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 le 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 du carbone dans la cellulose des cernes annuels 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 $Pinus banksiana$ 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.

[Traduit par la Rédaction]

Received October 9, 1997. Accepted January 15, 1998.

J.R. Brooks.1 Department of Biology, University of South Florida, Tampa, FL 33620-5150, U.S.A.
J.B. Flanagan.2 Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 4N1, Canada.
J.R. Ehleringer. Department of Biology, Stable Isotope Ratio Facility for Environmental Research, University of Utah, Salt Lake City, UT 84112, U.S.A.

1 Author to whom all correspondence should be addressed. e-mail: jrbrooks@chuma.cas.usf.edu
2 Present address: Department of Biological Sciences, University of Lethbridge, 4401 University Drive, Lethbridge, AB T1K 3M4, Canada.

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 characteristics 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 characteristics (Farquhar et al. 1982, 1989) as expressed in the following equation:

$$\delta^{13}C_{\text{plant}} = \delta^{13}C_{\text{air}} - a - (b - a) \frac{c_i}{c_o}$$

where $\delta^{13}C_{\text{plant}}$ and $\delta^{13}C_{\text{air}}$ 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 $c_o$ are the intercellular and ambient CO$_2$ concentrations, respectively. The ratio $c_i/c_o$ is important because it is a function of the photosynthetic rate and stomatal conductance. With constant $\delta^{13}$C$_{\text{air}}$, changes in $\delta^{13}$C$_{\text{plant}}$ 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 $c_i/c_o$ (Franey 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-OB5 (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: T6RSS, 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

© 1998 NRC Canada
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, precipitation-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.

© 1998 NRC Canada
had a representative yearly at 90° from each other on the disk. Pooling samples insured that we
a binocular scope. Yearly wood was pooled from four sections taken
Each year's growth was carefully separated with a razor knife under
tree rings were clearly visible. Tree rings were counted and cross-
d and the resulting CO₂ was analyzed on an isotope ratio mass spec-
milligram subsamples of the holocellulose were combusted on-line
and at BLC. In this case, yearly wood was separated back to 1962,
isotope analysis, except for the comparison between a disk at DBH
1994). The last 21 years of growth (1974–1994) were used for carbon
Thompson for the northern site. We compared annual variation in
δ¹³C with monthly climate data, seasonal climate data, and estimates of
PET. Climate parameters were kept in the model if they were signif-
ificant at the 0.05 level. The final models were selected on the basis
r² and F statistics.

Results

Tree-ring width chronologies

The two southern sites had much older trees than the two north-
ern sites (Table 1; Fig. 1). The oldest stand was SSA-OBS
where some trees date back to the 1860s. The SSA-OBS chron-
ology 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 be-
fore 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 aver-
age. 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 corre-
lations were between species, but not between locations, north
and south (Fig. 2). Generally, there were few significant cor-
relations 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

<table>
<thead>
<tr>
<th>Tree-ring width chronologies</th>
</tr>
</thead>
</table>
| 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 Δ¹³C 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 CO₂ was analyzed on an isotope ratio mass spectrometer (Delta S, Finnigan Mat, Bremen, Germany) for Δ¹³C (see Boutton 1991 for more detail on δ¹³C 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 Δ¹³C 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 δ¹³C 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 r² and F statistics.

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

<table>
<thead>
<tr>
<th>Characteristics of the tree-ring chronologies developed for the four BOREAS sites.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Picea mariana</td>
</tr>
<tr>
<td>SSA-OBS</td>
</tr>
<tr>
<td>Number of trees</td>
</tr>
<tr>
<td>Mean ring width (±SD)</td>
</tr>
<tr>
<td>Mean sensitivity</td>
</tr>
</tbody>
</table>

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

(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.

<table>
<thead>
<tr>
<th>Site</th>
<th>Independent variables</th>
<th>Effect</th>
<th>p</th>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$R^2$</td>
</tr>
<tr>
<td>SSA-OJP</td>
<td>PET</td>
<td>+</td>
<td>0.0003</td>
<td></td>
</tr>
<tr>
<td></td>
<td>P-PET</td>
<td>+</td>
<td>0.006</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Growing season precipitation</td>
<td>–</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Growing season temperature</td>
<td>–</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>NSA-OJP</td>
<td>Growing season precipitation</td>
<td>–</td>
<td>0.007</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter precipitation</td>
<td>+</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tree</td>
<td></td>
<td>0.002</td>
<td></td>
</tr>
</tbody>
</table>

Note: The variable effect indicates whether the variable increased (+) or decreased (–) the δ¹³C ratio. “Tree” represents a dummy variable for the individual trees.

