

Time-series analysis of $\delta^{13}\text{C}$ from tree rings. I. Time trends and autocorrelation

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Summary Univariate time-series analyses were conducted on stable carbon isotope ratios obtained from tree-ring cellulose. We looked for the presence and structure of autocorrelation. Significant autocorrelation violates the statistical independence assumption and biases hypothesis tests. Its presence would indicate the existence of lagged physiological effects that persist for longer than the current year. We analyzed data from 28 trees (60–85 years old; mean = 73 years) of western white pine (*Pinus monticola* Dougl.), ponderosa pine (*Pinus ponderosa* Laws.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*) growing in northern Idaho. Material was obtained by the stem analysis method from rings laid down in the upper portion of the crown throughout each tree's life. The sampling protocol minimized variation caused by changing light regimes within each tree. Autoregressive moving average (ARMA) models were used to describe the autocorrelation structure over time. Three time series were analyzed for each tree: the stable carbon isotope ratio ($\delta^{13}\text{C}$); discrimination (Δ); and the difference between ambient and internal CO_2 concentrations ($c_a - c_i$). The effect of converting from ring cellulose to whole-leaf tissue did not affect the analysis because it was almost completely removed by the detrending that precedes time-series analysis. A simple linear or quadratic model adequately described the time trend. The residuals from the trend had a constant mean and variance, thus ensuring stationarity, a requirement for autocorrelation analysis. The trend over time for $c_a - c_i$ was particularly strong ($R^2 = 0.29$ – 0.84). Autoregressive moving average analyses of the residuals from these trends indicated that two-thirds of the individual tree series contained significant autocorrelation, whereas the remaining third were random (white noise) over time. We were unable to distinguish between individuals with and without significant autocorrelation beforehand. Significant ARMA models were all of low order, with either first- or second-order (i.e., lagged 1 or 2 years, respectively) models performing well. A simple autoregressive (AR(1)), model was the most common. The most useful generalization was that the same ARMA model holds for each of the three series ($\delta^{13}\text{C}$, Δ , $c_a - c_i$) for an individual tree, if the time trend has been properly removed for each series. The mean series for the two pine species were described by first-order ARMA models (1-year lags),

whereas the Douglas-fir mean series were described by second-order models (2-year lags) with negligible first-order effects. Apparently, the process of constructing a mean time series for a species preserves an underlying signal related to $\delta^{13}\text{C}$ while canceling some of the random individual tree variation. Furthermore, the best model for the overall mean series (e.g., for a species) cannot be inferred from a consensus of the individual tree model forms, nor can its parameters be estimated reliably from the mean of the individual tree parameters. Because two-thirds of the individual tree time series contained significant autocorrelation, the normal assumption of a random structure over time is unwarranted, even after accounting for the time trend. The residuals of an appropriate ARMA model satisfy the independence assumption, and can be used to make hypothesis tests.

Keywords: ARMA models, Box-Jenkins models, conifers, discrimination, global climate change, *Pinus monticola*, *Pinus ponderosa*, *Pseudotsuga menziesii*, stable carbon isotope ratio, water-use efficiency.

Introduction

Variation in stable carbon isotopic composition among plant species was first noted by geochemists in the 1950s, and by the 1970s it was accepted that stable carbon isotope ratios ($\delta^{13}\text{C}$) could distinguish among photosynthetic pathways (Farquhar et al. 1989, Ehleringer 1991). A potential advantage of carbon isotope analyses over instantaneous observations is the long-term integration provided by isotopically fractionated organic matter accumulated in leaves or tree rings (Ehleringer 1991). A second potential advantage is that the carbon isotopes are recorded in annual rings of trees, providing a record of the past. Tree-ring isotopic data have been used to reconstruct past atmospheric composition (Tans and Mook 1980) and photosynthetic gas exchange (Marshall and Monserud 1996).

Isotopic data have also been used to analyze interannual variation, especially in relation to climate (Leavitt and Long 1989b, Leavitt 1993, Brooks et al. 1998). Because series of consecutive observations are collected from the same trees (e.g., annual rings from an increment core), autocorrelation

may arise. Autocorrelation describes the correlation between successive measurements on the same individual across a range of time lags. Its presence violates the independence assumption necessary for most statistical analyses, and thereby biases hypothesis tests (e.g., an analysis of variance). Monserud (1986) demonstrated both the prevalence of autocorrelation and the importance of removing it in dendrochronological tree-ring analyses. Once the autocorrelation structure has been described with an appropriate statistical model, the residuals can be analyzed directly without biasing hypothesis tests (Monserud 1986).

Little is known about the stochastic properties of $\delta^{13}\text{C}$ over the lifetime of forest-grown trees. Berninger et al. (2000) examined annual variation in discrimination (Δ) in four, old-growth, *Pinus sylvestris* L. trees in Finland and found a long-term increase in Δ , and also observed that the series were highly autocorrelated; however, they did not explicitly model and remove the autocorrelation. Dupouey et al. (1993) analyzed tree-ring cellulose in breast-high (1.37 m) cores from four beech trees over a 40-year period (1950–1990) and found a significant linear trend, but the autocorrelations in $\delta^{13}\text{C}$ were not significant for any time lag. Leavitt and Long (1987) analyzed tree ring series from long-lived mixed conifers (mostly *Pinus ponderosa* Laws.) in southwestern USA, but failed to find any effects of environmental disturbances (e.g., fire, thinning, insect defoliation) on $\delta^{13}\text{C}$. Leavitt and Long (1987) focused on graphical techniques, and did not examine the statistical time-dependent properties of their time series.

We focused on the time-dependent properties of the stable isotope ratio $\delta^{13}\text{C}$ in tree-ring cellulose, based on material from 28 forest-grown trees (mean age of 73 years) of three conifer species. Time series of the major transformations of $\delta^{13}\text{C}$ were analyzed for each tree, concentrating on both the long-term trend and the stochastic autocorrelation structure.

Gas exchange variables

All C_3 plants, which includes most temperate-zone species including the three conifer species studied here, discriminate against ^{13}C relative to ^{12}C as they assimilate atmospheric CO_2 , because ^{13}C has intrinsically lower reactivity than ^{12}C (Farquhar et al. 1982). The ratio of ^{13}C to ^{12}C in a plant sample is determined relative to an accepted standard with a mass spectrometer, and expressed in δ notation in per mil units (‰):

$$\delta^{13}\text{C}_{\text{plant}} = \left(\frac{^{13}\text{C}/^{12}\text{C}_{\text{plant}}}{^{13}\text{C}/^{12}\text{C}_{\text{standard}}} - 1 \right) 1000, \quad (1)$$

where $\delta^{13}\text{C}_{\text{plant}}$ is the ratio of ^{13}C to ^{12}C in the plant tissue expressed relative to the Pee Dee Belemnite (PDB) standard (‰).

Farquhar and Richards (1984) proposed a more physiologically relevant measure, Δ , the isotopic discrimination of ^{13}C relative to ^{12}C by the leaf:

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p / 1000}, \quad (2)$$

where δ_a and δ_p are the isotopic compositions, $\delta^{13}\text{C}$ (‰), of air and plant tissue, respectively. Hereafter, the simpler δ_p notation is used rather than $\delta^{13}\text{C}_{\text{plant}}$. For the period 1905–1989, δ_a has ranged between -6.54 and -7.78 ‰ relative to the PDB standard (Friedli et al. 1986, Keeling et al. 1989). We used linear interpolation to estimate δ_a values between the relatively infrequent observations before 1980 (the exponential smoothing of Feng (1999) would not change conclusions). Note that the denominator is close to 0.975 (for δ_p of -25 ‰), which means that Δ is approximately 2 to 3% larger than the difference $\delta_a - \delta_p$.

Discrimination Δ has the advantage of measuring isotopic composition relative to the source of carbon (atmospheric CO_2) rather than to an arbitrary standard such as PDB limestone (Ehleringer 1991). Thus, it directly expresses the consequences of biological processes, whereas δ_p is the result of both source isotopic composition and biological activities (Ehleringer 1991).

Farquhar et al. (1982) determined that the difference $\delta_a - \delta_p$ is linearly related to the ratio of internal to ambient CO_2 concentrations (c_i/c_a):

$$\delta_a - \delta_p = a + (b - a)(c_i/c_a), \quad (3)$$

where a is fractionation by diffusion through stomata (4.4‰), b is a fitted parameter determined mostly by the fractionation of the carboxylating enzymes (27‰; Farquhar and Richards 1984), c_i is the intercellular CO_2 concentration (ppm) in leaf mesophyll, and c_a is the concentration of CO_2 in the air surrounding the leaf (ppm). Annual records of past δ_a and c_a were obtained from published data from Antarctic ice cores (Friedli et al. 1986) and direct measurements summarized by Keeling et al. (1989). There has been a shift in δ_a of atmospheric CO_2 by about -1.2 ‰ during the 20th century (Friedli et al. 1986). The ice core data have been corroborated by the isotopic record in cellulose of C_4 plants (Marino and McElroy 1991).

Equation 3 can be solved for c_i (Farquhar et al. 1982):

$$c_i = \frac{c_a(\delta_a - \delta_p - a)}{b - a}. \quad (4)$$

Thus, the slope of this equation depends on the CO_2 concentration. Once c_i has been determined, the ratio c_i/c_a and the difference $c_a - c_i$ can be determined for each observation. The advantage of $c_a - c_i$ is its direct relationship with both net photosynthetic rate and photosynthetic water-use efficiency.

We focused on the stochastic properties of δ_p , Δ , c_i/c_a and $c_a - c_i$. These series are not independent of each other (Figure 1). The ratio c_i/c_a is directly proportional to the difference $\delta_a - \delta_p$, (Equation 3) and Δ is dominated by the numerator $\delta_a - \delta_p$ in Equation 2. Thus, we can conclude that the time-series properties of Δ and c_i/c_a will be almost identical, because the variates differ only by a factor of proportionality.

