

Climatic Signals in δ 13C and δ 18O of Tree-rings from White Spruce in the Mackenzie Delta Region, Northern Canada

Authors: Porter, Trevor J., Pisaric, Michael F. J., Kokelj, Steven V., and Edwards, Thomas W. D.

Source: Arctic, Antarctic, and Alpine Research, 41(4): 497-505

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1938-4246-41.4.497

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Climatic Signals in δ^{13} C and δ^{18} O of Tree-rings from White Spruce in the Mackenzie Delta Region, Northern Canada

Trevor J. Porter*
Michael F. J. Pisaric*\$
Steven V. Kokelj† and
Thomas W. D. Edwards‡

*Department of Geography and Environmental Studies, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, K1S 5B6, Canada †Renewable Resources and Environment, Department of Indian Affairs and Northern Development, P.O. Box 1500, Yellowknife, Northwest Territories, X1A 2R3, Canada ‡Department of Earth and Environmental Sciences, University of Waterloo, 200 University Avenue West, Waterloo, Ontario, N2L 3G1, Canada \$Corresponding author: michael_pisaric@carleton.ca

Abstract

Here we present the first tree-ring series (1850–2003) of stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope ratios from a high-latitude treeline site in northwestern Canada. Both $\delta^{13}C$ and $\delta^{18}O$ were measured at annual resolution from whole-ring α -cellulose of three white spruce trees (*Picea glauca* [Moench] Voss) growing in the Mackenzie Delta. There is a strong positive association between $\delta^{13}C$ and maximum summer temperatures. This relation likely results from the influence of temperature-induced drought stress on stomatal conductance. Mean summer relative humidity is also significantly correlated, inversely, with $\delta^{13}C$ reflecting its direct influence on stomatal conductance. The $\delta^{18}O$ record is strongly and positively correlated with early-spring to mid-summer minimum temperatures likely owing to the temperature dependence of $\delta^{18}O$ in precipitation and uptake of this water during the growing season. Mean summer relative humidity is also significantly and inversely correlated with $\delta^{18}O$ due to leaf water evaporative enrichment. Our $\delta^{13}C$ and $\delta^{18}O$ records contain a large amount of climate-driven variability indicating their considerable potential to infer past climate changes in the Mackenzie Delta region.

DOI: 10.1657/1938-4246-41.4.497

Introduction

The arctic climate system has experienced rapid and widespread change during recent decades, including reductions in sea ice extent and snow cover, increases in annual precipitation, and pronounced surface air warming (Serreze and Barry, 2005). Many of these changes have been attributed to anthropogenic forcing (Overpeck et al., 1997; ACIA, 2005), but some can also be linked to natural modes of variability (Serreze et al., 2000). Regardless, recent climate change appears to be having significant impacts on northern ecosystems, including the boreal forest.

Tree-ring studies near or at boreal treeline have documented a recent change in the sensitivity of ring-width and maximum density to summer temperatures (Briffa et al., 1998; Jacoby et al., 2000; Wilmking et al., 2005; Pisaric et al., 2007; D'Arrigo et al., 2008), a phenomenon characterized as a divergence between these tree-ring properties and late 20th century temperatures at sites where summer warmth had previously been a fundamental biological limitation. Changing climate-growth relations at boreal treeline remain poorly understood partly due to sparse climate data coverage at higher latitudes and inherent difficulties in separating effects of covarying environmental factors that may also affect tree growth (D'Arrigo et al., 2008). Regardless, this phenomenon suggests that paleoclimate inferences at some highlatitude sites based on ring-width or maximum density alone may be problematic and highlights the need to explore other climatically sensitive tree-ring properties.

Stable isotopes in tree rings are sensitive to a suite of environmental variables including temperature, relative humidity, soil moisture, and irradiance (McCarroll and Loader, 2004) and, therefore, offer potential to improve understandings of past climate. Here, we report the first stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope ratio tree-ring records from a high-latitude treeline site in northwestern Canada (Fig. 1). This study gives initial insights into $\delta^{13}C$ and $\delta^{18}O$ variability in white spruce trees from a region where stable-isotope records are lacking. Our objectives are to probe the statistical relations between these records and instrumental climate data and explain their physical basis.

Theory

STABLE CARBON ISOTOPES

Stable carbon-isotope ratios of a sample are expressed as δ^{13} C values representing the 13 C/ 12 C deviation of the sample relative to the VPDB (Vienna Pee Dee Belemnite) standard in per mille (‰). The δ^{13} C of plant matter (δ^{13} C_p) (e.g., cellulose) is controlled fundamentally by the isotopic composition of atmospheric CO₂ (δ^{13} C_a) and modified by isotopic discrimination occurring during CO₂ uptake and photosynthesis as described by Farquhar et al. (1982):

$$\delta^{13}C_{p} = \delta^{13}C_{a} - a - (b - a)c_{i}/c_{a}$$
 (1)

where a is the ¹³C discrimination due to the slower diffusion of ¹³CO₂ relative to ¹²CO₂ in air (a = 4.4%), b is the ¹³C discrimination associated with Rubisco ($b \approx 27\%$), and c_i/c_a is the ratio of CO₂ partial pressures of intercellular leaf spaces (c_i) to the atmosphere (c_a). Assuming constant c_a , variations in c_i can be attributed to the balance between carbon assimilation (A) and leaf boundary layer and stomatal pore conductance (g) (Francey and Farquhar, 1982):

$$c_{\rm i} = c_{\rm a} - A/g \tag{2}$$

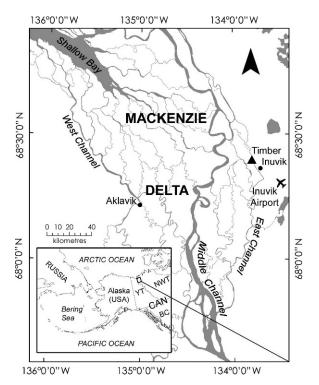


FIGURE 1. Map of the Mackenzie Delta, Northwest Territories, Canada. Timber is located along East Channel (68°24′00″N, 133°48′40″W), approximately 15 km northwest of the Inuvik Airport.

thus providing a realistic link between $\delta^{13}C_p$ and climate as both A and g are influenced by environmental variables. In moisture-limited environments, atmospheric and/or soil moisture stress may exert the strongest influence on ^{13}C discrimination in plants leading to changes in $g,c_i,$ and $\delta^{13}C$ (Brooks et al., 1998; Barber et al., 2004; Gagen et al., 2004), but where moisture is abundant, factors that control A such as light and temperature may be more important (McCarroll et al., 2003; Gagen et al., 2007).

