RELATIONSHIPS BETWEEN RING-WIDTH VARIATION AND SOIL NUTRIENT AVAILABILITY AT THE TREE SCALE

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ABSTRACT

Within the framework of the linear aggregate model of dendrochronology, the potential role of soil nutrient availability in explaining multi-decadal variation in radial growth at the tree level was studied in the central Spanish Pyrenees. Increment cores were collected from 20 mature *Pinus uncinata* Ram. and analyzed dendrochronologically. One ion-exchange resin capsule was buried within the root zone of each sampled tree for just over eight months. The resins were chemically extracted and measured for NH_4, NO_3, PO_4, Ca, and K. Statistical relationships between indexed tree growth and soil nutrient availability were determined with regression analysis and bivariate plots.

The single most important soil nutrient with respect to decadal-scale dendrochronological tree-growth variables in this study was N in the form NO_3, which explained 22% of variation of trend in growth since 1950. The 20 values of NO_3 availability fell into two subgroups, one of trees with relatively higher NO_3 availability and the other with lower NO_3 availability. When the tree-growth data were grouped based on NO_3 availability, the two resultant index chronologies had different low-frequency features since 1950. Trees with low NO_3 availability have been growing as expected based on past growth, but trees with high NO_3 availability have been growing better than expected. Measuring and analyzing soil nutrient availability at the tree level might enhance environmental applications of dendrochronological research. With soils information at this spatial scale, it is possible to distinguish between subgroups of trees within a tree-ring site and thereby construct subchronologies that differ significantly, especially for variation at the decadal scale. Subsite-chronologies may then lead to different and presumably more informative environmental interpretations relative to those based on a full-site chronology.

Keywords: dendrochronology, ion-exchange resins, soil nutrients, Spanish Pyrenees, *Pinus uncinata*.

INTRODUCTION

An underlying basis for environmental applications of dendrochronology is the linear aggregate

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model (Cook 1987):

$$R_t = A_t + C_t + \delta D1_t + \delta D2_t + E_t \quad (1)$$

where t indicates time in calendar year and R is an observed time series of ring widths of a tree (or more broadly, any ring-growth variable), which can be explained by some combination of variation

related to age or size of the tree (A), climate (C), endogenous or local disturbances (D1), and exogenous or stand-wide disturbances (D2). The error term (E) represents variation in R that cannot otherwise be explained by the other terms. The δ with each disturbance term is a binary indicator of absence ($\delta = 0$) or presence ($\delta = 1$) of disturbance, while examples of endogenous disturbance include gap creation (Bosch and Gutiérrez 1996) and examples of exogenous disturbance include insect epidemics (Swetnam et al. 1985).

A general strategy in dendrochronology is to isolate the explainable variance of R_t into just one predictor term of the linear aggregate model by reducing the effect of the other terms. For example, age- or size-related variation can be accounted for by standardizing measured values with a tree-specific growth curve of expected values empirically estimated from the measurement data (Fritts 1976). The effects of disturbance ($D1_t$ and $D2_t$) can be avoided by sampling trees with no outward evidence of injury. The effects of climate (C_t) can be removed by quantitatively modeling out important climatic controls of tree growth.

One way of improving the environmental applications of the linear aggregate model is to add explanatory terms that decrease the error term (E_t). One such additional term could relate to the quality of soil, which provides moisture and nutrients for tree growth and whose physical, chemical, and biological properties vary at the tree spatial scale or even less (Arnold and Wilding 1991). Indeed, soil characteristics other than moisture availability, which is accounted for by the climate term, were specifically included as part of E_t (Cook 1987). Soil nutrient availability can vary dramatically in soils across short distances (Beckett and Webster 1971; George et al. 1997) such that trees within a typical dendrochronological site might be growing in soils of different quality. Adding a soil nutrient availability term to the linear aggregate model may broaden the range of environmental applications of dendrochronology as well as improve interpretations of radial growth patterns. The primary objective of this research was to assess the relationship between ring-width variation and soil nutrient availability at the tree scale, with the potential goal of adding a soil nutrient availability term to the linear aggregate model.

