# Quantifying the effects of climate change, carbon fertilization and modern sample bias in boreal jack pine (*Pinus banksiana*) forests

### Jacob Cecile1, F. Wayne Bell2, Lucas Silva3, William Horwarth3, Madhur Anand1

# Abstract

Climate change and increasing atmospheric carbon dioxide levels are thought to be responsible for recent shifts in global forest growth. Tree ring chronologies are a crucial tool for identifying and understanding these changes, but their use for reliably reconstructing long-term trends in growth is hampered by the presence of modern sample bias. Modern sample bias arises from systematic uncorrected correlations between tree productivity and age, which skew the resulting trends in tree growth. Using factor regression standardization (a regression-based extension of regional curve standardization), we demonstrate and correct modern sample bias in a young living jack pine (*Pinus banksiana* Lamb.) chronology from northwestern Ontario, Canada, by accounting for tree-level productivity. Ignoring the effect of tree-level productivity exaggerated the underlying trend in tree growth over time (1879-2010), with a strong universal negative trend observed after correction. Using generalized additive models, we found that this corrected chronology exhibited strong nonlinear responses to summer climate and water use efficiency (as determined by whole wood carbon isotope discrimination). Growth decreased with increased water use efficiency, which appeared to be an indicator of drought stress. Rising levels of atmospheric carbon dioxide (CO2) substantially increased calculated water use efficiency with no corresponding increase in growth, suggesting that CO2 fertilization via this mechanism was unlikely for these trees. Our results showed that factor regression standardization corrected for modern sample bias in ways that traditional dendrochronological practices could not, producing a clearer picture of long-term patterns of tree growth and climate response.

**Keywords:** factor regression standardization, δ13C, climate response, dendrochronology, water use efficiency

# 1. Introduction

Since the industrial revolution, a shifting climate and increasing carbon dioxide (CO2) levels have disrupted patterns of forest growth [*Newman et al.*, 2011]. Evidence for a positive effect of CO2 on forest growth, often referred to as “carbon fertilization”, is mixed and controversial. Laboratory experiments and theoretical expectations show that tree growth increases due to improved photosynthetic efficiency and decreased in stomatal conductance, which reduce water requirements [*Conroy et al.*, 1986; *Huang et al.*, 2007]. But as CO2 levels increase other developmentaland ecological changes occur, making it difficult to extrapolate these results to a more natural setting, [*Asshoff et al.*, 2006; *Stewart and Hoddinott*, 1993]. As a result, outdoor large-scale Free Air Carbon dioxide Enrichment (FACE) experiments have been set up to examine the effects of carbon fertilization[*Asshoff et al.*, 2006; *Körner et al.*, 2005; *Norby et al.*, 2005]. Reviews of the findings suggest that direct CO2 enrichment typically increases tree productivity but these gains are often slowed as other factors (typically nutrients, with nitrogen being the most studied) become more limiting; plant species composition may also shift [*Ainsworth and Long*, 2005; *Norby and Zak*, 2011].

Tree rings can serve as a record of tree growth long into the past, and are a powerful tool for understanding the link between growth and the environment. Attempts to find evidence for carbon fertilization in the tree ring records suffer from several methodological difficulties, but recent global analyses suggests that the effect is largely absent [*Gedalof and Berg*, 2010; *Peñuelas et al.*, 2011; *Silva and Anand,* 2012]*.*The primary challenge in dendrochronological analysis is the extraction of a reliable index of tree growth over time (or alternate measurements such as wood isotope ratios). The analysis of tree ring data cannot be divorced from its fundamentally biological nature; growth varies not only by year but with age and species and microsite as well. To address this, dendrochronologists turn to the techniques of standardization, controlling for unwanted effects (typically age-driven) to extract a common, climate-sensitive chronology. The two broad approaches to this problem are individual series standardization and regional curve standardization. Individual series standardization is intended to remove the age-driven trend in one series (a tree ring record from a single tree) at a time, using parametric models of the change in growth by age or by removing low-frequency (presumably age-driven) variability. As a result, individual series standardization is a poor approach for capturing long-term trends in growth [*Cook et al.*, 1995]. In contrast, regional curve standardization is used to estimate the common effect of age on each tree, remove it, and then estimate the time-driven variability (referred to as forcing) [*Briffa and Melvin*, 2011].

If, however, the observed tree ring data varies systematically by tree as well, the estimates produced by regional curve standardization are flawed. This is known as differing-contemporaneous-growth-rate bias, and when the link between tree productivity and either age or year is persistent, it results in modern sample bias [*Briffa and Melvin*, 2011]. In that case, the forcing is underestimated in years where the mean intrinsic growth rate of the trees in the chronology is low, and overestimated where it is high. The high frequency variability is retained accurately, but the long-term trend is compromised, making the detection of carbon fertilization or climate change effects extremely difficult [*Brienen et al.*, 2012a,b]. Factor regression standardization extends regional curve standardization using classical regression techniques to account for tree-level productivity as well, providing a simple solution to the problem of modern sample bias [*Cecile and Anand*, in review]*.*

Once forcing is extracted, the major challenge is to show that the increasing atmospheric CO2 levels are positively affecting tree growth. Merely showing that tree growth is increasing [c.f. *LaMarche et al.,* 1984] is not sufficient; investigators need to control for other important environmental changes, especially climate [*Gedalof and Berg*, 2010; *Jacoby*, 1997].