For modern tree-ring records, however, a constant c_a is an invalid assumption. CO2 measurements from ice cores and modern air indicate a c_a rise from pre-industrial levels of ~280 ppm (Etheridge et al., 1996) to ~386 ppm at present (Tans, 2009) with the largest increases occurring during recent decades. Further, because fossil fuel burning releases isotopically light carbon, $\delta^{13}C_{a}$ has decreased over time, a process known as the "Suess-effect" (Keeling, 1979). The changes to $\delta^{13}C_a$ and c_a imply that tree rings may exhibit declining $\delta^{13}C$ values over time unrelated to climate variability. Fortunately, the Suess-effect can be removed from δ¹³C_p records using δ¹³C_a correction values available in McCarroll and Loader (2004). However, some Suess-corrected tree-ring records may still exhibit low δ^{13} C values towards the late 20th century, apparently associated with rising c_a (Treydte et al., 2001; Waterhouse et al., 2004; Gagen et al., 2007). There is no perfect correction for effects of rising c_a on $\delta^{13}C_p$, but empirically constrained corrections offer some promise (McCarroll et al.,

STABLE OXYGEN ISOTOPES

Stable oxygen-isotope ratios are expressed as $\delta^{18}O$ values signifying the $^{18}O/^{16}O$ deviation of the sample relative to the VSMOW (Vienna Standard Mean Ocean Water) standard in per mille. The $\delta^{18}O$ of plant cellulose ($\delta^{18}O_c$) reflects the $\delta^{18}O$ of water

in which cellulose and its precursors are formed, mainly a function of the $\delta^{18}O$ of source water ($\delta^{18}O_s$) and leaf water evaporative enrichment ($\Delta^{18}O_e$):

$$\delta^{18}O_c = \delta^{18}O_s + f\Delta^{18}O_e + \varepsilon_{wc}$$
 (3)

where $\varepsilon_{\rm wc}$ is the isotopic exchange between carbonyl oxygen of cellulose precursors and surrounding water ($\varepsilon_{\rm wc} \approx 27\%$) (DeNiro and Epstein, 1981; Sternberg et al., 1986) and f is the so-called "dampening factor" which accounts for processes that work to nullify leaf water enrichment signals (e.g., the Péclet effect or reequilibration of cellulose precursors with unaltered source water following sugar export from the leaf) (Farquhar and Lloyd, 1993; Saurer et al., 1997; Roden et al., 2000; Barbour et al., 2005). Values of f may vary between 0.3 and 0.5 (Saurer et al., 1997; Roden et al., 2000) and allow for the preservation of $\Delta^{18}O_{\rm e}$ signals in $\delta^{18}O_{\rm c}$ (Edwards and Fritz, 1986; Robertson et al., 2001; Anderson et al., 2002; Barbour et al., 2002).

Leaf water ¹⁸O enrichment depends largely on the δ^{18} O of atmospheric vapor (δ^{18} O_v) and δ^{18} O_s, and the ratio of ambient to intercellular vapor pressure (e_a/e_i):

$$\Delta^{18}O_e = \varepsilon_k + \varepsilon^* + (\delta^{18}O_v - \delta^{18}O_s - \varepsilon_k)e_a/e_i$$
 (4)

where ε_k accounts for the diffusion difference between $H_2^{18}O$ and $H_2^{16}O$ during their movement through the stomata ($\varepsilon_k = 32\%$) and laminar boundary layer ($\varepsilon_k = 21\%$), and ε^* is the depression of water vapor pressure by $H_2^{18}O$ ($\varepsilon^* = 9.1\%$ at 25 °C and 9.5% at 20 °C) (Dongmann et al., 1974; Saurer et al., 1997; Roden et al., 2000; Barbour et al., 2002). Ambient relative humidity is often tightly coupled with e_a/e_i and, therefore, $\Delta^{18}O_e$ (Roden et al., 2000; Barbour et al., 2002; Helliker and Ehleringer, 2002).

Because the $\delta^{18}O$ of precipitation, and to a large extent $\delta^{18}O_s$, at mid- to high latitudes covaries seasonally and annually with local air temperature (Dansgaard, 1964; Rozanski et al., 1993; Fricke and O'Neil, 1999), many tree-ring studies have provided good evidence for the use of $\delta^{18}O_c$ as a proxy for temperature (Libby et al., 1976; Burk and Stuiver, 1981; Barbour et al., 2001). However, where the effects of both temperature and relative humidity are strongly embedded in $\delta^{18}O_c$, it may be possible to tease apart their separate influence if change in $\delta^{13}C_p$ is also considered (Saurer et al., 1997; Edwards et al., 2000, 2008; Scheidegger et al., 2000; Barbour et al., 2002).

Materials and Methods

STUDY AREA AND SITE DESCRIPTION

The Mackenzie Delta is a vast alluvial landform which contains the northernmost extent of white spruce in Canada (Fig. 1). Terrain in the delta is underlain by permafrost, but channel shifting, flooding, ecological succession and snow accumulation influence the local variation in permafrost thickness and temperature (Mackay, 1963; Smith, 1975). Old-growth spruce forests develop on delta surfaces that have been cryostatically uplifted above the level of regular flooding (Kokelj and Burn, 2005). Fire has an important ecological role in boreal forests (Black and Bliss, 1978), but wildfire in the Mackenzie Delta is rare resulting in the development of old-growth forests and preservation of standing deadwood (Pearce et al., 1988; Kokelj and Burn, 2004).

During winter months, the Mackenzie Delta is dominated by cold, dry arctic air (Burns, 1973; Dyke, 2000). Summers are short but may be relatively warm as arctic high pressure retreats northward allowing low-pressure systems from the North Pacific

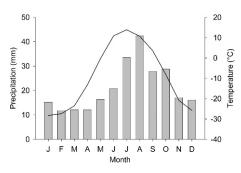


FIGURE 2. Climograph representing mean monthly temperature (line) and total precipitation (bars) recorded at the Inuvik Airport (1957–2003).

and Beaufort Sea to move into the area (Dyke, 2000). During 1957–2003, mean annual, January, and July air temperatures for Inuvik were -9 °C ($\sigma = 1.5$ °C), -28.3 °C ($\sigma = 4.7$ °C), and 13.9 °C ($\sigma = 1.8$ °C), respectively (Fig. 2). Annually, Inuvik receives approximately 254 mm ($\sigma = 48$ mm) of precipitation, with nearly 70% falling as snow.

White spruce trees were sampled from a spruce/feathermoss forest site (Timber) approximately 5 km northwest of Inuvik along East Channel (Fig. 1). The soil is fine-grained alluvial silt and the terrain is approximately 5 m above sea level. Trees at this site grow in an active layer ranging from 40 to 70 cm in thickness, but an aggrading permafrost table may effectively anchor the roots of some trees in permafrost (Kokelj and Burn, 2004). Liquid water is not available to the root system until the active layer has thawed in late spring. The study site is prone to ice-jam flooding approximately once every five years (Kokelj and Burn, 2005). Flooding may promote active layer thaw so that tree-growth commences earlier than on adjacent upland terrain during flood years.

