

Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada

Giovanni Leonelli, Bernhard Denneler, and Yves Bergeron

Abstract: Growth–climate relationships were analyzed for 15 stands of trembling aspen (*Populus tremuloides* Michx.) along a productivity gradient in northeastern British Columbia. Productivity was evaluated with a site index model whose values varied between 6.65 and 26.93 m height at age 50 years. To assess the role of climate on radial growth, we built a tree-ring chronology for each site and then performed a dendroclimatic analysis by means of bootstrapped correlation functions using monthly and annual climatic variables. We found that trembling aspen sensitivity to climate varied across stands with different productivities in the study area. At the more productive sites, trees were more sensitive to climate, and ring widths were positively correlated, particularly with summer month precipitation prior to the year of growth. The different responses to climate along the productivity gradient are likely related to the differences in substrate properties; substrates at the more productive sites are richer in nutrients and have a better water holding capacity than those of the less productive sites. Our study suggests that the effects of future climate change on tree growth may not only increase towards the limit of a species distribution, but also towards richer and wetter stands.

Résumé : Quinze populations de peuplier faux tremble (*Populus tremuloides* Michx.) du nord-est de la Colombie Britannique représentant un gradient de productivité ont été analysés en regard des relations entre la croissance radiale et le climat. La productivité a été évaluée par l'indice de qualité de site qui variait entre 6,65 et 26,93 m de hauteur à 50 ans. Afin d'évaluer le rôle du climat sur la croissance radiale, une chronologie maîtresse fut produite pour chacun des sites. Les chronologies ont par la suite été comparées aux données climatiques mensuelles et annuelles à l'aide d'une analyse dendroclimatique basée sur des fonctions de corrélation utilisant une procédure bootstrap. La sensibilité du peuplier faux tremble aux conditions climatiques variait avec le gradient de productivité. Ainsi, les sites les plus productifs montraient une plus grande sensibilité au climat particulièrement avec les précipitations durant les mois d'été de l'année précédente. Les différentes réponses observées selon le gradient de productivité pourrait s'expliquer par les caractéristiques des sols qui dans les sites les plus productifs sont plus riches en nutriments et possède une plus grande capacité à retenir l'eau. Notre étude suggère que l'effet du changement climatique sur la croissance des arbres pourrait se faire sentir non seulement à la limite de distribution des espèces mais aussi dans les sites riches et plus humides.

[Traduit par la Rédaction]

Introduction

Although the site productivity of trembling aspen (*Populus tremuloides* Michx.) stands has been shown to depend primarily on soil nutrient and moisture regimes (Hogg 1994; Chen et al. 1998, 2002), other ecological factors influencing tree health, including insect outbreaks and root diseases, also play a role (Hogg 1999; Brandt et al. 2003). In addition, aspen is highly sensitive to light availability (Hemming and Lindroth 1999) and soil temperature (Peng and Dang 2003). However, few studies have focused on the growth–climate relationships of trembling aspen despite it being the most widely distributed tree species in North America (Perala 1990). Chen et al. (1998) found that site productivity of aspen stands in northern British Columbia

was best predicted using a combination of climate surrogates, topographic characteristics, and soil properties. However, the combination of environmental factors predicting the site index, as well as their relative importance, varied for different biogeoclimatic zones (Chen et al. 2002). For example, Chen et al. (2002) found that water deficit was the most important limiting factor for aspen height growth in the warmer southern regions of British Columbia, whereas low temperatures limited aspen growth in the cooler northern regions or at high elevations. This conclusion was based on indirect measures of climate such as latitude, elevation, and slope aspect, with the study focusing on height growth and not radial growth. Hogg et al. (2005) observed that radial growth of aspen in the western Canadian interior was primarily limited by water deficit, with temperature having

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no distinct influence. Neither of the studies differentiated the climatic responses by site conditions. Differentiating the sites in such a manner would allow evaluation of the conditions under which aspen growth is most sensitive to temperature or precipitation.

Tree rings, which are capable of providing long-term annual information, are widely used in forestry studies to assess past stand dynamics and to reconstruct disturbance regimes, including fire (e.g., McBride 1983; Johnson and Fryer 1989) and insect outbreaks (e.g., Swetnam and Lynch 1989; Bergeron et al. 2002). Tree growth tends to be generally limited by climate, thus allowing annual growth rings to be used as one of the main proxies for climate reconstructions concerning temperatures (e.g., Tessier et al. 1997; Wilson and Luckman 2003) and precipitation (e.g., Case and MacDonald 1995; Watson and Luckman 2001). The dendroclimatological approach has also been used in forestry, because it allows long period of growth–climate relationships for specific sites, as well as large regions, to be assessed (e.g., Jean and Bouchard 1996; Brooks et al. 1998). Moreover, the parameterization of tree-ring growth–climate relationships into models of forest growth allows for the prediction of future forest responses under different climate change scenarios (e.g., Hogg 1999; Goldblum and Rigg 2005).

This study aims to examine how stand productivity affects aspen growth–climate relationships by establishing radial growth responses to climate variables along a site productivity gradient in northeastern British Columbia. Based on the limiting factor principle (Fritts 1976), we hypothesize that low-productivity aspen stands on drier sites will be more sensitive to climate (i.e., more strongly limited by climate) than high-productivity stands on moist sites. We also expect that, in less productive and drier sites, stressed trees will show higher year to year variation in ring widths, mostly related to climate conditions associated to soil moisture.

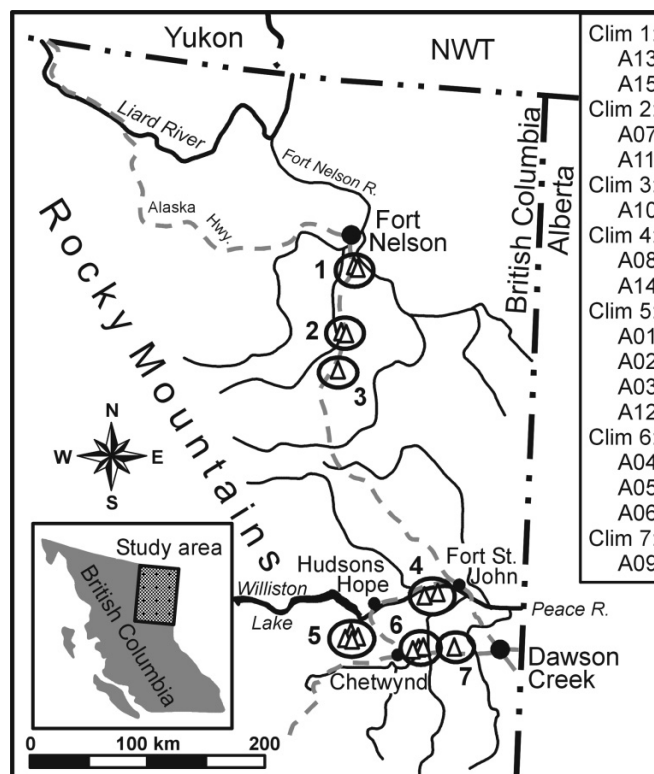
Methods

Study area and sampling sites

The study area is situated in the eastern foothills of the Rocky Mountains in northeastern British Columbia (Fig. 1). It is located in the Moist and Warm Boreal White and Black Spruce (BWBSmw) biogeoclimatic subzone that covers the latitudes between 55°N and 60°N and represents the main natural distribution zone of trembling aspen in British Columbia (Meidinger and Pojar 1991). Aspen is a typical pioneer species (shade intolerant, fast growing, and relatively short lived) that colonizes areas affected by disturbances, such as forest fires and clear-cutting, and can grow on many soil types (Perala 1990).