We investigate these questions in the context of a homogeneous chronosequence of even-aged jack pine (*Pinus banksiana* Lamb.) stands in northwestern Ontario. Ring-width measurements provided the central evidence for changes in tree growth from 1879-2010 while carbon isotope ratios (δ13C, or 13C:12C ) were used to reconstruct water use efficiency. Generalized additive models were used to model the links between climate, water use efficiency and growth.

# 2. Methods

## 2.1 Site description

Nineteen even-aged jack pine stands ranging in stand establishment dates from 1872-1999 (by date of pith emergence) in a 30 km radius near Silver Dollar, Ontario were studied (approximately centred around 49° 50' N, 91° 18' W) (Figure 1). Fifteen of the sites originated from stand-replacing fire, while four developed after a clearcut harvest. These sites are since undisturbed and unmanaged, with the exception of one harvest-origin site established in 1980 and thinned in 2008-2009. This relatively remote location in Northwestern Ontario helps reduce the effect of simultaneous anthropogenic changes in short- to medium range atmospheric pollutants, particularly NOx, SO2, ozone, and particulates that have been shown to have significant effects on tree growth and nutrient cycling [*Dietze and Moorcroft*, 2011]. All stands were jack pine dominated, with many of the older stands containing younger *Populus spp.* (poplar), *Abies balsamea* (balsam fir), *Picea mariana* (black spruce) or *Picea glauca* (white spruce) in the understory. The soil on all sites was a deep (>50 cm) OrthicHumo-Ferric Podzol[*SCWG*, 1998]. For the fire-origin sites, all Ae and Bf horizons were coarse sand, silty sand, or loamy sand (mean percent sand, silt, clay was 84.4±8.3, 11.5±7.8, 4.1±1.6, respectively) and mean pH was 5.4 ± 0.2 while the LFH layer was thin (1 to 2 cm) on all sites. Detailed soil data was not available for the remaining four harvest origin sites.

## 2.2 Climate data

Monthly interpolated climate data for a single centrally located point at 49.849915° N, 91.304131° W for the period 1901 to 2007 were obtained from Canadian Forest Service using the model outlined in *McKenney et al.* [2006]. The study sites had a mean annual precipitation of 690 mm per year, a mean annual temperature 1 °C, and typically experience a 165-day growing season. Rainfall is strongly seasonal, with about 65% occurring during the growing season. July is typically the hottest month of the summer, while August is the driest, so drought may occur during the growing season.

## 2.3 Species description

Jack pine is a short-lived, shade-intolerant pioneer species native to eastern and central boreal forests, with a range extending south to surround lakes Superior, Michigan, and Huron [*Rudolph and Laidly*, 1990]. Through the use of common garden trials, Thomson and Parker [2008] showed that the “optimum latitude” for this species is between 46°N and 47°N, slightly south of our study sites. Jack pine is frequently found on xeric, well-drained sites but grows faster in mesic conditions and is considered relatively drought tolerant [*Rudolph and Laidly*, 1990].

## 2.4 Sampling and chronology preparation

At each of the 19 sites, 10 dominant/codominant canopy trees were sampled at 25 m intervals along a linear transect, offsetting then doubling back if stand boundaries were reached. In July 2011, two perpendicular cores per tree were taken at 1.3 m above the ground, then sanded, scanned, and measured, taking care to avoid carbon isotope contamination. Cores with intact bark were dated directly; other cores were visually and statistically crossdated against these using t and trend statistics in Corina [*Brewer et al.*, 2010]. The stands were known to be even-aged; to reduce the effect of missing pith years when standardizing the chronology, all series were assumed to originate in the year of stand establishment for the purposes of determining age. The sample depth (number of series included in the chronology) by year and age is displayed in Figure 2.

## 2.5 Standardization

Factor regression standardization (an extension of regional curve standardization) was used to separate the effects of tree-level productivity, age, and year on ring width and correct for modern sample bias [*Cecile and Anand*, in review]. The tree ring data was strongly log-normal, so the following growth model was used to standardize the chronology:

Gitτ is the observed ring width at tree i, year t, and age τ. Q, F and A are latent factors that influence tree growth: Qi describes the intrinsic productivity of that tree, Ft is the forcing at that year (equivalent to the standardized chronology or ring width index) while Aτ is the value of the age trend (equivalent to the regional curve) at that age. Preliminary examination of the residuals using quantile-quantile plots and histograms revealed that the error term was more appropriately treated as lognormal and multiplicative, rather than normal and additive.

Keeping with common practice in regional curve standardization, the age trend was assumed to be a smooth function of age. To accomplish this, generalized additive regression was used on the log-transformed ring width data to produce a locally smooth estimate of the age trend in a single step. This smoothing was performed using locally linear polynomial regression (loess), with the span selected automatically based on minimum Akaike's information criterion. For a full theoretical justification of these concepts and their relation to regional curve and signal-free standardization, the interested reader is referred to *Cecile and Anand* [in review]

Two separate standardizations were carried out, one including and the other excluding Q (productivity) in our growth model to directly show the effect of modern sample bias.

## 2.6 Carbon isotope ratios and water use efficiency

Intrinsic water use efficiency (Wi) is the ratio between plant carbon fixation and stomatal conductance and can be approximately determined by the discrimination against 13C [*Farquhar et al.*, 1982]. Because compounds deposited in tree rings have fixed stable isotope ratios, historical records are commonly constructed using one of the various forms of the equation below [*Duquesnay et al.*, 1998], in which Ca is the atmospheric concentration of CO2, *a* is the diffusion fractionation across the boundary layer and the stomata (≈4.4‰), and *b* is the RuBisCo enzymatic biologic fractionation (≈27.0‰). Δ is defined as the isotopic discrimination, and is simply calculated from δ, the deviation from the PeedeeBelmenite (PDB) carbonate standard as follows:

Samples from the same site and year were pooled due to cost constraints, providing an increased sensitivity to interannual variation in climate compared to serial or “pentad” pooling at the cost of information about intertree variability [*Leavitt*, 2008, 2010; *Liñán et al.*, 2011]. δ13C for all the wood samples was determined by the Stable Isotope Facility at University of California Davis using a continuous flow Isotope Ratio Mass Spectrometer. Cellulose extraction was not performed, as studies show little or no accuracy improvement for 13C [*Barbour et al.*, 2001; *English et al.*, 2011].

