Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses

J. Renée Brooks, Lawrence B. Flanagan, and James R. Ehleringer

Abstract: Spatial distribution and species composition of the boreal forest are expected to change under predicted climate change scenarios. Current research indicates that water limitations control the southern boundary of the central Canadian boreal forest and temperature limitations control the northern boundary. As part of Boreal Ecosystem – Atmosphere Study (BOREAS), we examined this idea by comparing annual variation in tree-ring widths and carbon isotope ratios ($\delta^{13}C$) of tree-ring cellulose with annual climatic parameters in the northern and southern boreal forest. Contrary to expectations, climate correlations with ring widths at the northern and southern sites were similar in black spruce (*Picea mariana* (Mill.) BSP). Annual growth was favored by cooler and wetter conditions. For jack pine (*Pinus banksiana* Lamb.), increased temperature and spring precipitation favored annual growth at both sites. In the north, annual growth was negatively correlated with winter precipitation. The $\delta^{13}C$ – climate correlations in *Pinus banksiana* followed current distribution theories. In the south, potential evapotranspiration explained significant annual $\delta^{13}C$ variation, whereas in the north, winter and growing season precipitation influenced annual $\delta^{13}C$ variations. Our data support the concept that moisture limits the southern range of *Pinus banksiana* and cold soil temperatures limit the northern extent. However, colder, wetter conditions favored growth of *Picea mariana* throughout its range. These observations strengthen the concept that species respond individually to climate change, not as a cohesive biome.

Résumé : La distribution spatiale et la composition en espèces de la forêt boréale devraient changer selon les scénarios de changement climatique qui sont envisagés. Les travaux de recherche en cours montrent que la forêt boréale située dans la partie centrale du Canada est limitée au sud par la disponibilité en eau et au nord par la température. Dans le cadre du projet « Étude de l'atmosphère et des écosystèmes boréaux » (BOREAS) nous avons examiné cette situation en comparant la variation annuelle dans la largeur des cernes et les ratios isotopiques ($\delta^{13}C$) du carbone dans la cellulose des cernes annuels avec les variables climatiques annuelles au sud et au nord de la forêt boréale. Contrairement aux attentes, les corrélations entre le climat et la largeur des cernes étaient semblables au sud et au nord chez l'épinette noir (*Picea mariana* (Mill.) BSP). La croissance annuelle était favorisée par des conditions plus froides et plus humides. Dans le cas du pin gris (*Pinus banksiana* Lamb.), l'augmentation de la température et les précipitations printanières ont favorisé la croissance annuelle dans les deux sites. Au nord, la croissance annuelle était négativement corrélée avec la précipitation hivernale. Dans le cas du *Pinus banksiana*, les corrélations entre $\delta^{13}C$ et le climat allaient dans le sens des théories actuelles sur la distribution. Au sud, l'évapotranspiration potentielle expliquait l'importante variation annuelle de $\delta^{13}C$ tandis qu'au nord, la précipitation hivernale et celle qui survient durant la saison de croissance influençaient les variations annuelles de $\delta^{13}C$. Nos données supportent l'idée que l'humidité limite l'aire de distribution du *Pinus bankasiana* au sud et que les températures froides du sol limitent son étendue vers le nord. Cependant, des conditions plus froides et plus humides favorisent la croissance du *Picea mariana* partout dans son aire de distribution. Ces observations renforcent l'idée que les espèces réagissent individuellement au changement climatique et non comme un biome cohésif.

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Introduction

Because boreal forests store vast amounts of organic carbon, they are extremely important in understanding the global carbon budget (Apps et al. 1993). Recently, research efforts have focused on understanding how boreal forests interact with the atmosphere and how the distribution of these forests will change in response to climate change (Bonan et al. 1995; Sellers et al. 1995; Price and Apps 1996). Past research indicates that the northern boundary of the boreal forest is affected by temperature (Shugart 1984; Earle et al. 1994; Briffa et al. 1995). However, Bonan and Sirois (1992) found that air temperature did not have a direct affect on tree growth, suggesting that the correlations found in the past may be related to more

complex ecological processes. The southern boundary of the boreal forest in central and western Canada has been related to moisture limitations and fire frequency (Hogg 1994).

The goal of Boreal Ecosystem – Atmosphere Study (BOREAS), a large-scale international interdisciplinary experiment in the boreal forests of Canada, was to improve our understanding of boreal forests: how they interact with the atmosphere, how much CO_2 they can store, and how climate change may affect them. One BOREAS task was to assess the sensitivity of the boreal forest biome to changes in the physical climate system. The BOREAS project was intensive, but of short duration (1993–1996). This was a relatively short time period for understanding processes that ultimately affect the distribution of the boreal forest. Therefore, one important component of BOREAS was a temporal perspective that integrated important processes over the last several decades or more. Activities and approaches that added the long-term perspective were (*i*) modeling studies (Price and Apps 1996), (*ii*) studies of spatial relationships between climate and vegetation zonation that have developed over time (Hogg 1997), and (*iii*) the study of historical variation in growth and physiological charateristics using tree rings (present study).

Tree-ring research in the boreal areas has been used to understand climatic factors influencing growth over the last century. Research at the extreme northern limit of trees in the Northern Hemisphere has found that warm summer temperatures and the number of growing degree-days significantly increase the growth and productivity of these trees (Garfinkel and Brubaker 1980; Jacoby and Cook 1981; Earle et al. 1994; Briffa et al. 1995). However, studies conducted at slightly lower latitudes where the boreal forest is more contiguous have observed contrasting results. Dang and Lieffers (1989) found that growth in black spruce (*Picea mariana* (Mill.) BSP) was negatively correlated with summer temperatures, but positively related to summer precipitation. Larsen and MacDonald (1995) found that ring widths in white spruce (*Picea glauca* (Moench) Voss) and jack pine (*Pinus banksiana* Lamb.) were negatively correlated with the duration of fire weather during the summer. These different observations indicate that boreal tree growth and the climate factors influencing it are complex and perhaps unique to a species, thus meriting more investigation.