Climate in the study area is continental and highly influenced by the rain shadow effect of the Rocky Mountain range, which forms a barrier to the warmer and wetter air masses coming from the Pacific Ocean. The northern part of the study area (N) is generally warmer and wetter during the summer months than the southern part (S). Climate normals for the 1971–2000 period from the four closest weather stations (Dawson Creek, Baldonnel, Fort St. John (S), and Fort Nelson (N)) display these differences: mean annual temperature varies between -0.7°C (N) and 2.0°C (S), mean

Fig. 1. Location of the study area and sampling sites A01 to A15 in British Columbia, Canada (triangles). Circles surround sites sharing the same climatic data set for the dendroclimatological analysis.



temperature of the warmest month (July) from 15.2°C (S) to 16.8°C (N), and mean temperature of the coldest month (January) from -12.9°C (S) to -21.2°C (N). The mean annual precipitation at these weather stations varies between 452 mm (N) and 482 mm (S), with 44% (S) and 49% (N) of it falling during the three summer months of June through August. During these months, total precipitation ranges between 207.5 mm (S) and 222.9 mm (N) (Environment Canada: http://climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html; accessed 15 August 2007).

The most common soils in the study area are fine-textured gray luvisols and, to a lesser extent, brunisols, gleysols, and regosols (Green and Lord 1978).

Site selection was restricted to a subset of the sampling sites used in the study on the productivity of aspen stands conducted by Chen et al. (1998) in the BWBSmw zone. In this study, the authors examined the relationships between aspen height growth and site quality as well as foliar nutrients, to predict the productivity of aspen stands. Productivity was thereby related to a site index (SI), defined as the mean height of dominant and codominant trees at the age of 50 years at breast height. A total of 60 almost pure and even-aged postfire aspen stands were deliberately selected to capture a variety of soil moisture and nutrient regimes. For our dendroclimatological study, we selected 15 sites from the 60 sites with the goal of covering the entire SI gradient established by Chen et al. (1998). These sampling sites were located south of Fort Nelson and west of Dawson Creek (Fig. 1). For the determination of SI within each plot, the three largest dominant trees (by diameter at breast

Table 1. Characteristics of the studied sites (data from Chen et al. 1998).

| Site | Latitude (N) | Longitude (W) | Site index (m) | Elevation (m above sea level) | DBH (cm) | Slope (°) | Aspect | Soil moisture regime | Soil nutrient regime |
|------|--------------|---------------|----------------|-------------------------------|----------|-----------|-----------|----------------------|----------------------|
| A15 | 58°35' | 122°40' | 26.93 | 450 | 19.0 | 12 | South | Subhygric | Rich |
| A14 | 56°08' | 121°23' | 25.06 | 630 | 26.1 | 3 | South | Subhygric | Rich |
| A13 | 58°35' | 122°40' | 22.79 | 450 | 14.0 | 0 | - | Mesic | Poor |
| A12 | 55°48' | 122°12' | 22.61 | 750 | 29.5 | 8 | South | Subhygric | Rich |
| A11 | 58°07' | 122°44' | 22.45 | 525 | 17.9 | 2 | Northeast | Submesic | Medium |
| A10 | 57°51' | 122°51' | 21.45 | 750 | 20.3 | 15 | East | Mesic | Medium |
| A09 | 55°47' | 122°49' | 20.41 | 740 | 24.4 | 1 | West | Mesic | Medium |
| A08 | 56°12' | 121°11' | 20.24 | 630 | 16.6 | 5 | Southwest | Mesic | Medium |
| A07 | 58°10' | 122°44' | 19.94 | 525 | 13.9 | 2 | Northeast | Submesic | Medium |
| A06 | 55°43' | 121°22' | 17.23 | 710 | 17.0 | 6 | Southwest | Mesic | Poor |
| A05 | 55°43' | 121°21' | 15.48 | 710 | 13.9 | 2 | East | Submesic | Poor |
| A04 | 55°43' | 121°22' | 15.43 | 710 | 12.3 | 2 | South | Mesic | Poor |
| A03 | 55°48' | 122°10' | 12.82 | 750 | 15.0 | 5 | West | Submesic | Poor |
| A02 | 55°48' | 122°07' | 10.83 | 750 | 13.5 | 40 | South | Submesic | Poor |
| A01 | 55°48' | 122°09' | 6.65 | 750 | 8.1 | 0 | - | Submesic | Very poor |

Note: Sites are ordered according to decreasing site index values from top to bottom.

height, DBH) with no visible evidence of growth abnormalities or damage were felled for stem analysis. Site index (height at 50 years) values varied between 6.65 m (S) and 26.93 m (N), mean DBH varied between 8.1 and 29.5 cm, and the altitude of the sampling sites ranged from 450 to 750 m a.s.l. (Table 1). Most of the sites possessed a flat slope with a southern or western aspect. Low SIs were generally associated with relatively dry and poor soils, whereas the productive stands were characterized by rich and moist soils. In general, most productive sites were found in the northern part of the study area, where summer is characterized by a higher temperature (by about 1.6 °C) and a slightly wetter climate. However, the second and fourth most productive sites (A14 and A12, respectively) were located in the southern part, close to sites that were generally less productive.

Data collection and chronology development

At each site, two cores were sampled at breast height from approximately 15 dominant and undisturbed living aspen trees during October 2003. At sites A01 and A02, five and seven discs were also collected, respectively. The samples (cores and discs) were prepared for dendrochronological analysis using a belt sander, and razor blades and chalk were used, where necessary, to enhance the contrast between annual growth rings. Each sample was cross-dated using a simplified skeleton-plot method (Yamaguchi 1991) before measuring ring width with a Velmex measuring system (accuracy of 0.001 mm). Dating accuracy was both statistically and visually verified using the programs COFECHA (Grissino-Mayer 2001) and TSAP-Win Professional, version 0.30 (Rinntech, Heidelberg, Germany). Individual series that did not correlate well with their mean site chronology ($r < 0.4$) were eliminated, resulting in a total of 325 well cross-dated measurement series that were used for further analysis (Table 2).

The ring-width chronologies were developed using the program ARSTAN (Cook 1985). The raw measurements were first detrended to remove long-term variations in ring widths that are related to age or stand dynamics (Fritts 1976; Cook et al. 1990a). Based on the 67% criterion of Cook et al. (1990a) that was applied to the mean length of

all the series, we chose a cubic smoothing spline with a 50% cut-off at a 40 year wavelength to standardize the measurement series. The resulting indexed ring-width series, which retained high-frequency growth variations, were then prewhitened by autoregressive modeling to eliminate autocorrelation. The site residual chronologies were then obtained by averaging the individual indexed series of each site using a robust biweight mean, which reduces the influence of outliers and enhances the common signal of the data (Cook et al. 1990b). Finally, the 15 residual chronologies were cross-dated with the dating accuracy being verified amongst the sites.