Changing levels of atmospheric δ13C were compiled from ice core records as documented by McCarroll and Loader [2004], but extending the linear extrapolation to 2010. Annual atmospheric averages of CO2 concentration from Mauna Loa, Hawaii (www.esrl.noaa.gov/gmd/ccgg/trends/, courtesy of Dr. Pieter Tans (NOAA/ESRL) and Dr. Ralph Keeling (Scripps Institution of Oceanography)) were supplemented with Lawdome ice core records to construct a historical record of Ca[*Etheridge et al.*, 1998] .

Water use efficiency showed strong patterns by year, age, and site. Factor regression standardization was used, as above, to separate these effects. In contrast to the ring width chronology above, the canonical vectors were scaled such that the magnitude of the data was retained in the forcing (**F**) to aid reader interpretation of typical intrinsic water use efficiency values. Akaike's information criteria confirmed that in this case the full model was most appropriate.

## 2.7 Links between climate, water use efficienc,y and growth

The climate sensitivity and responses of jack pine chronologies are well-established in the literature, so we designed our analysis to test the previously observed relationships using our data. Drought-induced growth limitation is a common theme [*Brooks et al.*, 2011; *Girardin et al.,* 2012; *Hoffer and Tardif*, 2009; *Hofgaard et al.*, 1999; *Larsen and MacDonald*, 1995; *Savva et al.*, 2008; *Tardif and Conciatori*, 2001], but warm [*Botkin et al.*, 1991; *Despland and Houle*, 1997; *Hamel et al.*, 2004; *Huang et al.*, 2010] or extended growing seasons have also been found to increase jack pine growth [*Despland and Houle*, 1997; *Hofgaard et al.*, 1999; *Tardif and Conciatori*, 2001]. Growing season growing degree days and growing season precipitation were selected as the drought-linked climate variables as they are fairly general and simple to interpret while growing degree days provided a test for temperature limitation. Growing season length was selected as a largely orthogonal measurement to test the second hypothesis directly. Similarly, several studies have investigated carbon fertilization in jack pine (CITATIONS). Elevated water use efficiency is a compelling mechanistic explanation of this effect so we used the reconstructed typical intrinsic water use efficiency from the δ13C chronology to investigate it. By examining the response of ring width to these variables, we could explore the effect of climate change and carbon fertilization on tree growth, while examining the relationship between climate and water use efficiency helped to interpret δ13C measurements.

In dendrochronology, it is common practice to assume a linear relationship between tree growth and climate [*Biondi and Waikul*, 2004]. This simplifies analysis and interpretation considerably, especially when the final goal is climate reconstruction, and may be a good assumption when the observed range of variability is small or far from local optima [*Loehle*, 2009]. Nevertheless, nonlinear responses have been shown in tree-ring chronologies [*D’Arrigo*, 2004; *Graumlich and Brubaker*, 1986; *Helama et al.*, 2009; *Ni et al.*, 2002]. Agronomic, ecological, and physiological evidence argue for a nonlinear response to almost all environmental variables, at least over large ranges. Resource demands (CO2, water, nutrients) can be met but response to temperature is typically hump-shaped: when it is too low the rate of growth and metabolism is reduced and when it is too high drought ensues. To test for these effects, we used both generalized additive models (via thin-plate kernel regression smoothing with the R package *mgcv*, *Wood* [2006]), which assumed only a locally smooth additive fit, and traditional multivariate linear regression. Ring-width forcing was log-transformed to stabilize variance (the error structure is retained from the original growth model) before fitting climate-growth models.

# 3. Results

## 3.1 Tree ring width

Factor regression standardization splits the ring-width chronology into three components: the effects due to tree-level productivity (Figure 3), year-linked factors such as climate (Figure 4), and age (Figure 5). Each of these regressions shows the difference between the two models: G=GFA, in which tree-level productivity is accounted for, and G=FA, where it is not. Figure 2 shows the estimated productivity of each tree vs. their age to demonstrate the cause of the observed modern sampling bias. The three-factor model fit the data significantly better than the two-factor model (Table 1).

Tree-level productivity was strongly negatively correlated with tree age (Spearman's ρ=-0.86, p=0). Accounting for tree-level productivity in the model changed the long-term trend of the forcing. Rather than increasing and reaching a plateau around 1950 (Spearman's ρ=0.64, p=0), it declined throughout the study period (Spearman's ρ=-0.91, p=0). As expected, high-frequency variability is extremely similar between the two approaches. The derived age trend was similar for both models, peaking six years after pith emergence, declining until about age 30 to 40 and then gradually rising as the trees aged. Optimal span values for the smoothing of the age trend were quite similar between the two models and correspond to a neighbourhood of about eight or nine years.

