



WOOD $\delta^{13}\text{C}$ AS A MEASURE OF ANNUAL BASAL AREA GROWTH AND SOIL WATER STRESS IN A *PINUS STROBUS* FOREST¹

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Abstract. The relationships between annual wood tissue $\delta^{13}\text{C}$, growing season soil water potential, and basal area growth were studied in a mature, white pine (*Pinus strobus*) stand at the Coweeta Hydrologic Laboratory, in western North Carolina. In 1992, four bole-wood cores that spanned the years from 1980 to 1989 were extracted from each of ten equal-size, co-dominant white pine trees within the stand. The 1980s were a time of extreme climate with some of the hottest, driest, and wettest years recorded at Coweeta. Annual basal area growth ranged from 14.5 to 25.0 $\text{cm}^2\text{-tree}^{-1}\text{-yr}^{-1}$, and modeled values of average growing season soil water potential ranged from -0.21 to -5.58 MPa, when measured to a depth of 60 cm. After correcting annual wood tissue $\delta^{13}\text{C}$ for atmospheric changes in $\delta^{13}\text{C}$, carbon isotopic discrimination (A) ranged from 18.52 to 19.62‰. The A of annual wood tissue was positively correlated with average growing season soil water potential ($r^2 = 0.74$, $P = 0.0005$, $n = 10$ growing seasons) and average annual basal area growth ($r^2 = 0.78$, $P = 0.0002$, $n = 10$ seasons). Basal area growth and growing season soil water potential were also correlated ($r^2 = 0.64$, $P = 0.002$, $n = 10$ seasons). These results suggest that annual wood tissue $\delta^{13}\text{C}$ could potentially be useful in estimating historic changes in soil water potential and basal area growth in mature forest ecosystems.

Key words: basal growth; carbon; Coweeta (North Carolina USA); discrimination; isotope; soil water; white pine; wood tissue.

INTRODUCTION

Modern levels of atmospheric CO_2 -C contain ^{12}C , ^{13}C , and ^{14}C at a ratio of approximately 99:1:10⁻¹² (Stuiver 1982). When plant stomata are open and atmospheric CO_2 is readily transported into leaf intercellular spaces, ^{12}C is preferentially fixed compared to ^{13}C (O'Leary 1981). However, when stomata close and the intercellular CO_2 supply is limited, the $^{13}\text{C}/^{12}\text{C}$ fraction (expressed as $\delta^{13}\text{C}$) of plant material increases as proportionally more ^{13}C is incorporated into photosynthate. Once the C is fixed into plant tissue, the isotopic fractionation is preserved. Previous research has correlated plant tissue $\delta^{13}\text{C}$ with vegetative growth (Stuiver et al. 1984, Martin and Sutherland 1990), climate (Freyer and Belacy 1983, Van Deusen 1990, Korner et al. 1991, February and Van Der Merwe 1992), atmospheric CO_2 concentration (Tans and Mook 1980, Bender and Berge 1982, Epstein and Krishnamurthy 1990), nutrient availability (Wong and Osmond 1991, Polley et al. 1992), water use efficiency (Farquhar et al. 1982), and pollutant stress (Martin and Sutherland 1990). Most of this research has involved analysis of part or whole plant tissue $\delta^{13}\text{C}$ from small (<2 m tall) herbaceous or woody vegetation. Leaf tissue analysis provides a measure of current year, or in the case of conifers, 2-3 yr of $\delta^{13}\text{C}$ values. Woody tissue provides a much longer $\delta^{13}\text{C}$ signal, which could be related to

historic ecosystem conditions. Variations in annual wood tissue $\delta^{13}\text{C}$ have been observed (Bender and Berge 1982, Epstein and Krishnamurthy 1990, Leavitt 1992) but it is difficult to link changes in wood tissue $\delta^{13}\text{C}$ with ecosystem parameters such as soil water potential (SWP) due to ecosystem complexity and plant size. To develop relationships between wood tissue $\delta^{13}\text{C}$ and SWP at the forest level, detailed measurements of plant water demand, soil structure, and climate are required. The objective of this study was to correlate the $\delta^{13}\text{C}$ signature in annual bole wood from a mature *Pinus strobus* (white pine) stand located at the Coweeta Hydrologic Laboratory with measured annual basal area growth and with modeled average growing season SWP. The years 1980-1989 were selected for study because these were years of extreme climatic variation at Coweeta, including the wettest and driest years on record.