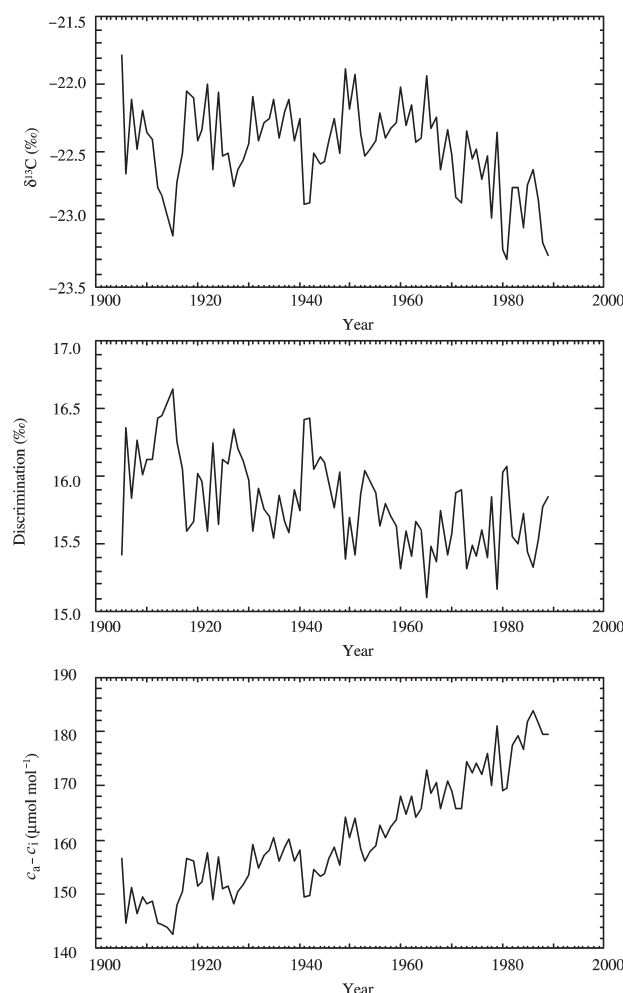


Figure 1. Correspondence over time of the overall mean time series for δ_p , Δ , and $c_a - c_i$. All variables are calculated from measured tree-ring cellulose data as well as predicted leaf whole-tissue data.

A second observation from Equation 2 is that Δ and δ_p are strongly related, but with opposite signs (Figure 1). Because δ_a is a stable and slow-moving time series, Δ and δ_p have similar residuals from their respective trend lines, but with opposite signs. These residuals contain the stochastic time-series information that we analyzed.

Materials and methods

We analyzed carbon isotope ratios of tree-ring cellulose deposited over the last 80 years in 28 trees of western white pine (*Pinus monticola* Dougl.), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*) growing naturally at the Priest River Experimental Forest (PREF) in northern Idaho, USA (48°21' N, 116°50' W) at altitudes between 800 and 950 m a.s.l. Our 28 trees are a random sample of eight Douglas-fir trees and 10 each of ponderosa pine and western white pine trees from an earlier study of trees that were destructively sampled in 1988 and 1989 by stem analysis methods. All trees were mature dominants or

codominants with a normal, healthy appearance. The sample trees ranged from 60 to 85 years old (mean = 73 years). Tree diameter at breast height (1.37 m) ranged from 28 to 55 cm (mean = 38 cm), and total height ranged from 24 to 39 m (mean = 32 m). The stands are the same as those used by Marshall and Monserud (1996) and Monserud and Marshall (1999). Any discrepancy between ring counts and whorl counts was resolved by splitting the stem section down the pith and identifying terminal bud scars.

Figure 2 depicts the sampling scheme for selecting annual rings within a tree, and Table 1 lists an example. Within the crown, sample disks were taken at every 10th whorl, and below the crown at every 5th whorl (Figure 2). No rings were taken below breast height (bh), and with the exception of the bh disk, no rings were taken closer than five rings from the pith. Finally, no rings were taken farther than 15 rings from the pith. This scheme ensured that the sample rings came from the same relative location in the upper portion of the crown

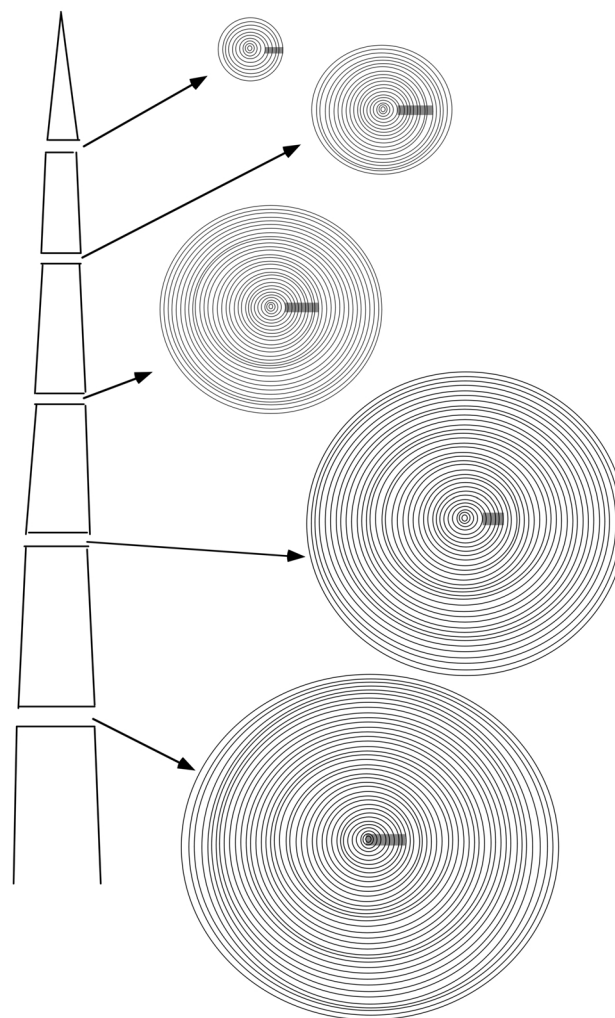


Figure 2. Schematic of sampling scheme for selecting tree rings within a typical tree. Only rings 5–15 from the pith were used to construct the time series, with cross sections taken every 10 whorls within the crown and every five whorls below the crown.

Table 1. Sampling scheme for selecting tree rings within a typical tree. Age at breast height (bh, 1.37 m) in this example is 67 years, and crown base is at Whorl 30 below the tip. Within the crown, sample disks were available only every 10 whorls, and below the crown every five whorls. No rings were used below bh and, with the exception of the bh disk, no rings were taken closer than five rings from the pith. Finally, no rings were taken farther than 15 rings from the pith. This scheme ensured that the sample rings came from the same relative location within the crown throughout the tree's life.

Whorl no. from top	Year pith formed	Total no. of rings sampled for $\delta^{13}\text{C}$	Ring numbers sampled, from pith	Years of sample ring formation	Observation no. in time series
0	1989	0	—	—	—
10	1979	5	6–10	1985–89	63–67
20	1969	10	6–15	1975–84	53–62
30	1959	10	6–15	1965–74	43–52
35	1954	5	6–10	1960–64	38–42
40	1949	5	6–10	1955–59	33–37
45	1944	5	6–10	1950–54	28–32
50	1939	5	6–10	1945–49	23–27
55	1934	5	6–10	1940–44	18–22
60	1929	5	6–10	1935–39	13–17
65	1924	5	6–10	1930–34	8–12
67 (bh)	1922	7	1–7	1923–29	1–7

throughout each tree's life. We intentionally sampled the innermost five rings only in the bh disk, thereby placing these innermost five rings at the start of the time series, where any transient effect resulting from proximity to the pith will have a minimum effect on the autocorrelation function. Examination of the ring width pattern for the sampled section of these disks provided no evidence of suppression by or strong shading from neighboring trees. We did not analyze a corresponding time series based on bh disks or bh cores from the same trees.

Each sample was dated and divided into earlywood and latewood based on color and resistance to peeling with a sharp blade. Holocellulose was extracted from the earlywood as described by Leavitt and Danzer (1993) and δ_p determined. No material was combined across trees, or across rings. The resulting δ_p values were concatenated into an annual time series for each sample tree.

The decision to use earlywood was based on several criteria. First, the narrowness of the latewood layer in some of these trees, especially the white pine, as well as the subjectivity in determining the location of the boundary, led to concern about sample size and sample quality. Second, latewood would almost certainly have shown a stronger record of conditions in the late summer than earlywood, but earlywood probably carries more information about the previous fall and current spring (Livingston and Spittlehouse 1996). Third, the relative value of data from the two tissue types depends on the question being asked. We were primarily interested in the annual carbon budget of the tree. Because earlywood represents the period of highest photosynthetic rates by the tree, and therefore contains information on the most important part of the year, we concluded that earlywood would be most informative.

A correction (or offset) is often used to account for the difference between ring cellulose and leaf whole tissue (but see Feng 1998, 1999). We examined the magnitude of this offset. First, we used the mean difference between cellulose and whole tissue measured in earlywood (1.7‰) for the three

study species (Marshall and Monserud 1996). This value is near the values reported by Benner et al. (1987) and Gleixner et al. (1993) in other species. Next, we accounted for the difference between stem wood and leaves using the difference measured by Leavitt and Long (1986) for pinyon pine *Pinus edulis* Engelm. (1.2‰). The net effect of these corrections was to reduce $\delta^{13}\text{C}$ by 2.9‰, which translates into an essentially constant increase in Δ by $3.02 \pm 0.01\text{‰}$. Values of $c_a - c_i$ estimated from these corrected values (whole leaf tissue) ranged from 38 to 45 $\mu\text{mol mol}^{-1}$ lower than estimates from the uncorrected values (ring cellulose). The similarity in the curves with and without the offset for all three variables is evident in Figure 1.