## 3.2 Water use efficiency

Figures 6 through 8 show the effects of intrinsic water use efficiency by stand, year, and age. The optimal age trend span parameter for this standardization was 0.13. Stand age and stand-level effects on water use efficiency were positively correlated (Spearman's ρ=0.81, p=2.5e-5) and stand-level variability was high (ranging from 0.8-1.2). Typical water use efficiency values increased rapidly when the trees were very young, seemingly approaching a plateau from ages 15 to 40, then declining and fluctuating inconsistently. Water use efficiency increased substantially from 1877-2010 (Spearman's ρ=0.76, p=0) but this effect seems to be largely due to increasing atmospheric CO2 levels (controlling for this effect yields a Spearman's ρ=-0.20, p=0.02) (Figure 9).

## 3.3 Links between climate, growth and water use efficiency

The three selected climatic variables were not stationary during the study period, with growing season growing degree days (Spearman's ρ=0.63, p=0), precipitation (Spearman's ρ=0.48, p=1.1e-7), and length (Spearman's ρ=0.43, p=3.1e-6) all increasing over time (Figure 10).

The three-factor forcing was more sensitive to historic climate (Table 2), with differences in climate responses observed (see Figure 11, Table 3 for details). Generalized additive model-based climate-response modelling had better performance and explained more variability for both forcing reconstructions (Table 2), and meaningful non-linearity was detected in the response to water use efficiency and precipitation for the three-factor forcing. Despite this, climate responses seen using generalized additive models were consistent, in terms of magnitude and direction, with their linear counterparts.

In all cases, water use efficiency was a significant negative predictor of growth. Accounting for tree-level productivity revealed that growing season growing degree days was a significant negative predictor of growth. Growing season precipitation had a similarly negative effect on growth, especially when precipitation increased. No response to changes in growing season length were observed.

A similar approach was used to investigate climatic drivers of intrinsic water use efficiency (see Table 4 for model fit statistics). Climate was found to be a fairly good predictor for the corresponding year. Table 5 and Figure 12 show the response of intrinsic water use efficiency, which showed a strong negative response to growing season precipitation but no response to growing season length. Although growing season length was a significant predictor for both the linear and generalized additive model, no clear relationship was evident.

# 4. Discussion

## 4.1 Presence of modern sample bias

Modern sample bias was clearly visible in the chronology. Productivity was strongly negatively correlated with age. As a result, long-term trends in forcing changed dramatically when tree-level productivity was accounted for. There is good reason to suspect the corrected approach is a better reflection of true historic patterns of tree growth. Model fit was much better and the climate signal was stronger after accounting for differences in productivity among trees.

Despite this, the origin of this bias is somewhat unclear. Big tree-selection bias (see [*Brienen et al.*, 2012b; *Cecile and Anand*, in review]) should not be present under the sampling design followed. No minimum diameter cutoff was used and the stands were almost completely even-aged. There was a deliberate bias towards the selection of locally large, dominant trees, but this will not produce modern sample-bias when the largest trees are of the same age as the smallest.

The survivorship patterns of jack pine, locally, favour the fastest growing trees via competitive dominance due to their shade-intolerant nature [*Rudolph and Laidly*, 1990]. Yet this chronology showed a strong negative correlation between productivity and age; slow-growing trees were more likely to survive (or at least be sampled). In some studies, there may be sampling biases due to patchy resources, in which the stem density on fertile sites drops more rapidly than it does on less productive sites, effective reducing the relative survivorship of fast-growing trees [*Cecile and Anand*, in review]. Yet this effect is unlikely here since a fixed number of trees were sampled from homogeneous sites and the stem density of the stands was irrelevant to their representation in the chronology.

Macro-scale disturbance biases may hold the answer however. The area around Silver Dollar, Ontario where this study occurred is actively managed. If disturbances affect large or productive trees, slow-growing trees will live longer, causing modern sample bias. Harvesting operations may be artificially biasing the stands selected for study. If a stand is highly productive, it is more likely to be logged (and thus wouldn't be sampled). If this was the case, only unproductive old stands would remain. This is a fairly plausible explanation for the modern sample bias observed in the chronology but one caveat remains. Trees are harvested only when it is economically viable to do so; they much reach a marketable size. As such, the signature of harvest-driven modern sample bias would show no relation between productivity and age at very young ages, and then the most productive stands would be gradually removed from the population. The trend seen here was a consistent decline, with no real flat unmarketable segment observed even for very young trees. Nevertheless, this is a fairly subtle signature and the sample here may not have been sufficiently large or robust to detect it. Harvest-driven survivorship bias remains the most plausible explanation of the observed modern sample bias.

## 4.2 Climate, growth and water use efficiency

The climatic drivers of jack pine growth have been extensively surveyed. Summer water limitation is cited in the negative response to growing degree days [*Hofgaard et al.*, 1999; *Larsen and MacDonald*, 1995] and water use efficiency [*Brooks et al.*, 2011; *Hoffer and Tardif*, 2009; *Savva et al.*, 2008; *Tardif and Conciatori*, 2001]. The positive effects seen in other studies for warmer temperatures [*Botkin et al.*, 1991; *Despland and Houle*, 1997; *Hamel et al.*, 2004; *Huang et al.*, 2010] and longer growing seasons [*Despland and Houle*, 1997; *Hofgaard et al.*, 1999; *Tardif and Conciatori*, 2001] were not evident in our study, likely due to the central location of the study sites.

The relationships between precipitation, growth, and water use efficiency deserve special attention. Water use efficiency seemed to act as a mediating variable, integrating and translating changes in water balance into growth. Consistent with research in plant physiology, water use efficiency was negatively associated with growth and precipitation, suggesting that water use efficiency gains were likely driven by decreased stomatal conductance at the cost of photosynthesis [*Blum*, 2005].