SAMPLING AND ISOTOPIC MEASUREMENT

In August of 2004, 72 tree cores were collected from 36 trees at Timber (2 cores/tree; opposite sides of the tree) using Hagloff increment borers (internal diameter of ~4.3 mm). Of the cores collected, only six cores from three trees were used to develop δ^{13} C and δ^{18} O chronologies. Cores with relatively large ring-widths were preferentially selected to ensure adequate biomass for isotope analysis; however, many rings from 1975-2003 still did not yield sufficient material due to low wood production. Longevity was also a criterion for core selection so that the isotope chronologies would span 1850-2003. The innermost rings of the selected trees were dated to 1775, 1823, and 1846; however, these dates likely underestimate their actual age because the cores were not collected at ground level. Prior to isotope analysis, cores were visually crossdated and measured using a Velmex tree-ring measuring system. Cross-dating was later verified using COFECHA (Holmes, 1983). The six cores selected for isotope analysis were all highly correlated with the master ring-width series (r = 0.66, 0.62, 0.64,0.68, 0.67, and 0.70; p < 0.001). Standard ring-width indices (RW) for these trees were developed in ARSTAN (Cook, 1985).

The six sample cores were separated into their annual wholering units under magnification using a Nikon SMZ-1000 stereomicroscope and a scalpel. For each tree, two corresponding annual rings (i.e., from different radii but from the same tree and year) were pooled to yield three individual chronologies spanning 1850–2003. The sample wood was pulverized to a homogenous mixture of very fine particles using a Retsch MM200 Mixer Mill and purified to α -cellulose in open test tubes, helping to further homogenize the wood mixture. The chemical procedure, adapted from Sternberg (1989), included: a solvent extraction to remove lipids, resins, and tannins; bleaching to remove lignin; and alkaline hydrolysis to remove xylan, mannan, and other non-glucan polysaccharides.

Isotope ratios were measured at the Environmental Isotope Laboratory, University of Waterloo. For $\delta^{13}C$, samples were combusted to CO_2 in a Carlo Erba CN Elemental Analyzer interfaced to a GV Isochrom CF-IRMS (Continuous Flow–Isotope Ratio Mass Spectrometer). For $\delta^{18}O$, samples were pyrolyzed to CO in a HEKAtech furnace linked to an elemental analyzer (EA3028) and GV Isoprime CF-IRMS. Blanket precisions for $\delta^{13}C$ and $\delta^{18}O$ were $\pm 0.2\%$ and $\pm 0.4\%$, respectively.

CLIMATE DATA AND STATISTICAL PROCEDURES

Values of monthly temperature (min., mean, max.), June–August relative humidity (mean only), and total precipitation recorded at the Inuvik Airport (Environment Canada, http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html) were obtained for the climate-isotope analysis. Temperature and precipitation data cover 1957 to present, whereas relative humidity data are only available from 1961 onwards.

As a measure of signal strength between trees, 30-year running inter-correlation coefficients (RBAR) were calculated for the isotope series. The relation between mean δ^{13} C and δ^{18} O was also assessed using a 30-year running RBAR. Pearson's product-moment correlation coefficients were calculated for relations between monthly climate data and the mean isotope series to identify those months with a significant control on treering isotopic variability. In some instances, several months were combined to create seasonal climate indices and correlations between the indices, and mean isotope records were calculated. Correlations were examined at annual and supra-annual (3-yr running mean applied to climate/isotope series) resolution. Supraannual correlations are referred to as 3-yr correlations. The running mean serves to remove some annual resolution noise from the isotope series related to non-dominant environmental effects and, therefore, 3-yr correlations can help identify climate indices that are more important to lower-frequency variability. Univariate and bivariate models were then used to characterize proportions of isotopic variability explained by the dominant climate indices.

Results and Discussion

TIMBER STABLE ISOTOPE CHRONOLOGIES

Figure 3 shows the $\delta^{13}C$ (Suess-corrected), $\delta^{18}O$, and corresponding ring-width series from three trees at Timber. The $\delta^{13}C$ series (Fig. 3a) have been adjusted to a common long-term mean to avoid biasing the mean chronology during intervals where missing data points exist (e.g., 1975–1982). The $\delta^{18}O$ series (Fig. 3c) did not require any standard adjustments.

Unlike δ^{13} C tree-ring records from other high-latitude treeline sites (e.g., Gagen et al., 2007), our δ^{13} C series do not show any apparent downward trends during the late 20th century that can be attributed to rising c_a (Fig. 3a). This suggests that the gas exchange physiology of our trees may be relatively plastic, compared to other trees, allowing them to maintain a nearconstant c_i/c_a . Evidence for differential c_i/c_a responses to rising c_a was provided by Waterhouse et al. (2004) in their comparison of trees in western Europe. Furthermore, no juvenile trends were found in our δ^{13} C series, as are commonly observed in tree-ring

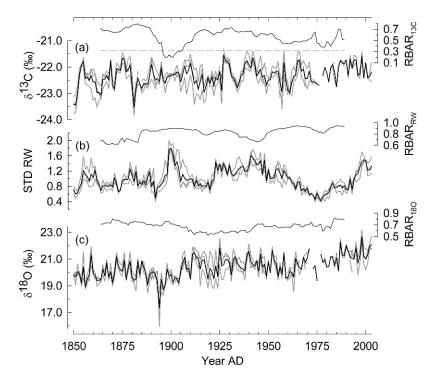


FIGURE 3. Time-series (1850-2003) of (a) δ^{13} C, (b) standardized ring-width (STD RW), and (c) δ^{18} O for three individual trees (gray lines) at Timber. Mean series are shown as thick black lines. Thirty-year running intertree correlation coefficients (RBAR) are indicated above the series they apply to. Significance levels ($p \le 0.05$) are indicated for RBAR_{13C} as a dashed line. RBAR_{RW} and RBAR_{18O} are always significant ($p \le 0.001$).

 δ^{13} C records (McCarroll and Loader, 2004), but might have been expected in the two youngest trees with inner ring dates of 1846 and 1823, but not in the eldest tree with an inner ring of 1775. Regardless, all of the δ^{13} C series are closely aligned at the start of the record (Fig. 3a).

The RBAR for $\delta^{13}C$ (RBAR $_{13C}$) is highly variable but indicates the $\delta^{13}C$ series are mostly well correlated throughout the record (Fig. 3a). RBAR $_{13C}$ is particularly high from 1864 to 1889 but declines sharply to 0.18 (not significant) in 1897 before rising to previous levels by 1915. A general RBAR $_{13C}$ decline after $\sim\!1940$ characterizes the remainder of the record. The low RBAR $_{13C}$ between 1890 and 1915 is driven mainly by the differential $\delta^{13}C$ response of a single tree (Fig. 3a). RBAR $_{13C}$ calculations for the 1890–1915 period using the two remaining trees yield higher values of 0.72–0.85 ($p \leq 0.001$). The cause of the differential response is unknown, but it appears to follow an abrupt increase in tree growth recorded by all three trees (Fig. 3b).

While the cause of the growth spike is also unknown, it may have had a prolonged (10–15 years) effect on ¹³C discrimination in one of the trees.

