

Climate sensitivity of thinleaf alder growth on an interior Alaskan floodplain¹

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Abstract: This study examined the climate sensitivity of the growth of riparian *Alnus incana* ssp. *tenuifolia* (thinleaf alder), a keystone nitrogen-fixer, on the Tanana River floodplain of interior Alaska. We investigated correlations between alder radial growth and inter-annual variation in monthly meteorology and hydrology, spatial patterns of alder climate sensitivity in relationship to depth of subsurface water, and long-term climatic trends. Annual radial growth of alder was positively correlated with June precipitation, river discharge, and Palmer Drought Severity Index values and was negatively correlated with June temperature, suggesting a susceptibility of growth to early-season moisture limitation, due to the co-occurrence of dry meteorological conditions and low levels of hyporheic flow. Alder radial growth was positively correlated with August discharge and July temperature, suggesting that moisture may also be limiting in August, but not in July. The sensitivity of alder growth to variation in temperature and precipitation was greater on higher terraces where depth to water table was greater, while the sensitivity to variation in river level was greater on lower terraces, suggesting that subsurface water more strongly influences moisture availability at these sites. Long-term climatic trends in this region suggest increasing drought conditions; however, the overall influence on alder growth and associated rates of nitrogen fixation are uncertain due to the contrasting relationship of growth with climate in June/August versus July.

Keywords: *Alnus*, climate change, dendroecology, drought stress, nitrogen fixation.

Résumé : Cette étude a examiné la sensibilité climatique de la croissance de l'espèce riveraine *Alnus incana* ssp. *tenuifolia* (aulne à feuilles minces), une espèce clé pour la fixation d'azote dans la plaine inondable de la rivière Tanana à l'intérieur de l'Alaska. Nous avons examiné les corrélations entre la croissance radiale de l'aulne et les variations interannuelles dans les conditions météorologiques et hydrologiques mensuelles, les patrons spatiaux de sensibilité climatique de l'aulne par rapport à la profondeur d'eau sous la surface et les tendances climatiques à long terme. La croissance radiale annuelle de l'aulne était corrélée de façon positive avec les précipitations en juin, le débit de la rivière et les valeurs de l'indice de sécheresse de Palmer, et était corrélée de façon négative avec la température de juin, suggérant une susceptibilité de la croissance aux limitations hydriques en début de saison en raison de la co-occurrence de conditions météorologiques sèches et de faibles niveaux de flux hyporhéique. La croissance radiale de l'aulne était corrélée de façon positive avec le débit en août et la température de juillet, suggérant que l'humidité puisse aussi être un facteur limitatif en août, mais non en juillet. La sensibilité de la croissance de l'aulne aux variations de température et de précipitation était plus grande sur les terrasses plus élevées où la nappe phréatique est plus profonde, tandis que la sensibilité à la variation du niveau de la rivière était plus grande sur les terrasses plus basses, suggérant que l'eau sous la surface influence plus fortement la disponibilité en eau dans ces sites. Les tendances climatiques à long terme dans cette région suggèrent une augmentation des conditions de sécheresse; cependant, l'influence générale sur la croissance de l'aulne et les taux de fixation d'azote associés est incertaine en raison de la relation inverse de la croissance avec le climat en juin/août par rapport à juillet.

Mots-clés : *Alnus*, changement climatique, dendroécologie, fixation d'azote, stress hydrique.

Nomenclature: Hultén, 1968.

Introduction

Increased levels of greenhouse gases are causing rapid climate warming in the circumboreal north (Serreze *et al.*, 2000), and the rate of warming has accelerated over the last 30 y (Chapin *et al.*, 2005). The temperature-induced increase in summer drought is one of the most important and rapidly changing features of the physical environment of the boreal forest in western North America (Oechel

et al., 2000). Increased summer air temperatures in interior Alaska have accelerated evapotranspiration rates and led to a net reduction in soil moisture, with summer water deficits increasing 6.5 cm·decade⁻¹ (Oechel *et al.*, 2000; McGuire *et al.*, 2007). Some coniferous and deciduous boreal tree species that are sensitive to the increased summer water deficit exhibit drought stress, growth suppression, and susceptibility to disease (Barber, Juday & Finney, 2000; Brandt *et al.*, 2003; Juday *et al.*, 2005; Lloyd & Bunn, 2007; Hogg, Brandt & Michaelian, 2008; Winslow, 2008). This study addresses the patterns of climate sensitivity in the growth of an important nitrogen (N)-fixing shrub, *Alnus incana* ssp.