Constant differences between the two estimates (ring cellulose versus whole leaf tissue) for $\delta^{13}\text{C}$ and Δ do not affect the analysis. Differences (ring cellulose versus whole leaf tissue) in $c_a - c_i$ are not constant. Because the differences drift slowly and smoothly (as a result of changes in c_a during the 85-year period of study), they are essentially removed by the detrending that precedes the time-series analysis (described below). We report results of analyzing $c_a - c_i$ without the offset to whole leaf tissue, although we also analyzed the $c_a - c_i$ time series with the offset. We adjusted all $c_a - c_i$ estimates in the figures for the 2.9‰ offset.

To determine whether a shift in the leaf area/sapwood area ratio might help to explain the long-term isotopic trends, we also analyzed a separate data set (described in Monserud and Marshall 1999) containing a broader range of tree ages and sizes from the same stands.

Analysis

Box-Jenkins ARMA models

We analyzed the time-dependent structure of the various carbon isotope series by means of a class of stationary time-series models called autoregressive moving average (ARMA) mod-

els (Box and Jenkins 1970). The ARMA (p, q) model, which has autoregressive terms up to order p and moving average terms up to order q , is given by the following linear stochastic difference equation:

$$Z_t - \varphi_1 Z_{t-1} - \varphi_2 Z_{t-2} - \dots - \varphi_p Z_{t-p} = a_t - \theta_1 a_{t-1} - \theta_2 a_{t-2} - \dots - \theta_q a_{t-q}, \quad (5)$$

where Z_t is the deviation at time t from the mean of an equally spaced stationary time series of length n , a_t is an independently distributed normal deviate with zero mean and constant variance σ^2 (a_t is called white noise), φ_i are the p autoregressive parameters, and θ_j are the q moving average parameters. The current value Z_t of the time series (Z) thus depends on a linear combination of the past p values of the time series, the current random shock a_t , and the past q random shocks.

High-order ARMA models are rarely needed in tree-ring studies. Monserud (1986) analyzed 33 historic dendrochronologies that ranged from several hundred to several thousand years in length. With few exceptions, he found that simple two-parameter models described the autocorrelation structure quite well. Thus, we consider the following low-order variants of the general ARMA (p, q) process:

AR(1), the first-order autoregressive model:

$$Z_t = \varphi_1 Z_{t-1} + a_t. \quad (6)$$

AR(2), the second-order autoregressive model:

$$Z_t = \varphi_1 Z_{t-1} + \varphi_2 Z_{t-2} + a_t. \quad (7)$$

MA(1), the first-order moving average model:

$$Z_t = a_t - \theta_1 a_{t-1}. \quad (8)$$

MA(2), the second-order moving average model:

$$Z_t = a_t - \theta_1 a_{t-1} - \theta_2 a_{t-2}. \quad (9)$$

ARMA(1,1), the mixed first-order model:

$$Z_t = \varphi_1 Z_{t-1} + a_t - \theta_1 a_{t-1}. \quad (10)$$

Models 6 and 7 are analogous to regression models using lagged variables, specifically, deviations from the previous year (Z_{t-1}) or the previous 2 years (Z_{t-2}) as independent variables. Models 8 and 9 also use lagged variables, but the variables are the unobservable past random shocks external to the tree (a_{t-1} and a_{t-2}). These MA models rely on simultaneous, iterative fitting of all variables on the right-hand side of the equation by procedures described below. The key difference between the AR and MA models is that Models 6 and 7 rely on explained variance associated with previous values in the series, whereas Models 8 and 9 rely on the magnitude and direction of unexplained variance (random shocks) associated with previous values in the series. Model 10 relies on a combination of explained and unexplained variance.

A key assumption is that the underlying time series is stationary. This means that the joint probability distribution between Z_t and Z_{t-s} depends only on the interval s and not on time t . Changing the time origin of a stationary time series has no effect on the joint probability distribution of any m consecutive observations in the series (Box and Jenkins 1970). Heuristically, the stationary property means that all observations in the time series are equally important and that the mean is a meaningful measure of central tendency (Monserud 1986).

Removing the time trend

The importance of the stationarity property means that care should be taken to describe and remove the trend in the data over time. Traditionally, dendrochronologists have considered this step (akin to standardization) crucial to their analyses, for their goal is to isolate the influence of climate on tree growth, while excluding factors such as tree size and age, stand density, and site productivity (Fritts 1976). The residual variation about the trend contains this climatic information (Monserud 1986).

Dendrochronologists have used a variety of methods for describing the time trend: regression methods such as linear or quadratic polynomials, the negative exponential, a multiplicative power function (Monserud 1986), and smoothing splines (Cook and Briffa 1990). Because the goal is to remove only the non-climatic trend while retaining the underlying variation, simple, parsimonious methods are preferable. If splines are used, they are usually stiff, to avoid overfitting the data. Both Cook and Briffa (1990) and Schweingruber (1996) caution against using any automatic detrending or standardization method or program, because an automatic procedure could remove the variation that is the subject of investigation.

For many physiologists, the trend itself may be the subject of interest. Whether the focus is on an examination of the long-term trend or annual variation, the first step is to describe the trend in succinct mathematical terms so that the residuals have a constant mean and variance. We fit either a linear or quadratic trend to the original data. The residuals of this trend had the necessary properties of a constant mean (zero) and a constant variance. We used standard statistical procedures (e.g., t -test) to decide between the linear and quadratic forms. More complicated curve forms were not needed to describe the trends in our data.

ARMA model fitting

An iterative three-stage procedure is central to fitting ARMA models using Box-Jenkins techniques: identification, estimation, and diagnostic checking (Jenkins 1982). In the identification phase, the modeler tries to infer the orders p and q of a parsimonious ARMA model. The main tool is the sample autocorrelation function (ACF), which is a simple summary (usually a graph: the correlogram) of the correlation structure within the series at increasing lags (e.g., the Lag 2 autocorrelation is the correlation between all observations that are 2 years apart). Almost as useful is the partial ACF (partial autoregressions), and the extended ACF (Tsay and Tiao 1984). After inferring several likely candidate models, the pa-

rameters are estimated and the models checked and compared with standard diagnostic tools. If deficiencies are found, the modeler returns to the identification stage and looks more closely for information on model form. The interpretation of the ACF (and the companion partial ACF) is one of the hardest aspects of time-series analysis and requires practical experience (Chatfield 1996).

We illustrate preliminary model identification with two examples, the mean series δ_p data for Douglas-fir and western white pine (Figure 3). As in all our ARMA analyses, the data are deviations from the mean, meaning the trends have been removed. For the mean western white pine series, the autocorrelation function (ACF) shows a combination of exponential decay and sine waves, whereas the partial autocorrelation function (PACF) shows a significant spike (i.e., significant autocorrelation) at Lag 1 followed by no apparent pattern (Figure 3). These are the indications of an AR(1) model (Jenkins 1982); an MA(1) is also a good choice. In the second example, the ACF for the mean Douglas-fir series has only weak autocorrelation at Lag 1 and a significant spike at Lag 2, followed by a pattern that could be a mixture of exponential decay and sine waves; the same general pattern also appears to hold for

the PACF (Figure 3). This information indicates that Douglas-fir could be represented by a second-order model, with both MA(2) and AR(2) as good candidates. As we will see after parameter estimation and diagnostic testing, both models describe the mean Douglas-fir data well. These patterns correspond closely to the theoretical ACF and PACF for these respective models (Box and Jenkins 1970). Note that the Lag 3 autocorrelation was not significant for either of our examples, indicating that there is no need to consider higher order models such as AR(3) and MA(3). This was true for all trees and mean series in the study.

Parameter estimation is straightforward with AR models (linear regression), but the MA models require maximum likelihood or nonlinear procedures to estimate the parameters of the unobservable a_{t-q} terms. We used Proc ARIMA in the Econometric Time Series package of the SAS Institute (1993) for most univariate modeling, supplemented by the SCA system (Liu and Hudak 1992) for the EACF and additional diagnostic tools.

Often a time-series analysis will uncover several competing models, each with significant parameters (we determined significance at the $\alpha = 0.05$ level). This is because of the inverse duality between the AR and MA models (Box and Jenkins 1970). For example, an AR(1) process can be represented by an infinite series of MA terms with coefficients that decay exponentially, but usually only the first one or two MA terms are needed for a good approximation. As a result, it is not unusual for both an AR model and an MA model of the same order to explain nearly the same amount of variation. Thus, it is often necessary to determine which of two or more competing models represents the underlying system the best. We note that the ease of computation and estimation with AR models is a considerable advantage over comparable MA models (Chatfield 1996).

The adequacy of the model is examined by a series of diagnostic checks, such as comparing the ACF of the residuals to that expected for white noise. Testing the residuals with the portmanteau Q -statistic of Ljung and Box (1978) over a range of time lags is often useful, although the power of this χ^2 test can be low, especially when sample sizes are less than 100 (Davies and Newbold 1979, Hosking 1986). Akaike's Information Criterion (AIC) is helpful for comparing competing models, as is a Bayesian variant (BIC) that more severely penalizes models that contain additional parameters (Chatfield 1996). Parsimony is an obvious goal, so that the model with the fewest parameters is preferable when other diagnostic statistics are similar (Ledolter and Abraham 1981). We used a combination of all of these diagnostics to eliminate unsuitable models and to find the best or near-best models. The competing "best" models always had Information Criteria (whether AIC or BIC) that were essentially the lowest, although we did not use such a criterion blindly when deciding.