With water use efficiency largely indicating drought-stress, a strange, significant negative response to summer precipitation emerged. In a drought-limited ecosystem, precipitation should increase growth. But if this effect is accounted for more reliably by water use-efficiency, subtler effects may come into play. Sunlight is an important factor in tree growth, but is rarely analyzed in dendroclimatological studies due to the scarcity of data [*Friedrichs et al.*, 2009; *Nelson*, 2012; *Young et al.*, 2010]. In the absence of direct measurements of cloud cover, the negative response at higher levels of precipitation may reflect reductions in sunlight. At low and moderate precipitation levels, the benefit from increased water may counteract any negative effects, yet during extremely wet, cloudy summers solar radiation may become limiting instead.

## 4.3 Carbon fertilization

Carbon fertilization was not evident in this study. Changes in climate have had a largely negative effect on the jack pine studied and its growth continues to decline. Water use efficiency, expected to increase as CO2 concentrations rise, is a negative predictor of growth and appears to show drought stress rather than efficiency in any beneficial sense.

This, by and large, is consistent with the literature on the subject. Large scale reviews [*Boisvenue and Running*, 2006; *Gedalof and Berg*, 2010; *Peñuelas et al.*, 2011; *Silva and Anand*, 2012] show that any carbon fertilization effect that may occur is likely weak and that intrinsic water use efficiency is a poor predictor of the strength of these effects. *Girardin et al.* [2011] compared a process-based model to study the observed tree ring growth in jack pine. As in this study, they found that CO2 fertilization was not necessary to explain the changes observed in growth.

The three major challenges facing those wanting to detect carbon dioxide fertilization using tree ring chronologies are as follows: First, confounding climate variables must be controlled for. This is often challenging when only a relatively short (approximately 100 year) calibration period is available. However, process-based models and more sophisticated regression techniques such as the generalized additive models used here may help. An increase in growth as CO2 levels rise does not necessarily imply that carbon fertilization is occurring.

Second, long-term trends need to be appropriately reconstructed. Individual-series standardization is still widely used despite its long-known limitations for reconstructing long-term trends. Furthermore, modern sample bias may be a major problem when estimating trends longer than the lifespan of a single tree. Fortunately, as clearly demonstrated here, factor regression standardization can be used to address this bias.

Finally, more subtlety is needed in the search for bioclimatic signals of carbon fertilization. The physiological literature makes specific predictions about the effect of carbon fertilization on water use efficiency: plants will become more drought tolerant and the trade-off between stomatal conductance and photosynthesis will be reduced. This combination should manifest in a shift in climatic optima. Drier, hotter weather will have less effect on tree growth and necessitate smaller increases in water use efficiency [*Soulé and Knapp*, 2006]. Future research needs to move beyond linear climate response models to look for these shifts, rather than focusing on simple increases in growth.

# References

Ainsworth, E. A., and S. P. Long (2005), What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2, *New Phytologist*, *165*, 351–372.

Asshoff, R., G. Zotz, and C. Körner (2006), Growth and phenology of mature temperate forest trees in elevated CO2, *Global Change Biology*, *12*(5), 848–861.

Barbour, M. M., T. J. Andrews, and G. D. Farquhar (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.

Biondi, F., and K. Waikul (2004), DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies, *Computers and Geosciences*, *30*(3), 303–311.

Blum, A. (2005), Drought resistance, water-use efficiency, and yield potential—are they compatible, dissonant, or mutually exclusive?, *Australian Journal of Agricultural Research*, *56*(11), 1159, doi:10.1071/AR05069.

Boisvenue, C., and S. W. Running (2006), Impacts of climate change on natural forest productivity evidence since the middle of the 20th century, *Global Change Biology*, *12*(5), 862–882.

Botkin, D. B., D. A. Woodby, and R. A. Nisbet (1991), Kirtland’s Warbler habitats: a possible early indicator of climatic warming, *Biological Conservation*, *56*, 63–78.

Brewer, P. W., K. Sturgeon, L. Madar, and S. W. Manning (2010), A new approach to dendrochronological data management, *Dendrochronologia*, *28*(2), 131–134.

Brienen, R. J. W., E. Gloor, and P. A. Zuidema (2012a), Can we detect evidence for CO2 fertilization from tree rings?, *Global Biogeochemical Cycles*, *26*, GB1025.

Brienen, R. J. W., E. Gloor, and P. A. Zuidema (2012b), Detecting evidence for CO2 fertilization from tree ring studies: The potential role of sampling biases, *Global Biogeochemical Cycles*, *26*(1), GB1025, doi:10.1029/2011GB004143.

Briffa, K. R., and T. M. Melvin (2011), A closer look at regional curve standardization of tree-ring records: justification of the need, a warning of some pitfalls, and suggested improvements in its application, in *Dendroclimatology*, vol. 11, edited by M. K. Hughes, T. W. Swetnam, and H. F. Diaz, pp. 113–145, Springer Netherlands.

Brooks, J. R., L. B Flanagan, and J. R Ehleringer (2011), Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses,

Cecile, J., and M. Anand (in review), Regional curve standardization as regression: eliminating modern sample bias,

Conroy, J., E. W. R. Barlow, and D. I. Bevege (1986), Response of Pinus radiata seedlings to carbon dioxide enrichment at different levels of water and phosphorus: growth, morphology and anatomy, *Annals of Botany*, *57*(2), 165–177.

Cook, E. R., K. R. Briffa, D. M. Meko, D. A. Graybill, and G. Funkhouser (1995), The “segment length curse” in long tree-ring chronology development for palaeoclimatic studies, *The Holocene*, *5*(2), 229–237, doi:10.1177/095968369500500211.