METHODS

Study Site

The study site was located within the Aigüestortes and Sant Maurici Reservoir National Park of Catalunya (42°35'00"N, 1°0'00"E, 2,000 m elevation) of the central Spanish Pyrenees (Figure 1a). The site had a subsite with a 30° slope angle and an adjacent flat subsite, which allowed for the evaluation of topography and geomorphic position on the relationship between ring-width trends and soil nutrient availability. Because the study site was small at only 0.2-ha, trees within it have been experiencing essentially the same climate through time, thereby equalizing the effect of C_t on R_t for all trees.

Weather records at the nearby town of Capdella (42°27'55"N, 0°59'28"E, 1,270 m elevation, records from 1945 to 1997, Figure 1a) show a mean total annual precipitation of 1,261 mm evenly distributed across all months of the year and a mean annual temperature of 9°C with a range of 16°C between January and July average temperatures (Figure 2). A field survey of the soil indicated that it is generally shallow (<0.5 meters deep), dark brown, and sandy loamy in texture with abundant (~20%) cobbles and weak granular structure; the soil probably classifies as lithic Haplumbrept (Soil Survey Staff 1990). The study site has a stem density of ~200 trees/ha with Pinus uncinata Ram. as the dominant overstory tree species and Vaccinium spp. and grasses as the understory and ground cover species.

Field Sampling

Ten trees per subsite were sampled in October 1996 (Figure 1b). To equalize the effects of A_t on R_t for all trees, mature, dominant trees of approximately the same age were selected. To avoid the effects of $D1_t$ and $D2_t$ on R_t, trees were selected that did not have abrasion scars or other visible evidence of injury. Two increment cores were collected from each tree along opposing radii that were parallel to the slope contour for trees of the
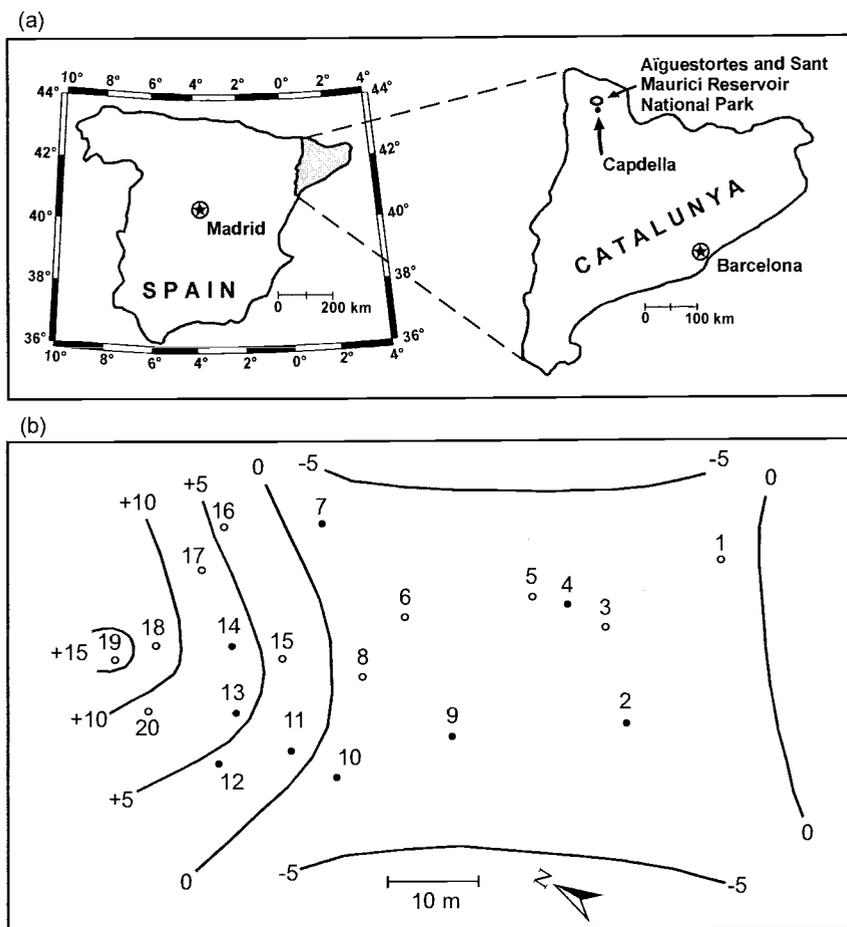
(a)

(b)