METHODS

Data necessary to examine correlations between $\delta^{13}\text{C}$, and growth or SWP were collected at the Coweeta Hydrologic Laboratory (latitude 35°03'N, longitude 83°25'W). The laboratory is in the Nantahala Mountain Range within the Blue Ridge Physiographic Province, which was characterized by Swank and Crossley (1988) as normally having a growing season that is warm (average annual air temperature 12.7°C) and moist (total average annual precipitation 180 cm/yr).

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Climatic data

Daily climate data were collected at climatic station 1 (CS1), located =300 m from the sampled plot (Swank and Crossley 1988). Precipitation was measured using an 20.32-cm standard rain gauge. Solar radiation, air temperature, and wind speed were measured every 5 min and recorded on data loggers (Swank and Crossley 1988). Mean daily values were calculated by averaging time-point data within each day.

Wood tissue sampling

Ten co-dominant white pine trees were selected from Watershed 1, a 16-ha plantation at an elevation of 720 m. The stand was planted in 1957 and basal area growth began to fluctuate around a mean growth value after 1978. The stand has not been actively managed since planting. A wood core was extracted from each of 10 trees within the stand, at the four cardinal compass points. All samples were collected at a height 1.4 m above the forest floor to remove the potential influence of collection height on wood tissue $\delta^{13}\text{C}$ (Schleser 1992). The cores were brought to the laboratory where core radius was measured from the outer growth ring to the pith. Annual tree ring widths were measured using a Model 3 increment measurer (Fred C. Henson Co., Mission Viejo, California, USA), which has an accuracy of ± 0.01 mm. Tree ring growth was converted to annual basal area growth (cm^2/tree) using πr^2 , assuming that the cross-sectional area of the bole is circular. After measuring annual basal area growth increments, annual wood tissue produced by each tree during the period 1980-1989 was separated by year. To assure that an adequate amount of tissue was available for $\delta^{13}\text{C}$ analysis, samples from the four wood cores from each tree were combined into a single sample for each year. Samples were first ground through a 0.25 mm mesh screen using a Wiley Mill. Since most error associated with isotopic measurements results from poor sample preparation (Boutton 1991), the samples were homogenized and the wood tissue particle size was further reduced by placing each sample in a Wig-L-Bug Homogenizer (Crescent Dental, Lyons, Illinois) for 30 min. The grinding and pulverization provided a sample of =30 mg for each annual growth increment.

Annual wood tissue isotopic measurements

Wood samples were sent to IRMS (Isotope Ratio Imaging Spectrometer) Laboratories (Sioux Falls, South Dakota), and measured for $\delta^{13}\text{C}$ using a dual-inlet gas isotope ratio mass spectrometer, following analysis procedures described by Boutton (1991). No pretreatment (e.g., to remove cellulose fraction) was conducted on the wood tissue since others (Tans and Mook 1980, Schleser 1992) have found that pretreatment does not change the pattern of isotopic concentration, only the absolute amount. Careful attention was

given to repeatability of sample $\delta^{13}\text{C}$ values. Five replicative measurements were run on randomly selected samples during the analysis to check mass-spectrometer precision, and three blind replicates were included in the sample set to check intra-sample variability. The $\delta^{13}\text{C}$ of wood tissue was calculated as $[(^{13}\text{C}/^{12}\text{C})_{\text{sample}} - (^{13}\text{C}/^{12}\text{C})_{\text{PDB standard}}] / (^{13}\text{C}/^{12}\text{C})_{\text{PDB standard}} \times 10^3$, where PDB refers to Pee Dee belemnite (limestone).