Despland, E., and G. Houle (1997), Climate influences on growth and reproduction of *Pinus banksiana* (Pinaceae) at the limit of the species distribution in eastern North America, *American Journal of Botany*, *84*(8), 928–937.

Dietze, M. C., and P. R. Moorcroft (2011), Tree mortality in the eastern and central United States: patterns and drivers, *Global Change Biology*, *17*, 3312–3326.

Duquesnay, A., N. Bréda, M. Stievenard, and J. L. Dupouey (1998), Changes of tree-ring δ13C and water-use efficiency of beech (*Fagus sylvatica* L.) in north-eastern France during the past century, *Plant, Cell & Environment*, *21*, 565–572.

D’Arrigo, R. D. (2004), Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada, *Global Biogeochemical Cycles*, *18*(3), GB3021, doi:10.1029/2004GB002249.

English, N. B., N. G. McDowell, C. D. Allen, and C. Mora (2011), The effects of Î±-cellulose extraction and blue-stain fungus on retrospective studies of carbon and oxygen isotope variation in live and dead trees, *Rapid Communications in Mass Spectrometry*, *25*(20), 3083–3090.

Etheridge, D. M., L. P. amd. L. Steele R.L., L. J. Francey, J.-M. Barnola, and V. I. Morgan (1998), Historical CO2 records from the Law Dome DE08, DE08-2, and DSS ice cores, in *Trends: A Compendium of Data on Global Change*, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A.

Farquhar, G. D., M. H. O’Leary, and J. A. Berry (1982), On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves, *Functional Plant Biology*, *9*(2), 121–137.

Friedrichs, D. A., U. Büntgen, D. C. Frank, J. Esper, B. Neuwirth, and J. Löffler (2009), Complex climate controls on 20th century oak growth in Central-West Germany, *Tree physiology*, *29*(1), 39–51, doi:10.1093/treephys/tpn003.

Gedalof, Z., and A. A. Berg (2010), Tree ring evidence for limited direct CO2 fertilization of forests over the 20th century, *Global Biogeochemical Cycles*, *24*(3), 6.

Girardin, M. P., P. Y. Bernier, F. Raulier, J. C. Tardif, F. Conciatori, and X. J. Guo (2011), Testing for a CO2 fertilization effect on growth of Canadian boreal forests, *Journal of Geophysical Research*, *116*.

Girardin, M. P., X. J. Guo, P. Y. Bernier, F. Raulier, and S. Gauthier (2012), Changes in growth of pristine boreal North American forests from 1950 to 2005 driven by landscape demographics and species traits, *Biogeosciences Discussions*, *9*(1), 1021–1053.

Graumlich, L. J., and L. B. Brubaker (1986), Reconstruction of annual temperature (1590-1979) for Longmire, Washington, derived from tree Rings, *Quaternary Research*, *25*(2), 223–234.

Hamel, B., N. Bélanger, and D. Paré (2004), Productivity of black spruce and jack pine stands in Quebec as related to climate, site biological features and soil properties, *Forest Ecology and Management*, *191*(1–3), 239–251.

Helama, S., N. G. Makarenko, L. M. Karimova, O. A. Kruglun, M. Timonen, J. Holopainen, J. Merilainen, and M. Eronen (2009), Dendroclimatic transfer functions revisited: Little Ice Age and Medieval Warm Period summer temperatures reconstructed using artificial neural networks and linear algorithms, *Annales geophysicae*, *27*(3), 1097–1111.

Hoffer, M., and J. C. Tardif (2009), False rings in jack pine and black spruce trees from eastern Manitoba as indicators of dry summers, *Canadian Journal of Forest Research*, *39*(9), 1722–1736, doi:10.1139/X09-088.

Hofgaard, A., J. Tardif, and Y. Bergeron (1999), Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest, *Canadian Journal of Forest Research*, *29*(9), 1333–1346.

Huang, J., J. C. Tardif, Y. Bergeron, B. Denneler, F. Beringer, and M. P. Girardin (2010), Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest, *Global Change Biology*, *16*, 711–731.

Huang, J.-G., Y. Bergeron, B. Denneler, F. Berninger, and J. Tardif (2007), Response of forest trees to increased atmospheric CO2, *Critical Reviews in Plant Sciences*, *26*(5-6), 265–283.

Jacoby, G. C. (1997), Tree rings, carbon dioxide, and climatic change, *Proceedings of the National Academy of Sciences*, *94*(16), 8350–8353, doi:10.1073/pnas.94.16.8350.

Körner, C., R. Asshoff, O. Bignucolo, S. Hättenschwiler, S. G. Keel, S. Peláez-Riedl, S. Pepin, R. T. W. Siegwolf, and G. Zotz (2005), Carbon flux and growth in mature deciduous forest trees exposed to elevated CO2, *Science*, *309*(5739), 1360–1362.

LaMarche, V. C., D. A. Graybill, H. C. Fritts, and M. R. Rose (1984), Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural Vegetation, *Science*, *225*(4666), 1019–1021.

Larsen, C. P. S., and G. M. MacDonald (1995), Relations between tree-ring widths, climate, and annual area burned in the boreal forest of Alberta, *Canadian Journal of Forest Research*, *25*(11), 1746–1755, doi:10.1139/x95-189.

Leavitt, S. W. (2008), Tree-ring isotopic pooling without regard to mass: No difference from averaging d13C values of each tree, *Chemical Geology*, *252*, 52–55.