Figure 1. (a) Federal and autonomy maps of Spain and Catalunya and (b) plan view of study site. Contour lines are relative to the elevation of the flat subsite. Open circles denote trees with low NO_3 availability while closed circles denote trees with high NO_3 availability.
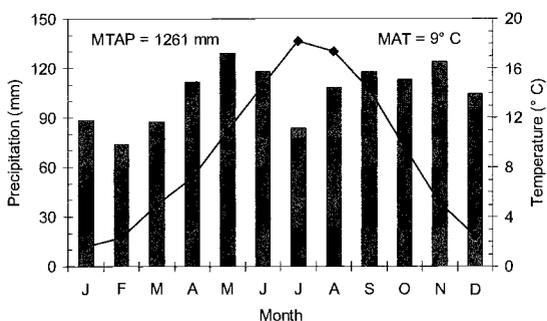

Figure 2. Climograph for Capdella (42°27'55"N, 0°59'28"E, 1270 m elevation, records from 1945 to 1997). Bars indicate mean total monthly precipitation (mm) and solid line indicates mean monthly temperature (°C). MTAP is the mean total annual precipitation and MAT is the mean annual temperature.

sloped subsite and randomly oriented for trees of the flat subsite. The location and topographic microsite conditions of each tree were recorded.

Measuring the total amount of a nutrient present in soil would have quantified the potential nutrient pool, but that may not relate reliably with what actually becomes available in mineralized forms (Binkley and Hart 1989). We measured potential soil nutrient availability using ion-exchange resins (IER), which approximate soil-root interactions with respect to nutrient availability (Gibson 1986; Skogley and Dobermann 1996). One IER capsule (UNIBEST PST-1 capsules, Bozeman, Montana) was buried within the root zone (1–2 meters from the trunk) for each sampled tree. Having more cap-

sules per tree would have been preferable because soil nutrient availability can vary at small spatial scales (Beckett and Webster 1971). The capsules were buried to a uniform depth of 10–15 cm with as little disturbance to the soil column as possible (Carlyle and Malcolm 1986). The soil particles removed while digging with soil corers were placed back into the hole over the capsule, and complete contact between the capsules and the surrounding mineral soil was attained (Gibson 1986; Skogley et al. 1996). The IER capsules were retrieved in May, 1997, after having resided in the soil for 247 days spanning autumn, winter, and the first half of spring. The capsules were lightly rinsed with deionized water in the field (Giblin et al. 1994) and stored individually in marked plastic bags (Skogley et al. 1997).

Laboratory and Quantitative Analysis

The tree cores were prepared and crossdated according to standard dendrochronological procedures (Douglass 1941; Swetnam et al. 1985). Width of all dated rings was measured to ±0.01 mm and checked for dating and measurement errors using cross-correlation testing (Holmes 1983). Measured values were then averaged within each tree for all years held in common by both cores of each tree. To remove the effect of A_t on R_t for all trees, measured values were converted to dimensionless indices by dividing them by curve fit values. For this step, the cubic-smoothing spline was selected whose flexibility retained 75% of the variation at the 100-year period in the resultant index series (Cook and Peters 1981). This strategy allowed for analysis of trends up to 50 years in length in tree growth. All resultant index series were averaged together into a standard chronology (Fritts 1976).

Correlation functions between the standard chronology and monthly precipitation and temperature variables were inspected to identify the important climatic controls of tree growth (Blasing et al. 1984). A dendroclimatological year was tested, extending from September of the prior year to September of the current year of growth. Regression analysis of the standard chronology and the strongest climate variables was used to model cli-

mate with tree growth. Model residuals were checked for the necessary assumptions of time-series regression analysis (Ostrom 1990). Once a model was identified, it was re-evaluated for the index series of each tree to remove the effects of C_t on R_t for all trees. This resulted in a time series of residual tree growth for each tree.

Ions absorbed by the IER were extracted in three steps using 20 ml of 2 M HCl agitated for a total of one hour (Dobermann et al. 1997; Skogley et al. 1997). This resulted in a 60-ml solution for each tree. Solutions were then measured for NH_4, NO_3, and PO_4 using colorimetry (Clesceri et al. 1989), Ca using atomic absorption spectrometry (Wright and Stuczynski 1996), and K using flame emission spectrometry (Wright and Stuczynski 1996).

Relationships between temporal trends of residual tree growth and soil nutrient availability were quantified using bivariate plots and regression analysis. Because we were interested primarily in analyzing relative tree growth of the last few decades, during which global deposition of N has been increasing (Mayewski et al. 1986), trends in growth indices since 1950 were tested as the dependent tree-growth variable. Model residuals were inspected for the necessary assumptions of regression analysis (Sokal and Rohlf 1981).