Overall, the strong RBAR_{13C} for most of the series lends support to the notion that a common and generally robust δ^{13} C signal is recorded among the sample trees. This is not surprising given the inter-tree radial growth similarity (Fig. 3b). The growth records suggest these trees have experienced similar growing conditions (e.g., light, temperature, humidity, and soil moisture) and that endogenous disturbance factors (e.g., tree-fall gaps) have not influenced the trees disproportionally. As such, one might expect the three trees to have similar carbon assimilation rates, stomatal conductance, and c_i/c_a leading to coherent changes in δ^{13} C.

The RBAR for $\delta^{18}O$ (RBAR_{18O}) is characterized by high initial values above 0.7 which decline to a low of 0.52 in 1919 and then recover until the end of the record (Fig. 3c). As a coarse

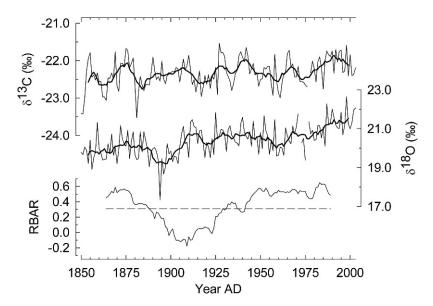


FIGURE 4. Mean δ^{13} C and δ^{18} O series for Timber. A 5-year running mean is indicated for each series. A 30-year running intercorrelation coefficient (RBAR) is used to highlight common trends between the mean δ^{13} C and δ^{18} O records. Significance level ($p \leq 0.05$) is indicated as a dashed line.

500 / ARCTIC, ANTARCTIC, AND ALPINE RESEARCH

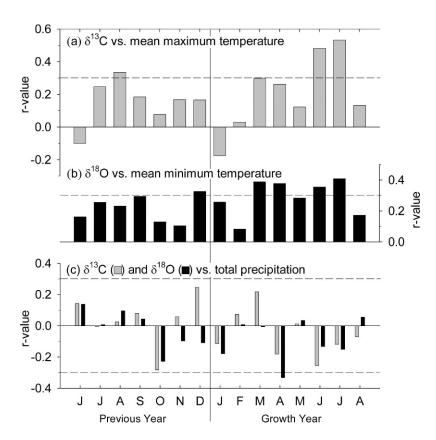


FIGURE 5. Monthly correlations (pJun–Aug) between (a) mean $\delta^{13}C$ and maximum temperature, (b) mean $\delta^{18}O$ and minimum temperature, and (c) mean $\delta^{13}C/\delta^{18}O$ and total precipitation over the period of Inuvik Airport climate data (1957–2003). Significance levels ($p \leq 0.05$) are indicated as dashed lines.

measure, the RBAR $_{18O}$ is evidence that our $\delta^{18}O$ series contain a high signal-to-noise ratio. The fact that our $\delta^{18}O$ series are better correlated with one another compared to our $\delta^{13}C$ series may relate to the fact that carbon isotope discrimination involves a number of active biological controls and, therefore, phenotypic differences may be expressed in the $\delta^{13}C$ of tree rings. Conversely, oxygen isotope discrimination is dominantly passive which may lead to greater coherence between trees.

The two mean stable isotope records ($\delta^{13}C_M$ and $\delta^{18}O_M$) contain considerable high- and low-frequency variability (Fig. 4). Furthermore, a 30-year running RBAR between $\delta^{13}C_M$ and $\delta^{18}O_M$ shows the records are significantly correlated (RBAR > 0.31, $p \le 0.05$) during the periods 1864–1888 and 1942–1989 (Fig. 4), indicating they may share some common forcing parameters (e.g., temperature or relative humidity).

TREE-RING STABLE ISOTOPE-CLIMATE RELATIONS

Relations between the isotope records and mean monthly climate were examined over the period 1957–2003 (Figs. 5 and 6). Since trees may integrate the effects of climate during previous

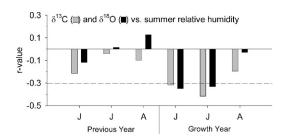


FIGURE 6. Monthly correlations (pJun-pAug and Jun-Aug) between mean δ^{13} C/ δ^{18} O and relative humidity (1961–2003). Significance level ($p \le 0.05$) is indicated as a dashed line.

growing seasons (Fritts, 1976), our analysis considered climate data from June of the previous growing season to the end of August of the growth year.

 $\delta^{13}C_M$ was most strongly associated with mean maximum temperatures (MaxT) in June and July of the current growth year and August of the previous growing season (Fig. 5a). Three-year correlations revealed that a climate index comprising $_{previous}Aug + Jun-Jul\ MaxT$ explained the greatest proportion of variability in the $\delta^{13}C_M$ record (Table 1).

The positive $\delta^{13}C_M$ -MaxT relation is consistent with $\delta^{13}C$ -temperature relations observed in a large number of field studies, but this result is not consistent with negative $\delta^{13}C$ -temperature relations commonly observed in climate-controlled growth chamber experiments (Edwards et al., 2000; Mayr et al., 2004). As discussed by Schleser et al. (1999), the common $\delta^{13}C$ -temperature

TABLE 1

Annual and supra-annual (3-year) correlations between mean Timber isotope chronologies and Inuvik Airport seasonal climate indices (MinT, MaxT, and RH). All correlations are significant at $p \leq 0.01$. Underlined coefficients are significant at $p \leq 0.001$.

Climate index	n-value	$\delta^{13}C_{M}\;(annual)$	$\delta^{13}C_{M}$ (3-year)
MaxT Jun–Jul	46	0.67	
MaxT Jun-Jul (3-year)	42		0.67
MaxT pAug + Jun-Jul	45	0.68	
MaxT pAug + Jun–Jul (3-year)	41		0.74
RH Jun-Jul	41	-0.47	<u>—</u>
Climate index	n-value	$\delta^{18}O_{M}$ (annual)	δ ¹⁸ O _M (3-year)
MinT Dec-Jul	45	0.51	
MinT Dec-Jul (3-year)	41		0.76
MinT Mar-Jul	46	0.50	
M:-T M I-1 (2)	42		0.78
MinT Mar–Jul (3-year)			

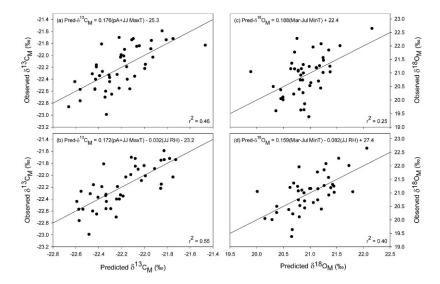


FIGURE 7. Annual resolution univariate and bivariate models of predicted $\delta^{13}C_M/\delta^{18}O_M$ based on climate variables determined to be important to $\delta^{13}C_M/\delta^{18}O_M$ variability. Univariate models (a) and (c) are calibrated with temperature data for the period 1957–2003, whereas bivariate models (b) and (d) are calibrated with temperature and relative humidity data for the period 1961–2003 since RH data are only available from 1961 onward.

discrepancy between field and laboratory studies may result from nonlinearity between temperature and biological processes, or perhaps the influence of temperature on other variables in an uncontrolled environment (Mayr et al., 2004). As was suggested by Barber et al. (2004) from studies of white spruce under similar conditions in Alaska, the $\delta^{13}C_M$ -MaxT relation observed here likely reflects the influence of temperature-induced drought stress on stomatal conductance, considering that white spruce trees in the Mackenzie Delta are growing at their ecological tolerance for minimum mid-summer precipitation (~34 mm, $\sigma=19$ mm at Inuvik, Fig. 2; ~20 mm minimum for white spruce, Barber et al., 2004).