Changes in atmospheric $\delta^{13}\text{C}$ and CO_2 concentration during the 1980s

Measurements collected at Manua Loa, Hawaii recorded that atmospheric CO_2 varied from 337 to 351 $\mu\text{L}/\text{L}$ and that atmospheric $\delta^{13}\text{C}$ varied from -7.59 to -7.85‰ from 1980 to 1989 (Keeling et al. 1989). To adjust for changes in atmospheric $\delta^{13}\text{C}$ between 1980 and 1989, carbon isotope discrimination (A) of wood, in parts per thousand, was calculated as $A = (\delta_a - \delta_p) / (1 + \delta_p)$ (Farquhar et al. 1988), where δ_a is $\delta^{13}\text{C}$ of the atmosphere and δ_p is the $\delta^{13}\text{C}$ of the wood. In the watershed where the samples were collected, the base of the forest canopy was >15 m above the forest floor, so inputs of CO_2 from decomposing organic material were assumed to have had minimal influence on the $\delta^{13}\text{C}$ of CO_2 fixed (Schleser and Jayasekera 1985).

Stand hydrology

Using PROSPER, a phenomenological one-dimensional hydrologic model that links the atmosphere, vegetation, and soil (Goldstein et al. 1975), we predicted average growing season stand level SWP to a depth of 60 cm for years 1980 through 1989. PROSPER uses daily inputs of solar radiation, relative humidity, temperature, and wind speed, which were taken at CS1. In addition to climate inputs, PROSPER was defined with vegetation and soils parameters (e.g., leaf area index, soil water holding capacity). PROSPER has previously been validated as a good predictor of stand level hydrology including SWP, for a wide range of forest types including Coweeta's Watershed 1 (Swift et al. 1975, Huff and Swank 1985).

RESULTS AND DISCUSSION

Wood tissue analysis

Annual wood tissue $\delta^{13}\text{C}$ varied from -26.81 to -25.76‰ and A varied between 18.52 and 19.62‰ respectively for the 10 yr of measurements (Table 1). Repeated measurement of sample $\delta^{13}\text{C}$ showed that variation was low (average $\delta^{13}\text{C}$ sample difference = $0.03 \pm 0.01\text{‰}$ [mean ± 1 SD], $n = 5$ samples). This degree of sample variation is within the range for average mass spectrometer precision of $\delta^{13}\text{C}$ measurements (Boutton 1991). Although $\delta^{13}\text{C}$ variation in the blind replicates was higher (average $\delta^{13}\text{C}$ intra-sample difference = $0.11 \pm 0.02\text{‰}$, $n = 3$ samples) than repeated-sample variation, these values were also well within the cited range of intra-sample variation (Bout-

TABLE 1. Coweeta Hydrologic Laboratory white pine stand climate, soil water potential (SWP), and wood tissue data (BA — basal area; A = carbon isotope discrimination). Values shown with variation are listed as mean \pm 1 SE.

Year	Precipitation (cm)		Avg. air temperature ($^{\circ}\text{C}$)		April-Sept. SWP (MPa)	Annual BA growth (cm^2/tree)	Wood tissue A (‰)
	Nov.-Oct.	April-Sept.	Jan.-Dec.	April-Sept.			
1989	260	127	13.0	18.4	-0.26	24.9 (4.8)	19.48 \pm 0.09
1988	160	53	12.3	18.6	-4.09	16.3 (3.4)	18.96 \pm 0.09
1987	144	71	12.7	18.8	-1.42	16.8 (3.0)	18.92 \pm 0.10
1986	150	37	13.3	19.0	-5.58	14.5 (2.9)	18.52 \pm 0.11
1985	119	66	12.7	18.1	-0.28	19.4 (3.9)	19.23 \pm 0.09
1984	143	79	12.7	18.6	-0.31	21.1 (3.8)	19.27 \pm 0.08
1983	209	84	12.4	18.7	-0.41	24.2 (4.2)	19.21 \pm 0.10
1982	187	58	13.3	18.6	-0.21	24.7 (4.6)	19.62 \pm 0.07
1981	167	61	12.0	18.0	-0.49	25.0 (5.6)	19.30 \pm 0.08
1980	133	79	12.5	18.8	-1.37	19.3 (3.9)	19.16 \pm 0.09
$\bar{X} \pm 1$ SE	167 (13)	72 (8)	12.7 (0.1)	18.6 (0.1)	-1.44 \pm 0.63	20.6 (1.3)	19.62 \pm 0.10