Finally, we note that the length n of the equally spaced time series is crucial, because the standard error of almost everything in time-series analysis is proportional to and dominated by: $1/\sqrt{n}$. The only information available to the analysis is contained in the series itself, and the measure of that informa-

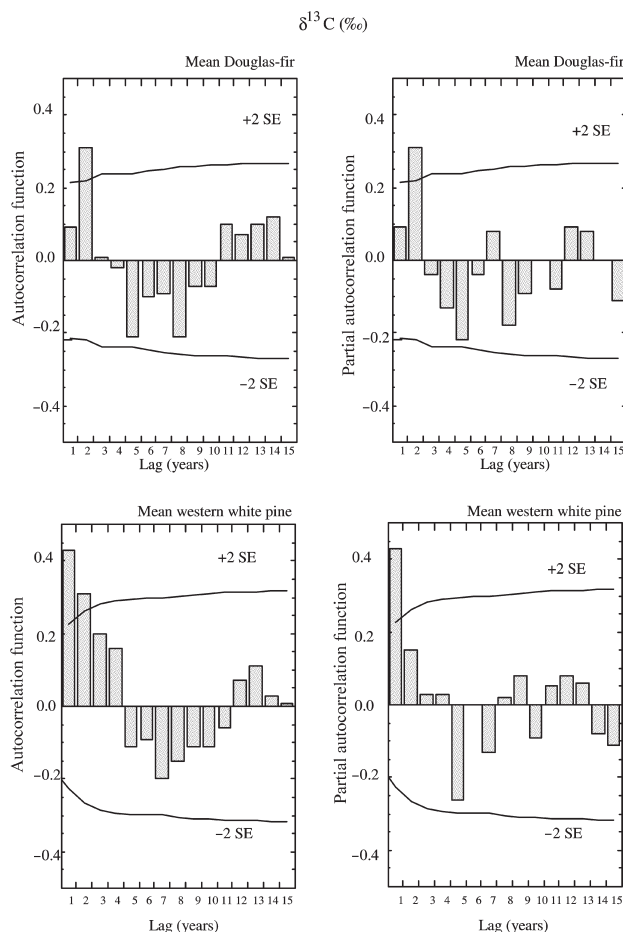


Figure 3. Autocorrelation function (ACF) and partial autocorrelation function (PACF) for the mean series for Douglas-fir and western white pine. Approximate ± 2 SE bounds are also plotted.

tion is n . For example, if n is increased from 16 to 64 then the ability to detect significant differences is doubled. Based on 2.0 as an approximate t -statistic for $\alpha = 0.05$, the magnitude of the confidence interval half-width decreases from about $2/\sqrt{16} = 0.5$ to $2/\sqrt{64} = 0.25$. Further increases in n , the length of the time series, will allow us to detect increasingly small differences from zero, the null hypothesis in parameter estimation.

Results

Time trends: individual trees

We analyzed 84 time series from 28 individual trees (three variables for each). All but 11 series had a significant slope with respect to time (Table 2). Either a linear or quadratic model was sufficient to account for the time trend and ensure stationarity. The trends over time for the δ_p and Δ series were weak, with a mean R^2 of about 0.22 for each variable. The trend over time for $c_a - c_i$ was strong ($R^2 = 0.29$ – 0.84 , with a mean of 0.60).

Some species-specific differences in time trends are apparent from Table 2. For Δ , the Douglas-fir series had almost no slope with respect to time (mean $R^2 = 0.04$), whereas the ponderosa pine series all had relatively strong slopes (mean $R^2 = 0.33$); western white pine was intermediate. For the $c_a - c_i$ time series, the slopes for Douglas-fir accounted for less variation with respect to time (mean $R^2 = 0.43$) than the strong relations found for ponderosa pine (mean $R^2 = 0.73$); again western white pine was intermediate. There were no apparent differences among species for the δ_p series. For the model form summarized in Table 2, half the trends were quadratic and the other half were either linear or not significant.

We analyzed $c_a - c_i$ both with and without the offset from tree-ring cellulose to predicted whole leaf tissue. Three generalizations are apparent with the offset: the time trends were of the same form (Table 2), the proportion of explained variation was smaller (mean R^2 was 51 versus 60%; Table 2), and the slopes were less positive (not shown). This third result was expected because the offset reduced $c_a - c_i$ from 38 to 45 $\mu\text{mol mol}^{-1}$ from the uncorrected values (tree-ring cellulose).

Failure to account properly for a significant time trend (Table 2) violates the stationarity assumption. The warning sign is an ACF that damps only slowly (see Box and Jenkins 1970 or Monserud 1986 for examples). This failure results in overly complex (and usually incorrect) ARMA models. Only the 11 series with no significant time trend would be unaffected by such an oversight.

Time trends: species means

We analyzed the species mean and the overall mean time series for each of our standard three variables. All but one series (mean Δ for Douglas-fir) had a significant slope with respect to time (Table 2). The trend over time for both the δ_p and $c_a - c_i$ mean series was quadratic for all three species and for the overall mean series (Figures 4 and 5). The trend over time for the Δ mean series was linear, except for the insignificant slope

for Douglas-fir (Figure 6). In most instances, the amount of explained variation attributable to the trend was larger for the mean time series than it was for the individual tree series. For example, the linear trend for the mean Δ series for ponderosa pine had an $R^2 = 0.66$ (Table 2), which was larger than any individual Δ series for ponderosa pine (maximum $R^2 = 0.52$). This effect was even stronger for the $c_a - c_i$ mean series, with trends explaining 0.69, 0.92, 0.81, and 0.88 of the variation for our three species and the overall mean series, respectively (Table 2; Figure 5). The cause was a common c_a signal that remained after individual tree variation in c_i was reduced by averaging to produce the mean series (Figure 7). Thus, working with a mean of several individual trees usually resulted in a stronger signal over time. Note that the c_a signal would not have much influence on the autoregression analyses of residuals, because it would be removed with the long-term trend. As before, the proportion of explained variation was smaller for the $c_a - c_i$ mean series with the offset to predicted whole leaf tissue. The pronounced differences among time trends of the three standard variables (δ_p , Δ and $c_a - c_i$) do not imply that the residuals should similarly differ.

Species-specific differences in time trends are most apparent for the mean Δ series (Table 2). The mean Douglas-fir Δ series was flat over time, with no significant trend, whereas the mean ponderosa pine series was highly significant ($R^2 = 0.66$). The trend for western white pine was significant but weak ($R^2 = 0.12$). Combining all Δ data into one overall series resulted in a significant trend ($R^2 = 0.31$). In all cases the sign of the significant slope for the trend in mean Δ was negative (Figure 6).

ARMA models: individual trees

Time-series analyses of the residuals from these time trends found that two-thirds of the series contain significant autocorrelation, whereas the remaining third were random white noise over time (by species: three Douglas-fir, five ponderosa pine, two western white pine; Table 3). Significant ARMA models were all of low order, with either first- or second-order autoregressive or moving average models performing well (Table 3). The most common model was a simple AR(1) process. Second-order models were significant for only a few of the trees from the two pine species, but were significant for half of the Douglas-fir trees (Table 4). Only one tree's time series was best described as a mixed ARMA(1,1) process.

No strong species-specific generalizations are apparent from the results summarized in Tables 3 and 4, although the western white pine series are more strongly autocorrelated than those of the other two species (note the lower frequency of nonsignificant results in Table 3 and the larger parameter estimates in Table 4). Furthermore, the individual trees with and without significant autocorrelation cannot be identified without statistical analysis. One useful generalization is shown in Table 3; i.e., that the same ARMA model holds for each of the three series (δ_p , Δ and $c_a - c_i$) for an individual tree, provided that the time trend has been properly removed for each series.

Table 2. Linear (L) or quadratic (Q) time trends by tree for each of three time-series variables (δ_p , Δ , and $c_a - c_i$). Results for the difference $c_a - c_i$ between ambient and internal CO_2 concentration are tabulated both for tree-ring cellulose and for predicted whole-leaf tissue (i.e., with the offset). The percentage of explained variation (adjusted R^2) is given by tree and species (D = Douglas-fir, P = ponderosa pine, and W = western white pine); ns indicates not significant ($\alpha = 0.05$). The species and overall mean trends are fit to the respective mean time series obtained by averaging for each year.

Tree ID	Time-series variable								Length of series (years)
	δ_p		Δ and c_i/c_a		$c_a - c_i$ (tree-ring cellulose)		$c_a - c_i$ (predicted leaf tissue)		
	Trend	R^2 (%)	Trend	R^2 (%)	Trend	R^2 (%)	Trend	R^2 (%)	
D16G	Q	18	L	11	L	64	L	56	77
D46	Q	31	Q	5	L	29	L	17	84
D62	Q	49	Q	17	L	34	L	18	66
D102	Q	16	ns	0	L	43	L	31	85
D106	Q	12	ns	1	L	42	L	31	78
D109	Q	34	ns	1	L	34	L	21	75
D112	Q	30	ns	0	Q	51	Q	37	74
D122	Q	12	ns	1	L	46	L	34	78
Mean D	Q	45	ns	0	Q	69	L	54	85
P2	Q	24	Q	40	L	81	L	76	78
P4	Q	37	Q	20	L	66	L	56	77
P44	L	13	L	50	Q	80	Q	75	78
P46	L	6	L	52	Q	84	Q	79	63
P50	L	13	L	5	Q	65	Q	54	73
P52	L	23	L	52	Q	80	Q	75	77
P59	ns	0	L	19	Q	60	Q	53	62
P62	ns	11	Q	35	Q	75	Q	69	73
P66	Q	17	Q	20	L	68	L	60	72
P67	L	5	L	38	Q	76	Q	71	79
Mean P	Q	16	L	66	Q	92	Q	89	79
W13	Q	21	Q	37	L	76	L	70	60
W17	L	15	ns	0	L	42	L	31	67
W21	Q	48	Q	16	L	40	L	25	65
W462	L	10	ns	0	Q	48	Q	37	77
W47	Q	25	ns	0	L	50	L	37	76
W48	Q	47	Q	51	Q	75	Q	70	70
W49	ns	0	L	9	Q	62	Q	52	76
W51	Q	49	Q	47	Q	79	Q	72	64
W57	Q	42	Q	49	Q	76	Q	70	63
W78	Q	43	Q	6	L	52	L	38	66
Mean W	Q	30	L	12	Q	81	Q	73	77
Overall mean	Q	26	L	31	Q	88	Q	83	85

We also compared parameter estimates for a given ARMA model across each of our three main variables. Results (Table 4) lend further support to the conclusion that the same ARMA model holds for each of the three series for an individual tree, after the time trend has been removed. Note that we intentionally tabulated insignificant estimates in Table 4 so that the full range of variability can be seen and borderline cases can be examined (e.g., the MA(1) estimates for Trees P44 and P50 are nearly significant, whereas those for P59 and P62 are not significant).