While tree-ring widths have been related to rates of productivity under past climatic conditions (Fritts 1976), the carbon isotope ratio of cellulose in annual rings also provides information relating the balance of CO_2 uptake and water vapor loss during photosynthetic gas exchange (Livingston and Spittlehouse 1996). The carbon isotope ratio of plant material is more depleted in ^{13}C than atmospheric CO_2 because of two main fractionation processes during photosynthesis. The first fractionation process occurs during diffusion of CO_2 into the leaf; $^{13}CO_2$ diffuses slower than $^{12}CO_2$. The second fractionation process occurs during carboxylation in C_3 plants; the enzyme ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) reacts with $^{12}CO_2$ molecules faster than with $^{13}CO_2$ molecules. The extent that these two fractionation processes are expressed during photosynthesis depends on leaf physiological properties (Farquhar et al. 1982, 1989) as expressed in the following equation:

$$[1] \quad \delta^{13}C_{plant} = \delta^{13}C_{air} - a - (b-a)\left(\frac{c_i}{c_a}\right)$$

where $\delta^{13}C_{plant}$ and $\delta^{13}C_{air}$ are the carbon isotope ratios of leaf tissue and atmospheric CO_2, respectively, *a* is the fractionation associated with diffusion (4.4‰), *b* is the net fractionation associated with carboxylation (27‰), and c_i and c_a are the intercellular and ambient CO_2 concentrations, respectively. The ratio c_i/c_a is important because it is a function of the photosynthetic rate and stomatal conductance. With constant $\delta^{13}C_{air}$, changes in $\delta^{13}C_{plant}$ values occur because of changes in either or both photosynthetic rate and stomatal conductance. Tree rings record the isotopic fractionation that occurs during photosynthetic gas exchange, thereby providing an integrated history of c_i/c_a (Francey and Farquhar 1982). The impact of drought and other abiotic parameters on season-long gas exchange activity is detectable as changes in the carbon isotopic composition of tree rings (Dupouey et al. 1993; Leavitt 1994; Livingston and Spittlehouse 1996). Isotopic analysis of carbon in cellulose of tree rings provides critical long-term information to extend the relatively short-term studies of BOREAS.

Our objectives were to determine temporal and spatial variability in growth and carbon isotope composition for two boreal tree species. Specifically, we were interested in whether conifers in the northern and southern parts of the boreal forest responded differently to climate variables. We hypothesized that trees in the south would respond to factors related to water stress and trees in the north would respond to factors related to temperature. In addition, we were interested in whether the two species, *Picea mariana* and *Pinus banksiana*, responded similarly to variations in climate variables. Finally, we wanted to determine whether the primary BOREAS years (1993–1994) were typical years in terms of growth and carbon isotope composition.
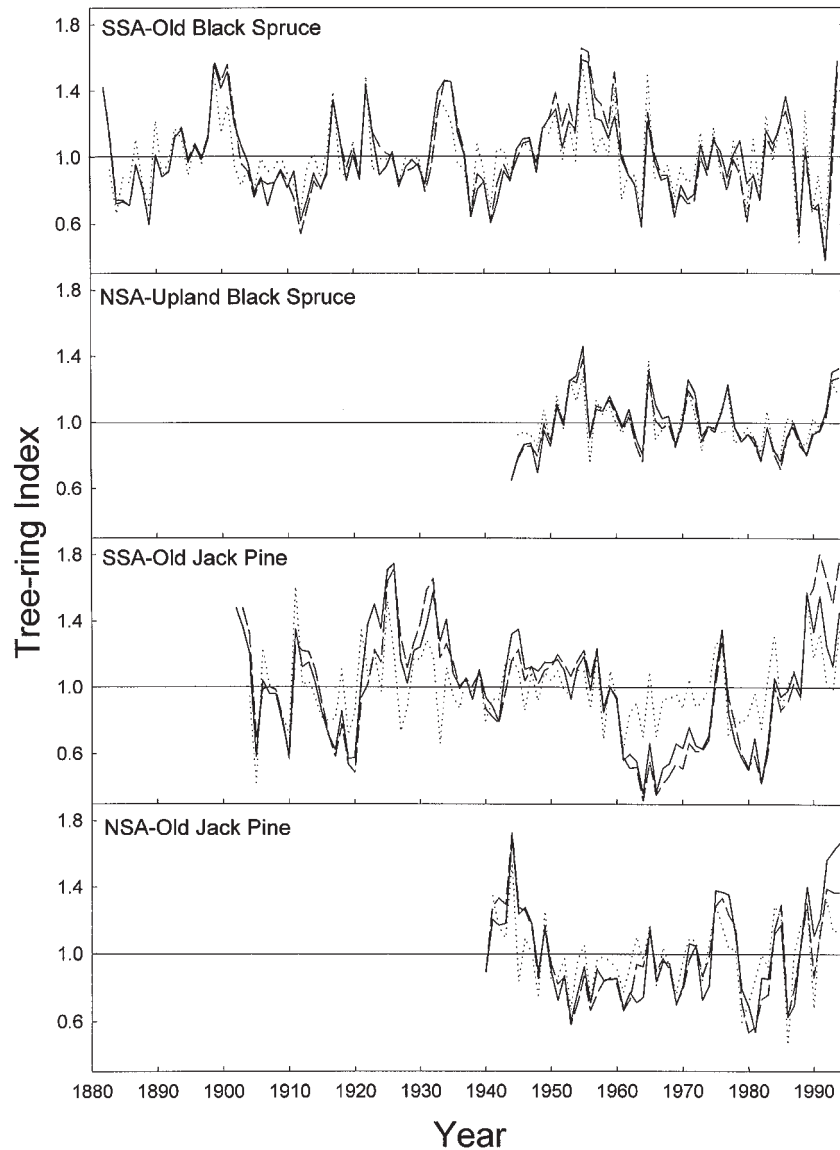
Methods

Study site
In association with the BOREAS, we conducted our study at the northern and southern limits of the boreal forest in central Canada in stands dominated by *Picea mariana* and *Pinus banksiana*. The Southern Study Area (SSA) was located 40 km north of Prince Albert, Saskatchewan, and covered an area 130 km wide by 90 km. The average annual precipitation and temperature since 1889 are 406 mm and 0.7°C, respectively. The Northern Study Area (NSA) was 100 by 80 km and included the town of Thompson, Manitoba. The average annual precipitation and temperature since 1967 (the year Thompson was founded) are 522 mm and –3.2°C, respectively.

