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Evidence of Reduced Photosynthetic Rates in Old Trees

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ABSTRACT. Wood production generally declines as forests age. The decrease in production has been attributed to higher respiration associated with increasing biomass, but direct measurements fail to support this assumption. An alternate hypothesis is that the growth decline is caused by reduced net photosynthesis. To test this hypothesis, we compared the net photosynthetic rates of foliage from trees that had ceased height growth with foliage from actively growing, mature trees. Results showed that net photosynthesis per unit area of 1-yr-old foliage from old *Pinus contorta* and *P. ponderosa* averaged 14–30% lower than the same-aged foliage from younger trees. Computer simulations from a previous study indicated that differences of this magnitude are sufficient to explain the lower wood production in old trees. The cause of the photosynthetic decline is not clear, but it did not appear to be due to a reduction in the maximum capacity for photosynthesis. Ratios of stable carbon isotopes from leaves and wood indicated a greater stomatal limitation of photosynthesis in older trees. A possible relationship between lower hydraulic conductance in the vascular systems of older trees leading to greater stomatal closure is discussed. FOR. SCI. 40(3):513–527.

ADDITIONAL KEY WORDS. *Pinus ponderosa, Pinus contorta,* photosynthesis, senescence, hydraulic conductance.

AS TREES PROGRESS FROM MATURITY TO OLD AGE, height growth eventually ceases and volume growth is sharply reduced (e.g., Pienaar and Turnbull 1973, USDA Forest Service 1990). This reduced growth in old trees is well documented (e.g., Young 1982, Waring and Schlesinger 1985) but has not been fully explained (Leshem et al. 1986). The rate that growth declines with age increases with rising temperature (Whittaker 1975, Waring 1987). The reduced growth, therefore, has been widely assumed to be caused by increased annual respiration costs associated with the greater living biomass in old forests.

Foliage contains the highest concentration of protein among plant tissues, with the highest maintenance cost, but leaf biomass levels off as stands mature and usually declines in old age (Tadaki et al. 1977). The phloem tissue, located beneath the bark of branches and stems, is the next most metabolically active tissue above ground. As a forest ages, however, the amount of phloem present also reaches a plateau because the surface area of bark and stem levels off or decreases as tree mortality occurs (cf. Sprugel 1984, Ryan, unpublished data). This leaves sapwood, with 5–30% living cells, as the most likely source of increasing

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respiration as forests age (Yoda et al. 1965, Whittaker and Woodwell 1967, Kira and Shidei 1967, Kramer and Kozlowski 1979).

Recently, Ryan and Waring (1992) made direct measurements of maintenance respiration of woody tissues in lodgepole pine (*Pinus contorta* var. *latifolia* Englem.) stands varying in age from 40 to 245 yr. When scaled to the entire stand, estimates of maintenance respiration only accounted for about 10% of the observed 78% decrease in growth between 40 and 250 years. Ryan and Waring (1992) used a process model, FOREST-BGC (Running and Coughlan 1988), to assess possible alternative explanations for the growth reduction observed as the pine forests aged. On those study sites the nitrogen content of leaves remained steady (Schoettle 1994 and this paper) whereas the total foliage weight and leaf area decreased by >35% as stands aged. Because light interception by a canopy is a negative exponential function of leaf area, modeled canopy photosynthesis was reduced by only 10% when projected LAI decreased from 5.1 to 3.3 $m^2 m^{-2}$, insufficient to account for the remaining unexplained reduction in forest growth with age. The modeling exercise indicated another likely possibility: a 15% decrease in photosynthetic rates per unit of leaf area would account for the remaining unexplained reduction in above-ground growth.

In this paper, we return to the now 45- and 250-yr-old lodgepole pine stands previously studied and evaluate whether differences in photosynthetic rates occur at the level predicted. In addition, to make the test independent of possible subtle differences between the young and old stands, we report a parallel study in ponderosa pine (*Pinus ponderosa* Laws.), where pairs of young and older trees were compared side by side on a uniform site. In addition to photosynthetic rates, we measured several other environmental and physiological attributes of the trees and study sites to evaluate possible causes of any differences observed in gas exchange.