In all cases, graphs of the distribution of parameter estimates for a given ARMA model form were nearly overlapping across our three main variables. For example, the mean estimate of ϕ_1 in the AR(1) model for all 28 trees (see Table 4)

was 0.27, 0.29 and 0.29 for δ_p , Δ and $c_a - c_i$, respectively; the standard deviation was 0.19 for each of the three variables. (Note that the mean of these individual estimates is different from the estimate of ϕ_1 for the mean series, also shown in Table 4.) The strong overlap across variables held for second-order models as well: the average estimate of (θ_1, θ_2) in the MA(2) model was $(-0.26, -0.15)$, $(-0.27, -0.16)$ and $(-0.26, -0.17)$ for δ_p , Δ and $c_a - c_i$, respectively; the standard deviations of the estimates of θ_1 and θ_2 were 0.20 and 0.12, respectively, for all three variables. Clearly, these models were not significantly different across the three dependent variables. Thus, not only does the same model form hold across variables, but essentially the same parameter values also hold across variables.

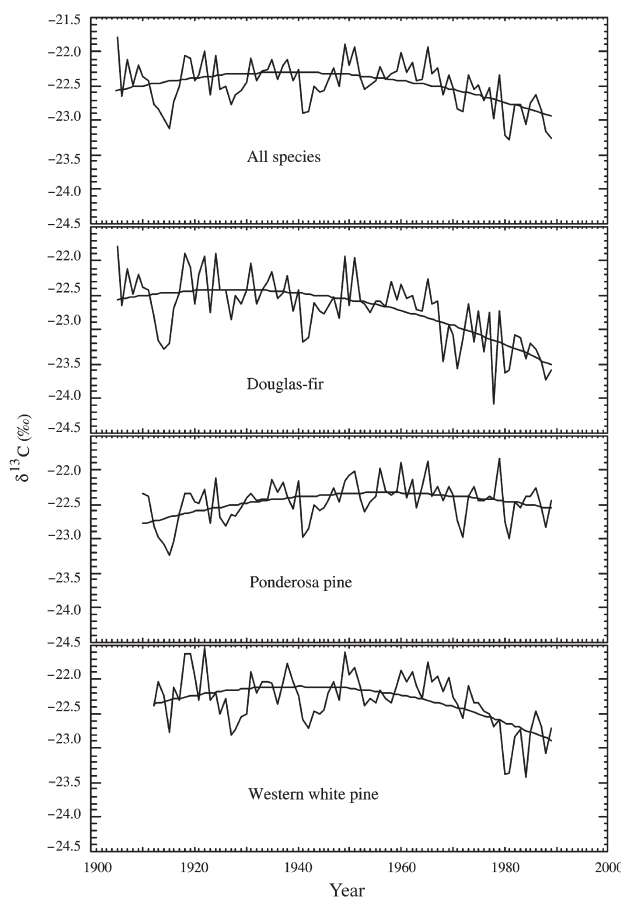


Figure 4. Overall mean and species mean time series for stable carbon isotope ratio, δ_p , of tree-ring cellulose.

We also compared time-series models for $c_a - c_i$ both with and without the offset from tree-ring cellulose to predicted whole leaf tissue. Generally, both model form and parameter estimates were similar for the corresponding series (not shown), usually differing by only about 0.01. There were a few exceptions (all of which were ponderosa pine), where a significant model was found for $c_a - c_i$ with the offset and no model was significant without the offset (e.g., P50, P67).

ARMA models: species means

The autocorrelation structure persisted after averaging individual tree series to produce a mean series. Analyzing the species-specific and overall mean time series for each of the three variables produced consistent results: none of the mean series was white noise, and all mean series contained significant autocorrelation that required either a first- or second-order AR or MA model (Table 3). Even though the mean Δ series for Douglas-fir did not have a significant trend over time (Table 2), it nevertheless contained significant autocorrelation (Table 3).

Examination of the model forms listed in Table 3 and the parameter estimates in Table 4 revealed that second-order models were significant for only seven of the 28 trees. Never-

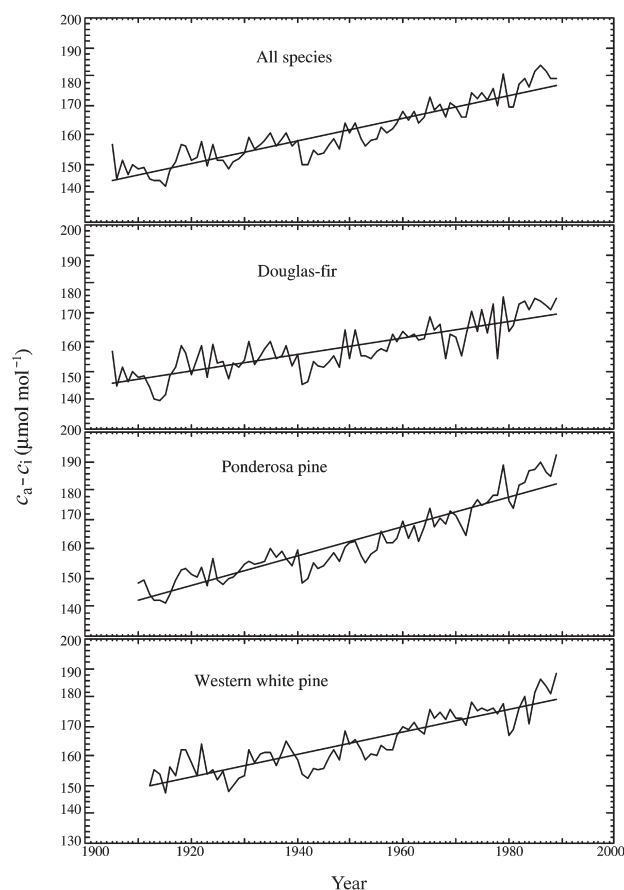


Figure 5. Overall mean and species mean time series for the difference between ambient and internal CO_2 concentrations, $c_a - c_i$, estimated following correction for the offset between tree-ring cellulose and whole tissue in leaves.

theless, both the AR(2) and MA(2) models were significant for the overall mean series, for each of the three variables. Clearly, the best model for the overall mean series cannot be inferred from a consensus of the individual tree model forms (Table 3), nor can its parameters be estimated reliably from the mean value of the individual tree parameters (Table 4).

Species-specific differences arose in the model form (Table 4). The mean series for the two pine species was described by significant first-order ARMA models. In contrast, the Douglas-fir mean series was dominated by significant second-order effects, but negligible first-order effects.

Discussion

Long-term trends

The first step in a time-series analysis of physiological variables is to account for a time trend. Failure to remove a significant trend violates the stationarity assumption and results in mis-specified and overly complicated autocorrelation models. The actual form of this trend is not crucial as long as the residuals have a constant mean and variance, ensuring a stationary

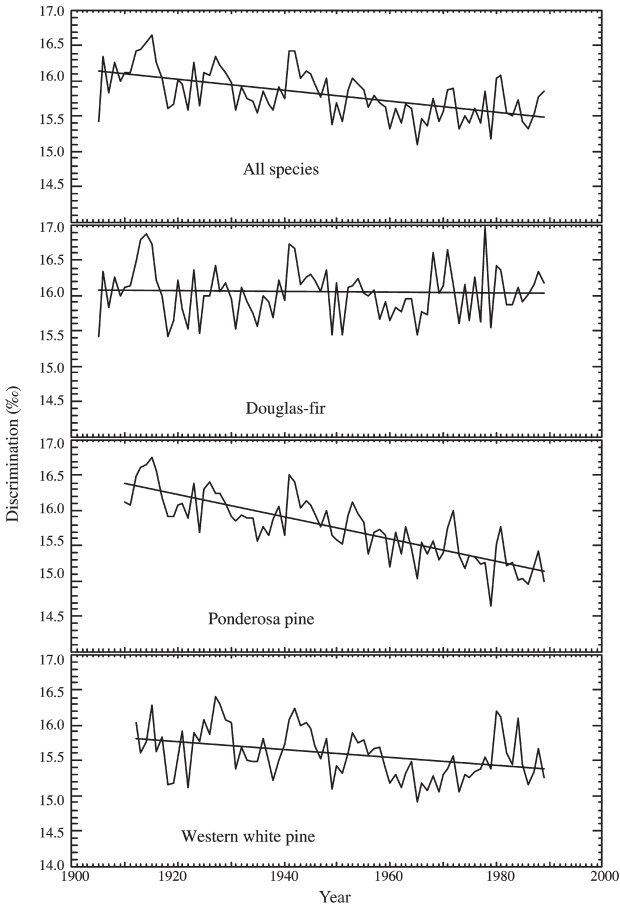


Figure 6. Overall mean and species mean time series for Δ of tree-ring cellulose.

series for autocorrelation analysis. We found considerable variation in the form of the trend among variables, trees, and species. In all cases, they could easily be described with either

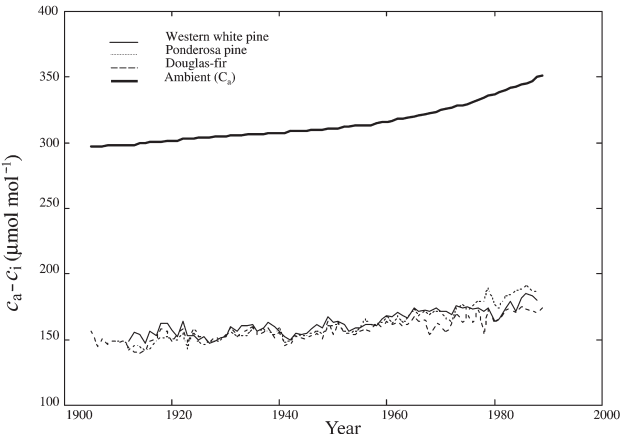


Figure 7. Ambient CO_2 concentration, c_a , and the species-specific mean time series for $c_a - c_i$, the difference between ambient and internal CO_2 concentration, which is estimated following correction for the offset between tree-ring cellulose and whole tissue in leaves.