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tenuifolia, hereafter *Alnus tenuifolia* (thinleaf alder), on the Tanana River floodplain of interior Alaska. The response of this keystone N-fixer to a warmer, drier climate could have major implications for ecosystem function in the boreal forest floodplains (Ruess *et al.*, 2009).

Dendroecological studies of moisture limitation have traditionally focused on upland environments, where sensitivity to meteorological drought is expected to be greater due to the presumably reduced access to groundwater (Fritts, 1971). However, recent studies are beginning to show that some riparian plants are also vulnerable to drought stress, despite their relative proximity to subsurface water (Dawson & Pate, 1996; Leffler & Evans, 1999; Horton, Kolb & Hart, 2001; Cooper, D'Amico & Scott, 2003; Li *et al.*, 2007; Winslow, 2008; McGuire *et al.*, 2010). Surface soil moisture in the Tanana River floodplains is influenced by the depth of hyporheic flow, which is a function of river level (Viereck *et al.*, 1993). River level is controlled indirectly by air temperature, primarily through the rate of glacial melt (Swanson *et al.*, 1998), as the Tanana River derives 85% of its water from glacially fed tributaries (Yarie *et al.*, 1998). Interestingly, while increased summer air temperatures would be predicted to decrease soil moisture through increased evapotranspiration (Oechel *et al.*, 2000), warmer summer temperatures may also be predicted to increase floodplain soil moisture by increasing glacial melt (Woo *et al.*, 2008) and the height of hyporheic flow (Viereck *et al.*, 1993; Clilverd, Jones & Kielland, 2008). These opposing consequences of warming on floodplain soil moisture are separated in time within the growing season, where drought stress may be more likely to occur before river levels peak. Evaporation rates are highest in June and July, but river levels of the Tanana do not typically peak until mid-July (Viereck *et al.*, 1993), and the capillary rise of hyporheic water does not reach the rooting zone of willow until late June (Clilverd, Jones & Kielland, 2008). If air temperature is high and precipitation is low in June, then increased glacial melt later in the season may not offset the effect on plants of low soil moisture experienced earlier in the growing season. Thus, floodplain vegetation may be vulnerable to moisture stress in years of early-season meteorological drought, despite the late-season increase in hyporheic flow.

The goal of this study was to understand the temporal and spatial patterns in the sensitivity of thinleaf alder growth to climatic variables in the Tanana River floodplains. Our specific objectives were to (1) determine the influence of inter-annual variation in monthly meteorological and hydrological variables on annual alder radial growth, (2) assess the variability in alder climate sensitivity across the landscape in relationship to variations in the depth of the water table, and (3) explore the implications of long-term trends in climate and hydrology for future alder growth in this region. We expected to find that the growth of thinleaf alder along the Tanana River would be sensitive to meteorological drought during periods of low hyporheic flow, and that this sensitivity would vary spatially, dependent on the vertical distance to subsurface water.

Methods

STUDY AREA

The study area encompasses an 80-km reach of the Tanana River floodplain in interior Alaska, from Fairbanks (64.9° N, 147.9° W) to Nenana (64.5° N, 148.7° W), between the Chena and Nenana rivers. The Tanana River is a meandering, glacially fed river that drains the north slope of the Alaska Range into the Yukon River. The Tanana River carries a high sediment load, and continued deposition creates new silt bars and increases terrace elevations. Early successional alder stands occur nearly contiguous to the river edge on terraces just above the average maximum river height. Differences in depositional rates and stand age combine to naturally distribute these stands across terraces of heights that differ by up to 2 m. The substrate of alder stands is alluvium, consisting of loess-derived silts and silt loams, and a thin layer of leaf litter, with older stands developing a thin organic layer (Viereck, Dyrness & Foote, 1993). A common sequence of primary succession on this floodplain shifts in dominance from *Salix* to *Alnus tenuifolia*, to *Populus balsamifera*, to *Picea glauca*, and eventually, perhaps through secondary succession, to *Picea mariana* (Viereck, Dyrness & Foote, 1993; Hollingsworth *et al.*, 2010).