METHODS

STUDY AREA

The lodgepole pine site is located at the Fraser Experimental Forest near Winter Park, Colorado (N39° 54′ W105° 52′). The growing season on this site is short, and soil moisture is generally high during the growing season. Further details are described in Ryan and Waring (1992). The ponderosa pine site is located near Black Butte, OR (N44° 25′ W121° 40′), elevation 1027 m. In this area nearly all of the annual precipitation falls during the winter months, and drought-tolerant ponderosa pine is the only tree species on the site. Thinning and partial harvesting over many years has produced an open stand of trees of differing age classes, ranging from 3 to more than 250 yr. Because of the open condition of the stand, most trees receive full sunlight most of the day.

PHYSIOLOGICAL MEASUREMENTS

At both sites we measured net photosynthesis and stomatal conductance in full sun [photosynthetic photon flux density (PPFD) >800 $\mu mol\ m^{-2}\ s^{-1}$] and at ambient temperature and humidity. The photosynthetic light saturation of ponderosa pine occurs between 700 and 800 μmol m^{-2} s^{-1} (Hadley 1969), and lodgepole pine is expected to behave similarly. At the ponderosa pine site we sampled trees in pairs of old and younger trees growing within 10 m of one another, with only a few minutes elapsing between the measurements of a pair. Sixteen pairs were measured in July, 1990, and six pairs were measured in July, 1991, between the hours of 0900 and 1330. In August, 1991, repeated measurements were made on two old/young pairs of trees at hourly intervals between 0700 and 1700. At this site we used a LiCor 6200 gas exchange system with a 1/4-l cuvette. One-yr-old, sunlit foliage was removed from midcanopy with either a shotgun or a pole pruner, and gas exchange measurements were completed within 3 minutes. In preliminary measurements we found no measurable differences in photosynthesis and stomatal conductance between attached and detached foliage during this period.

We used an open system (LCA 2 or LCA 3, Analytical Development Company) to measure gas exchange at the lodgepole pine site. Measurements were made during the morning, until clouds lowered PPFD below photosynthetic saturation, on four dates through the summer of 1991. For each measurement we used three two-needle fascicles of sunlit, one-yr-old foliage from the upper third of the canopy. Foliage was obtained either by shotgun (sampling periods 1–3) or accessed by scaffolding (sampling period 4), and photosynthesis and stomatal conductance were determined within three minutes of detachment. As with ponderosa pine, preliminary studies confirmed that gas exchange of detached lodgepole pine foliage was not measurably different from attached foliage for at least 3 minutes after detachment. Each sample was taken from a different tree, and because temperature and relative humidity changed over the 2–5 hr sampling period, we alternated samples from the old and young stands.

The surface area of needles in cuvettes at both sites was determined from caliper measurements of enclosed needles and the width of the chamber. For lodgepole pine we assumed each fascicle was a right elliptical cylinder, and for ponderosa pine we assumed that each fascicle was a right circular cylinder divided into thirds. Photosynthesis is expressed per unit area of total needle surface.

At both sites we used a pressure chamber to measure leaf water potential (Ψ_{leaf}). For the diurnal cycle at the ponderosa pine site we measured Ψ_{leaf} before dawn and concurrently with leaf gas exchange on either a fascicle or a small stem near the foliage used for gas exchange. At the lodgepole pine site we measured (Ψ_{leaf}) before dawn and midday on foliage from nine branches accessible from the scaffolding towers. Soil water content was measured weekly at the lodgepole pine site using time-domain reflectometry (TDR) at ten points near the scaffolding towers. We used a Tektronix 1502 cable tester attached with coaxial cable to a wave guide formed by two steel rods 5 cm apart and inserted 1 m into the soil (Dalton et al. 1984). An equation developed by Topp et al. (1980) was used to estimate soil moisture content from the measured dielectric constant.