Further, the $\delta^{13}C_M$ -MaxT relation may partially relate to temperature effects on the carbon assimilation rate. Such a relation might be expected at northern treeline where summer warmth is limited and may stimulate carbon assimilation rates, reduce c_i/c_a , and lead to higher $\delta^{13}C_M$. Moreover, air temperatures correlate well with sunlight amount and, therefore, some of the $\delta^{13}C_M$ -MaxT relation may reflect photoassimilation effects. However, such temperature-related assimilation effects are suspected to be of secondary importance to temperature-induced drought stress given the lack of summer moisture in this region available to meet white spruce moisture requirements.

The existence of a pAug MaxT signal in $\delta^{13}C_M$ can be explained as a carryover effect where carbohydrates produced at the end of a growing season are stored through winter and remobilized to initiate radial expansion at the start of the following growing season (Fritts, 1976).

 $\delta^{18}O_{M}$ was most strongly correlated with mean minimum temperatures (MinT) during several winter, spring, and summer months (Fig. 5b). Dec–Jul and Mar–Jul MinT were both significantly correlated with $\delta^{18}O_{M}$ (Table 1); however, three-year correlations reveal that Mar–Jul MinT tracks $\delta^{18}O_{M}$ variability better than Dec–Jul MinT (Table 1). The observed $\delta^{18}O_{M}$ -MinT relation is consistent with the notion that our trees inherit a strong temperature-dependent "Dansgaard" signal from the isotopic composition of soil water derived from snowmelt and summer rain. It is interesting to note that $\delta^{18}O_{M}$ -MinT correlations are similar in strength during snowfall months (i.e., Mar–May) and rainfall months (i.e., Jun–Jul) even though rainfall accounts for a greater proportion of the Mar–Jul precipitation budget (Fig. 2). Snowmelt can move into frozen soils along frost cracks or by thermally induced suction gradients (Mackay, 1983; Marsh, 1988)

and may become accessible to plants as the active layer thaws. Analogous isotopic evidence for the importance of snowmelt to soil water recharge and tree rings has been observed in oak from eastern England (Robertson et al., 2001), juniper from the Karakorum, Pakistan (Treydte et al., 2006), alpine conifers in southern British Columbia, Canada (Clague et al., 1992), and maple in southern Ontario, Canada (Buhay and Edwards, 1995).

Precipitation is not significantly correlated with $\delta^{13}C_M$, but April precipitation correlates significantly with $\delta^{18}O_M$ (Fig. 5c). Significant negative correlations between relative humidity (RH) and $\delta^{13}C_M$ and $\delta^{18}O_M$ occur during June and July (Fig. 6) and with combined Jun–Jul (Table 1). The negative $\delta^{13}C_M$ -RH association at Timber has similarly been observed in a number of field (Lipp et al., 1991; Robertson et al., 1997; Anderson et al., 1998; Hemming et al., 1998) and laboratory (Edwards et al., 2000; Mayr et al., 2004) studies, and reflects changes in stomatal conductance with atmospheric moisture demand. The $\delta^{18}O_M$ -RH relation is also consistent with existing models of $\delta^{18}O$ variability in tree rings owing to the preservation of leaf water evaporative enrichment signals (Roden et al., 2000) and confirms these trees are effective oxygen-isotope archives of local climate.

The climate-isotope correlation results reveal that $\delta^{13}C_M$ and $\delta^{18}O_M$ may indeed share common forcing parameters, notably Jun–Jul temperatures and relative humidity, potentially explaining why these series are significantly correlated during some intervals (Fig. 4). Shared climate-isotope parameters may result in correlated isotopic trends when non-overlapping climate-isotope parameters (e.g., pAug MaxT- $\delta^{13}C_M/Mar-May$ MinT- $\delta^{18}O_M)$ are not significantly out of phase.

MODELING $\delta^{13}C_M$ -CLIMATE RELATIONS

Our correlation results guided the development of two linear models to help quantify the relative importance of the climate indices determined to be most significant to $\delta^{13}C_{\rm M}$: a univariate model which includes pAug + Jun–Jul MaxT as a predictor (Fig. 7a) and a bivariate model which includes pAug + Jun–Jul MaxT and Jun–Jul RH (Fig. 7b). The inter-correlation between pAug + Jun–Jul MaxT and Jun–Jul RH is not significant ($r=-0.24, p\leq0.13$), but the correlation between Jun–Jul MaxT and Jun–Jul RH is moderate ($r=-0.36, p\leq0.02$). Even though there is significant mutual correlation between MaxT and RH for Jun–Jul, much of the variability in these indices remains independent of

each other and will be used, with due caution, in the bivariate model. The univariate model explains 46% of $\delta^{13}C_M$ inter-annual variability over 1957–2003 (Fig. 7a). As shown in the bivariate model, the addition of RH helps to explain an additional 9% of $\delta^{13}C_M$ variability (Fig. 7b). These results show that MaxT is the dominant climate variable controlling $\delta^{13}C_M$ variability but also affirms the influence of RH.

It is tempting to assume that the bivariate model incorporating pAug + Jun–Jul MaxT and Jun–Jul RH (Fig. 7b) accurately resolves the separate influence of soil and atmospheric moisture stress, yet the existence of moderate covariance between Jun–Jul MaxT and Jun–Jul RH tempers confidence in this model. As a result, we propose $\delta^{13}C_{\rm M}$ is probably best considered a proxy of temperature-induced drought stress. However, $\delta^{13}C_{\rm M}$ may be better suited to explore lower-frequency trends in summer temperature.

At 3-year resolution, where the independent effects of atmospheric humidity and other non-dominant effects are likely smoothed out, $\delta^{13}C_M$ may explain as much as 55% of summer temperature variability (r=0.74; Table 1). If the relation between $\delta^{13}C_M$ and pAug + Jun–Jul MaxT was relatively stable over the full record, a linear transfer function of $\delta^{13}C_M$ (3-year smoothed) to pAug + Jun–Jul MaxT (3-yr smoothed) calibrated over the period 1957–2003 would estimate that summer temperatures in this region have risen by \sim 0.8 °C since 1850 and \sim 1 °C since 1950. Although considered only broad estimates, it is interesting to note that these trends are consistent with gridded instrumental data for the region compiled by Serreze et al. (2000) and a circumpolar summer temperature proxy record by Overpeck et al. (1997).