ton 1991). Therefore, despite the small range in wood tissue A, the low variation in intra-sample A strongly suggests that observed differences in inter-annual wood tissue A reflect certain changes in ecosystem conditions, and not simply sample noise about a small isotopic signal.

Factors influencing wood tissue $\delta^{13}\text{C}$

It has long been recognized that part of the difficulty in using wood tissue $\delta^{13}\text{C}$ as a tool for measuring historic ecosystem components (e.g., SWP) involves factoring out potential influences on wood tissue $\delta^{13}\text{C}$ other than water stress (Farmer 1979). Plant $\delta^{13}\text{C}$ discrimination is a function of the different rates at which $^{13}\text{CO}_2$ and $^{12}\text{CO}_2$ diffuse through stomata and are fixed during carboxylation. These processes are regulated by species type, plant tissue type and location, climate, plant age, and pollution levels. To assess the control of climate on wood tissue $\delta^{13}\text{C}$, effects of non-climate factors need to be removed.

Since all wood tissue samples were collected at the same height above the forest floor from an even-age, mature, mono-cultural forest stand, the effects of species, tissue location, and age variation can be excluded. Coweeta's location in the southwestern North Carolina removes it from major sources of sulfur deposition ($\text{SO}_4\text{-S} < 10 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, Swank and Waide 1988), which is well below the level shown to affect wood tissue $\delta^{13}\text{C}$ (Martin and Sutherland 1990). While high daily atmospheric O_3 levels have been recorded at Coweeta ($=100 \text{ nL/L}$, Taylor et al. 1992), O_3 levels are also well below levels that influence plant $\delta^{13}\text{C}$ (Saurer et al. 1991, Elsik et al. 1993).

Atmospheric CO_2

Atmospheric CO_2 concentration increased $\approx 4\%$ during the 1980s (Keeling et al. 1989). In this study, changes in atmospheric CO_2 concentration were not correlated with basal area growth ($r^2 = 0.05$, $P = 0.28$), SWP ($r^2 = 0.03$, $P = 0.34$), or A ($r^2 = 0.00$, $P = 0.42$). A analysis of annual wood tissue may be useful for detecting changes in ecosystem parameters attributed

to changes in atmospheric CO_2 but a much longer tree ring record would be required (Bender and Berge 1982, Epstein and Krishnamurthy 1990).

Climate

From 1980 through 1989, average annual and growing season precipitation were 176.7 and 79.8 cm, respectively. These averages are very close to the 58-yr record of average annual (180.0 cm) and growing season (78.5 cm) precipitation recorded at CS1. However, the 1980s were characterized by extreme events. For example, 1989 growing season precipitation was the highest on record, while precipitation during 1986 and 1988 were the lowest and third lowest annual levels ever recorded at Coweeta (Table 1).

Neither annual nor growing season precipitation, annual air temperature nor growing season air temperature, were well correlated with wood tissue A. Precipitation and temperature may be partially responsible for changes in A, but other regulators of plant water stress (e.g., soil water holding capacity, vapor pressure deficit) can buffer or magnify plant water stress and therefore influence wood fixation of ^{13}C .