In the SSA, the *Picea mariana* site (BOREAS site: SSA-OBS (Old Black Spruce), 53.985°N, 105.12°W) was located on poorly drained sandy–clayey soils. The oldest trees on the site were established around the mid-1800s, and the average age of dominant canopy trees is between 100 and 150 years. *Pleurozium schreberi* with patches of *Sphagnum* spp. covered the ground in an almost continuous layer throughout the site. The *Pinus banksiana* site (BOREAS site: SSA-OJP (Old Jack Pine), 53.916°N, 104.69°W) was located in a well-drained sandy area. Average stand age of canopy dominants was around 70 years. Stand density was approximately 1300 trees/ha. Green alder (*Alnus crispa* (Ait.) Pursh) was the dominant shrub in the understory, and the ground was covered with lichens and occasional patches of feather moss.

In the NSA, the *Picea mariana* site (BOREAS site: T6R5S, labeled in text as NSA-UBS (Upland Black Spruce), 55.908°N, 98.519°W) was located in an upland area with poorly drained clay soils. This stand was more productive and younger than its southern counterpart. The stand was approximately 50 years of age and was

Fig. 1. Tree-ring chronologies from each of the four sites standardized to remove long-term growth trends. These are the three chronologies generated by the ARSTAN program (Cook and Kairiukstis 1990): the solid line represents the standard chronology, the dotted line represents the residual chronology, and the dashed line represents the ARSTAN chronology.

very dense (approximately 9300 trees/ha). Similar to the southern *Picea mariana* site, the ground was covered with a deep layer of feather moss. The *Pinus banksiana* site (BOREAS site: NSA-OJP, 55.928°N, 98.622°W) was similar to the southern *Pinus banksiana* site in that the soils were sandy and well drained with an understory of *Alnus crispa* and a ground cover of lichen. However, the stand was younger (40–60 years old) and more dense (approximately 2000–3000 trees/ha) than in SSA.

At each of the four study sites, four to seven dominant trees were selected for analysis. Three of these trees were the same dominant trees used by Gower et al. (1997) for biomass analysis at the sites, so we were able to obtain disks at the diameter at breast height (DBH) and the base of live crown (BLC). Otherwise, trees were cored at DBH using an increment borer (Haglöf Inc., Långsele, Sweden). Four cores were taken from each tree, one from each of the cardinal directions. Ring widths were measured on all sampled trees, but carbon isotope analysis was restricted to *Pinus banksiana* trees. Disks from two *Pinus banksiana* trees at each site were cut into two disks; one

was kept for ring width measurements and the other was used for carbon isotope analysis.

Climate data

Climate data were obtained for both Prince Albert and Thompson from the Atmospheric Environment Service (Environment Canada) and include monthly totals of precipitation and monthly averages of daily maximum and minimum temperatures. The data date back to 1889 for Prince Albert, while the record for Thompson starts in 1967. Potential evapotranspiration (PET) and a simple climatic moisture index, precipitaion-PET (P-PET), were calculated using a simplified version of the Penman–Monteith equation that relies only on these monthly climate statistics (Hogg 1994, 1997). In addition, we compiled seasonal temperature averages and precipitation totals to use in our correlation analysis with the tree-ring carbon isotope data. The growing season was defined as May through September and winter (the dormant season) as October through April.

Table 1. Characteristics of the tree-ring chronologies developed for the four BOREAS sites.

	Picea mariana		*Pinus banksiana*	
	SSA-OBS	NSA-UBS	SSA-OJP	NSA-OJP
Number of trees	6	4	7	6
Interval	1882–1994	1944–1994	1902–1994	1940–1994
Mean ring width (±SD)	0.51±0.27	1.17±0.54	1.10±0.79	0.86±0.53
Mean sensitivity	0.239	0.168	0.235	0.241

Note: Mean sensitivity is the mean percentage change from each measured ring to the adjacent ring (Fritts 1976).

Tree-ring width chronologies

Disks and cores were air dried and sanded to enhance ring boundaries. Samples were cross-dated visually to identify common marker years and ring width patterns. In general, all ring patterns matched within a site and there was no evidence of missing rings. Ring widths were measured on a measuring stage (Fred C. Henson Co., Mission Viejo, Calif.) with a precision of 0.01 mm. On each disk, rings were measured from four locations 90° apart. Measurements from each tree were averaged to produce one chronology per tree. Individual tree chronologies were standardized to remove long-term growth trends in ring widths by fitting a smooth curve to the data. For these chronologies, a negative exponential curve was the most appropriate curve. Each ring width was divided by the corresponding fitted value producing an index series with a mean of 1. These standardized mean chronologies (standard, residual, and ARTSAN) were created using the program ARSTAN (Cook and Kairiukstis 1990) from the International Tree-Ring Data Bank Program Library (version 2.1, Grissino-Mayer et al. 1992).

Because of the limited data from Thompson, tree-ring chronologies from the northern sites were correlated with climate data from both locations. As a result of the limited degrees of freedom using the Thompson weather data, we are reporting the ring width results using Prince Albert weather data for all the sites, although both climate data sets produced similar results. We used the program PRECON (Fritts 1994) to correlate our tree-ring chronologies with the monthly climate data. Pearson correlation coefficients were calculated for monthly climate data from May in the year preceding ring formation through September in the year of ring formation, a 17-month period. We selected this time period because it includes two complete growing seasons. The year prior to ring formation may affect growth indirectly through such factors as stored carbon reserves, root formation, and bud size.

Carbon isotope analysis

We analyzed the carbon isotope ratios of cellulose for four trees from the two *Pinus banksiana* sites. Disks were dried and then sanded so that tree rings were clearly visible. Tree rings were counted and cross-dated with the cores and disks used for tree-ring width chronologies. Each year's growth was carefully separated with a razor knife under a binocular scope. Yearly wood was pooled from four sections taken at 90° from each other on the disk. Pooling samples insured that we had a representative yearly $\delta^{13}C$ value for the tree (Leavitt and Long 1984). The last 21 years of growth (1974–1994) were used for carbon isotope analysis, except for the comparison between a disk at DBH and at BLC. In this case, yearly wood was separated back to 1962, when the disk at BLC was initiated. In addition, for one tree, we separated early- and late-wood and weighted each sample so that we could calculate whole-ring values.