MODELING $\delta^{18}O_{M}$ -CLIMATE RELATIONS

The relative importance of climate indices to $\delta^{18}O_{\rm M}$ was assessed using two linear models: a univariate model which includes Mar–Jul MinT as a predictor (Fig. 7c) and a bivariate model which includes Mar–Jul MinT and Jun–Jul RH (Fig. 7d). A test of co-linearity between Mar–Jul MinT and Jun–Jul RH revealed that the two indices were poorly correlated (r=-0.04, p=0.78), indicating that they may be used together in a statistically meaningful approach. MinT alone accounts for 25% of annual $\delta^{18}O_{\rm M}$ variability (Fig. 7c) and an additional 15% is explained by the inclusion of RH in the bivariate model (Fig. 7d).

The bivariate model explains roughly 40% of interannual $\delta^{18}O_M$ variability. Model performance is remarkable considering likely sources of noise such as: the link between air temperature and the $\delta^{18}O$ of precipitation; mixing of snowmelt water with residual soil water from previous years; snow removal by flood events; and other factors that diminish the climate signal at annual resolution.

The absence of a statistically significant relation between Mar–Jul MinT and Jun–Jul RH in the calibration data set suggests that the bivariate model can reliably separate the contribution of these factors to interannual $\delta^{18}O_{\rm M}$ variability. The lower magnitude of the MinT coefficient in the bivariate model versus the univariate model (0.159 vs. 0.188) indicates that, on average, RH-dependent signals tend to reinforce MinT-dependent signals. This raises the possibility that the bivariate model may still slightly underestimate the proportional influence of RH, but $\delta^{18}O_{\rm M}$ does appear to be a reasonable first-order proxy for spring/summer temperatures, especially at lower-frequencies (~60% variance explained at 3-yr resolution, r=0.78; Table 1) where non-dominant interannual effects are effectively muted. This would seem to extend over the 20th century, at least, judging

by the general pattern of $\delta^{18}O_M$ at Timber (Fig. 4), a pattern that is reminiscent of regional and circumpolar temperature trends (Serreze et al., 2000). Also of note is the sharp drop in $\delta^{18}O_M$ to an extreme low in 1894 (Fig. 4) which happens to correspond with the second lowest spring temperature value recorded at Fort McPherson since 1892 (115 km to the southwest of Inuvik) (Environment Canada, http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html).

Conclusions

This study has provided initial observations of $\delta^{13}C$ and $\delta^{18}O$ variability in tree rings from three trees at a high-latitude treeline site in northwestern Canada. Variability in the composite $\delta^{13}C_M$ record was best modeled by summer maximum temperatures accompanied by secondary relative humidity effects. Analysis of the composite $\delta^{18}O_M$ record reveals that spring/summer minimum temperatures and growing season relative humidity are most important to $\delta^{18}O_M$ variability. At lower frequencies, both $\delta^{13}C_M$ and $\delta^{18}O_M$ appear to track summer and spring/summer temperatures, respectively, quite well indicating their potential to probe multiple aspects of past temperature variability in the region. However, the opportunity to recover interannual relative humidity signals from these series may also exist.

As demonstrated by Edwards et al. (2008), when $\delta^{13}C$ and $\delta^{18}O$ are influenced by the same two climate variables (e.g., temperature and relative humidity), their coupled response can be used to resolve the separate influence of both climate variables. Our results provide a foundation for the development of a multivariate model that couples $\delta^{13}C$ and $\delta^{18}O$ data and, perhaps, other tree-ring variables such as ring-width and density, to investigate the long-term climate history of the Mackenzie Delta region. Such an approach may also prove useful in exploring changing climate-growth relations noted in tree ring-width chronologies in this region (Pisaric et al., 2007).

Acknowledgments

Financial support was provided by Indian and Northern Affairs Canada: Water Resources Division and a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to Pisaric. Field and laboratory support from J. Bailey, R. Jenkins, P. Morse, and M. Palmer is gratefully acknowledged. We also thank M. Gagen, P. Sullivan, and one anonymous reviewer for their useful comments on earlier versions of this paper.

References Cited

ACIA, 2005: Arctic Climate Impact Assessment. Cambridge: Cambridge University Press, 1042 pp.

Anderson, W. T., Bernasconi, S. M., McKenzie, J. A., and Saurer, M., 1998: Oxygen and carbon isotopic record of climatic variability in tree ring cellulose (*Picea abies*): An example from central Switzerland (1913–1995). *Journal of Geophysical Research*, 103: 31,625–31,636.

Anderson, W. T., Bernasconi, S. M., McKenzie, J. A., Saurer, M., and Schweingruber, F., 2002: Model evaluation for reconstructing the oxygen isotopic composition in precipitation from tree ring cellulose over the last century. *Chemical Geology*, 182: 121–137.

Barber, V. A., Juday, G. P., Finney, B. P., and Wilmking, M., 2004: Reconstruction of summer temperatures in interior Alaska from tree-ring proxies: evidence for changing synoptic climate regimes. *Climatic Change*, 63: 91–120.