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, δ¹³C values from the northern site were more variable than values from the southern site. In contrast with the ring width data, δ¹³C 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 δ¹³C variation in the south and 40% in the north (Table 2). Neither model was particularly good at predicting the extreme δ¹³C values (Fig. 4, solid line). For example, 1980 (SSA) and 1981 (NSA) produced highly positive δ¹³C values that the regression model could not predict. Climatically, these years do not stand out, and yet the δ¹³C values were the most positive produced in the chronology. However, some variation in δ¹³C 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, δ¹³C 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, δ¹³C becomes more enriched in ¹³C (positive), opposite to expectations. However, when considered alone, the moisture index was negatively related to δ¹³C, 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, δ¹³C 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 δ¹³C in opposite ways. High amounts of precipitation during the growing season correlated with more depleted δ¹³C values, which was similar to the results from SSA. Abundant winter precipitation was associated with more enriched δ¹³C values. In addition, the trees in the northern site used for δ¹³C analysis were significantly different from each other, although the pattern of annual variation was similar (Fig. 4).
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 \( \delta^{13}C \) values from the southern site were lower in 1993 and 1994 than the average \( \delta^{13}C \) 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, \( \delta^{13}C \) 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 \( \delta^{13}C \) between late- and early-wood cellulose using the regression models in Table 3. In 1993, late- and early-wood cellulose had similar \( \delta^{13}C \) 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.

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

<table>
<thead>
<tr>
<th>Climate variable</th>
<th>Effect</th>
<th>( R^2 )</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Earlywood</td>
<td>Winter precipitation</td>
<td>+</td>
<td>0.22</td>
<td>19</td>
<td>5.4</td>
</tr>
<tr>
<td>Latewood</td>
<td>Growing season precipitation</td>
<td>-</td>
<td>0.27</td>
<td>18</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>Winter precipitation</td>
<td>+</td>
<td>0.22</td>
<td>19</td>
<td>5.5</td>
</tr>
</tbody>
</table>

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 \( \delta^{13}C \) values, indicating that the two variables are responding to different factors. This was also evident in the climatic correlations with annual \( \delta^{13}C \) 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 \( \delta^{13}C \), whereas in the northern site, PET was not significant. In addition, \( \delta^{13}C \) 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 \( \delta^{13}C \) 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>
<thead>
<tr>
<th></th>
<th>SSA-OIP</th>
<th>NSA-OIP</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average 1993</td>
<td>1994 0.52</td>
</tr>
<tr>
<td>Ring width (mm)</td>
<td>0.57±0.18</td>
<td>0.42</td>
</tr>
<tr>
<td>Cellulose δ13C (%)</td>
<td>–24.2±0.5</td>
<td>–25.0</td>
</tr>
<tr>
<td>Precipitation (mm)</td>
<td>430±74</td>
<td>427</td>
</tr>
<tr>
<td>Growing season precipitation (mm)</td>
<td>260±65</td>
<td>288</td>
</tr>
<tr>
<td>Winter precipitation (mm)</td>
<td>125±36</td>
<td>90</td>
</tr>
<tr>
<td>PET (mm)</td>
<td>488±43</td>
<td>439</td>
</tr>
<tr>
<td>P-PET (mm)</td>
<td>–6±1±04</td>
<td>–12.8</td>
</tr>
<tr>
<td>Mean annual temperature (°C)</td>
<td>1.0±1.1</td>
<td>1.5</td>
</tr>
<tr>
<td>Growing season temperature (°C)</td>
<td>14.8±1.0</td>
<td>13.8</td>
</tr>
<tr>
<td>Winter temperature (°C)</td>
<td>–8.0±2.0</td>
<td>–7.2</td>
</tr>
</tbody>
</table>

Note: Winter is assumed to be October through April, and the growing season is May through September.
and temporally. As a result, many different climate conditions can result in an average δ13C value. In some cases, monthly temperature and precipitation data may not be related to variation in δ13C and therefore the c/f 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 δ13C chronology from a mesic forest in China.

Other climate variables besides monthly temperature and precipitation data may be significant in explaining the variation of δ13C as well. For example, solar radiation during the growing season was the only variable that explained variation in tree-ring δ13C values in a cool temperate deciduous forest of Japan (Hanba et al. 1996). Niemelä et al. (1997) noted that δ13C values became more enriched in 13C with increasing air pollution along a gradient of sulfur and nitrogen emissions. These differences between species and their correlations between δ13C 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/f) will vary with climatic fluctuations.

Seasonal variation in climate and δ13C may also make it difficult to predict annual variation. Livingston and Spittlehouse (1996) were able to improve on their relationship between transpiration and δ13C values by separating early- and late-wood in Pseudotsuga menziesii. They found that they could explain 93% of the variation in latewood δ13C 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 δ13C was most strongly influenced by winter precipitation and both winter and growing season precipitation influenced latewood δ13C 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 13C than earlywood, whereas we found that latewood was almost always more enriched in 13C. Leavitt (1993) also observed that latewood was generally more enriched in 13C than earlywood.

General circulation models (GCMs) predict that the area from Prince Albert to Thompson will become warmer and wetter with a doubling of CO2 (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 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 CO2 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

We thank Kevin Rapp for all his assistance in the field and in the laboratory, especially during cellulose extractions. A special thanks goes to Ted Hogg for providing his model of PET calculations, C.F. Kitty and C. Cook for assistance with isotope analysis, and Steve Leavitt, Hal Fritts, and Henri Grissino-Mayer for assistance with the tree-ring analysis. Nina Buchmann and Steve Leavitt provided valuable comments on an earlier draft of this manuscript. This research was supported by a grant from NASA BOREAS to J.R.E. and by grants to L.B.F. from the Natural Sciences and Engineering Research Council of Canada.

References


© 1998 NRC Canada