Leavitt, S. W. (2010), Tree-ring C–H–O isotope variability and sampling, *Science of The Total Environment*, *408*(22), 5244–5253.

Liñán, I. D., E. Gutiérrez, G. Helle, I. Heinrich, L. Andreu-Hayles, O. Planells, M. Leuenberger, C. Burger, and G. Schleser (2011), Pooled versus separate measurements of tree-ring stable isotopes, *Science of The Total Environment*, *409*, 2244–2251.

Loehle, C. (2009), A mathematical analysis of the divergence problem in dendroclimatology, *Climatic Change*, *94*(3-4), 233–245, doi:10.1007/s10584-008-9488-8.

McCarroll and Loader

McKenney, D. W., J. H. Pedlar, P. Papadopol, and M. F. Hutchinson (2006), The development of 1901–2000 historical monthly climate models for Canada and the United States, *Agricultural and Forest Meteorology*, *138*(1–4), 69–81.

Nelson, E. A. (2012), Climate change in the canadian boreal forest: the effect of warming, frost events, cloud cover and CO2 fertilization on conifer tree rings, University of Toronto, PhD thesis.

Newman, J. A., M. H. Anand, H. A. L. Henry, and S. L. Hunt (2011), *Climate Change Biology*, CABI.

Ni, F., T. Cavazos, M. K. Hughes, A. C. Comrie, and G. Funkhouser (2002), Cool-season precipitation in the southwestern USA since AD 1000: comparison of linear and nonlinear techniques for reconstruction, *International Journal of Climatology*, *22*(13), 1645–1662, doi:10.1002/joc.804.

Norby, R. J. et al. (2005), Forest response to elevated CO2 is conserved across a broad range of productivity, *Proceedings of the National Academy of Sciences of the United States of America*, *102*(50), 18052–18056.

Norby, R. J., and R. D. Zak (2011), Ecological lessons from free-air CO2 enrichment (FACE) experiments, *Annual Review of Ecology, Evolution, and Systematics*, *42*, 181–203.

Peñuelas, J., J. G. Canadell, and R. Ogaya (2011), Increased water-use efficiency during the 20th century did not translate into enhanced tree growth, *Global Ecology and Biogeography*, *20*(4), 597–608, doi:10.1111/j.1466-8238.2010.00608.x.

Rudolph, T. D., and P. R. Laidly (1990), Pinus banksiana Lamb. jack pine, in R.M. Burns and B.H. Honkala (eds.), *Silvics of North America*, *Vol. 1, Conifers*, USDA Forest Service, Agricultural Handbook 654, Washington, DC. , 280-293

Savva, Y., Y. Bergeron, B. Denneler, A. Koubaa, and F. Tremblay (2008), Effects of interannual climate variations on radial growth of jack pine provenances in Petawawa, Ontario, *Canadian Journal of Forest Research*, *38*, 619–630.

Silva, L. C. R., and M. Anand (2012), Probing for the influence of atmospheric CO2 and climate change on forest ecosystems across biomes, *Global Change Biology*.

Soil Classification Working Group [SCWG] (1998), *The Canadian System of Soil Classification*, Agriculture and Agri-Food Canada, Ottawa, Canada.

Soulé, P. T., and P. A. Knapp (2006), Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO2 fertilization effect?, *New Phytologist*, *171*, 379–390.

Stewart, J. D., and J. Hoddinott (1993), Photosynthetic acclimation to elevated atmospheric carbon dioxide and UV irradiation in *Pinus banksiana*, *PhysiologiaPlantarum*, *88*(3), 493–500.

Tardif, J., and F. Conciatori (2001), Comparative analysis of the climatic response of seven boreal tree species from northwestern Quebec, Canada, *Tree-Ring Research*, *57*(2), 169–181.

Thompson and Parker

Wood, S. N. (2006), *Generalized Additive Models: An Introduction with R*, Chapman &Hall/CRC, New York, NY.

Young, G. H. F., D. McCarroll, N. J. Loader, and A. J. Kirchhefer (2010), A 500-year record of summer near-ground solar radiation from tree-ring stable carbon isotopes, *The Holocene*, *20*(3), 315–324, doi:10.1177/0959683609351902.

# Tables

**Table 1:** Model fit statistics for factor regression standardization of tree ring width data for a two- (FA) and three- (QFA) factor model. Q = productivity ; F = forcing of year; A = age trend.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Model** | **Span** | Akaike information criterion | Bayesian information criterion | **Geometric standard**  **deviation of residuals** |
| G=QFA | 0.0606 | 19600 | 23600 | 0.400 |
| G=FA | 0.0614 | 27200 | 28300 | 0.503 |

**Table 2:** Model fit statistics for climate-ring width models. Akaike information criterion (AIC)/Bayesian information criterion (BIC) comparisons among models are invalid because the dependent variables differ. Q = productivity ; F = forcing of year; A = age trend.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Standardization model** | **Climate-growth model** | **AIC** | **BIC** | **Adjusted R2** |
| G=QFA | Generalized additive model | -33.6 | 14.7 | 0.706 |
| G=QFA | Linear | -10.5 | 5.5 | 0.612 |
| G=FA | Generalized additive model | -117.6 | -77.3 | 0.392 |
| G=FA | Linear | -79.3 | -63.3 | 0.062 |