- Barbour, M. M., Andrews, T. J., and Farquhar, G. D., 2001: Correlations between oxygen isotope ratios of wood constituents of *Quercus* and *Pinus* samples from around the world. *Australian Journal of Plant Physiology*, 28: 335–348.
- Barbour, M. M., Walcroft, A. S., and Farquhar, G. D., 2002: Seasonal variations in δ^{13} C and δ^{18} O of cellulose from growth rings of *Pinus radiata*. *Plant, Cell and Environment*, 25: 1483–1499.
- Barbour, M. M., Cernusak, L. A., and Farquhar, G. D., 2005: Factors affecting the oxygen isotope ratio of plant organic material. *In Flanagan*, L. B., Ehleringer, J. R., and Pataki, D. E. (eds.), *Stable Isotopes and Biosphere-Atmosphere Interactions: Processes and Biological Controls*. San Diego: Elsevier Academic Press, 9–28.
- Black, R. A., and Bliss, L. C., 1978: Recovery sequence of *Picea mariana–Caccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. *Canadian Journal of Botany*, 56: 2020–2030.
- Briffa, K. R., Schweingruber, F. H., Jones, P. D., Osborn, T. J., Shiyatov, S. G., and Vaganov, E. A., 1998: Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature*, 391: 678–682.
- Brooks, J. R., Flanagan, L. B., and Ehleringer, J. R., 1998: Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. *Canadian Journal of Forest Research*, 28: 524–533.
- Buhay, W. M., and Edwards, T. W. D., 1995: Climate in southwestern Ontario, Canada, between AD 1610 and 1885 inferred from oxygen and hydrogen isotopic measurements of wood cellulose from trees in different hydrologic settings. *Quaternary Research*, 44: 438–446.
- Burk, R. L., and Stuiver, M., 1981: Oxygen isotope ratios in trees reflect mean annual temperature and humidity. *Science*, 211: 1417–1419.
- Burns, B. M., 1973: *The Climate of the Mackenzie Valley–Beaufort Sea.* Toronto: Environment Canada, Climatological Studies, 1, Number 24.
- Clague, J. J., Mathewes, R. W., Buhay, W. M., and Edwards, T. W. D., 1992: Early Holocene climate at Castle Peak, southern Coast Mountains, British Columbia, Canada. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 95: 153–167.
- Cook, E. R., 1985: A Time Series Analysis Approach to Tree Ring Standardization. Ph.D. dissertation. Tucson, Arizona, U.S.A., University of Arizona, School of Renewable Natural Resources.
- Dansgaard, W., 1964: Stable isotopes in precipitation. *Tellus*, 16: 436–468.
- D'Arrigo, R., Wilson, R., Liepert, B., and Cherubini, P., 2008: On the 'Divergence Problem' in northern forests: a review of the tree-ring evidence and possible causes. *Global and Planetary Change*, 60: 289–305.
- DeNiro, M. J., and Epstein, S., 1981: Isotopic composition of cellulose from aquatic organisms. *Geochimica et Cosmochimica Acta*, 45: 1885–1894.
- Dongmann, G., Nurnberg, H. W., Förstel, H., and Wagener, K., 1974: On the enrichment of H₂¹⁸O in the leaves of transpiring plants. *Radiation and Environmental Biophysics*, 11: 41–52.
- Dyke, L. D., 2000: Climate of the Mackenzie River valley. In Dyke, L. D., and Brooks, G. R. (eds.), *The Physical Environment of the Mackenzie Valley, Northwest Territories: a Baseline for the Assessment of Environmental Change.* Ottawa, Ontario: Geological Survey of Canada Bulletin, 547: 21–30.
- Edwards, T. W. D., and Fritz, P., 1986: Assessing meteoric water composition and relative humidity from ¹⁸O and ²H in wood cellulose: paleoclimatic implications for southern Ontario, Canada. *Applied Geochemistry*, 1: 715–723.
- Edwards, T. W. D., Graf, W., Trimborn, P., Stichler, W., Lipp, J., and Payer, H. D., 2000: δ^{13} C response surface resolves humidity and temperature signals in trees. *Geochimica et Cosmochimica Acta*, 64: 161–167.

- Edwards, T. W. D., Birks, S. J., Luckman, B. H., and MacDonald, G. M., 2008: Climatic and hydrologic variability during the past millennium in the eastern Rocky Mountains and northern Great Plains of western Canada. *Quaternary Research*, 70: 188–197.
- Etheridge, D. M., Steele, L. P., Langenfelds, R. L., Francey, R. J., Barnola, J.-M., and Morgan, V. I., 1996: Natural and anthropogenic changes in atmospheric CO₂ over the last 1000 years from air in Antarctic ice and firn. *Journal of Geophysical Research*, 101: 4115–4128.
- Farquhar, G. D., and Lloyd, J., 1993: Carbon and oxygen isotope effects in the exchange of carbon dioxide between terrestrial plants and the atmosphere. *In* Ehleringer, J. R., Hall, A. E., and Farquhar, G. D. (eds.), *Stable Isotopes and Plant Carbon-Water Relations*. San Diego: Academic Press, 47–70.
- Farquhar, G. D., O'Leary, M. H., and Berry, J. A., 1982: On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, 9: 121–137.
- Francey, R. J., and Farquhar, G. D., 1982: An explanation of ¹³C/¹²C variations in tree rings. *Nature*, 297: 28–31.
- Fricke, H. C., and O'Neil, J. R., 1999: The correlation between ¹⁸O/¹⁶O ratios of meteoric water and surface temperature: its use in investigating terrestrial climate change over geologic time. *Earth and Planetary Science Letters*, 170: 181–196.
- Fritts, H. C., 1976: *Tree Rings and Climate*. New York: Academic Press.
- Gagen, M., McCarroll, D., and Edouard, J. L., 2004: Latewood width, maximum density, and stable carbon isotope ratios of pine as climate indicators in a dry subalpine environment, French Alps. *Arctic, Antarctic, and Alpine Research*, 36: 166–171.
- Gagen, M., McCarroll, D., Loader, N. J., Robertson, I., Jalkanen, R., and Anchukaitis, K. J., 2007: Exorcising the 'segment length curse': summer temperature reconstruction since AD 1640 using non-detrended stable carbon isotope ratios from pine trees in northern Finland. *The Holocene*, 17: 435–446.
- Helliker, B. R., and Ehleringer, J. R., 2002: Grass blades as treerings: environmentally induced changes in the oxygen isotope ratio of cellulose along the length of grass blades. *New Phytologist*, 155: 417–424.
- Hemming, D. L., Switsur, V. R., Waterhouse, J. S., Heaton, T. H. E., and Carter, A. H. C., 1998: Climate variation and the stable carbon isotope composition of tree ring cellulose: an intercomparison of *Quercus robur*, *Fagus sylvatica* and *Pinus sylvestris*. *Tellus B*, 50: 25–33.
- Holmes, R. L., 1983: Computer-assisted quality control in treering dating and measurement. *Tree-Ring Bulletin*, 43: 69–78.
- Jacoby, G. C., Lovelius, N. V., Shumilov, O. I., Raspopov, O. M., Karbainov, J. M., and Frank, D. C., 2000: Long-term temperature trends and tree growth in the Taymir region of northern Siberia. *Quaternary Research*, 53: 312–318.
- Keeling, C. D., 1979: The Suess Effect: ¹³Carbon-¹⁴Carbon interrelations. *Environment International*, 2: 229–300.
- Kokelj, S. V., and Burn, C. R., 2004: Tilt of spruce trees near ice wedges, Mackenzie Delta, Northwest Territories, Canada. Arctic, Antarctic, and Alpine Research, 36: 615–623.
- Kokelj, S. V., and Burn, C. R., 2005: Near-surface ground ice in sediments of the Mackenzie Delta, Northwest Territories, Canada. *Permafrost and Periglacial Processes*, 16: 291–303.
- Libby, L. M., Pandolfi, L. J., Payton, P. H., Marshall, J., III, Becker, B., and Giertz-Sienbenlist, V., 1976: Isotopic tree thermometers. *Nature*, 261: 284–288.
- Lipp, J., Trimborn, P., Fritz, P., Moser, H., Becker, B., and Frenzel, B., 1991: Stable isotopes in tree ring cellulose and climatic change. *Tellus B*, 43: 322–330.
- Mackay, J. R., 1963: The Mackenzie Delta area, N.W.T. Ottawa, Ontario: Department of Mines and Technical Surveys, Geographical Branch Memoir, 8: 202.