The climate of the region is strongly continental, with low precipitation (annual average precipitation of 269 mm), and is characterized by a short growing season and extreme seasonal variation in day length and temperature (Viereck *et al.*, 1993). Local climate and hydrological variables vary widely throughout the course of the growing season (late May–early September) (Figure 1). Mean monthly temperature from 1930 to 2008 approaches its peak in June and

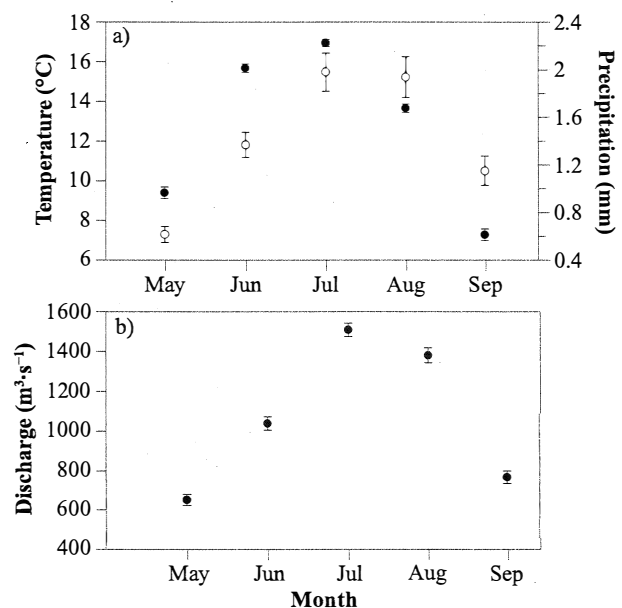


FIGURE 1. Temporal variation (May–September) in (a) air temperature (solid circles) and precipitation (open circles) in Fairbanks, Alaska (1930–2008) and in (b) Tanana River discharge in Nenana, Alaska (1962–2009). Data are monthly means $\pm$ SE.

reaches its maximum in July (Figure 1a). Mean monthly precipitation follows a similar pattern but peaks in July and August (Figure 1a). Mean Tanana River discharge and gauge height rapidly increase from May through July and decrease from July through September (Figure 1b).

In 2006, 45 transects (50 × 5 m) were established in alder-dominated stands that represented a wide range of alder stand structures and terrace heights. Each transect was subdivided into ten 5 × 5-m plots. After initial vegetation sampling, multivariate analyses of community structure were conducted to aggregate plots of each transect into larger zones of homogenous vegetation that were then used for subsequent sampling (Nossov, 2008). We refer to the aggregated plots from each transect as sites. Of the 89 sites established for a larger study, we randomly selected 27 sites that represent the range of variability in terrace heights throughout the study area.

TERRACE HEIGHT SAMPLING

Terrace height was used as a proxy for the maximum depth of the water table at each site. We calculated terrace height as the relative elevation of the soil surface above the mean summer river level. Terrace heights were surveyed and calculated through differential levelling at 5-m intervals along transects, and were averaged for each site. Hourly Tanana River gauge height readings from the Fairbanks US Geological Survey (USGS) site (#15485500) were used as benchmark elevations. While there is a slight downstream change in river gradient between sites that may affect the accuracy of our terrace height estimates, our estimates were not spatially biased, as the terrace heights of our sites were distributed randomly throughout the longitudinal gradient of the river.

TREE RING SAMPLING AND CHRONOLOGY DEVELOPMENT

At each of the 27 sites, we collected disks at ground level from up to 10 live alder stems for each of 3 size classes based on diameter at breast height (dbh) (0–2.9 cm, 3–4.9 cm, and ≥ 5 cm). The disks were oven-dried and sanded with 400–600 grit sandpaper. Tree rings were counted and measured on a sliding bench micrometer to a precision of 0.001 mm. Three to 4 radii from each disk were sampled, ring counts were compared, and disks with any ring count discrepancies were excluded from analyses.