Dendroclimatic analysis

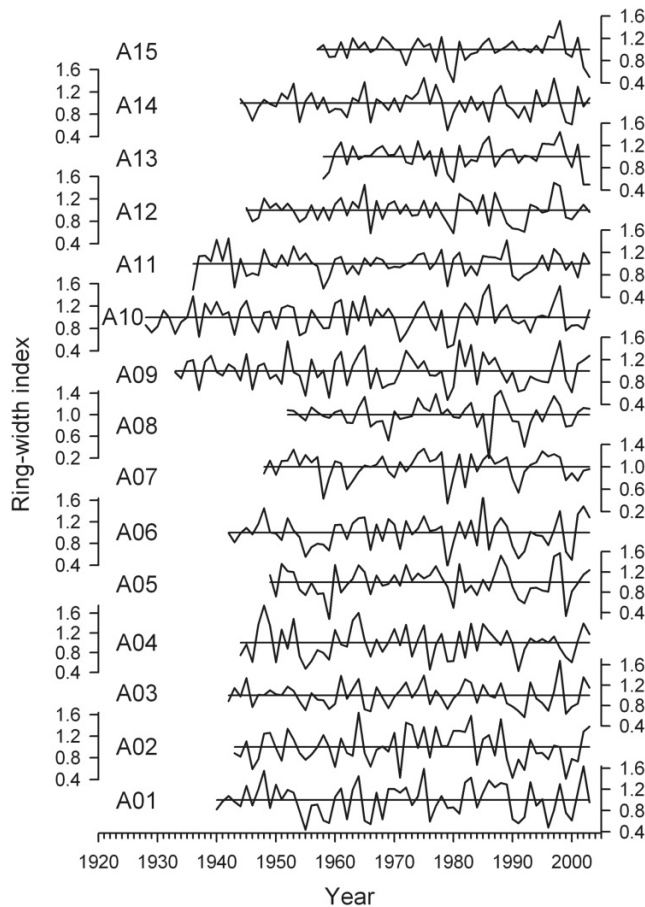
The interannual, high-frequency, responses of radial growth to climate were assessed using Pearson's correlation coefficients (Fritts 1976; Fritts and Guiot 1990) calculated between residual chronologies and climate variables using the software package DENDROCLIM2002 (Biondi and Waikul 2004). In contrast to other programs used in dendroclimatology, this program uses bootstrapping to test the significance of the correlation coefficients at the 0.05 level, which increases the accuracy of the results. The correlations were performed over the 1952–2003 interval, except for the slightly shorter chronologies A13 (1962–2003) and A15 (1958–2003), whose starting years corresponded to the first year with a subsample signal strength of at least 85% (Briffa and Jones 1990). The observation of “white rings”, i.e., narrow and pale-colored tree rings mainly caused by severe, early season insect defoliation (Hogg et al. 2002b; Sutton and Tardif 2005) in samples from the five northernmost stands suggests that growth in these stands was affected by major outbreaks of the forest tent caterpillar (*Malacosoma disstria* Hbn.), because these white-ring years correspond with known outbreak years in nearby northwestern Alberta (Hogg et al. 2002a, 2005). Thus, the years 1971 (A10), 1979 (A07, A10, and A11), 1980 (A07, A10, A13, and A15), and 2003 (A13 and A15) were removed from the dendroclimatic analysis of the corresponding chronologies to further minimize ring-width variations not related to climate.

Table 2. Descriptive statistics of the trembling aspen residual chronologies.

| | A15 | A14 | A13 | A12 | A11 | A10 | A09 | A08 | A07 | A06 | A05 | A04 | A03 | A02 | A01 |
|---|-------|-------|-------|------|-------|-------|-------|-------|-------|-------|-------|-------|------|-------|-------|
| First year of chronology | 1957 | 1944 | 1958 | 1945 | 1936 | 1928 | 1933 | 1952 | 1948 | 1942 | 1949 | 1944 | 1942 | 1942 | 1940 |
| First year with subsample signal strength >85% | 1958 | 1944 | 1962 | 1946 | 1950 | 1930 | 1934 | 1952 | 1949 | 1942 | 1949 | 1948 | 1948 | 1945 | 1942 |
| Last year of chronology | 2003 | 2003 | 2003 | 2003 | 2003 | 2003 | 2003 | 2003 | 2003 | 2003 | 2003 | 2003 | 2003 | 2003 | 2003 |
| Chronology length (years) | 47 | 60 | 46 | 59 | 68 | 76 | 71 | 52 | 56 | 62 | 55 | 60 | 62 | 62 | 64 |
| No. of trees | 12 | 11 | 12 | 12 | 12 | 14 | 12 | 13 | 14 | 13 | 13 | 14 | 10 | 12 | 10 |
| No. of radii | 22 | 21 | 21 | 16 | 22 | 26 | 22 | 22 | 27 | 25 | 23 | 26 | 14 | 20 | 18 |
| No. of eliminated radii for cross-dating problems | 6 | 9 | 5 | 12 | 8 | 4 | 10 | 8 | 3 | 5 | 7 | 4 | 12 | 2 | 4 |
| Mean ring width (mm) | 1.96 | 1.67 | 1.27 | 1.85 | 1.48 | 1.25 | 1.25 | 1.29 | 1.23 | 1.23 | 1.06 | 0.88 | 0.78 | 0.76 | 0.46 |
| Mean sensitivity | 0.21 | 0.26 | 0.23 | 0.23 | 0.23 | 0.27 | 0.30 | 0.24 | 0.24 | 0.30 | 0.31 | 0.36 | 0.25 | 0.32 | 0.33 |
| SD | 0.20 | 0.21 | 0.22 | 0.21 | 0.20 | 0.24 | 0.26 | 0.23 | 0.22 | 0.26 | 0.28 | 0.30 | 0.22 | 0.28 | 0.29 |
| Autocorrelation order 1 ^a | 0.30 | 0.24 | 0.41 | 0.27 | 0.30 | 0.30 | 0.25 | 0.22 | 0.50 | 0.36 | 0.29 | 0.40 | 0.13 | 0.18 | 0.32 |
| Variance due to autoregression (%) ^a | 11 | 26 | 13 | 8 | 7 | 0 | 0 | 0 | 27 | 14 | 23 | 18 | 20 | 7 | 0 |
| Autoregression model | 1 | 3 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 0 | 1 | 3 |
| Common interval analysis (1952–2003)^b | | | | | | | | | | | | | | | |
| Signal to noise ratio | 16.80 | 13.54 | 14.32 | 9.46 | 11.67 | 14.47 | 25.10 | 20.04 | 10.79 | 43.06 | 27.10 | 14.25 | 8.07 | 11.05 | 19.14 |
| Expressed population signal | 0.94 | 0.93 | 0.93 | 0.90 | 0.92 | 0.94 | 0.96 | 0.95 | 0.92 | 0.98 | 0.96 | 0.93 | 0.89 | 0.92 | 0.95 |
| Principal component 1 variance (%) | 61 | 64 | 58 | 59 | 58 | 54 | 69 | 63 | 54 | 81 | 70 | 68 | 56 | 67 | 71 |
| Intercore correlation | 0.59 | 0.61 | 0.55 | 0.55 | 0.55 | 0.52 | 0.68 | 0.61 | 0.51 | 0.80 | 0.68 | 0.65 | 0.51 | 0.63 | 0.69 |
| Intertree correlation | 0.58 | 0.60 | 0.54 | 0.54 | 0.54 | 0.51 | 0.68 | 0.61 | 0.50 | 0.80 | 0.68 | 0.64 | 0.50 | 0.61 | 0.68 |
| Intratree correlation | 0.76 | 0.71 | 0.76 | 0.67 | 0.72 | 0.74 | 0.66 | 0.70 | 0.73 | 0.88 | 0.78 | 0.74 | 0.60 | 0.82 | 0.77 |