RESULTS

The length of individual tree index series averaged 159 years and ranged from 128 to 184 years, long enough for all trees to express departures of 50 years in length (Cook et al. 1995). The index chronology did not show a significant trend since 1950 (Figure 3a).

Precipitation of fall and winter prior to the growing season tended to correlate positively with the standard chronology (Figure 4a). The strongest multi-month season of precipitation was September of the prior year through January of the current year of growth, with a correlation of +0.42. Spring temperatures tended to correlate positively with tree growth (Figure 4b). The strongest multi-month season of temperature was April through May of the current year, with a correlation of +0.41. Neither of the seasonal climate variables
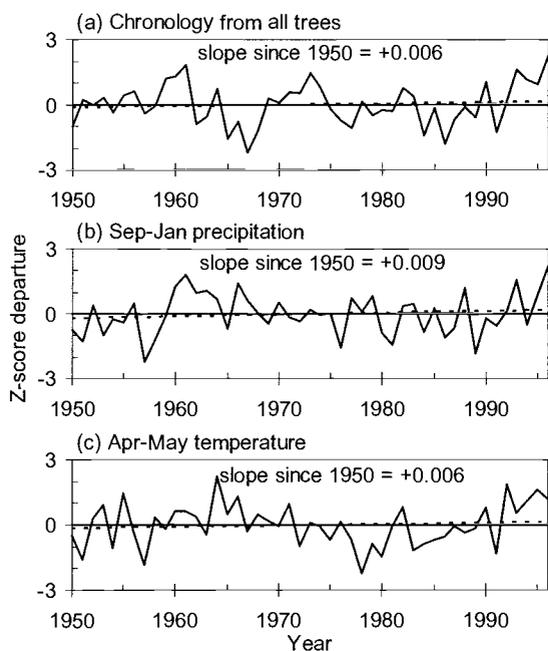
Figure 3. (a) Index chronology derived from all trees of the study site, (b) mean total precipitation at Capdella for the season from September to January, (c) mean temperature at Capdella for the season from April to May. All series were truncated to show the period 1950 to 1996. All original values have been converted to z-scores to facilitate comparison between series. Flat solid lines are the means while dashed lines are the linear trends since 1950.
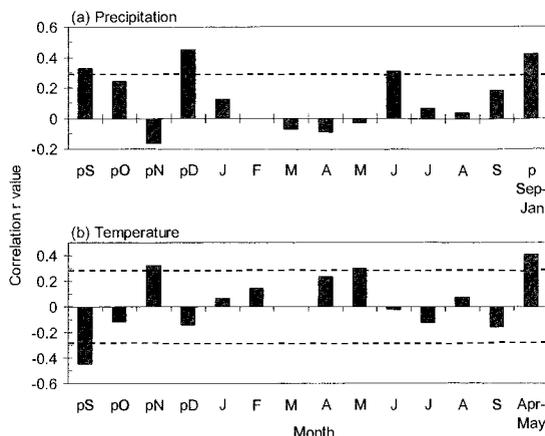

Figure 4. Correlation functions for the index chronology using all trees and (a) monthly total precipitation and (b) monthly average temperature, recorded at Capdella. Dashed lines indicate significant r values (n = 53, α = 0.05, Rohlf and Sokal 1981). The "p" in front of months indicates a prior-year month, otherwise months are for the current year of tree growth. The pSep–Jan indicates the season of September through January and the Apr–May indicates the season of April through May.

showed a significant trend since 1950 (Figures 3b and 3c). The best dendroclimatic model used both of the seasonal climate variables to explain 22% of variation in the index chronology since 1950. The model was significant (p < 0.01) and had residuals that were normally distributed, that showed no relationship with predicted or predictor values, and that were not significantly autocorrelated. The model was re-evaluated for each tree to provide a time series of residual tree-growth for each tree.

The best one-variable model of soil nutrients and trends in residual tree growth used NO_3 as an independent variable to explain 22% of variation of trends in growth since 1950 (Figure 5). This model was significant (p < 0.05) and had normally distributed residuals that did not relate with predictor or predicted values. No other single soil nutrient variable correlated significantly with the tree-growth variables.