Each raw tree ring-width series was detrended to remove the growth trend that could be attributable to aging or stand dynamics in order to isolate the climatic signal (Fritts, 1971). The predominant radial growth trend of thinleaf alder exhibited a steep increase in ring-width for the first several years of growth followed by a more gradual non-linear decline. The first few years of rapidly changing growth were disregarded (Fritts, 1976), and a flexible cubic spline was fit to the remaining ring-widths of each series (Cook & Peters, 1981). Ring-width indices were calculated using residuals from each growth curve and were normalized (Cook & Peters, 1997). Correlation coefficients between each detrended series and the site mean were used to identify potentially misdated series, which were visually examined, recounted as necessary, or excluded from analysis. Only stems that were at least 10 y old were included

in the ring-width chronologies. A standard landscape-level chronology was calculated by averaging ring-width indices from all sites, with a minimum sampling depth of 10 data points per year. The landscape-level chronology represents growth data from 456 stems across 27 sites, spanning 1968–2006 (minimum age = 10 y, maximum age = 56 y). Standard site-level chronologies were calculated by averaging ring-width indices within each site, with a minimum sampling depth of 4 data points per year. Mean series inter-correlation, the average correlation of each individual ring-width chronology with the site chronology, was rather high ($r = 0.65$), suggesting the presence of a fairly strong climate signal in the ring-widths. The chronologies represent the high-frequency variation in ring-width, and are analyzed at the inter-annual time scale (Johnson, Cook & Siccama, 1988; Lebourgeois *et al.*, 2005; Liang *et al.*, 2006).

DATA ANALYSIS

The climatic variables considered in this study were air temperature, precipitation, Palmer Drought Severity Index (PDSI), and Tanana River discharge and gauge height. Temperature and precipitation data were from the Fairbanks International Airport for the period 1930–2008 (climate.gi.alaska.edu/). Hydrological data for the Tanana River were obtained from US Geological Survey (USGS) website (waterdata.usgs.gov/nwis/) for sites in Fairbanks (#15485500) and in Nenana (#15515500). Tanana River gauge height data (1991–2009) were from the Fairbanks site, and Tanana River discharge data were from the Nenana site (1962–2009). The PDSI data (1949–2006) were obtained from the Bonanza Creek Long-Term Ecological Research (LTER) program, and were calculated with climate data from the Fairbanks International Airport and soil data from an early successional site on the Tanana River floodplain (McGuire, 2006).

The PDSI is a standardized index of meteorological drought that approximates the departure from the local mean atmospheric moisture supply and demand at the soil surface (Palmer, 1965). The water balance approach of the PDSI utilizes temperature, precipitation, and local soil available water content data to estimate evapotranspiration, soil recharge, runoff, and moisture loss (Thorntwaite, 1948; Palmer, 1965). Despite the limitations of this index (Alley, 1984), the PDSI provides a useful approximation of relative meteorological drought that is typically a stronger predictor of soil moisture than either temperature or precipitation alone (Dai, Trenberth & Quian, 2004) and is often correlated with ring widths of drought-stressed trees (Cook *et al.*, 1999). Although the PDSI was developed to estimate meteorological drought, this index is also frequently correlated with river discharge (Dai, Trenberth & Quian, 2004; MacDonald *et al.*, 2007); therefore, the PDSI functions as a hydrometeorological index for our application with riparian vegetation. Note that low soil moisture is associated with negative values of the PDSI.

Spearman's rank correlations were conducted between the landscape-level ring-width chronology and climate indices (mean temperature, total precipitation, mean river discharge, and PDSI) for June, July, August, and September to identify the factors most closely associated with variations

in alder radial growth. The climate indices were used to emphasize the high-frequency variation in climate and were calculated as the residuals of a spline of the raw climate data. In addition, bootstrapped correlation functions were computed using DendroClim2002 to verify the significance of these results (Biondi & Waikul, 2004). To address the spatial variation in alder climate sensitivity in relationship to terrace height, Spearman's rank correlations were conducted between the site-level ring-width chronologies and mean temperature, total precipitation, and mean gauge height indices for the months where significant relationships between climate and the landscape-level ring-width chronology were found. The statistically significant rank correlation coefficients resulting from these analyses were plotted against terrace height in order to identify the spatial trends in climate sensitivity. Long-term trends in the climate and hydrological variables were assessed using simple linear regression. Prior to regression analyses, all variables were tested for normality using the Shapiro–Wilk test and deviations from normality were corrected using the appropriate data transformation (June precipitation, August precipitation, and August PDSI were square root transformed; July precipitation and June, July, and August river discharge were log-transformed). All results were considered statistically significant at $\alpha = 0.05$. Analyses were conducted with JMP 8.0.2 (SAS Institute, 2009) and DendroClim2002 (Biondi & Waikul, 2004).