Table 3. Results of a Box-Jenkins autocorrelation analysis for each of three detrended carbon isotope variables, by individual tree, species mean, and overall mean. The best and second best ARMA models are indicated; ns indicates that no significant models were found (white noise) with $\alpha = 0.05$. The species and overall mean time series are obtained by averaging for each year. Tree ID prefixes are D = Douglas-fir, P = ponderosa pine, and W = western white pine.

Tree ID	Time-series variable					
	δ_p		Δ and c_i/c_a		$c_a - c_i$	
	Best ARMA	2nd Best	Best ARMA	2nd Best	Best ARMA	2nd Best
D16G	MA(2)	AR(1)	MA(2)	AR(1)	MA(2)	AR(2)
D46	AR(2)	MA(2)	AR(2)	MA(2)	AR(2)	MA(2)
D62	ns	ns	ns	ns	ns	ns
D102	ns	ns	ns	ns	ns	ns
D106	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)
D109	MA(2)	AR(2)	MA(2)	AR(2)	MA(2)	AR(2)
D112	ns	ns	ns	ns	ns	ns
D122	ARMA (1,1)	AR(2)	ARMA (1,1)	AR(2)	ARMA (1,1)	AR(2)
Mean D	MA(2)	AR(2)	MA(2)	AR(2)	MA(2)	AR(2)
P2	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)
P4	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)
P44	AR(1)	ns	AR(1)	ns	AR(1)	MA(1)
P46	ns	ns	ns	ns	ns	ns
P50	ns	ns	ns	ns	MA(1)	ns
P52	AR(1)	MA(2)	AR(1)	MA(2)	AR(1)	MA(2)
P59	ns	ns	ns	ns	ns	ns
P62	ns	ns	ns	ns	ns	ns
P66	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)
P67	ns	ns	ns	ns	ns	ns
Mean P	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)
W13	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)
W17	MA(2)	AR(1)	MA(2)	AR(1)	MA(2)	AR(1)
W21	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)
W462	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)
W47	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)
W48	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)
W49	AR(2)	AR(1)	AR(2)	AR(1)	AR(2)	AR(1)
W51	ns	ns	MA(1)	ns	ns	ns
W57	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)
W78	ns	ns	ns	ns	ns	ns
Mean W	AR(1)	MA(1)	AR(1)	MA(1)	AR(1)	MA(1)
Overall mean	AR(2)	MA(2)	MA(2)	AR(2)	AR(2)	MA(2)

linear or quadratic models. The trick is to remove just enough of the trend so that the residuals are stationary (Cook et al. 1990), without heavily removing the additional information (the underlying δ_p signal) that we seek to analyze.

There have been few long-term analyses of individual tree records of stable carbon isotope composition; usually material from several trees or years have been combined before analysis (Feng 1998). One of the few long-term studies on individual trees was conducted by Berninger et al. (2000), who examined annual variation in Δ in four subarctic *Pinus sylvestris* trees. Their trees were 100 to 300 years old, and their analyses

Table 4. Parameter estimates by tree and variable (δ_p , Δ , and $c_a - c_i$) for each of four models: AR(1), AR(2), MA(1), and MA(2). Species prefixes are D = Douglas-fir, P = ponderosa pine, and W = western white pine. The species mean and overall mean time series are obtained by averaging for each year and fit separately; parameter estimates are not averages. Note that both significant and nonsignificant estimates are listed to illustrate the full range of possible values; significant parameter estimates are listed in bold ($\alpha = 0.05$).

Tree ID	AR(1)			AR(2)						MA(1)			MA(2)					
	δ_p	Δ	$c_a - c_i$	δ_p	Δ	$c_a - c_i$	δ_p	Δ	$c_a - c_i$	δ_p	Δ	$c_a - c_i$	δ_p	Δ	$c_a - c_i$	δ_p	Δ	$c_a - c_i$
	φ_1	φ_1	φ_1	φ_1	φ_2	φ_1	φ_2	φ_1	φ_2	θ_1	θ_1	θ_1	θ_1	θ_2	θ_1	θ_2	θ_1	θ_2
D16G	0.23	0.30	0.33	0.20	0.16	0.25	0.20	0.25	0.25	-0.17	-0.20	-0.21	-0.23	-0.25	-0.27	-0.29	-0.27	-0.31
D46	0.07	0.12	0.18	0.05	0.28	0.08	0.32	0.12	0.34	-0.05	-0.08	-0.11	-0.06	-0.28	-0.08	-0.31	-0.11	-0.33
D62	0.14	0.13	0.12	0.11	0.21	0.10	0.20	0.09	0.22	-0.10	-0.09	-0.08	-0.09	-0.17	-0.09	-0.17	-0.06	-0.18
D102	0.14	0.15	0.14	0.13	0.08	0.14	0.08	0.13	0.11	-0.12	-0.13	-0.12	-0.11	-0.11	-0.12	-0.12	-0.10	-0.15
D106	0.36	0.38	0.40	0.38	-0.06	0.40	-0.05	0.42	-0.04	-0.34	-0.35	-0.37	-0.39	-0.10	-0.40	-0.12	-0.42	-0.13
D109	0.01	0.03	0.10	0.01	0.25	0.03	0.26	0.07	0.32	-0.01	-0.02	-0.06	-0.03	-0.29	-0.04	-0.30	-0.05	-0.33
D112	0.06	0.03	0.06	0.06	0.09	0.03	0.06	0.06	0.08	-0.05	-0.03	-0.05	-0.09	-0.14	-0.05	-0.11	-0.05	-0.10
D122	0.48	0.46	0.43	0.37	0.23	0.36	0.22	0.34	0.21	-0.33	-0.33	-0.31	-0.37	-0.28	-0.36	-0.27	-0.34	-0.26
Mean D	0.10	0.08	0.06	0.06	0.32	0.05	0.32	0.04	0.33	-0.06	-0.05	-0.04	0.01	-0.38	0.02	-0.38	0.05	-0.39
P2	0.47	0.48	0.50	0.53	-0.13	0.55	-0.14	0.55	-0.10	-0.46	-0.48	-0.47	-0.50	-0.21	-0.51	-0.22	-0.51	-0.27
P4	0.32	0.35	0.40	0.32	-0.02	0.35	0.01	0.39	0.03	-0.31	-0.34	-0.36	-0.33	-0.06	-0.35	-0.08	-0.39	-0.12
P44	0.26	0.26	0.31	0.23	0.10	0.23	0.13	0.26	0.14	-0.21	-0.21	-0.23	-0.24	-0.13	-0.23	-0.14	-0.27	-0.16
P46	0.12	0.12	0.14	0.11	0.10	0.11	0.11	0.13	0.10	-0.10	-0.10	-0.11	-0.10	-0.11	-0.09	-0.15	-0.10	-0.12
P50	0.18	0.19	0.19	0.20	-0.16	0.21	-0.16	0.23	-0.18	-0.24	-0.24	-0.26	-0.19	0.13	-0.20	0.11	-0.21	0.12
P52	0.50	0.45	0.40	0.41	0.18	0.38	0.16	0.34	0.14	-0.33	-0.31	-0.28	-0.44	-0.30	-0.41	-0.29	-0.36	-0.25
P59	0.07	0.10	0.09	0.06	0.16	0.09	0.19	0.08	0.18	-0.05	-0.08	-0.07	-0.01	-0.16	-0.03	-0.18	-0.01	-0.18
P62	0.03	0.02	0.06	0.03	0.03	0.02	0.03	0.06	0.06	-0.03	-0.02	-0.06	-0.04	-0.07	-0.04	-0.06	-0.09	-0.13
P66	0.49	0.52	0.50	0.59	-0.21	0.61	-0.20	0.60	-0.21	-0.53	-0.54	-0.54	-0.62	-0.13	-0.64	-0.16	-0.63	-0.14
P67	0.06	0.08	0.08	0.05	0.09	0.07	0.11	0.07	0.12	-0.05	-0.07	-0.06	-0.13	-0.16	-0.16	-0.19	-0.15	-0.20
Mean P	0.25	0.26	0.31	0.27	-0.07	0.27	-0.03	0.30	0.02	-0.27	-0.26	-0.29	-0.27	-0.01	-0.27	-0.05	-0.30	-0.09
W13	0.40	0.45	0.43	0.46	-0.16	0.50	-0.11	0.48	-0.12	-0.51	-0.53	-0.52	-0.50	0.01	-0.54	-0.04	-0.52	-0.01
W17	0.64	0.63	0.66	0.71	-0.12	0.70	-0.13	0.73	-0.11	-0.49	-0.48	-0.43	-0.72	-0.41	-0.70	-0.41	-0.72	-0.42
W21	0.43	0.48	0.50	0.39	0.10	0.43	0.11	0.46	0.10	-0.34	-0.37	-0.40	-0.37	-0.19	-0.41	-0.22	-0.44	-0.22
W462	0.45	0.45	0.49	0.42	0.06	0.42	0.07	0.45	0.08	-0.42	-0.42	-0.45	-0.41	-0.10	-0.41	-0.11	-0.44	-0.13
W47	0.49	0.51	0.48	0.44	0.11	0.45	0.13	0.42	0.12	-0.39	-0.39	-0.38	-0.41	-0.20	-0.41	-0.22	-0.39	-0.19
W48	0.34	0.41	0.39	0.28	0.17	0.32	0.20	0.30	0.21	-0.26	-0.29	-0.28	-0.28	-0.15	-0.33	-0.19	-0.30	-0.18
W49	0.43	0.43	0.41	0.33	0.22	0.33	0.23	0.32	0.22	-0.30	-0.30	-0.29	-0.30	-0.28	-0.30	-0.29	-0.29	-0.28
W51	0.17	0.20	0.20	0.19	-0.16	0.23	-0.14	0.22	-0.13	-0.22	-0.25	-0.24	-0.16	0.16	-0.22	0.10	-0.21	0.08
W57	0.34	0.32	0.35	0.29	0.11	0.28	0.11	0.32	0.09	-0.27	-0.26	-0.29	-0.30	-0.16	-0.28	-0.16	-0.32	-0.17
W78	-0.11	-0.09	-0.12	-0.12	-0.04	-0.09	-0.01	-0.13	-0.05	0.12	0.09	0.14	0.11	0.03	0.09	0.00	0.13	0.04
Mean W	0.43	0.44	0.38	0.37	0.15	0.37	0.17	0.33	0.14	-0.32	-0.32	-0.29	-0.37	-0.18	-0.37	-0.20	-0.32	-0.15
Mean all	0.31	0.28	0.24	0.23	0.25	0.20	0.25	0.18	0.23	-0.20	-0.18	-0.16	-0.22	-0.29	-0.20	-0.29	-0.17	-0.26

concentrated on the past century. They found a long-term trend of increasing Δ since 1920 of about 0.016‰ year^{-1} . This positive trend in Δ contrasts sharply with our results for the same time period: no trend for Douglas-fir, a strongly negative trend for ponderosa pine, and a negative but intermediate trend for western white pine (Figure 6). We examine whether differences in hydraulic conductance could account for these pronounced species differences.