Soil water potential

The integration of climate (e.g., precipitation, air temperature, vapor pressure) with soil and vegetation data simulated with PROSPER, provides an estimation of average annual SWP that is a meaningful measure of plant moisture stress. Predicted growing season SWP varied substantially during the 1980s (-5.58 to -0.21 MPa, Table 1).

When soil H_2O is limited, the frequency and duration of stomatal closures increase (Shimshi 1964), and the wood tissue A should increase. If other factors have greater influence on stomatal closure as soil water potential increases (tends towards zero), the relationship between soil water potential and A should decrease. In this study, the deviation about the regression line of A and SWP changed little as SWP increased (Fig. 1). This suggests that under closed canopy conditions, A could

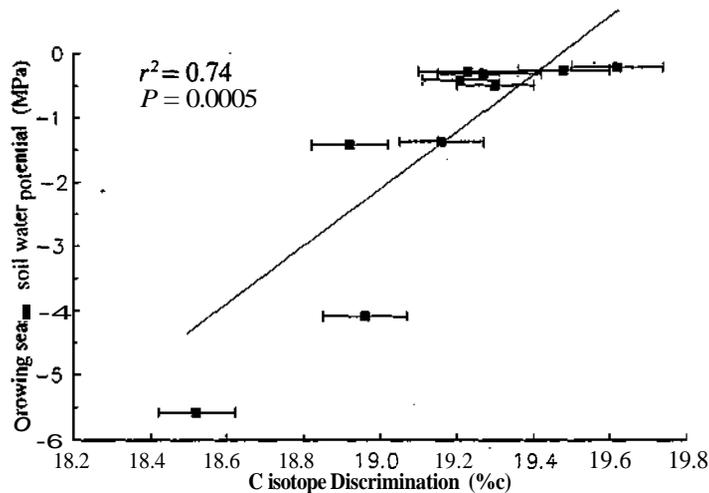


FIG. 1. Regression of carbon isotope discrimination (A) against soil water potential for 10 yr of wood tissue samples collected 1.4 m above the forest floor, in a mature white pine (*Pinus strobus*) stand.

be used to predict SWP across a range of climatic conditions.

During many years, average growing season SWP was > -1.0 (Fig. 1). When SWP > -1.0 , A ranged from 19.2 to 19.6‰, but there was no correlation ($P > 0.5$, $n = 6$ seasons) between the two variables. Even in soils with little water stress, mid-day tree water stress is common because transpiration exceeds water uptake (Waring et al. 1980). As stomata close, wood tissue Δ could be reduced despite high SWP. Annual variation in midday tree water stress were not factored into the regression and could be responsible for some of the deviation about the regression line of SWP and A. Changes in inter-annual average midday water stress could have the greatest influence on wood tissue A when SWP is greatest (i.e., average growing season water stress is least).

Growth

Following canopy closure in the late 1970s, the co-dominant trees within the stand exhibited considerable variation in annual basal area growth (14.5-25.0

$\text{cm}^2 \cdot \text{tree}^{-1} \cdot \text{yr}^{-1}$, Table 1), which was only weakly correlated with annual precipitation ($r^2 = 0.40$, $P = 0.03$, $n = 10$ growing seasons) and was not correlated ($P > 0.05$) with growing season precipitation or air temperature. However, when climate, soils, and vegetation data were entered into PROSPER to estimate SWP, a linear relationship between growing season SWP and basal area growth was observed ($r^2 = 0.64$, $P = 0.002$, $n = 10$ seasons). As was observed between A and SWP, the slope of the regression tended toward zero when basal area growth $> 20 \text{ cm}^2 \cdot \text{tree}^{-1} \cdot \text{yr}^{-1}$ and SWP > -1 MPa (Fig. 2). Basal area growth was not related to SWP when SWP > -1 MPa ($P > 0.05$); instead, some other factor (e.g., solar radiation, amount of insect herbivory) appeared to determine growth.