^aValues related to the standard chronology.^bFor chronologies A15, A13, and A08, the common interval analysis encompassing the maximum number of tree-ring series, starts, respectively, in 1962, 1968, and 1959.

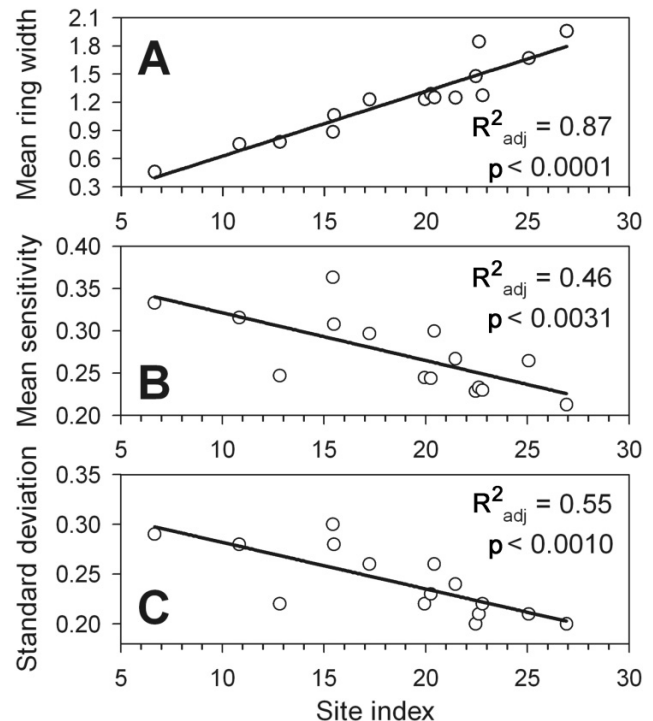
Fig. 2. Residual site chronologies ordered along the site index gradient.



The 15 residual chronologies were compared with the monthly mean temperatures and monthly total precipitation for the period beginning in May prior to the year of growth to August of the year of growth, as well as to the monthly mean Canadian Drought Code (CDC) from May to October of the previous year and from May to August of the year of growth. The CDC is a slow drying index with a time lag estimated at 52 days (Turner 1972), and it varies as a function of daily maximum temperature and total precipitation values. CDC values in the study area generally increase during the summer and towards the end of the growing season. Annual and growing season mean temperature and total precipitation, as well as annual maximum CDC, were also used in the dendroclimatic analysis. The growing season was considered to start when the mean daily temperature was $\geq 5^{\circ}\text{C}$ for five consecutive days after 1 March and to end when the minimum temperature reached -2°C or less after 1 August (MacKey et al. 1996).

To best approximate climate conditions at the different study sites, we used seven site-specific climate data sets provided by the Great Lakes Forestry Centre of the Canadian Forest Service (D. McKenney, personal communication, 2006; see Fig. 1). These data sets were created with ANUSPLIN version 4.3, a spatially explicit model using thin-plate smoothing splines to interpolate climate data from sparse weather station networks (McKenney et al. 2006). The ac-

Fig. 3. Linear regressions of (A) mean ring width in millimetres, (B) mean sensitivity, and (C) standard deviation of the ring width indices on site index. The coefficient of determination and the p value are given for each regression.



curacy of the modeled historical climate data was verified by correlating the monthly temperatures and precipitation of the data sets for the two northernmost sites (A13 and A15) with the recorded data from the nearby weather station Fort Nelson A, using all monthly values from the period 1943–2003 ($n = 732$ months). The correlations for both temperature and precipitation were highly significant (temperature: $r = 0.9995$, $p < 0.0001$; precipitation: $r = 0.9746$, $p < 0.0001$). The same verification was done with the climate data sets for sites A08 and A14, which were compared with the recorded data from the nearby weather station Fort St. John A (temperature: $r = 0.9992$, $p < 0.0001$; precipitation: $r = 0.9456$, $p < 0.0001$).

Because ANUSPLIN does not provide daily data, we used records from the Fort St. John A and Fort Nelson A weather stations to create two sets of CDC indices to be compared with the ring-width chronologies from the 10 southern and 5 northern sites, respectively (Environment Canada: <http://climate.weatheroffice.ec.gc.ca>; accessed 25 January 2004). The drought codes were computed using the CDC calculator of Girardin et al. (2004a, 2004b).

Linear regressions of the growth–climate correlation coefficients on site index were applied to assess the changes in the growth–climate relationships along the site productivity gradient.

Results

Site chronologies

The 15 residual chronologies possess different lengths and

Table 3. Cross-correlation matrix of the ring-width chronologies for the period 1952–2003 ($n = 52$ years).

| | A15 | A14 | A13 | A12 | A11 | A10 | A09 | A08 | A07 | A06 | A05 | A04 | A03 | A02 |
|-----|-------------|-------------|--------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| A14 | 0.27 | | | | | | | | | | | | | |
| A13 | 0.88 | 0.12 | | | | | | | | | | | | |
| A12 | 0.29 | 0.57 | 0.17 | | | | | | | | | | | |
| A11 | 0.19 | 0.38 | 0.23 | 0.29 | | | | | | | | | | |
| A10 | 0.59 | 0.39 | 0.54 | 0.50 | 0.46 | | | | | | | | | |
| A09 | 0.25 | 0.47 | 0.19 | 0.69 | 0.32 | 0.55 | | | | | | | | |
| A08 | −0.04 | 0.59 | −0.19 | 0.51 | 0.24 | 0.07 | 0.37 | | | | | | | |
| A07 | 0.38 | 0.44 | 0.44 | 0.26 | 0.79 | 0.47 | 0.34 | 0.19 | | | | | | |
| A06 | 0.19 | 0.56 | 0.09 | 0.67 | 0.43 | 0.50 | 0.72 | 0.42 | 0.35 | | | | | |
| A05 | 0.24 | 0.57 | 0.16 | 0.60 | 0.48 | 0.43 | 0.61 | 0.54 | 0.39 | 0.67 | | | | |
| A04 | 0.14 | 0.43 | 0.17 | 0.45 | 0.39 | 0.41 | 0.53 | 0.15 | 0.35 | 0.69 | 0.53 | | | |
| A03 | 0.08 | 0.33 | 0.01 | 0.59 | 0.32 | 0.39 | 0.67 | 0.38 | 0.28 | 0.64 | 0.55 | 0.49 | | |
| A02 | −0.25 | 0.34 | −0.33 | 0.34 | 0.15 | 0.16 | 0.45 | 0.34 | 0.14 | 0.48 | 0.39 | 0.39 | 0.64 | |
| A01 | −0.01 | 0.23 | −0.02 | 0.41 | 0.31 | 0.36 | 0.51 | 0.17 | 0.24 | 0.64 | 0.44 | 0.67 | 0.75 | 0.51 |

