations due to soil moisture availability would be similar in both the drought and control plots, since both plots received soil moisture recharge from snowmelt. Since the majority of tree growth occurs early in the growing season, late-season (mid-July and August) rainfall events do not play a major role in controlling tree diameter growth. Based on these results, it can be hypothesized that removal of spring snowmelt should cause a significant reduction in tree growth.

Fundamental differences in water sources and associated root depth distributions of white spruce between upland and floodplain landscapes may explain differential ANPP responses to experimental rainfall exclusion in these two landscapes. Data from our experimental control plots indicate that ANPP of midsuccessional white spruce is almost twice as great in floodplain compared with upland landscapes, despite the fact that rainfall is 22% greater in upland landscapes. The most likely explanation for this is the access and reliance on subsurface water in floodplain environments. Three factors are thought to influence soil water profiles in floodplain landscapes: (i) evapotranspiration, (ii) capillary effects, and (iii) osmotic effects due to the salt concentrations in the soil solution (Van Cleve et al. 1993). Potential evapotranspiration, which is greater than precipitation in the summer, may become particularly important for trees with a shallow rooting distribution. The majority of roots that play a role in moisture uptake could have been located at shallow depths (<30 cm) in the soil profile (Ruess et al. 1996). The coarse-textured soils that are common on the floodplain could limit capillary rise from the water table. In comparison with the uplands, the lower rainfall and coarse-textured soils in the floodplains will result in faster water utilization. Third, ground water ion concentrations were sufficiently high to limit water (Yarie et al. 1993). Rowell (1988) indicated that an electrical conductivity value of 4 dS·m⁻¹ or greater will indicate sufficient salt content in the soil solution to have a detrimental effect on salt-sensitive plants. Measured values for electrical conductivity in floodplain soil solution were in the range of 0.7–3.6 dS·m⁻¹ depending on floodplain terrace height and soil depth.

White spruce displayed higher growth rates in midsuccessional floodplain stands compared with upland control sites. Growth of white spruce on the floodplain was almost twice as high compared with upland sites (Yarie 2008) even though floodplain sites received less precipitation. It was thought that the water for tree growth on the floodplain was principally supplied by the ground water proximity to the rooting system. This could reduce dependence on growing season precipitation to satisfy moisture requirements. However, the results of this study indicate that both the ground water and summer precipitation sources of moisture are critical to support the higher levels of observed growth. The relative importance of these sources is not clear and work using an isotope ratio method is indicated to delineate the actual source of water for tree growth on the floodplain.

How can we relate the results of this experiment to white spruce growth responses to changes in future climate? It has been suggested that there will be a substantial increase in air temperature especially during the winter months (Keyser et

al. 2000), and over the past 20 years, there has been no clear change in summer precipitation (Juday et al. 2003; Hinzman et al. 2005). If we assume that precipitation quantity and distribution will remain constant, the following scenario emerges from the experimental results. For upland sites, there will be very little or no change in tree growth dynamics. Both spring snowmelt and the seasonal distribution and quantity of rainfall will adequately restore soil water. Restoration of soil water will also occur on the floodplain, but it will last for a smaller portion of the growing season due to the higher sand content found in the soil profile. Tree growth on the floodplain will then have a greater dependence on rainfall. If the growing season continues to lengthen, then the duration of a potential moisture deficit will also lengthen and the growth capability on the floodplain sites will decrease.

Synthesis of the different perspectives

The dendrochronological analyses presented here indicate that climate warming has led to widespread declines in white spruce growth throughout interior Alaska from the Alaska Range in the south to the Brooks Range in the north. Negative responses to warming have become more prevalent during the 20th century. In comparing the analyses between the dendrochronological and demographic perspectives, it is important to note that the demographic analyses are limited to approximately the last 15 years and are spatially restricted to the vicinity of the Bonanza Creek Experimental Forest. Despite differences in the scope of the data sets, the results from demographic analyses are generally consistent with those of the dendrochronological perspective, as white spruce tree ANPP was substantially limited by soil moisture availability in both mid- and late-successional stands. Furthermore, the finding that there is more synchrony in inter-annual variability of tree NPP among stands within a landscape position than between landscape positions agrees with tree ring studies that have shown that the response of white spruce growth to temperature depends on landscape position and prevailing climate.

Results from the white spruce summer drought experiment were, in some respects, inconsistent with the demographic and dendrochronological analyses. The drought experiment was conducted in floodplain and upland midsuccessional forests where the more recently conducted demographic analyses have identified that July precipitation was strongly correlated with white spruce ANPP. Surprisingly, the drought experiment did not limit growth in the upland stands. The demographic analyses also indicated that the ANPP of both floodplain and upland trees is related to river stage, with a stronger sensitivity for the floodplain stands. One issue that the demographic perspective identifies is the dependence of current year production on the previous year's climate conditions. Climate factors in one year may affect environmental conditions the next year. For example, the relationship between current year ANPP and previous year August PDSI could be indicative of low soil moisture at the end of the previous growing season that translates into low soil moisture at the beginning of the current growing season depending on snow conditions during the winter. It is also possible that climate factors that limit the current year's carbon uptake, which if stored belowground, may re-

sult in carbon not being available to drive wood production early in the next growing season. The hypothesis that white spruce production depends primarily on early-season soil moisture is currently being tested with snow-exclusion experiments, and it will indeed be interesting to see whether this makes a difference in upland stands. This experiment also has the potential to shed light on whether changing seasonality in climate will be a major factor in determining future forest growth in different landscape positions.

Together, the three approaches analyzed in this study indicate that response of white spruce tree growth is vulnerable to warming through effects on water availability. The dendrochronological analyses indicate that warming in many areas of Alaska may have passed a critical threshold with respect to the response of white spruce growth and that further warming will result in more of the population responding negatively to temperature. Ongoing tree ring studies are attempting to clarify the degree to which white spruce growth responses are continuing to change and how landscape positions are influencing those dynamic responses. The high level of variation in response among individuals within a population is also a crucial area of future research to address the question: do individuals differ in growth response because of fine-scale variation in environmental conditions or is there genetic variation responsible for climate response? Ongoing demographic studies conducted by the BNZ LTER are attempting to understand sensitivities and controls at interannual to multidecadal scales. In an attempt to resolve inconsistencies of the experimental findings with the dendrochronological and demographic findings, the BNZ LTER is conducting a spring snow removal experiment to evaluate the degree to which spring water recharge of soils plays a role in white spruce growth. These ongoing studies will enrich our understanding of ecosystem responses to a changing climate and can inform models designed to project changes in ecosystem structure and function in interior Alaska.

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