Results

RELATIONSHIPS BETWEEN CLIMATIC VARIATION AND ALDER GROWTH

The strength and direction of the correlations between landscape-level alder ring-width indices and monthly climate indices exhibited intra-seasonal patterns (Figure 2). Alder ring-width was positively correlated with June PDSI, precipitation, and river discharge ($r_s = 0.49$, $P < 0.01$; $r_s = 0.35$, $P < 0.05$; $r_s = 0.32$, $P < 0.05$, respectively) and was negatively correlated with June temperature ($r_s = -0.37$, $P < 0.05$) (Figures 2 and 3). During July, when both atmospheric and subsurface water availability increased

(Figure 1), ring-width was positively correlated with temperature ($r_s = 0.37$, $P < 0.05$) (Figures 2 and 3). Ring-width was positively correlated with August river discharge ($r_s = 0.37$, $P < 0.05$) (Figures 2 and 3). No significant relationships between ring-width and September climate indices were found. Bootstrapped correlation functions confirmed the statistical significance of these findings (data not shown).

SPATIAL VARIATION IN CLIMATE SENSITIVITY OF ALDER GROWTH

The climate variables that were significantly correlated with landscape-level alder ring-widths were correlated with site-level ring-widths to evaluate the influence of terrace height on variation in alder climate sensitivity (Figure 4). Ring-width sensitivity to variations in gauge height (positive correlations) tended to occur at sites on lower terraces, while sensitivity to variations in temperature (negative correlations) and precipitation (positive correlations) occurred mostly on higher terraces. There appears to be a threshold at approximately 1.25 m above mean summer river stage where ring-width sensitivities to meteorological *versus* hydrological indices diverge.

LONG-TERM TRENDS IN CLIMATE AND HYDROLOGY

We explored the long-term trends in climatic variables for the months that were associated with alder ring-width (June–August) using linear regression (Table 1). Fairbanks climate data from 1930 to 2008 showed that mean temperatures for June, July, and August have all increased, while total precipitation has declined for August and showed no trend for June or July. From 1962 to 2009, mean discharge of the Tanana River declined marginally for June but we did not detect a temporal trend in discharge for July or August. From 1949–2006, PDSI declined marginally for June, but did not change for July or August.

Discussion

The suppression of tree growth has been linked to moisture stress in several deciduous and coniferous species native to the boreal forest (Barber, Juday & Finney, 2000; Brandt *et al.*, 2003; Juday *et al.*, 2005; Lloyd & Bunn, 2007; Hogg, Brandt & Michaelian, 2008; Winslow, 2008). Because subsurface water is often important to riparian plant water balance (Busch, Ingraham & Smith, 1992; Leffler & Evans, 1999; Li *et al.*, 2007), we hypothesized that the growth of thinleaf alder along the Tanana River would be sensitive to meteorological drought during periods of low hyporheic flow, and that this sensitivity would vary spatially, dependent on the vertical distance to subsurface water.

Given the timing of the seasonal variation in climatic and hydrological patterns on this glacial floodplain, it was expected that riparian alder would be most sensitive to drought early in the growing season. The PDSI indicates a generally dry period from June through August, with evaporation rates at their highest in June and July (Viereck *et al.*, 1993). However, the level of the water table, which is directly related to river discharge and river stage (Viereck *et al.*, 1993; Clilverd, Jones & Kielland, 2008), typically peaks in July, potentially increasing soil moisture within the

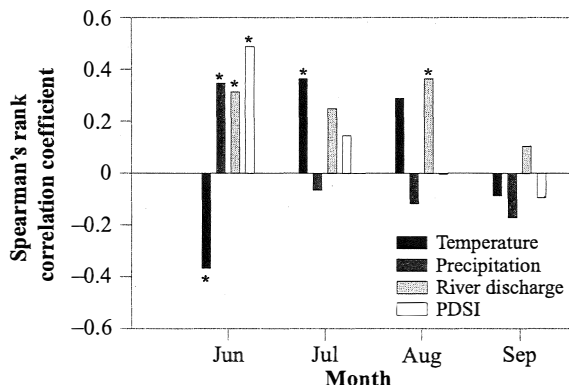


FIGURE 2. Correlations of landscape-level ring-width indices with indices of temperature, precipitation, discharge, and PDSI from June to September. Spearman's rank correlations, $n = 39$ y. Asterisks indicate correlations significant at $P < 0.05$.