Carbon isotope discrimination was significantly related to annual basal area growth during the 10-yr measurement period ($r = 0.78$, $P < 0.0002$, Fig. 3). Variation in inter-annual average midday tree water stress, which may not affect annual tree growth rates, could influence wood tissue A. Differences in midday water stress could account for some of the variation in A for

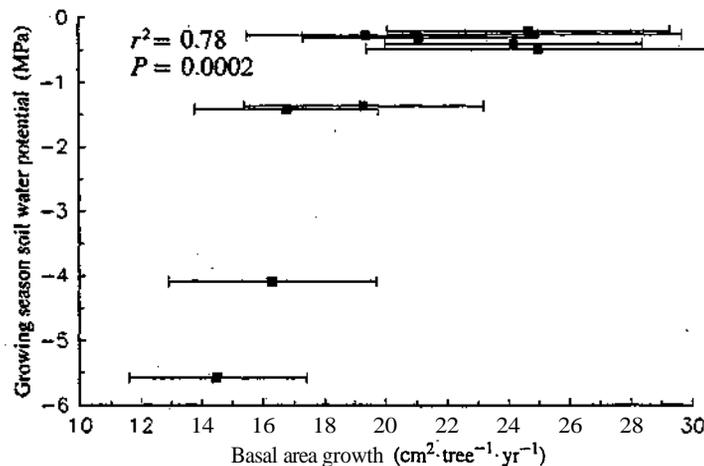
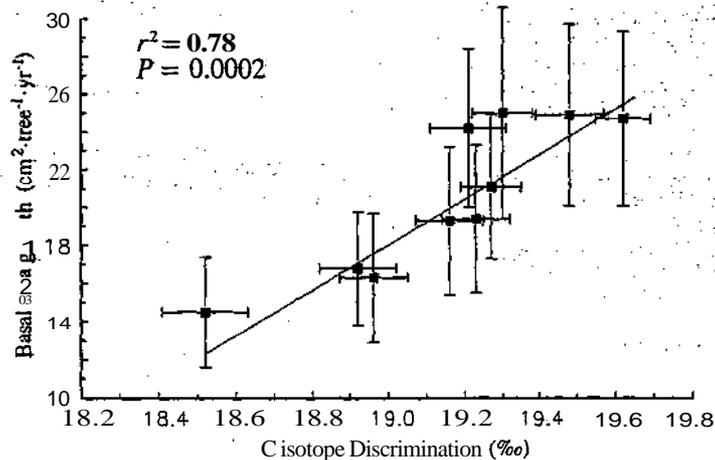


FIG. 2. Basal area growth regression against soil water potential for 1980 through 1989, from a closed canopy, mature white pine stand.

FIG. 3. Regression of carbon isotope discrimination (A) against basal area growth for 10 yr of wood tissue samples collected 1.4 m above the forest floor, in a mature white pine stand.



equal rates of basal area growth. There were also years in which basal area growth varied but there was not a large corresponding change in A (Fig. 3). As previously stated, inter-annual differences in leaf herbivory or solar radiation could impact the amount of C fixed (i.e., basal area growth), while having little influence on the C fractionation (i.e., A).

CONCLUSIONS

The range of annual wood tissue A was relatively small ($\approx 1\text{‰}$) during the 1980s, despite a wide range of climatic conditions. However, because the inter-tree A variation also was low, significant relationships between A vs. SWP and basal area growth were detected. Wood tissue Δ and basal area growth were both correlated with average growing season SWP over a wide range of annual precipitation inputs, probably because both were largely regulated by stomatal conductance of CO_2 .

These results are particularly significant since the sampling was conducted at a location which normally receives some of the highest rates of precipitation found in the U.S. Therefore, the future use of wood tissue A for predicting past long-term SWP appears promising. However, broad utility for the use of A in predicting average growing season SWP may be restricted in immature or sparsely stocked stands where water competition may be reduced and the degree of intra- and inter-species A variability could increase. These questions need to be addressed before wood tissue A can be widely used as a predictive tool for ecological interpretation of SWP and basal area growth.

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