The 20 measured soil NO_3 values happened to fall into two clear groups, one of trees with more than 10 μg/day/IER unit and the other of trees with less than 5 μg/day/IER unit. The groups did not correspond with the original flat or sloped subsites, which had average soil NO_3 values that did not differ significantly from one another. Instead, the majority of trees with high NO_3 (seven of nine) were in the transition zone between the two subsites, either in the lower half of the sloped subsite or in the part of the flat subsite that is adjacent to the margin of the two subsites (Figure 1b). Con-
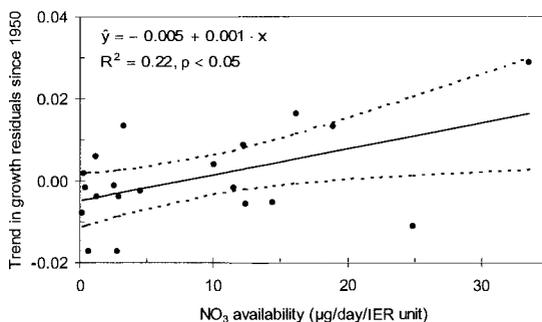

Figure 5. Regression results using NO_3 availability to explain trend in residual growth since 1950. Dashed lines are the 95% confidence limits of the predicted values.
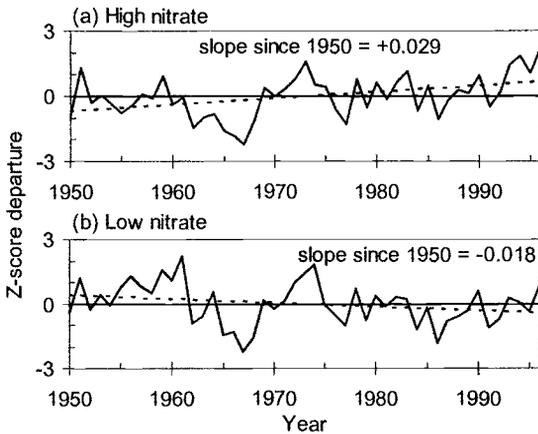
Figure 6. Residual chronologies for (a) trees with high NO_3 availability (>10 μg/day/IER unit), (b) trees with low NO_3 availability (<5 μg/day/IER unit). All original values have been converted to z-scores to facilitate comparison between series. Flat solid lines are the means while dashed lines are the linear trends since 1950.

versely, the majority of trees with low NO_3 (eight of eleven) were either on the summit of the sloped subsite or in the toeslope of the flat subsite.

After subdividing the residual index series of all trees into two subsets based on NO_3 availability, the resultant subsite chronologies showed different low-frequency features (Figure 6). The chronology composed of trees with high NO_3 availability had a significantly positive slope since 1950 (p < 0.05). By contrast, the chronology of trees with low NO_3 availability had a slope since 1950 that was actually negative though not significantly different from zero.

DISCUSSION

After removing or avoiding the effects of age or size, climate, and disturbance on tree growth, there was still variation in decadal-scale trends across trees in this study. Soil nutrient availability—most notably N in the form of NO_3—was useful in explaining some of that remaining variation between trees. Trees with currently relatively high NO_3 availability have been growing better than expected since 1950 based on their own past growth patterns. In contrast, trees with less NO_3 availability have been growing about as expected since 1950 based on their own past growth patterns.

It is impossible to know for certain from this study if the spatial pattern of soil N availability that exists now has existed for the last few decades. It would be best to answer this question by studying a forest site for which soil nutrient availability for individual trees has been measured more than once during the last few decades. Future research using dendrochemical analysis to determine N concentrations in crossdated tree rings might also help in this regard (Sheppard and Thompson 2000). For now, we assume that there is spatial persistence in soil properties regulating nutrient availability such that current spatial variability in relative nutrient availability reflects that of the recent past. We do not assume that current absolute values of soil nutrient availability are the same as those of the past, only that the spatial patterns of relative availability have not changed through time.

The two groups of trees with high- versus low-NO_3 availability transcended the original flat versus steep subsites, and instead they followed a pattern more related to geomorphic hillslope position. Most of the high-NO_3 trees were in or near the backslope-footslope (Hall and Olson 1991) transition of the site. The hillslope of our site had a convex contour and a weakly convex slope, which may cause surface and subsurface water and nutrients to accumulate in the backslope-footslope transition zone (Hall and Olson 1991). Trees of this geomorphic position may tend to have more available soil nutrients and therefore grow slightly better than other trees (Hammer et al. 1991). However, this geomorphic association was not perfect in this study: trees #6, #8 and #15 were growing in the backslope-footslope zone but had low NO_3 availability while trees #2 and #4 were in the toeslope zone but had high NO_3 availability (Figure 1b). Thus, quantifying the topographic microsite and geomorphic position of each tree may not suffice as a substitute for actually measuring soil nutrient availability for each sampled tree within a dendrochronological study.