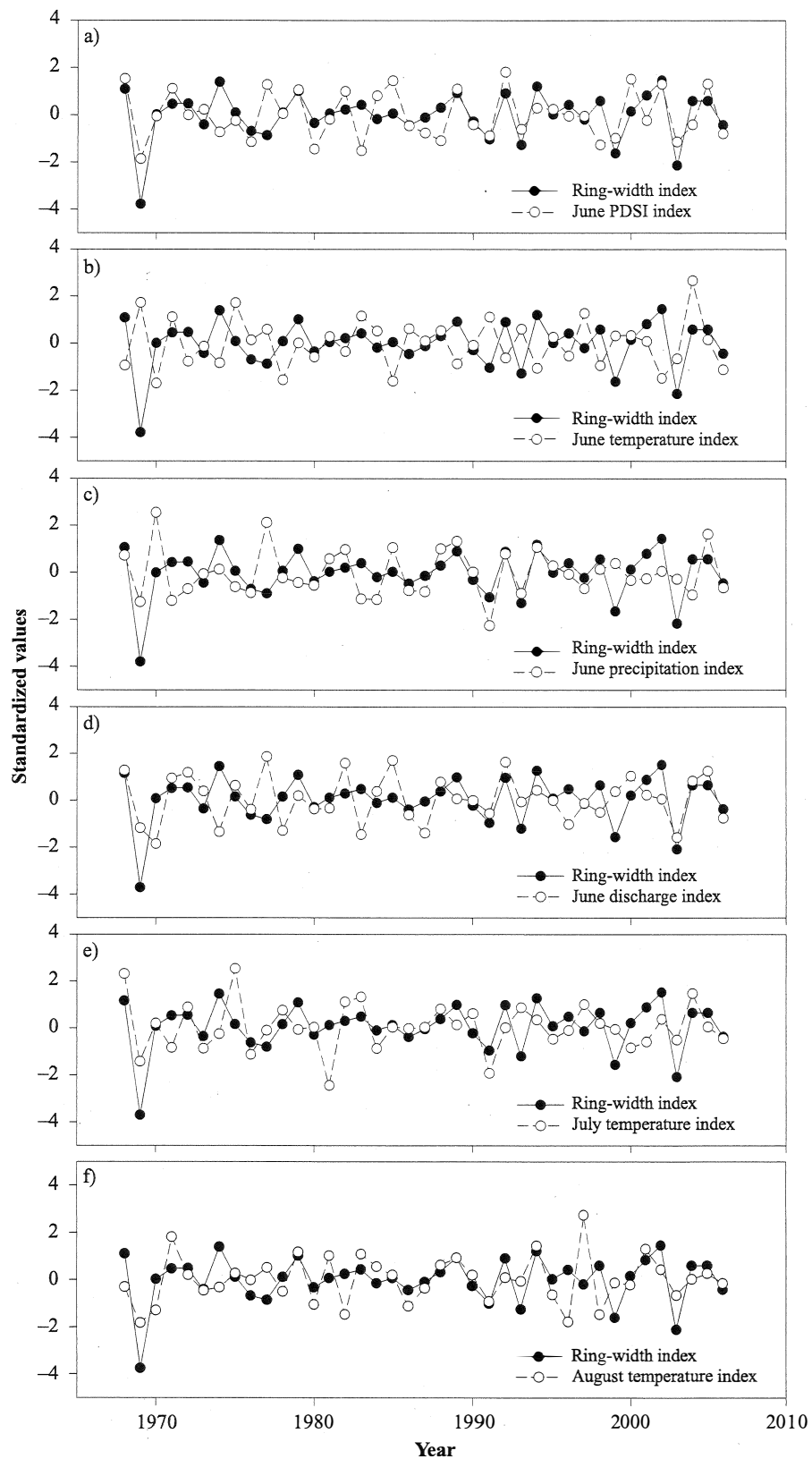


FIGURE 3. High-frequency variation in landscape-level ring-width indices in relationship to indices of a) June PDSI, b) June temperature, c) June precipitation, d) June river discharge, e) July temperature, and f) August river discharge. All values are standardized.