- Mackay, J. R., 1983: Downward water movement into frozen ground, western arctic coast, Canada. *Canadian Journal of Earth Sciences*, 20: 120–134.
- Marsh, P., 1988: Soil infiltration and snow melt run off in the Mackenzie Delta, NWT. *In Proceedings of the 5th International Conference on Permafrost*. Trondheim, Norway, 618–621.
- Mayr, C., Trimborn, P., Lipp, J., Grams, T. E. E., Graf, W., Payer, H. D., and Stichler, W., 2004: Climate information from stable hydrogen and carbon isotopes of C3 plants—Growth chamber experiments and field observations. *In* Fischer, H., Kumke, T., Lohmann, G., Flöser, G., Miller, H., von Storch, H., and Negendank, J. F. W. (eds.), *The Climate in Historical Times—Towards a Synthesis of Holocene Proxy Data and Climate Models*. Berlin: Springer-Verlag, 263–279.
- McCarroll, D., and Loader, N. J., 2004: Stable isotopes in tree rings. *Quaternary Science Reviews*, 23: 771–801.
- McCarroll, D., Jalkanen, R., Hicks, S., Tuovinen, M., Gagen, M., Pawellek, F., Eckstein, D., Schmitt, U., Autio, J., and Heikkinen, O., 2003: Multiproxy dendroclimatology: a pilot study in northern Finland. *The Holocene*, 13: 829–838.
- McCarroll, D., Gagen, M., Loader, N. J., Robertson, I., Anchukaitis, K. J., Los, S., Young, G. H. F., Jalkanen, R., Kirchhefer, A., and Waterhouse, J. S., 2009: Correction of tree ring stable carbon isotope chronologies for changes in the carbon dioxide content of the atmosphere. *Geochimica et Cosmochimica Acta*, 73: 1539–1547.
- Overpeck, J., Hughen, K., Hardy, D., Bradley, R., Case, R., Douglas, M., Finney, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonald, G., Moore, J., Retelle, M., Smith, S., Wolfe, A., and Zielinski, G., 1997: Arctic environmental change of the last four centuries. *Science*, 278: 1251–1256.
- Pearce, C. M., McLennan, D., and Cordes, L. D., 1988: The evolution and maintenance of white spruce woodlands on the Mackenzie Delta, N.W.T., Canada. *Holarctic Ecology*, 11: 248–258.
- Pisaric, M. F. J., Carey, S. K., Kokelj, S. V., and Youngblut, D., 2007: Anomalous 20th century tree growth, Mackenzie Delta, Northwest Territories, Canada. *Geophysical Research Letters*, 34: article L05714, doi:10.1029/2006GL029139.
- Robertson, I., Rolfe, J., Switsur, V. R., Carter, A. H. C., Hall, M. A., Barker, A. C., and Waterhouse, J. S., 1997: Signal strength and climate relationships in ¹³C/¹²C ratios of tree ring cellulose from oak in southwest Finland. *Geophysical Research Letters*, 24: 1487–1490.
- Robertson, I., Waterhouse, J. S., Barker, A. C., Carter, A. H. C., and Switsur, V. R., 2001: Oxygen isotope ratios of oak in east England: implications for reconstructing the isotopic composition of precipitation. *Earth and Planetary Science Letters*, 191: 21–31.
- Roden, J. S., Lin, G., and Ehleringer, J. R., 2000: A mechanistic model for interpretation of hydrogen and oxygen isotope ratios in tree-ring cellulose. *Geochimica et Cosmochimica Acta*, 64: 21–35.
- Rozanski, K., Araguás-Araguás, L., and Gonfiantini, R., 1993: Isotopic patterns in modern global precipitation. *In* Swart, P. K., McKenzie, J., Lohmann, K. C., and Savin, S. (eds.), *Climate*

- Change in Continental Isotopic Records. Washington D.C.: American Geophysical Union, Geophysical Monograph, 78: 1–37.
- Saurer, M., Aellen, K., and Siegwolf, R., 1997: Correlating δ^{13} C and δ^{18} O in cellulose of trees. *Plant, Cell and Environment*, 20: 1543–1550
- Scheidegger, Y., Saurer, M., Bahn, M., and Siegwolf, R., 2000: Linking stable oxygen and carbon isotopes with stomatal conductance and photosynthetic capacity: a conceptual model. *Oecologia*, 125: 350–357.
- Schleser, G. H., Helle, G., Lücke, A., and Vos, H., 1999: Isotope signals as climate proxies: The role of transfer functions in the study of terrestrial archives. *Quaternary Science Reviews*, 18: 927–943.
- Serreze, M. C., and Barry, R. G., 2005: Recent climate variability, trends and the future. *In The Arctic Climate System*. Cambridge, U.K.: Cambridge University Press, 291–334.
- Serreze, M. C., Walsh, J. E., Chapin, F. S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W. C., Morison, J., and Zhang, T., 2000: Observational evidence of recent change in the northern high-latitude environment. *Climatic Change*, 46: 159–207.
- Smith, M. W., 1975: Microclimatic influences on ground temperatures and permafrost distribution, Mackenzie Delta, Northwest Territories. *Canadian Journal of Earth Sciences*, 12: 1421–1438.
- Sternberg, L., DeNiro, M., and Savidge, R., 1986: Oxygen isotope exchange between metabolites and water during biochemical reactions leading to cellulose synthesis. *Plant Physiology*, 82: 423–427.
- Sternberg, L. S. L., 1989: Oxygen and hydrogen isotope measurements in plant cellulose analysis. *In* Linskens, H. F., and Jackson, J. F. (eds.), *Modern Methods of Plant Analysis: Plant Fibers, 10.* New York: Springer-Verlag, 89–99.
- Tans, P., 2009: Trends in Atmospheric Carbon Dioxide—Global. NOAA/ESRL. http://www.esrl.noaa.gov/gmd/ccgg/trends/ (accessed 24 April 2009).
- Treydte, K. S., Schleser, G. H., Schweigruber, F. H., and Winiger, M., 2001: The climatic significance of δ^{13} C in subalpine spruces (Lötschental, Swiss Alps): a case study with respect to altitude, exposure and soil moisture. *Tellus B*, 53: 593–611.
- Treydte, K. S., Schleser, G. H., Helle, G., Frank, D. C., Winiger, M., Haug, G. H., and Esper, J., 2006: The twentieth century was the wettest period in northern Pakistan over the past millennium. *Nature*, 440: 1179–1182.
- Waterhouse, J. S., Switsur, V. R., Barker, A. C., Carter, A. H. C., Hemming, D. L., Loader, N. J., and Robertson, I., 2004: Northern European trees show a progressively diminishing response to increasing atmospheric carbon dioxide concentrations. *Quaternary Science Reviews*, 23: 803–810.
- Wilmking, M., D'Arrigo, R., Jacoby, G. C., and Juday, G. P., 2005: Increased temperature sensitivity and divergent growth trends in circumpolar boreal forests. *Geophysical Research Letters*, 32: article L15715, doi:10.1029/2005GL023331.

MS accepted June 2009