Note: Chronologies are shorter for sites A15 (1958–2003) and A13 (1962–2003) based on the first year with subsample signal strength >85% (see Table 2). Values given in boldface are statistically significant at the 95% level.

display a good overall synchronicity despite presenting some differences in growth patterns (Fig. 2). The length of the chronologies varied between 46 and 76 years (Table 2). The descriptive statistics show that mean ring width increases from less than 0.5 mm to ca. 2 mm along the SI gradient, with the linear regression of mean ring width on SI being highly significant (Fig. 3A). Tree-ring chronologies of low-productivity stands showed a greater year to year variation in ring width expressed both by mean sensitivity (Fig. 3B), as well as by the SD (Fig. 3C) of the growth indices. However, the common variation amongst the individual trees (variance in the first eigenvector and intertree correlation) did not change significantly along the SI gradient. Over the 1952–2003 common period, most of the 15 residual chronologies (complete series) were significantly positively cross-correlated, except those from the two northernmost sites (A13 and A15), which showed different growth patterns for some of the years (Table 3).

Growth response to climate

The results of the dendroclimatic analysis reveal that the climatic conditions of the year preceding tree-ring formation ($t - 1$) had a much greater influence on radial growth than those of the year of growth (t) (Figs. 4 and 5). The ring-width indices were negatively correlated with the temperature of the summer months of the year prior to growth (May _{$t-1$} to August _{$t-1$} and growing season _{$t-1$}) (Fig. 5A). Except for March _{t} and April _{t} , temperatures of the year of growth were generally positively associated with growth, although the correlation coefficients were rarely significant. Precipitation of the summer months preceding growth positively influenced ring width, particularly July _{$t-1$} and August _{$t-1$} . Ten and 8 of the 15 chronologies were significantly correlated with precipitation of the growing season preceding growth and total annual precipitation of the year prior to growth, respectively (Fig. 5B). Precipitation during the winter months generally displayed negative relationships and did not emerge as significant predictors, except for March _{t} that possessed a positive correlation for several chronologies. Ring width tended to correlate nega-

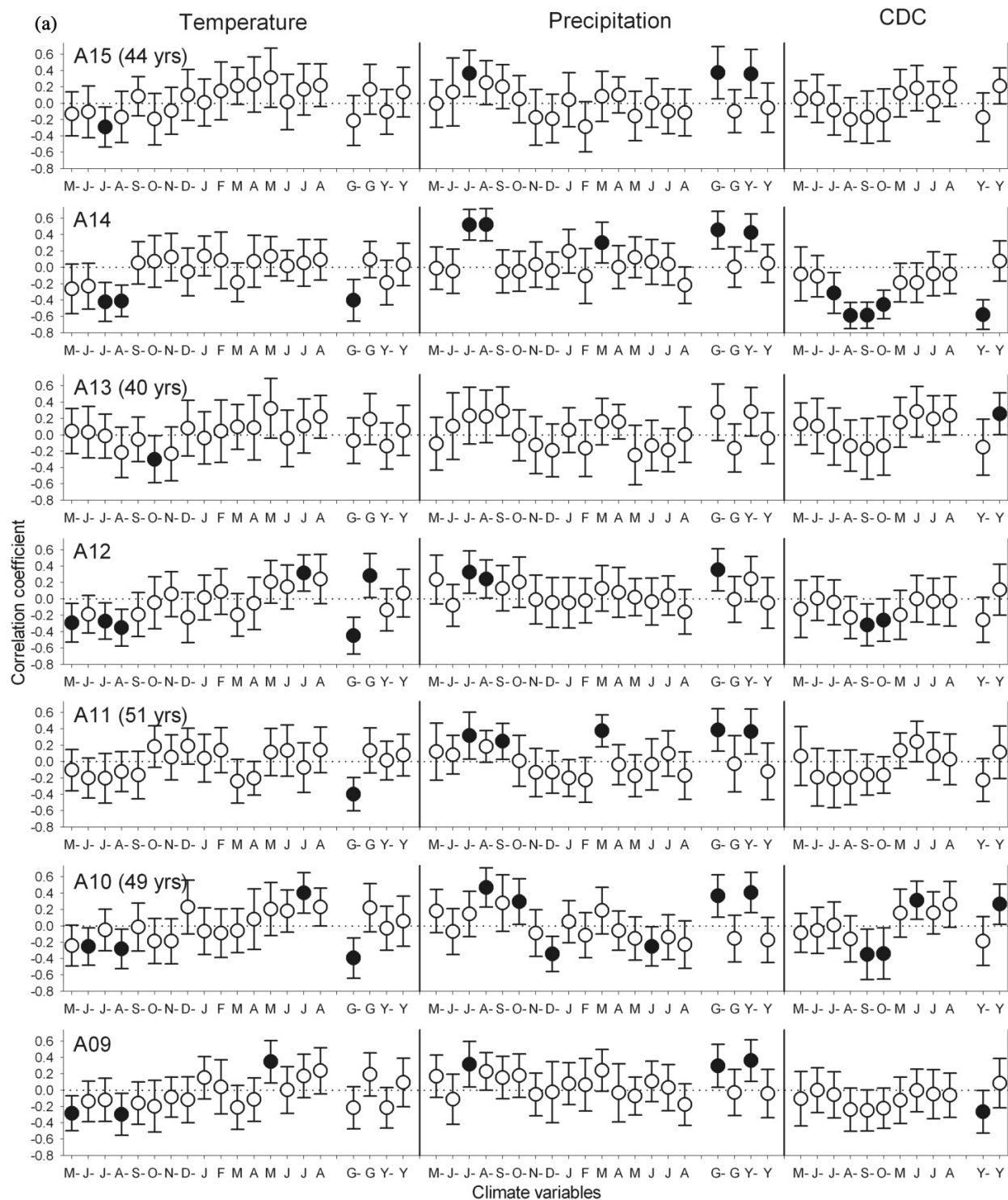
tively with the annual maximum CDC for the year preceding growth, as well as with the monthly mean CDC for August _{$t-1$} to October _{$t-1$} (Fig. 5C). For the year of growth, negative and positive correlations with the CDC were observed for about equal numbers of the chronologies, but only a few were significant (negative and positive correlation with mean annual CDC for A08 and A10, respectively).