**Table 3:** Responses (and coefficients) of ring width (log-transformed forcing) to climate variables and water use efficiency. Q = productivity ; F = forcing of year; A = age trend; GAM = generalized additive model; GDD = growing degree day; NA = not applicable.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Variable** | **Growth model** | **Climate-growth model** | **Coefficient** | **Effective degrees of freedom** | **Direction** | **p-value** |
| Intercept | G=QFA | GAM | -0.09 | NA | NA | 4.2e-6 |
| Intercept | G=QFA | Linear | 3.91 | NA | NA | 2.7e-12 |
| Intercept | G=FA | GAM | 0.10 | NA | NA | 1.1e-12 |
| Intercept | G=FA | Linear | 0.37 | NA | NA | 0.295 |
| Water use efficiency | G=QFA | GAM | NA | 4.7 | Negative | 3.6e-11 |
| Water use efficiency | G=QFA | Linear | -0.055 | NA | Negative | 4.1e-11 |
| Water use efficiency | G=FA | GAM | NA | 3.7 | Negative | -1.1e-6 |
| Water use efficiency | G=FA | Linear | -0.014 | NA | Negative | 0.012 |
| Growing season GDD | G=QFA | GAM | NA | 7.7 | Negative | 0.004 |
| Growing season GDD | G=QFA | Linear | -5.2e-4 | NA | Negative | 0.001 |
| Growing season GDD | G=FA | GAM | NA | 2.2 | Positive | 0.105 |
| Growing season GDD | G=FA | Linear | 1.1e-4 | NA | Positive | 0.328 |
| Growing season precipitation | G=QFA | GAM | NA | 4.7 | Negative | 0.004 |
| Growing season precipitation | G=QFA | Linear | -9.2e-4 | NA | Negative | 2.8e-5 |
| Growing season precipitation | G=FA | GAM | NA | 1.2 | Positive | 0.919 |
| Growing season precipitation | G=FA | Linear | 1.9e-5 | NA | Positive | 0.913 |
| Growing season length | G=QFA | GAM | NA | 1.0 | Positive | 0.727 |
| Growing season length | G=QFA | Linear | 1.6e-3 | NA | Positive | 0.500 |
| Growing season length | G=FA | GAM | NA | 6.0 | Positive | 0.105 |
| Growing season length | G=FA | Linear | 2.4e-3 | NA | Positive | 0.143 |

**Table 4:** Model fit statistics for climate-water use efficiency (WUE) models.

|  |  |  |  |
| --- | --- | --- | --- |
| **Climate-WUE model** | **AIC** | **BIC** | **Adjusted R2** |
| GAM | -339 | -308 | 0.281 |
| Linear | -326 | -312 | 0.208 |

**Table 5:** Responses (and coefficients) of water use efficiency to climate variables .

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Variable** | **Model type** | **Coefficient** | **Effective degrees of freedom** | **Direction** | **p-value** |
| Intercept | GAM | 4.0 | NA | NA | 0 |
| Intercept | Linear | -1.7 | NA | NA | 0 |
| Growing season GDD | GAM | NA | 7.6 | Mixed | 0.015 |
| Growing season GDD | Linear | 1.6e-4 | NA | Positive | 2.8e-6 |
| Growing season precipitation | GAM | NA | 1.0 | Negative | 0.008 |
| Growing season precipitation | Linear | 1.1e-4 | BA | Positive | 0.072 |
| Growing season length | GAM | NA | 1.0 | Negative | 0.416 |
| Growing season length | Linear | -9.9e-4 | NA | Negative | 0.068 |

# Figures



**Figure 1:** Location of jack pine stands used as study sites. See inset for location within Ontario.

a)



b)



**Figure 2:** Sample depth (number of series included in the chronology) by a) year and b) tree age for the jack pine ring-width chronology.

**Figure 3:** Tree-level productivity (**Q**) versus tree age for the jack pine ring-width chronology. The smooth line is a loess line of best fit for the QFA model and error bars show a 95% confidence interval for each data point.

**Figure 4:** Forcing (index of growth by year) for the jack pine ring-width chronology for two models. QFA = ???;FA= ???. The shaded region shows a 95% confidence interval.

**Figure 5:** Ring width relative to the age trend (expected growth by age) for the jack pine ring-width chronology. The shaded region shows a 95% confidence interval.

**Figure 6:** Stand-level effects on intrinsic water use efficiency (**Q**) versus stand age for the r intrinsic water use efficiency chronology. The smooth line is a loess line of best fit while error bars show a 95% confidence interval for each data point.

**Figure 7:** Standardized intrinsic water use efficiency by year. The shaded region shows a 95% confidence interval.

**Figure 8:** Age trend(index of intrinsic water use efficiency by age, analogous to the regional curve) for the intrinsic water use efficiency chronology. The shaded region shows a 95% confidence interval.

**Figure 9:** Standardized water use efficiency (Wi) divided by atmospheric carbon dioxide levels from 1879-2010. This is a simple method of adjusting atmospheric carbon dioxide levels. The shaded region shows a 95% confidence interval.

a)

b)

c)

**Figure 10:** Climate data from 1901-2007 for Silver Dollar, Ontario, showing variation in growing season a) growing degree days (GDD), b) precipitation, and c) length.

a)

b)

c)

d)

**Figure 11:** Response of standardized ring-width to climate and water use efficiency within the same year for two generalized additive models (GAM) and two linear models (LM). Plotted is the partial response to a) intrinsic water use efficiency (Wi), and growing season b) growing degree days (GDD), c) precipitation, and d) length. The shaded region shows a 95% confidence interval.

a)

b)

c)

**Figure 12:**Response of standardized water use efficiency to climate of the same year for a generalized additive model (GAM) and a linear model (LM). Plotted is the partial response to growing season a) growing degree days, b) precipitation and c) length. The shaded region shows a 95% confidence interval.