Samples were milled to 40 mesh and reduced to holocellulose using the method described in Leavitt and Danzer (1993). Two-milligram subsamples of the holocellulose were combusted on-line and the resulting CO_2 was analyzed on an isotope ratio mass spectrometer (Delta S, Finnigan Mat, Bremen, Germany) for $\delta^{13}C$ (see Boutton 1991 for more detail on $\delta^{13}C$ measurements and notation). All isotope analysis took place at the Stable Isotope Ratio Facility for

Environmental Research, University of Utah. The overall precision of the isotope measurements was ±0.11‰.

Regression analysis for the carbon isotope data was conducted using S-plus (version 3.3, Mathsoft Inc., Seattle, Wash.). The $\delta^{13}C$ chronologies from the two trees at each site were kept separate for regression analysis, and dummy variables were introduced into the model to test for differences between trees. Since the isotope chronologies spanned the last 20 years, we used climate data from Thompson for the northern site. We compared annual variation in $\delta^{13}C$ with monthly climate data, seasonal climate data, and estimates of PET. Climate parameters were kept in the model if they were significant at the 0.05 level. The final models were selected on the basis r^2 and F statistics.
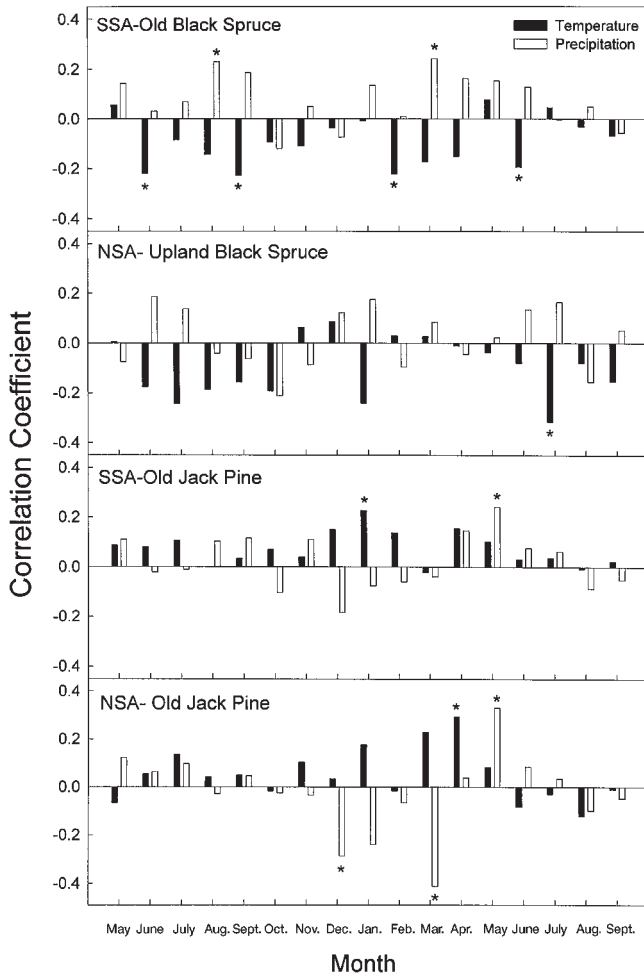
Results

Tree-ring width chronologies

The two southern sites had much older trees than the two northern sites (Table 1; Fig. 1). The oldest stand was SSA-OBS where some trees date back to the 1860s. The SSA-OBS chronology begins at 1880. The second oldest stand is SSA-OJP with the oldest trees being established around the turn of the century. On one tree, a fire scar was found dating to 1921 and other trees were established about 5–10 years after this fire event. At the sites in the north, the trees only date back to the early 1940s. Trees at NSA-OJP reached DBH a few years before the trees at NSA-UBS, so it is possible that both stands were initiated after the same disturbance.

The average annual increment for the chronologies was the smallest in the SSA-OBS site, which is not unexpected in older *Picea mariana* trees (Table 1). However, the largest average annual increment occurred in the northern *Picea mariana* site (NSA-UBS), which is also the youngest site. This site also had the lowest mean sensitivity in ring widths. The other three sites had similar values for mean sensitivity of the ring widths. For each site, there are distinct periods of above- and below-normal growth (Fig. 1), with the most recent years being above average. Both *Pinus banksiana* sites had periods of low growth in the early 1980s, and the southern site had a pronounced period of low growth in the 1960s and 1970s.

If the hypothesized weather patterns that caused the northern and southern boundaries of the boreal forest were affecting growth, we would expect correlations between tree-ring widths and climate to be very different at the two locations. However, the most striking differences with the climate correlations were between species, but not between locations, north and south (Fig. 2). Generally, there were few significant correlations with climate, but some very striking patterns did emerge from the data. Ring widths at both *Picea mariana* sites (SSA-OBS and NSA-UBS) were negatively associated with temperature, whereas ring widths at the *Pinus banksiana* sites

Fig. 2. Correlation coefficients for the four standard tree-ring chronologies with the monthly temperature and precipitation data. Correlations are calculated for the period from May the year prior to ring formation through September during the year of ring formation. A star over the bar indicates that the correlation coefficient was significant at the $\alpha = 0.05$ level.