Growth–climate relationships along the site productivity gradient

Significant trends of growth–climate correlations along the SI gradient were found for four temperature variables, with 25%–42% of the variance being explained by the linear regression models (Fig. 6). The correlation coefficients between ring width and August _{$t-1$} and annual temperature of the year prior to growth decreased with increasing SI from values close to zero to negative values. However, only August _{$t-1$} showed significant growth–climate correlation coefficients with most of the chronologies from intermediate- to high-productivity stands. June _{t} temperature also showed a negative trend, with correlation coefficient values varying from positive to ca. zero; only the chronology with the lowest SI had a significant growth–climate correlation coefficient. The opposite trend was observed for April _{t} temperatures, for which the correlation coefficients increased along the productivity gradient from slightly negative to slightly positive values. However, none of the values were significant.

Five of the six precipitation variables possessed a significant trend of growth–climate correlations and displayed a positive trend along the SI gradient (Fig. 7). The correlation coefficients between ring width and June _{$t-1$} precipitation increased from negative to slightly positive values, but none were significant. The correlation coefficients for July _{$t-1$} , August _{$t-1$} , growing season _{$t-1$} , and year _{$t-1$} precipitation all increased from approximately zero to significantly positive values for the high-productivity sites. The strongest linear relationship ($R^2 = 0.77$) was observed for growing season _{$t-1$} precipitation. This climatic variable also

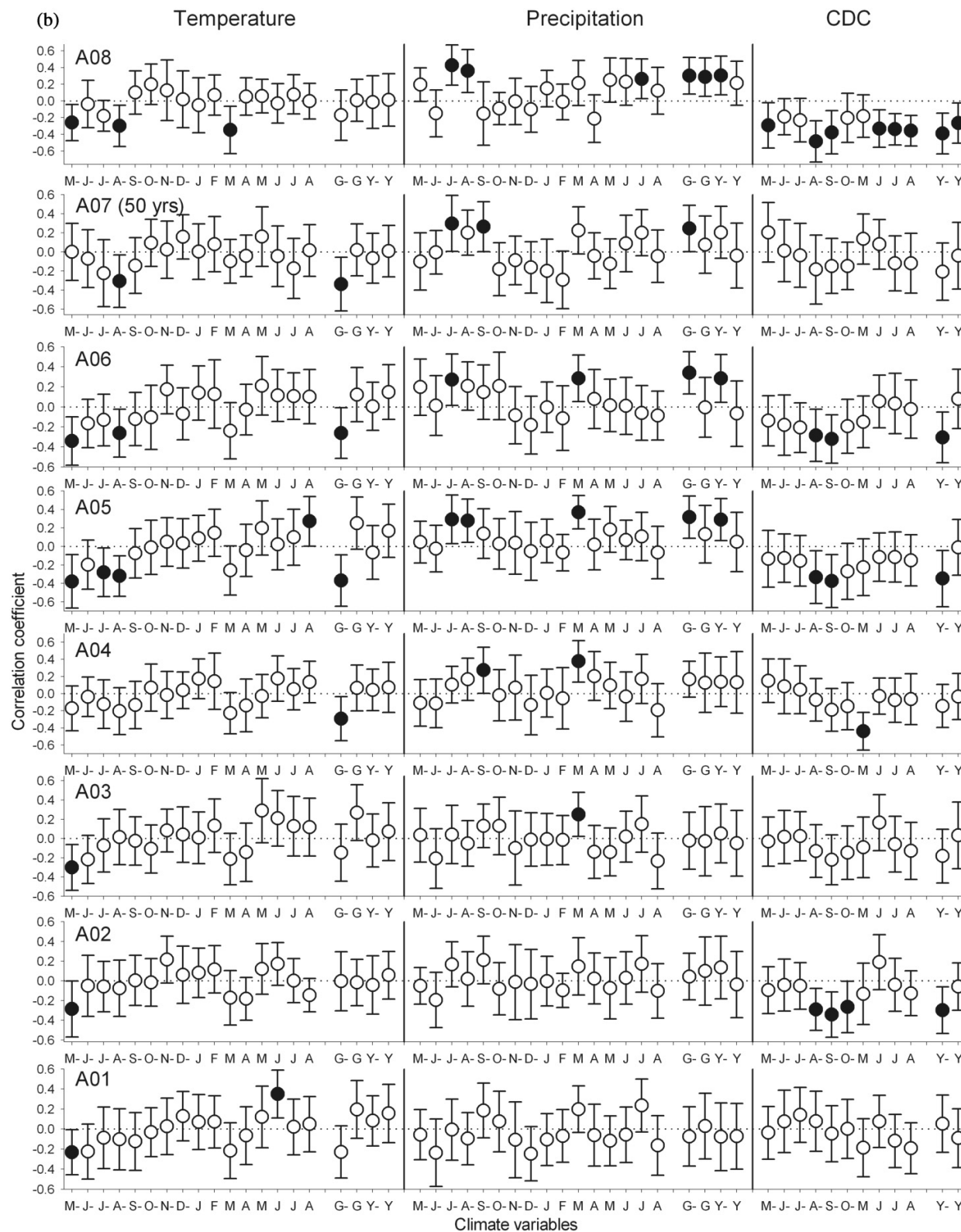
Fig. 4. Bootstrapped correlation coefficients between the trembling aspen residual chronologies and climate variables: monthly (J–D, January–December), seasonal (G, growing season), and annual (Y) values of mean temperature, sum of precipitation, and mean Canadian Drought Code (CDC), except the yearly CDC, which represents the maximum daily CDC observed between May and October. Climate variables referring to the year prior to growth are followed by a minus sign. The error bars show the 95% confidence intervals, and solid circles are significant correlation coefficients. The correlations encompass 52 years (1952–2003); exceptions due to the exclusion of the years of insect outbreaks are indicated in parentheses. (*Fig. 4 continued next page*)



showed the highest number of significant correlation coefficients (10 of 15). The correlation coefficients for July_t precipitation changed from slightly positive to slightly negative values along the SI gradient. However, the regression explained only 29% of the variation, and only one coefficient was significant.

The growth–climate correlations for the Canadian Drought Code showed a decreasing trend along the SI

Fig. 4 (concluded).



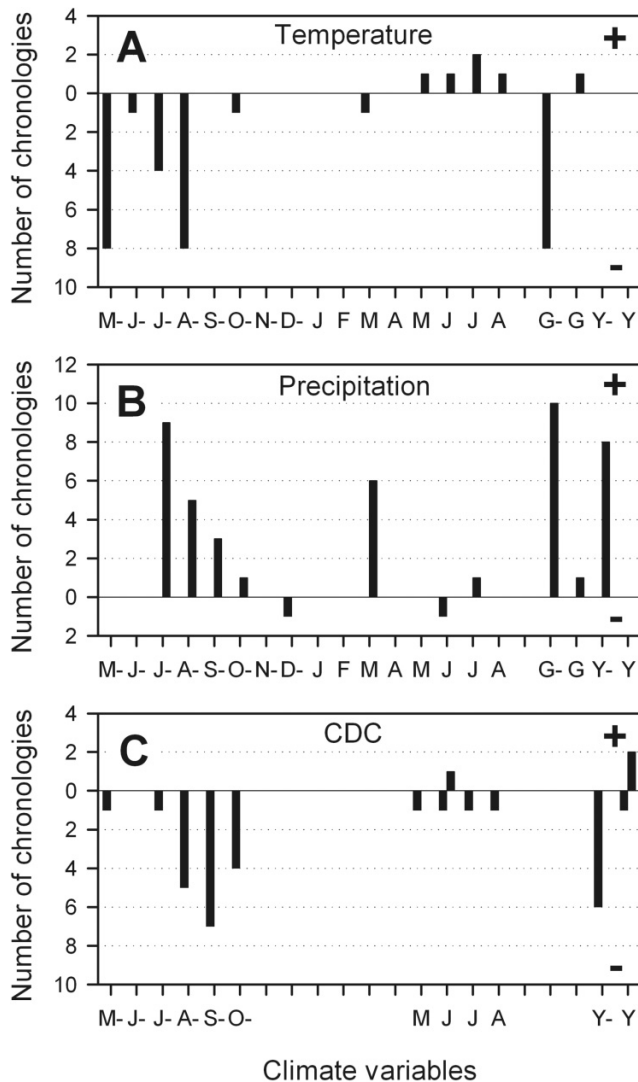
gradient with slightly positive to negative coefficients for July_{t-1} , and an increasing trend for August_t and year_t (Fig. 8). However, only a few correlation coefficients were significant, and the regressions explained only 22% and 24% of the variation for August_t and year_t, respectively.