The interpretability of the separate subsite-chronologies was more informative than that of the full-site chronology. The different decadal-scale patterns of the two subsite-chronologies in this study were statistically related to current N avail-

ability at the tree level, and additional research should focus on the mechanisms that could cause this relationship. At least three possibilities exist. First, light selection harvesting of trees took place around the study site in the late 1950s and late 1960s (personal communication with national park authorities), and this type of disturbance can change below-ground competition for N (Pritchett and Fisher 1987), perhaps more so for some remaining trees than for others. Second, grazing has been allowed in the national park, and this activity can redistribute nutrients in tree-specific ways (Beckett and Webster 1971). Third, recent N deposition of the central Spanish Pyrenees has been enhanced anthropogenically, though not to the level of central Europe (Camarero and Catalan 1993). Nitrogen deposition is a low-concentration nutrient input that might significantly affect tree growth over decades, especially in cool, coniferous forests, where N is often limiting to tree growth (Pritchett and Fisher 1987).

If chronic atmospheric deposition is adding N to the study site, then it is reasonable that soil and slope position play a role at the tree level in mediating the availability of N from chronic pollution to trees (Lammers and Johnson 1991) because trees take in much of their N as ionic forms through their roots (Kramer and Kozlowski 1979). Trees growing in zones of natural accumulation of soil moisture and nutrients might be fertilized more effectively with N from atmospheric deposition than trees growing in zones of natural surface/subsurface runoff of water and nutrients.

The ability to distinguish between trees within a site on the basis of environmental variables that are independent of their growth data—NO_3 availability in this case—is the essence of adding an additional explanatory term to the linear aggregate model of dendrochronology and decreasing the error term. Because the measurements of nutrient availability in this study were for only a single point in time, the time subscript is not applicable, as follows:

$$R_t = A_t + C_t + \delta D1_t + \delta D2_t + \Sigma SN_n + E_t \quad (2)$$

where ΣSN_n is the sum of effects of all n soil nutrients that significantly affect tree growth.

The SN_n term undoubtedly plays a variable role across dendrochronological sites depending on the spatial variability of soil nutrients within sites. The SN_n term should play its strongest role in sites with thin, poorly developed soils on complex geomorphic terrain, where soil nutrient availability is likely to vary at the individual tree spatial scale (Beasley 1972). Conversely, the SN_n term should play a weaker role in sites with well-developed soil on uniform terrain, where soil nutrient availability is likely to be relatively uniform across the individual tree spatial scale. In either case, accounting for the SN_n term in the linear aggregate model of tree growth could improve the interpretation of the other terms of the model, or it could be useful in its own right in environmental studies of the effects of spatial variation and temporal alterations in nutrient availability on tree growth.

CONCLUSIONS

Measuring and analyzing soil nutrient availability at the tree level can enhance environmental applications of dendrochronological research. Although hillslope position can explain much of the soil NO_3 variability at the tree scale, hillslope position may not be a perfect surrogate for actual soil availability measurements. Ion-exchange resins appear to be a reasonable approach for measuring soil nutrient availabilities in dendrochronological studies.

With soils information at the tree spatial scale, it is possible to distinguish between subgroups of trees within a tree-ring site and thereby construct subchronologies that differ significantly, especially for variation at the decadal scale. Subsite-chronologies may then lead to different and presumably more informative environmental interpretations relative to those based on a full-site chronology.

Further testing of relationships between tree growth and soil nutrient availability, across different forest types and levels of soil development, is merited to determine the general utility of this concept in dendrochronological research. Tree growth relationships with soil nutrients should be stronger at sites with high topographic relief (and therefore high soil variability) and weaker at sites with little topographic relief. Furthermore, dendrochronological studies of the role of increasing N deposition

on tree growth might best be focused on sites with sluggish soil nutrient cycling where N deposition may be relatively important compared to natural soil nutrient availability.

ACKNOWLEDGMENTS

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