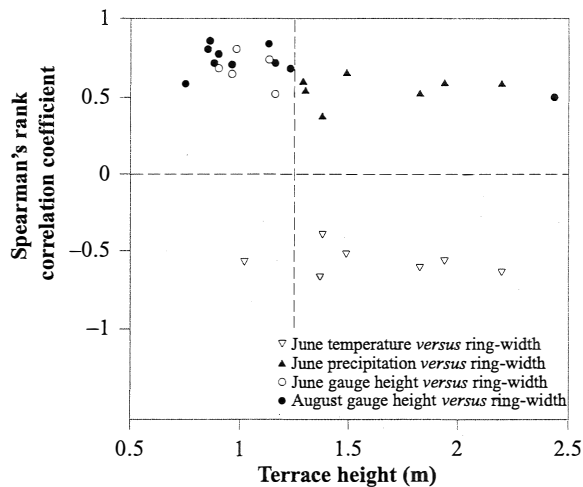


FIGURE 4. Statistically significant Spearman's rank correlations of site-level ring-width indices with meteorological and hydrological indices, by terrace height above summer mean river stage. The horizontal dashed line represents zero-correlation, and the vertical dashed line depicts a potential terrace height threshold.

TABLE I. Regression statistics of long-term trends in monthly mean temperature, total precipitation, mean discharge, and mean PDSI for June–August. Significant positive changes are indicated by “+”; significant negative changes are indicated by “–”; weak changes are bracketed by “()”; and zero changes are indicated by “0.”

Variable	Direction of change	r^2	P	df	F
June temperature	+	0.135	0.001	77	11.823
June precipitation	0	0.000	0.883	77	0.022
June discharge	(–)	0.048	0.134	47	2.328
June PDSI	(–)	0.042	0.124	57	2.443
July temperature	+	0.281	< 0.0001	77	29.672
July precipitation	0	0.011	0.216	78	0.846
July discharge	0	0.000	0.933	47	0.007
July PDSI	0	0.007	0.547	57	0.368
August temperature	+	0.130	0.001	78	11.458
August precipitation	–	0.058	0.034	77	4.664
August discharge	0	0.016	0.391	46	0.750
August PDSI	0	0.000	0.996	57	0.000

rooting zone of plants and alleviating drought conditions for vegetation during the mid and late growing season (Figure 1b) (Viereck, Dyrness & Foote, 1993; Viereck *et al.*, 1993). In June, mean air temperatures are relatively high and precipitation low, while river stage has yet to reach the seasonal peak (Figure 1).

Our results support the hypothesis that riparian thinleaf alder growth is particularly vulnerable to drought stress early in the growing season (Figure 2), as the annual radial growth of alder had strong positive relationships with the Palmer Drought Severity Index (PDSI) and precipitation and a strong negative relationship with air temperature for the month of June. These relationships demonstrate the tendency for alder growth to increase in years when June weather was cooler and wetter and decrease in years when it was warmer and drier. June PDSI was a better predictor of alder annual growth than either temperature or precipitation

alone, perhaps because PDSI takes into account both variables to more accurately characterize soil moisture (Palmer, 1965; Dai, Trenberth & Quian, 2004). The positive relationship between ring-width and river discharge in this month, as well as in August, reflects the importance of subsurface water to alder water balance. In July, moisture does not appear to be limiting to alder growth, as ring-width was not closely related to July PDSI, precipitation, or discharge; rather, it was positively correlated with temperature during this month.

In the early growing season, the co-occurrence of meteorological drought (influenced directly by high temperatures and low precipitation) and hydrological drought (influenced directly by low levels of the water table) explains the high sensitivity of alder radial growth to the inter-annual variation in climate. The spatial patterns of the sensitivity of alder growth to drought offer further compelling evidence to support this explanation.