Fig. 3. Comparison between tree-ring chronologies taken from two positions along the stem of the same tree: one chronology was taken from the BLC and the other chronology was taken at DBH. Both carbon isotope data from cellulose and tree-ring widths are presented for a dominant tree at the northern *Pinus banksiana* site (NSA-OJP). Each $\delta^{13}C$ and tree-ring width chronology represents four radii pooled from the cross section. The chronology presented in the figure begins when growth in the BLC disk was initiated in 1961.
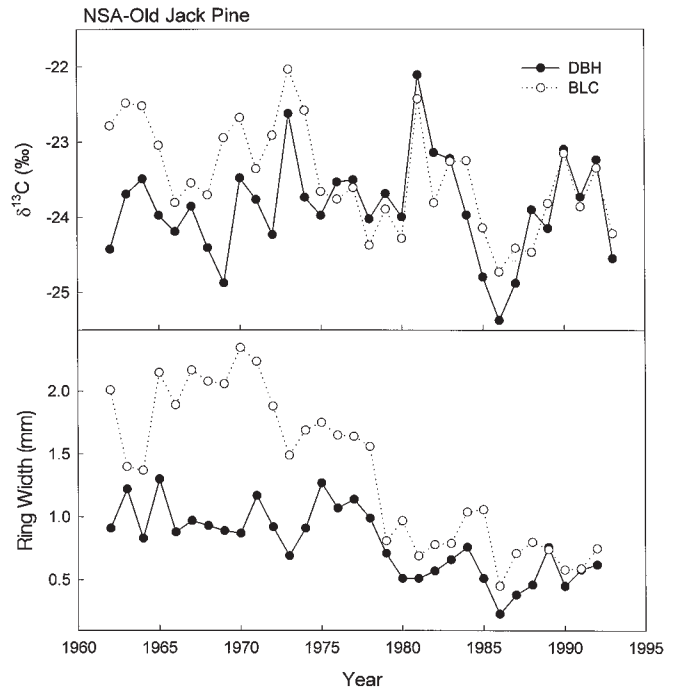

(SSA-OJP and NSA-OJP) were positively associated with temperature. In addition, ring widths at both *Pinus banksiana* sites were positively associated with spring precipitation. At the northern *Pinus banksiana* site, winter precipitation had a negative impact on ring widths. However, this winter precipitation association was not apparent at the northern *Picea mariana* site. Interestingly, ring widths at the *Picea mariana* site in the south were generally positively associated with precipitation, even though this site was the wettest site of all four sites.

Carbon isotope – ring width comparisons

Carbon isotope ratios from tree-ring cellulose add another dimension of information about the past history of a tree (Fig. 3). Comparing ring width and $\delta^{13}C$ series from two positions within the same tree, we can see several interesting patterns. First, both ring width and $\delta^{13}C$ data reflect differences in crown activity in the upper and lower canopies. Prior to 1978, growth in the BLC disk was about twice the rate of growth in the DBH disk; however, the difference between the $\delta^{13}C$ series was approximately 0.5‰. Rapid growth in the upper canopy

and slower growth near the base of the stem is a typical growth pattern in trees and can be observed in the time series of the BLC disk. The data in Fig. 3 begin when growth in the BLC disk was first initiated (1961), whereas the DBH disk dates back to 1940. The BLC series represents a growth transition from the upper active crown to below the crown, whereas the DBH disk always represents stem growth below the crown. Initially when the BLC was in the upper part of the canopy, annual increments were twice that of the DBH disk, and the $\delta^{13}C$ values were also about 0.5‰ higher. This difference in the $\delta^{13}C$ could indicate that carbon sources for bolewood production differ from the upper to the lower part of the canopy. Since carbon fixed in the upper canopy generally has a more enriched or higher $\delta^{13}C$ value than carbon fixed in the lower canopy (Brooks et al. 1997b), this pattern suggests that upper branches supply carbon to bolewood in the upper canopy. In the mid- to late 1970s, growth in the BLC disk slows and the annual increment becomes similar to that in the DBH disk and there is virtually no difference in $\delta^{13}C$ between the DBH and BLC disks. Most probably, this timing correlates with when the BLC section of the tree became part of the lower canopy rather than the upper, more active portion of the canopy. Despite the differences between the disks in terms of canopy position, the $\delta^{13}C$ series are closely matched.

The variation in ring width was not correlated with variation in $\delta^{13}C$ ratios ($p = 0.82$). For example, in 1973, $\delta^{13}C$ values peaked for both disks and this was associated with a

Table 2. Regression models for temporal variation in carbon isotope ratios at the northern and southern *Pinus banksiana* sites.

| Site | Independent variables | | | Model | | | |
	Climate variable	Effect	p	R^2	df	F	p
SSA-OJP	PET	+	0.0003				
	P-PET	+	0.006	0.43	37	7.03	0.0002
	Growing season precipitation	–	0.01				
	Growing season temperature	–	0.03				
NSA-OJP	Growing season precipitation	–	0.007				
	Winter precipitation	+	0.01	0.40	38	8.52	0.0002
	Tree		0.002				

Note: The variable effect indicates whether the variable increased (+) or decreased (–) the $\delta^{13}C$ ratio. "Tree" represents a dummy variable for the individual trees.
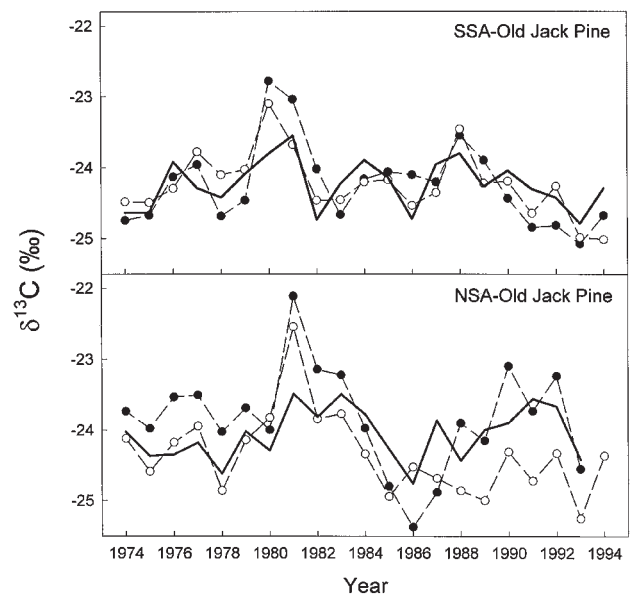
decline in ring width (Fig. 3). However, in 1981, $\delta^{13}C$ peaked again, but this time there was no associated decrease in ring width. In fact, in 1986 when there was a large decline in growth, this corresponded to the lowest $\delta^{13}C$ values for the series. Several anomalous years for $\delta^{13}C$ were noted (1986, 1981, and 1973), yet only 1986 stands out as a climate anomaly being the wettest year on record in Thompson. In 1986, annual precipitation was 670 mm, with 435 mm of rainfall occurring during the growing season. However, 1981 and 1973 were not climatically unusual. Both years had average rainfall and were slightly warmer than average, which would increase evaporative demand; however, other years were similar and did not produce such a dramatic shift in $\delta^{13}C$ values.