Discussion

Growth-climate relationships

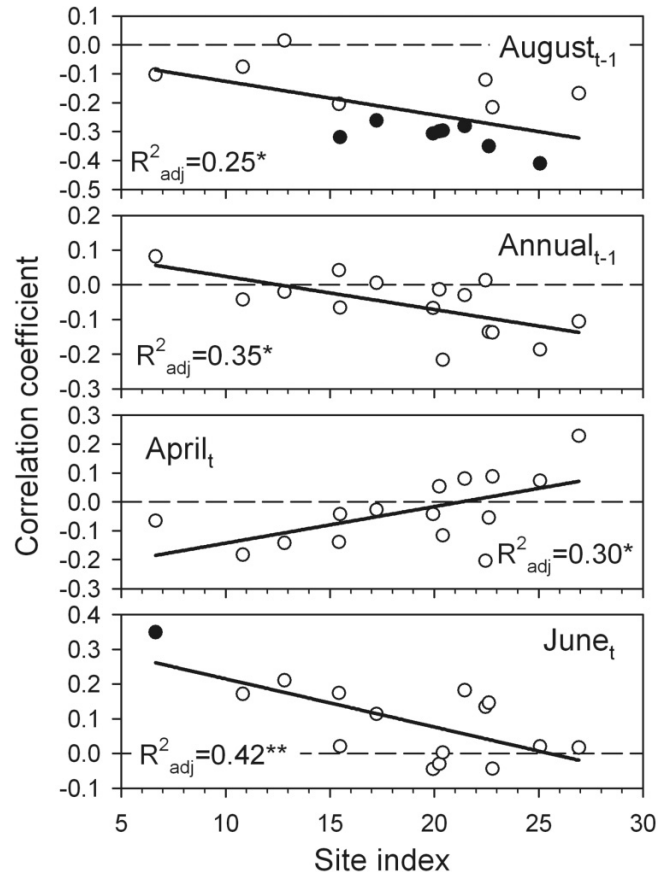
The results of the dendroclimatic analysis show that aspen radial growth variations were influenced mainly by the pre-

Fig. 5. Number of chronologies showing significantly positive or negative correlation with (A) temperature, (B) precipitation, and (C) CDC for the period 1952–2003. See Fig. 4 for abbreviations of the climate variables.



vious year's climatic conditions. Positive correlations with precipitation and negative correlations with temperature and CDC suggest that soil moisture condition is the main factor controlling aspen growth at our sites. At the boreal forest's northern tree limit, growth is particularly enhanced during warm summers and when long growing seasons occur (Jacoby and Cook 1981; Briffa et al. 1994). The aspen populations in this study lie well within their natural range limit, and their growth does not appear to be limited by temperature. The inverse relationship with temperature is not surprising, because negative correlations with summer temperature are reported for many species when moisture is the limiting factor (e.g., Dang and Lieffers 1989; Abrams et al. 1998; Archambault and Bergeron 1992). Negative effects of drought on tree growth are well reported for semiarid regions of southwestern United States (e.g., Fritts et al. 1965; Ogle et al. 2000). In a study concerning aspen growth in the boreal forest, Hogg et al. (2005) reported that drought could induce strong growth reductions with its impact lasting up to

Fig. 6. Linear regression of the radial growth–temperature correlation coefficients on site index. Solid circles are significant correlation coefficients, and open circles are not significant. Temperature variables without a significant trend along the productivity gradient are not shown. Asterisks indicate the statistical significance level: *95% and **99%.



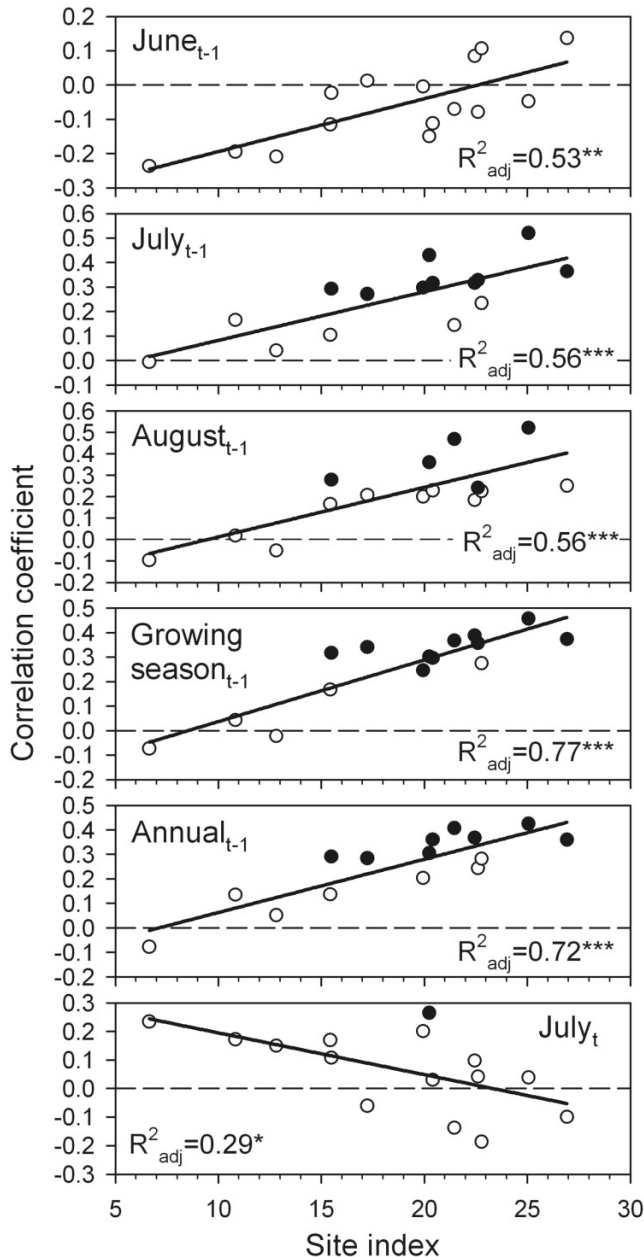
4 years following the drought event. Although not in an extremely arid environment, the location of aspen populations in the rain shadow of the Rocky Mountains likely explains the correlation with the drought signal.