The trees studied by Berninger et al. (2000) are essentially old-growth *Pinus sylvestris*, typified by a near cessation in height growth, especially for the three trees that were > 125 years old in 1920. Hydraulic conductance to the crowns of these old trees should be nearly constant during this time period (1920–present). We speculate that the positive trend in Δ found in these trees by Berninger et al. (2000) is probably as-

sociated with the documented increase in atmospheric c_a this century and the associated decrease in δ_a (Equation 3). Similar trends have been observed in old trees over long time periods (Freyer 1979, Freyer and Belacy 1983, Stuiver et al. 1984, Stuiver and Braziunas 1987, Leavitt and Long 1988, 1989a, Leavitt 1993, Saurer et al. 1997, Feng 1998, 1999).

Marshall and Monserud (1996) found a similar positive trend in Δ this century in an experiment that held tree height constant. They worked with the same three species in the same stands as our current study, but focused on saplings. In contrast, we followed 28 trees for the 70+ years from reaching breast height until reaching their final heights of 30–40 m. We did not try to hold the effects of age constant. Marshall and Monserud (1996) found clear decreases in δ_p , increases in Δ , and no change in $c_a - c_i$ over the same time period as that stud-

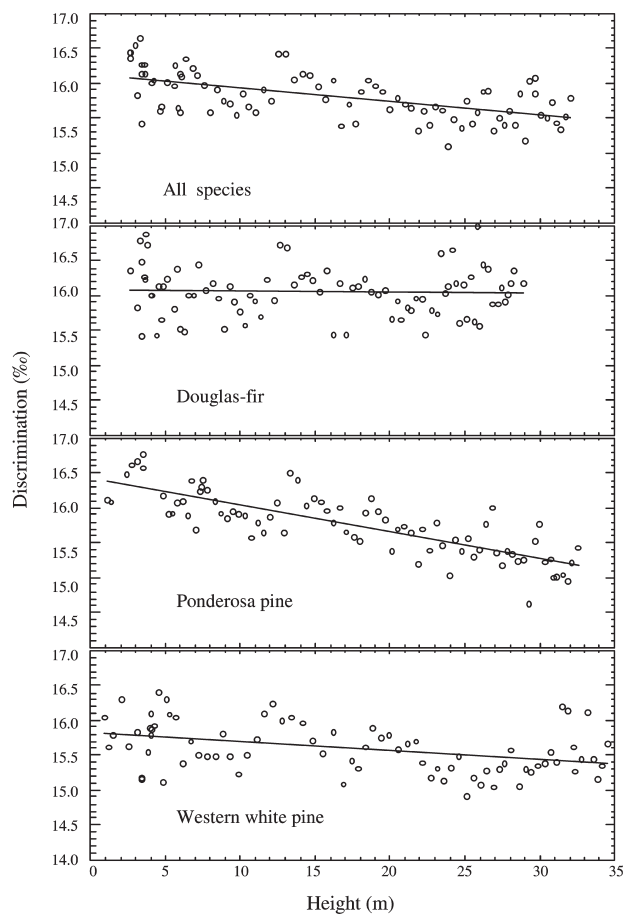


Figure 8. Discrimination, Δ , of tree-ring cellulose versus height for each species and all species combined, with each value corresponding to the mean for one calendar year.

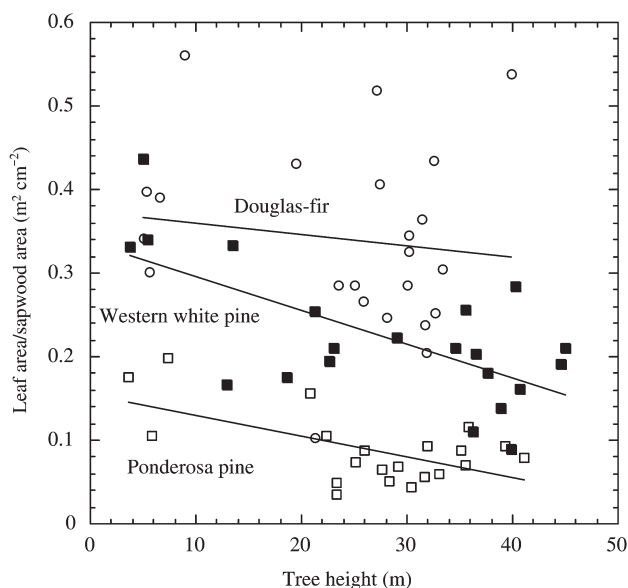


Figure 9. Leaf area/sapwood area (LA/SWA) ratio versus height. Data are from Monserud and Marshall (1999) who used a wider range of tree sizes and ages from the same stands as sampled for Figure 8.

ied here. We found rather different trends including minor changes in δ_p and Δ , and strong increases in $c_a - c_i$.

Based on a simple physical analysis of water flow, one might expect increasing water stress as trees gain height (Whitehead et al. 1984, Yoder et al. 1994). Elevation of the canopy would both lengthen the path of water flow and decrease the gravitational component of water potential at the top of the stem. As a consequence of lower water potential, stomata would partially close and Δ would tend to decline (Zhang et al. 1994). Such a decrease was expected as our trees aged and grew in height. Because all of our sample trees had a complete stem analysis, we could examine this hypothesis by comparing the observed height and Δ for each tree ring in our analysis. Figure 8 shows the Δ versus height relationship for each species and all species combined, with each plotted datum corresponding to the mean for one calendar year. The slope for Douglas-fir is insignificant, whereas the slope for ponderosa pine is highly significant ($P < 0.0001$) and negative (-0.038), with $R^2 = 0.63$. The relationship for western white pine is intermediate: the slope is also highly significant but less negative (-0.014), with $R^2 = 0.15$ (Figure 8). These general results and trends do not change when all 2033 observations of Δ versus height are analyzed by species (data not shown), except that the amount of explained variation is reduced ($R^2 = 0.02, 0.20$, and 0.06 for Douglas-fir, ponderosa pine, and white pine, respectively).

One strategy a tree could employ to reduce water stress as it grows in height is to reduce leaf area per unit of sapwood area (LA/SWA). If this strategy were effective, we predicted that marked reductions in LA/SWA would be found in species with less pronounced reductions in Δ . We tested this hypothesis by analyzing the trees described by Monserud and Marshall (1999), because they were from the same stands as the current study, and both LA and SWA were measured on each. We found (Figure 9) that LA/SWA decreased with height in western white pine ($P = 0.011$) and ponderosa pine ($P = 0.005$), the same species that showed significant reductions in Δ with increasing tree height (cf. Figure 8). The slope of the relationship was negative for both western white pine and ponderosa pine (Figure 9). The greatest reduction in LA/SWA was found in ponderosa pine, the species with the steepest declines in Δ (Figure 6). In contrast, Douglas-fir showed no significant change in LA/SWA with height ($P = 0.55$), which was the same relationship found between Δ and height (Figure 8). Thus, the reduction in LA/SWA does not compensate for the decline in Δ with increasing height.

The height effects on Δ are particularly straightforward to interpret because our sampling protocol minimized shading as a source of variation. Shading tends to increase discrimination (Ehleringer et al. 1986). Because the samples were collected at progressively higher positions on the tree, they were constantly in the upper portion of the canopy (Figure 2, Table 1). Also the ring width patterns for our sample discs showed no indication of suppression or strong shading from neighboring trees. A secondary concern, that foliage from deep in the canopy may be strongly influenced by isotopically light CO_2 from

soil respiration (Brooks et al. 1997), was also eliminated by our tree-ring sampling scheme (Figure 2).

Dendrochronologists frequently design their sampling strategies to minimize the “juvenile effect” when young trees are increasing rapidly in size (Fritts 1976). With respect to isotope composition, the juvenile effect is expressed as a tendency for young trees to show more negative stable carbon isotope ratios than older trees (Francey and Farquhar 1982). It is sometimes correlated with the occurrence of “juvenile wood” (e.g., low density xylem with thin-walled cells) found near the pith in young trees (Fritts 1976). A variant of juvenile wood, referred to as “crown wood,” is frequently found near the pith in the crowns of older trees (Kennedy 1995). Because of the correlation between wood anatomy and extremely negative δ_p in young trees, a dendrochronologist might also be concerned about the sampling of crown wood. However, we found that the inner rings of the tree grew out of the isotopic juvenile effect within a few years, resulting in δ_p values from the inner rings at the tops of trees that were quite different from the inner rings of young trees grown at the same time (Marshall and Monserud 1996). We interpret the increase in δ_p with age as evidence that the juvenile effect disappeared early in the lives of these trees, and that the correlation between negative δ_p and crown wood characteristics broke down. It appears that characteristics other than wood morphology cause the isotopic juvenile effect.