Climate-related changes in carbon isotopes

The carbon isotope ratios of cellulose for this study (Fig. 4) varied between –25.4 and –22.1‰ in the northern site and between –25.1 and –22.8‰ in the southern site, with an average of –24.0 (±0.7SD) and –24.2‰ (±0.5SD) for the northern and southern sites, respectively. In general, $\delta^{13}C$ values from the northern site were more variable than values from the southern site. In contrast with the ring width data, $\delta^{13}C$ patterns in the northern site were influenced by different climatic variables than the values from the southern site, and these correlations tend to support the hypothesized reason for the northern and southern boundaries of the boreal forest. Using regression analysis, climatic variables could explain 43% of the $\delta^{13}C$ variation in the south and 40% in the north (Table 2). Neither model was particularly good at predicting the extreme $\delta^{13}C$ values (Fig. 4, solid line). For example, 1980 (SSA) and 1981 (NSA) produced highly positive $\delta^{13}C$ values that the regression model could not predict. Climatically, these years do not stand out, and yet the $\delta^{13}C$ values were the most positive produced in the chronology. However, some variation in $\delta^{13}C$ was strongly associated with climate. In both the north and south, precipitation variables were more important in the regression models than were temperature variables.

At the southern sites, PET and P-PET were highly significant in the model (Table 2). In years when PET was high, $\delta^{13}C$ was also more positive, indicating greater water use efficiency (PET alone, $R^2 = 29\%$, $F = 16$, $p = 0.0003$). Interestingly, the moisture index also had a positive relationship in the multiple regression model (Table 2), which implies that when rainfall is greater than PET, $\delta^{13}C$ becomes more enriched in ^{13}C (positive), opposite to expectations. However, when considered

Fig. 4. Annual variation in $\delta^{13}C$ for two dominant trees at the southern *Pinus banksiana* sites (SSA-OJP) and two dominant trees at the northern *Pinus banksiana* sites (NSA-OJP). The solid line with no symbols represents predictions of $\delta^{13}C$ values based on the regressions in Table 2. At the NSA-OJP site, the $\delta^{13}C$ chronology with solid symbols is from the same tree as in Fig. 3 and the $\delta^{13}C$ chronology with open symbols is from the same tree as in Fig. 5.

alone, the moisture index was negatively related to $\delta^{13}C$, although only weakly so ($R^2 = 13\%$, $F = 6.1$, $p = 0.02$). The other significant climate variables in the model were growing season precipitation and temperature; when these variables were high, $\delta^{13}C$ values were more negative.

At the northern sites, PET and the moisture index were not significant. Instead, precipitation variables were the only significant climate variables in the model (Table 2). Growing season precipitation and winter precipitation affected $\delta^{13}C$ in opposite ways. High amounts of precipitation during the growing season correlated with more depleted $\delta^{13}C$ values, which was similar to the results from SSA. Abundant winter precipitation was associated with more enriched $\delta^{13}C$ values. In addition, the trees in the northern site used for $\delta^{13}C$ analysis were significantly different from each other, although the pattern of annual variation was similar (Fig. 4). One *Pinus banksiana*

Table 3. Regression models for carbon isotope ratios in late- and early-wood at the northern *Pinus banksiana* site (NSA-OJP).

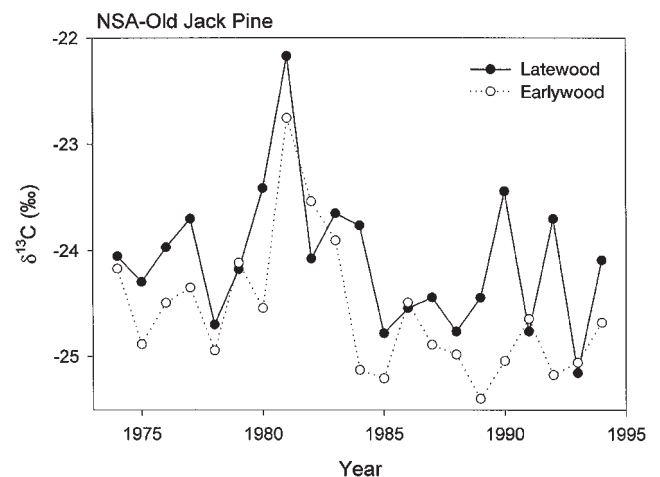|	Climate variable	Effect	R^2	df	F	p
Earlywood	Winter precipitation	+	0.22	19	5.4	0.03
Latewood	Growing season precipitation	−	0.27	18	3.5	0.05
	Winter precipitation	+				
Earlywood – latewood	P-PET	+	0.22	19	5.5	0.03

tree was consistently lower by about 0.5‰; thus, a dummy variable that represented the different trees was significant within the model.

For one *Pinus banksiana* tree at the northern site, we separated the cellulose of late- and early-wood and ran separate chronologies for each (Fig. 5). In general, the cellulose of earlywood was more depleted in ^{13}C than that in latewood. In correlating with climate variables, high amounts of winter precipitation were correlated with more enriched δ^{13}C values of earlywood cellulose (Table 3). The δ^{13}C of latewood cellulose was correlated most strongly with growing season precipitation but also with winter precipitation. In some years, the cellulose of early- and late-wood had very similar δ^{13}C values (1979, 1986, 1991, and 1993), whereas in others, they were different by over 1‰ (1980, 1984, 1990, and 1992). When regressing this difference value (early – late) against climate variables, the moisture index was the only significant variable (Table 3). In years when precipitation inputs were greater than PET, earlywood cellulose and latewood cellulose were more similar. In years when PET was greater than or equal to precipitation, latewood cellulose was much more enriched in ^{13}C than earlywood cellulose.