The strong correlation found in our analysis between tree-ring chronologies and the previous year's climate variables (particularly precipitation) suggests that aspen radial growth may be highly influenced by stored reserves. According to Landhäusser and Lieffers (2003), trembling aspen trees use nonstructural carbohydrates stored primarily in branches and stems for foliage growth at the time of flush, whereas the more abundant root reserves are used during root growth after soil thawing in summer, as well as towards the end of the growing season. At the beginning of the growing season (well before soil has reached the threshold temperature of 5 °C; Steele et al. 1997) reserves stored mainly in the crown and stem are used for breaking buds, flushing leaves, and building new wood tissue. In addition, the tree growth of a given year may also be influenced by the still-living wood vessels produced during the past few growth seasons resulting in the autocorrelation of the ring-width series (Fritts 1976).

Growth–climate responses along the productivity gradient

Our analysis provides evidence that aspen sensitivity to

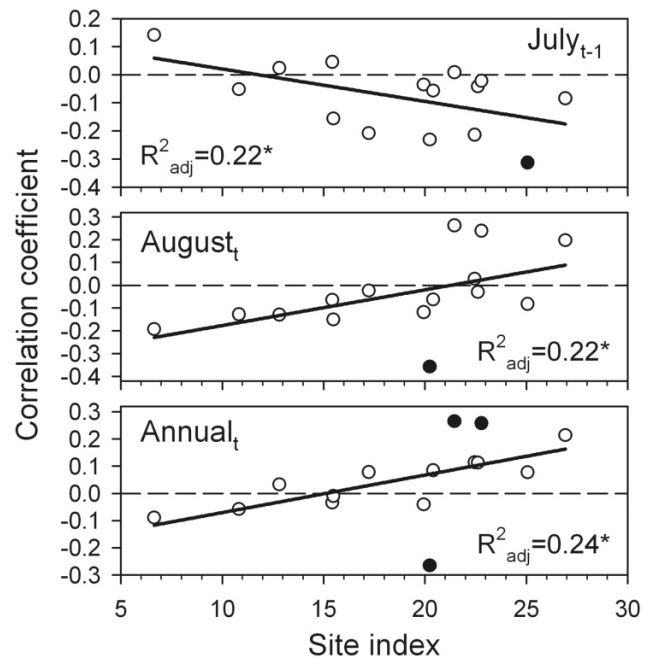
Fig. 7. Linear regression of the radial growth-precipitation correlation coefficients on site index. Solid circles are significant correlation coefficients, and open circles are not significant. Precipitation variables without a significant trend along the productivity gradient are not shown. Asterisks indicate the statistical significance level: *95%, **99%, and ***99.9%.



climate varies along the productivity gradient but that, contrary to the initial hypothesis, correlations with climatic variables are generally stronger in wetter and more productive sites.

In general, high-productivity sites showed higher negative and positive correlations for the monthly temperature and precipitation variables of the previous year, respectively. The positive correlation with precipitation, along with the negative correlation with temperature and CDC during the summer of the year prior to growth, suggests that summer water balance limits the production of assimilates that are

Fig. 8. Linear regression of the radial growth-CDC correlation coefficients on site index. Solid circles are significant correlation coefficients, and open circles are not significant. CDC variables without a significant trend along the productivity gradient are not shown. Asterisks indicate the statistical significance level: *95%.



used for tree-ring formation in the following year, particularly at high-productivity sites. Thus, we hypothesize that the lower sensitivity to the previous year's precipitation at low-productivity sites can be explained by poorer site conditions and lower amounts of reserves allocated to the stressed trees, which likely do not allow for rapid adjustments to specific annual weather conditions. The lower sensitivity to precipitation at these sites could also be partially explained by the kind of standardization performed on tree-ring series, which does not retain low-frequency growth variations. For example, the lasting effect of severe droughts on tree-ring growth would not be fully detected, thus lowering the correlation with the precipitation variables. However, the effect of drought on growth is stronger during the year of growth and becomes weaker in the following years. Our analysis considered also the climatic variables of the year prior to growth, thus covering the period where the drought effect on growth should be stronger.

Aspen stand productivity is known to be limited by a lack of soil moisture in the boreal forest and aspen parkland of western Canada (Hogg 1999; Hogg et al. 2005). At our sites, SI depends strongly on soil moisture but also on the nutrient regime (Chen et al. 2002). Although differences in precipitation could explain a portion of the differences in SI, especially between the southern and northern sectors, aspen sensitivity to climate are highly influenced by the quality of the local substrate. In fact, trees growing in different productivity sites from the same sector (e.g., the southern sector), and therefore affected by the same climate, show different responses to climate, whereas trees growing in similar productivity sites, both in the northern and southern sectors, showed similar responses to climate.

Aspen trees growing in high-productivity sites are readily able to respond to climate, because they are not limited by water or nutrients. In contrast, aspen trees at low-productivity sites may be unable to take advantage of good weather conditions either because a lack of moisture has already caused growth cessation or because nutrients are the limiting factor. A carbon-based model simulating aspen growth at two sites in the dry transition zone between the boreal forest and the aspen parkland in Saskatchewan, Canada, also showed that aspen growth was relatively insensitive to changes in soil hydrology and transpiration (Hogg 1999).

Although low-productivity aspen stands show weaker correlations with climatic variables, they also show higher year to year variability (Fig. 3B). Although higher variability in stressed environments is commonly observed (e.g., Fritts et al. 1965; Mäkinen et al. 2000), it generally corresponds to a higher response to climatic variables. At the moment, we are not able to explain this paradox. Although we cannot exclude a climatic influence, it appears that the climatic variables used in this study (i.e., the ones that are most commonly used for dendroclimatic analysis) are not responsible for this higher year to year variability. Alternative hypotheses include nonclimatic factors, such as damage related to insects outbreaks, which can strongly influence year to year growth variations (Hogg et al. 2005) or other biotic factor related to tree health, such as root diseases (Brandt et al. 2003). Delays in responses to drought (Hogg et al. 2005) or between weather conditions and the release of nutrients in poor soils (Berninger et al. 2004) could also potentially explain why year to year fluctuations are not well correlated with climatic variables.

Conclusions

The 15 chronologies considered in this study showed complex relationships with climatic variables and some of these relationships varied significantly across the site productivity gradient. Aspen radial growth was mainly influenced by climate of the year prior to growth, with precipitation playing a key role. The strength of aspen growth responses to climate varied across stands with different productivities, likely because of differences in substrate quality. The stronger influence of the previous year's precipitation was noticed both at the northern and southern high-productivity sites and is probably linked to a high soil water holding capacity along with a richer soil nutrient regime that allow trees to produce and store more reserves and consequently start the next growing season more efficiently.

Future climate change involving changes in the precipitation regime will likely affect high-productivity sites, which possess richer soils. Furthermore, our study suggests that climatic controls on tree growth may not only increase towards the limit of a species distribution, but also towards richer and wetter stands where the nutrient regime is less of limiting factor.

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