Our results show that the sensitivity of alder growth to inter-annual variation in meteorology and hydrology varied across the landscape in relationship to terrace height and, therefore, depth to water table (Figure 4). The association of suppressed alder radial growth with increased temperatures and decreased precipitation occurred at sites on relatively high terraces (> 1.25 m above mean summer river stage), while the positive relationship between radial growth and river stage tended to occur on relatively low terraces (< 1.25 m above mean summer river stage). This spatial variation in the strength of the relationship of alder growth to temperature, precipitation, and river level suggests that alder growth is more susceptible to drought stress on higher terraces, where distance to the water table is greater and soil moisture replenishment through river level fluctuation is less likely. The strong relationship between alder growth and river level on low terraces suggests that alder growth is moisture-limited in these sites; but fluctuation in the depth of the water table plays an integral role in alleviating or exacerbating soil moisture deficits. The apparent dependence of alder on atmospheric moisture *versus* subsurface water varied even within this relatively minimal gradient in floodplain terrace height (range of < 2 m). While we are unaware of any other studies explicitly examining the effect of elevation on the vulnerability of plant growth to drought stress within a riparian landscape, our findings are conceptually analogous to those derived from the examination of wide elevation gradients (Li *et al.*, 2007) and variable levels of subsurface flow (Leffler & Evans, 1999; Horton, Kolb & Hart, 2001; Cooper, D'Amico & Scott, 2003).

The climate sensitivity of thinleaf alder growth may have important implications for the climatic controls on N input in the Tanana River floodplain, as most of the soil N in this N-limited ecosystem is derived through thinleaf alder N-fixation (Van Cleve, Viereck & Schlentner, 1971; Van Cleve *et al.*, 1991; Uliassi & Ruess, 2002), with dense stands contributing in excess of 100 kg N·ha⁻¹·y⁻¹ (Ruess *et al.*, 2009). Because symbiotic N-fixation is controlled by plant N demand (Wall & Huss-Danell, 1997), high rates of thinleaf alder growth are synonymous with high rates of N-fixation input in early successional environments where soil N is minimal (Uliassi & Ruess, 2002). Many

studies have demonstrated that moisture deficits can reduce N-fixation rates and nodulation (Dalton & Zobel, 1977; Dixon & Wheeler, 1983; Harrington & Seiler, 1988; Hennessey *et al.*, 1989; Huss-Danell, 1997), and with acute drought stress, an almost complete inhibition of N-fixation was observed in *Alnus incana* (Sundström & Huss-Danell, 1987). The early season moisture-limitation of thinleaf alder growth may therefore also represent an important constraint on floodplain soil N input.

In predicting the future response of floodplain vegetation to a changing climate, it will be important to consider the demonstrated temporal and spatial variation in drought sensitivity. We examined the long-term trends of Fairbanks temperature, precipitation, PDSI, and Tanana River discharge for the months of alder climate sensitivity (June, July, and August) (Table I). The local trends in temperature, precipitation, and PDSI documented here suggest increasing drought severity, and are consistent with findings for overall summer trends for interior Alaska (Oechel *et al.*, 2000; McGuire *et al.*, 2007). However, the implications for riparian vegetation are complex due to the influence of the seasonal variation in water table depth. While annual discharge rates of the Tanana River have significantly increased since the 1960s (Hinzman *et al.*, 2005; Woo *et al.*, 2008), this was attributable to changes in winter discharge (data not shown), and we detected no change in discharge rates for the summer, except for a marginal decline in June. Nevertheless, it appears that alder growth is sensitive to river discharge in warm, dry summers, particularly in June and August. If temperature continues to increase without concurrent increases in precipitation or river discharge, we predict that moisture limitation of thinleaf alder growth during June and August is likely to become more common and severe. However, given that increasing temperatures in July are likely to have a positive effect on alder growth, the net effect of a warming climate on annual alder growth remains uncertain.

Conclusion

The results of our study suggest that the radial growth of thinleaf alder along the Tanana River is susceptible to meteorological drought during periods of low hyporheic flow, and that this sensitivity varies spatially, dependent on terrace height, or depth to water table. The seasonality of both atmospheric and hydrologic water availability create a temporally changing environment on this floodplain, where the sensitivity of alder growth to drought conditions is most pronounced early in the growing season, when river levels are low, although fluctuation in water table depth remains important to alder growth later in the season. The apparent climatic and hydrologic controls on alder radial growth may also influence symbiotic N-fixation by this species. It is unclear what the net effect of a changing climate would be for thinleaf alder on the Tanana River floodplains due to the contrasting nature of the relationship between growth and climate for June/August *versus* July.

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