Comparison of 1993 and 1994 with the last 20 years

Field campaigns for BOREAS occurred in 1993, 1994, and 1996, a relatively short timeframe compared with the chronologies presented here. One of our objectives was to determine if two primary years (1993 and 1994) were typical in terms of past tree physiological characteristics, tree growth, and climate. The δ^{13}C values from the southern site were lower in 1993 and 1994 than the average δ^{13}C values by over 0.5‰ (Table 4). These values were also more depleted in ^{13}C than predicted by our regression analysis (Fig. 4), indicating that the weather variables we considered could not completely account for this downward shift. The climate variables from the southern site were about average in 1993 and 1994, except for the high amount of precipitation that fell during the 1994 growing season and the lower than average winter precipitation. In the northern site, δ^{13}C values in 1993 were more depleted in ^{13}C than average, but in 1994, values were closer to the average. Climatically in the northern site, 1993 was a typical year, whereas 1994 was dryer and colder than average.

The climate differences between 1993 and 1994 in the north produced the predicted differences in δ^{13}C between late- and early-wood cellulose using the regression models in Table 3. In 1993, late- and early-wood cellulose had similar δ^{13}C values, and precipitation was greater than PET (Fig. 5; Table 4). In 1994, PET was greater than precipitation inputs, and as the regression model indicated, latewood cellulose was more enriched in ^{13}C than earlywood cellulose.

Fig. 5. Annual variation in δ^{13}C for early- and late-wood cellulose of a dominant tree from the northern *Pinus banksiana* site (NSA-OJP).

Discussion

Increased temperature negatively affected annual growth of *Picea mariana*, whereas precipitation tended to have a positive effect (Fig. 2). Annual growth of *Pinus banksiana* responded favorably to temperature and to spring precipitation. Contrary to expectations, both species had similar climate correlations at the northern and southern sites with the exception that annual growth in *Pinus banksiana* was negatively correlated with winter precipitation only in the northern site. Carbon isotope ratios in tree-ring cellulose provided additional information to the annual growth data. Carbon isotope values were less variable than annual increments within the same tree (Fig. 3). In addition, the variation in annual increments was not correlated with the variation in δ^{13}C values, indicating that the two variables are responding to different factors. This was also evident in the climatic correlations with annual δ^{13}C values. In these correlations, there were distinct differences between the northern and southern sites. In the south, PET was a dominant factor in explaining the variation in annual δ^{13}C, whereas in the northern site, PET was not significant. In addition, δ^{13}C values in the northern site were more enriched in ^{13}C with high amounts of winter precipitation, whereas winter precipitation was not a factor for δ^{13}C values in the southern sites.

The northern boundary of the boreal forest coincides with temperature isoclines; thus, this boundary has been hypothesized to be related to temperature variables (Larsen 1980). Indeed, several studies of trees growing at their northern limit do show a significant growth correlation with summer temperatures (Garfinkel and Brubaker 1980; Jacoby and Cook

Table 4. Comparison of 1994 and 1993 with average of the last 20 years (1974–1994).

	SSA-OJP			NSA-OJP		
	Average	1993	1994	Average	1993	1994
Ring width (mm)	0.57±0.18	0.42	0.52	0.78±0.26	1.13	1.12
Cellulose δ^{13}C (‰)	−24.2±0.5	−25.0	−24.8	−24.0±0.7	−24.9	−24.4
Precipitation (mm)	430±74	427	453	501±87	428	348
Growing season precipitation (mm)	260±65	288	335	264±74	268	165
Winter precipitation (mm)	125±36	90	99	113±24	80.4	110.7
PET (mm)	488±43	439	493	372±33	336	406
P-PET (mm)	−61±104	−12.8	−40.1	130±99	91	−58
Mean annual temperature (°C)	1.0±1.1	1.5	0.7	−3.3±1.0	−2.9	−4.4
Growing season temperature (°C)	14.8±1.0	13.8	14.5	11.2±0.9	10.4	11.8
Winter temperature (°C)	−8.0±2.0	−7.2	−8.4	−13.6±1.4	−12.4	−15.9

Note: Winter is assumed to be October through April, and the growing season is May through September.

1981; Earle et al. 1994; Briffa et al. 1995). However, in our study, changes in temperature were not significantly correlated with variation in tree-ring widths. If anything, the two species had opposite responses to warmer temperature regardless of their location: *Picea mariana* had a negative response, whereas *Pinus banksiana* tended to have a positive response. Given that *Pinus banksiana* grows on the drier site and that the *Picea mariana* site had much lower soil temperatures (Brooks et al. 1997*b*), one might have expected the opposite pattern where growth in *Picea mariana* responded favorably to warmer temperatures. However, others have noted the negative association between growth in *Picea mariana* and temperature (Dang and Lieffers 1989; Larsen and MacDonald 1995). The two species also have different responses to precipitation: *Picea mariana* in the south responds favorably to precipitation throughout the year, whereas *Pinus banksiana* in the south only responds to spring precipitation. Similarly, Flanagan et al. (1997) observed from stem water δ^{18}O values that *Picea mariana* took up summer precipitation, whereas *Pinus banksiana* did not. Baldocchi et al. (1997) also noted that ecosystem gas exchange at the *Pinus banksiana* site in the south did not respond to summer precipitation events. This distinction between species rather than location at the northern or southern boundary of the boreal forest further illustrates that species will respond to climate change individually rather than as a cohesive biome (Schulze and Mooney 1994).

Carbon isotope ratios provide information that directly relates to photosynthetic gas exchange characteristics of the foliage. Annual variation in δ^{13}C in the tree rings reflects the year-to-year variation in foliage gas exchange, thereby providing a more direct link to leaf physiology than variation in annual growth rings (eq. 1, Francey and Farquhar 1982). Correlations between δ^{13}C and climate variables do reflect differences between the northern and southern sites. At the southern boundary, PET had the strongest relationship with δ^{13}C (Table 2). This correlation supports the current view that the southern boundary of the boreal forest is a function of moisture stress (Hogg 1994, 1997). In the northern site, PET was not a significant factor, but winter precipitation was significant, indicating that high snow loads may impede photosynthesis of *Pinus banksiana* through low soil temperatures in the spring. Low soil temperatures in the growing season can restrict root activity (Teskey et al. 1984). *Pinus banksiana* seedlings exposed to low soil temperatures at this critical time period do experience significant water stress (Grossnickle 1988) which would increase the δ^{13}C of carbon fixed during that time. Low soil temperatures in the early growing season would also explain the variation in ring width data where winter precipitation had a negative influence on growth. In addition, warm April temperatures and May precipitation (rain) have a positive influence on growth, and both would tend to increase soil temperatures in the early growing season.