Autocorrelation analysis

We undertook this analysis to determine the long-term autocorrelation structure of δ_p in individual tree rings. After detrending, we found significant autocorrelation in the majority of the trees, but we also found a lack of autocorrelation in the remaining third. Furthermore, we were unable to find any trait that identified trees that exhibited significant autocorrelation before doing a statistical analysis. Therefore, because autocorrelation exists in δ_p in individual tree rings over time, we recommend that precautions be taken to remove the autocorrelation before testing hypotheses to ensure that the normality assumptions are met and that statistical tests will be unbiased.

In all cases, the significant autocorrelation could be described by relatively simple, low-order ARMA models requiring only one or two parameters: AR(1), AR(2), MA(1), and MA(2). The most common model form was AR(1). The residuals of these models satisfy the standard normality assumptions necessary for hypothesis testing.

Careful examination of the ARMA parameter estimates in Table 4 reveal the importance of the series length when determining the significance of a parameter estimate. Consider tree W51, for which $n = 64$ years. The critical value for significance is close to 0.25 ($= 2/\sqrt{64}$). The estimates of ϕ_1 in the AR(1) model for each of the three variables are all slightly less than 0.25 and therefore insignificant (viz., 0.17, 0.20, 0.20). If the tree series had been a few years longer, then the critical value would have been less and the criterion for significance might have been met. The MA(1) model for this tree does meet the significance criterion for one of our three variables, even

though all three estimates of θ_1 are close to each other (-0.22 , -0.25 , -0.24).

The inverse duality between low order AR and MA models (Box and Jenkins 1970) is illustrated by several of the parameter estimates in Table 4. For example, tree P4 can be described almost equally well by an AR(1) or an MA(1) model with similar sized parameters with opposite signs. If we write out these models for δ_p we see that they are similar in form:

$$Z_t = 0.32Z_{t-1} + a_t, \quad (11)$$

$$Z_t = 0.31a_{t-1} + a_t. \quad (12)$$

In both models, the current value Z_t of the time series depends on both the current random shock a_t and approximately 30% of a past value from the previous year (0.32 or 0.31). In the first model (Equation 11), that past value is the series itself (Z_{t-1}), and in the second model (Equation 12), the past value is the previous year's random shock. The lagged memory in this system is about 30% (10% if we look at the variance), and can be carried in either the past year's deviation or the past year's random shock. We could think of the observed value Z_t as internal and the random shock a_t as external to the tree, but in reality the tree's state is strongly conditioned by all past values of both. The memory or rate of decay of the importance of these past values is measured by the estimated parameter 0.3, and this rate of decay is exponential.

The most useful generalization is that the same ARMA model holds for each of the three series (δ_p , Δ , $c_a - c_i$) for an individual tree, given that the time trend has been properly removed for each series (Table 3). Recall that δ_p is the raw datum derived from laboratory analysis of a given tree ring's cellulose. Discrimination Δ is algebraically related to δ_p (Equation 2), with only δ_a providing additional time-series information that could alter the autocorrelation function. Clearly, this additional source of variation is minor. The difference $c_a - c_i$ contains two additional sources of variation: ambient concentration c_a and the isotopic ratio δ_a of that air. Both c_a and δ_a are slow moving time series with small mean variation from year to year. Their net effect is either removed by the linear or quadratic time trend, or is much smaller than the highly stochastic δ_p . The net effect is that a thorough time-series analysis of δ_p (or Δ) contains almost all of the stochastic information for a given tree (see Figure 1), which reduces the necessary statistical analysis by two-thirds.

A potential diagnostic test is apparent from the preceding generalization on model form: if a given tree has dissimilar ARMA models as the best descriptors of two of the three different physiological variables, then it is likely that the trend was not removed properly for one of the variables. A careful re-analysis of the trend should solve the problem.

One mechanism that might give rise to autocorrelation occurs if photosynthate from a previous year is used to produce cellulose in the current year. Cellulose is not translocated across tree rings, which is one of the justifications for analyzing cellulose (Tans et al. 1978). However, photosynthate reserves are carried through the winter and might be used to

produce cellulose in the next year. Some authors have suggested analyzing latewood rather than earlywood to minimize the influence of the previous year (Lipp et al. 1991). However, correlations between isotopic composition of the previous year's latewood and the current year's earlywood were not significant in Douglas-fir (Livingston and Spittlehouse 1996).

There are alternative physiological mechanisms that might lead to autocorrelation. For example, the older leaves of evergreen species continue to produce photosynthate in the years after they are produced, often at high rates, but with limited ability to change such structural characteristics as stomatal density and number of layers of mesophyll cells (Niinemets 1997). One might, therefore, expect higher autocorrelation in evergreens than in deciduous species, and highest correlations in evergreens with the longest needle retention. We observed different patterns of autocorrelation among species with different needle retention times. Douglas-fir typically holds its needles for 7 years, white pine for 3 years, and ponderosa pine for 3 years in northern Idaho. Of the three species, Douglas-fir was the only one to have significant second-order ARMA models, whereas the two pine species were dominated by first-order models.

The 2-year lag in Douglas-fir might also be caused by the common occurrence of buds between the nodal branches. These buds break and produce significant amounts of foliage in the year after the main shoot elongates. If the buds were initiated the year before main stem elongation, they would be 2 years old by the time they break. These intra-nodal branches do not occur in pines. However, they occur in many other temperate conifer genera, including *Abies*, *Picea* and *Larix*. Still another possibility is that differences in root biomass carry over from year to year (Dupouey et al. 1993). At present we know of no test of these hypotheses.

Autoregressive effects were less important in the interpretation of isotopic tree ring studies conducted before the early 1990s because the isotopic data were frequently analyzed in bulk as groups of rings or groups of trees. Most common were groups of five (pentads) or 10 rings (decades). This grouping reduced the expense of isotopic analyses and reduced sample variation caused by individual years or trees, or both. One effect was to strengthen the focus on long-term trends in many of these studies. However, the development of continuous-flow techniques has considerably simplified isotopic analyses, resulting in more long-term analyses of single tree rings (e.g., Berninger et al. 2000). The ability to analyze long series of rings increases the probability of detecting significant autocorrelation, an effect primarily determined by a decreasing standard error as series length n increases. An additional problem with grouping rings over 5–10-year periods (e.g., bulk samples) is that annual or biennial variation is lost, and cannot be detected regardless of sample size. We are not implying that this approach is inaccurate, only that it removes variation and limits the class of hypotheses that can be tested and the range of inferences that can be made.

For some studies, it will be necessary to aggregate individual tree data annually to a group average (e.g., species) time series before proceeding with an analysis (e.g., Leavitt and

Long 1989b, Dupouey et al. 1993). When we aggregated, we found significant autocorrelation in the mean series for all three variables for all three species, as well as the overall mean series (Table 3). Apparently the process of constructing an average time series for a species preserves an underlying signal related to δ_p and cancels some of the random individual tree variation. Note that the process of combining individual tree samples for the same year into an average is the same as mixing equal amounts of material into a single bulk sample. Thus, pooling of samples before analysis effectively weights trees according to the mass of the rings they contribute to the pool.

In addition to reducing variation, the process of averaging tree ring data across individuals fundamentally changes the underlying model. For example, only half of the individual Douglas-fir trees were described by significant second-order models, yet the species average series was clearly a second-order model (Table 4). Furthermore, three of the Douglas-fir trees had significant AR(1) models (see D16G, D106, and D122 in Table 4), but the first-order effect was insignificant for the species average series. Thus, not all of the individual tree models were of the same form as the model for the species average series.

Several authors have considered memory effects. One approach has been to correlate current-year isotopic values with previous-year climate data (Brooks et al. 1998, Nguyen-Queyrens et al. 1998). Others have calculated first differences; i.e., the differences between the current-year value and the previous-year value (Freyer and Belacy 1983, Leavitt and Long 1988). Correlations between the first differences of isotopic data and weather data typically are stronger than analyses of the raw data (Tans and Mook 1980). Stuiver et al. (1984) recognized the autocorrelation problem, and attempted to correct his decadal data for the probable reduction in degrees of freedom caused by autocorrelation in the time series. Other authors have recognized the value of analyzing autocorrelation in their isotopic data, but have not done so because their series were too short (Pendall et al. 1999) or unevenly spaced (Tans and Mook 1980) to support autoregression analyses.

A few authors have tested for autocorrelation, with mixed results. There was no detectable autocorrelation in a study of *Pinus pinaster* even though the previous year's weather clearly influenced stable isotope ratios (Nguyen-Queyrens et al. 1998). Likewise, there was no correlation between previous-year latewood and current-year earlywood in *Pseudotsuga menziesii* trees (Livingston and Spittlehouse 1996). In contrast, previous-year isotopic ratio significantly correlated with the present-year value in *Fagus sylvatica* L.; inclusion of this memory effect significantly improved correlations with climate variables (Dupouey et al. 1993).

Because analyses of time series are repeated measures (Potvin et al. 1990), autocorrelation is likely to be observed, especially if individual tree rings are analyzed. Direct analysis of isotopic data without first removing significant autocorrelation runs the risk of biasing hypothesis tests. Heuristically, the problem with significant autocorrelation is that it decreases the number of degrees of freedom.

The next step following the analysis presented here is to an-

alyze correlations between the residuals of the models (the random shocks, a_t) with climate variables. Because the autoregressive effects have been removed from a_t , such an analysis would meet all the assumptions of an analysis of variance. Note that all climatic variation is potentially contained in the residuals a_t , because our analysis does not remove the correlation between the residuals a_t and climatic variables (Monserud 1986).

There may be valuable clues to mature tree function contained within these autocorrelations. Comparisons of lagged effects in isotopic data of tree rings grown under experimentally varied conditions may help to identify and quantify processes that operate on a time span longer than one year. Aside from our discussion of the role of intra-nodal buds, we are unable to offer a strong physiological explanation for the significant second-order model for Douglas-fir, especially in the absence of a significant first-order term. Knowledge of the physiological basis of such lagged processes is one key to scaling up our short-term physiological understanding to explain long-term growth effects in mature trees.

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