In most of the δ^{13}C tree-ring studies, δ^{13}C values were most strongly correlated with detailed measurements of water fluxes or soil water availability. The strength of the relationship improved with the detail of the long-term climate and soil moisture data. For example, Dupouey et al. (1993) were able to explain 70% of the variation in δ^{13}C at a site where detailed climate and soil water measurements had been conducted over the last 40 years. Thus, they were able to calculate annual variation in extractable soil water that accounted for much of the variation in δ^{13}C. Livingston and Spittlehouse (1993) were able to explain 67% of the variation in δ^{13}C by calculating accumulative transpiration for a stand of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in a site that had also been intensively studied and measured over the last 17 years. McNulty and Swank (1995) were able to explain 74% of the variation in δ^{13}C with growing season soil water potential in eastern white pine (*Pinus strobus* L.) at the Coweeta Hydrological Laboratory.

However, most forest study sites do not have such detailed data available. Most have climate data similar to those obtained for this study: a summary of monthly temperature and precipitation data and, in some cases, a calculation of drought severity. Leavitt (1994) explained 46% of the variation in δ^{13}C using the mean July Palmer drought severity index for Great Basin bristlcone pine (*Pinus longaeva* D.K. Bailey) in the White Mountains. Sheu et al. (1996) found that May–October temperature accounted for 56% of the variation in δ^{13}C for Taiwan fir (*Abies kawakamii*) at a high-elevation site in Japan. These were similar to our climate correlations with δ^{13}C values ($r^2 = 0.43$ (SSA-OJP) and $r^2 = 0.40$ (NSA-OJP)). In addition, many plants function in such a way that the c_i/c_a ratio remains stable over a wide range of environmental conditions (Ehleringer 1994). If trees in this study functioned in such a way, low correlations between δ^{13}C values and climate variables would be expected. For example, Brooks et al. (1997*a*) found that the δ^{13}C of *Pinus banksiana* foliage was fairly stable both spatially

and temporally. As a result, many different climate conditions can result in an average $\delta^{13}C$ value. In some cases, monthly temperature and precipitation data may not be related to variation in $\delta^{13}C$ and therefore the c_i/c_a ratio at all. For example, Leavitt et al. (1995) found that the traditional variables of precipitation and temperature did not significantly explain any variation in a $\delta^{13}C$ chronology from a mesic forest in China.

Other climate variables besides monthly temperature and precipitation data may be significant in explaining the variation of $\delta^{13}C$ as well. For example, solar radiation during the growing season was the only variable that explained variation in tree-ring $\delta^{13}C$ values in a cool temperate deciduous forest of Japan (Hanba et al. 1996). Niemelä et al. (1997) noted that $\delta^{13}C$ values became more enriched in ^{13}C with increasing air pollution along a gradient of sulfur and nitrogen emissions. These differences between species and their correlations between $\delta^{13}C$ and climate further illustrate that species from diverse climate zones have distinct genetic controls on how the ratio of photosynthetic capacity and stomatal conductance (c_i/c_a) will vary with climatic fluctuations.

Seasonal variation in climate and $\delta^{13}C$ may also make it difficult to predict annual variation. Livingston and Spittlehouse (1996) were able to improve on their relationship between transpiration and $\delta^{13}C$ values by separating early- and late-wood in *Pseudotsuga menziesii*. They found that they could explain 93% of the variation in latewood $\delta^{13}C$ with summer cumulative transpiration. However, in our study, separating between early- and late-wood did not improve the correlation with climate variables. Although the correlations were weaker, the same climate variables were significant; earlywood $\delta^{13}C$ was most strongly influenced by winter precipitation and both winter and growing season precipitation influenced latewood $\delta^{13}C$ values. Interestingly, Livingston and Spittlehouse (1996) found much more variation in latewood compared with earlywood, whereas we found a similar amount of variation in both. In addition, they noted that latewood was often more depleted in ^{13}C than earlywood, whereas we found that latewood was almost always more enriched in ^{13}C. Leavitt (1993) also observed that latewood was generally more enriched in ^{13}C than earlywood.

General circulation models (GCMs) predict that the area from Prince Albert to Thompson will become warmer and wetter with a doubling of CO_2 (Price and Apps 1996). The different GCMs predicted that Prince Albert would increase in mean annual temperature between 3 and 8°C and that annual precipitation would increase between 10 and 100 mm. Our results indicated that any increase in temperature would have a negative effect on growth in *Picea mariana*. Also, the increases in temperature would increase PET which would negatively impact *Pinus banksiana*, particularly if the precipitation increase was on the lower side of the scale. Using the gap-phase dynamic model FORSKA2, Price and Apps (1996) predicted that both species would dramatically decline if temperature increased by 7°C but precipitation increased by only 10 mm. However, if temperature increased by 4°C and precipitation increased by 65 mm, they predicted that the biomass of both species would remain relatively constant. Both of these predictions were consistent with our findings.

In Thompson, the GCMs predicted that mean annual temperature would increase between 3 and 9°C and annual precipitation would increase between 50 and 200 mm. Our results indicated that the seasonal distribution of precipitation is more important than annual amounts. If the increase in precipitation came mainly as snow, growth of *Pinus banksiana* would decline. However, if the extra precipitation came during the growing season, growth of *Pinus banksiana* would increase. Price and Apps (1996) predicted only minor fluctuations for both species under the different climate change scenarios predicted for the north. These predictions do not include plant responses to CO_2 fertilization or changes in disturbance, both of which would be important in predicting vegetation distributions in the future (Körner 1995; Starfield and Chapin 1996). Our results and observations strengthen the idea that each species will respond individually to climate change and the boreal forest cannot be viewed as a unified biome.

Acknowledgements

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