FOLIAR NUTRITION ANALYSES

More than 50 1-yr-old fascicles were selected from the same branches used for gas exchange measurements at the lodgepole pine site during sampling periods 2 and 3 and their foliar nitrogen contents analyzed individually. At the ponderosa pine site the foliage used for gas exchange measurements in 1990 (16 old/young pairs of trees) was returned to the laboratory. The foliage was dried at 70°C, and analyzed for total Kjeldahl nitrogen.

ANALYSIS OF STABLE ISOTOPES OF CARBON

Relative amounts of ^{13}C and ^{12}C were assessed in whole needle and whole wood tissue from the ponderosa pine site. Needle tissue was from 13 of the foliage samples used for gas exchange measurements in 1990. Wood tissue was taken from cores extracted from the south side of the same trees (with one additional tree from the 1990 sample set), 1.37 m above ground level. With a razor blade, earlywood from the 1989 growth ring was isolated from each core. Both leaf and wood tissue were oven-dried and subsequently ground in a mortar and pestle. Carbon isotope ratios were determined in the laboratory of Dr. Alan Mix at Oregon State University with a Finnigan/MAT 251 isotope ratio mass spectrometer equipped with a multiport and tube cracker for analysis of gases prepared in sealed 6-mm tubes. Isotope ratios were measured relative to a working CO_2 gas standard, but reported here in standard delta notation relative to the conventional isotopic standard PDB (Pee Dee Belemnite). Calibration of reference gas was done using National Institute of Standards and Technology (NIST) carbonate isotopic standard NBS-20, and was checked by analyzing oil isotopic standard NBS-22. The oil standard was prepared in the same way as the plant materials, with combustion in sealed quartz tubes with copper oxide, followed by isolation of the CO_2 gas in sealed pyrex tubes (Engel and Maynard 1989), and has a long-term precision for standard $\delta^{13}C$ of ± 0.03 per mil.

MEASUREMENT OF GROWTH

At the ponderosa pine site, radial growth for each tree was determined (to the nearest 0.0005 m) from measurements of the most recent growth increment cores taken from four sides of each tree at 1.37 m above ground level. Heights of all trees were measured in 1990 using triangulation. A second order polynomial expression was developed relating height to diameter at 1.37 m above ground level ($R^2 = 0.95$), and height growth was estimated from dH/dD of this curve. Total stem volumes for 1990 and 1991 were estimated from diameters and heights using equations in Walters et al. (1985). Sapwood thickness at 1.37 m was measured on increment cores to the nearest 0.001 m, and sapwood cross-sectional area calculated assuming the cross section was circular. Sapwood area at the base of the crown was estimated from sapwood at 1.37 m and the height to the crown using taper equations in Maguire and Hann (1987). Total leaf area was calculated assuming 0.24 m^2 leaf area per cm^2 sapwood cross-sectional area at the base of the crown (Waring et al. 1982). Growth efficiency was evaluated as the quotient of estimated volume growth and estimated leaf area. Growth measurements at the lodgepole pine site are described by Ryan and Waring (1991).[1]

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[1] The predictive equations for each step of these analyses have an associated error that is provided in the referenced studies. All of these equations were developed for similar vegetation at different sites; the error incurred by applying to the current study cannot be determined accurately. However, in each case the equations represent the best possible approximation known to the authors.

STATISTICAL ANALYSES

In most cases we used a paired t-test to assess significant differences. For the August samples at the lodgepole pine site, we used a one-way analysis of variance (ANOVA) because the samples were not strictly paired and environmental conditions changed little over the relatively short sampling period. Only two pairs were used for the diurnal cycle at the ponderosa pine site, so it was not possible to assess significance of differences between means. Standard errors (s.e.) are noted to indicate variability of these diurnal measurements. Carbon isotope data were analyzed with a two-way ANOVA using the SAS general linear models procedure (SAS Institute 1985). Tissue type (foliage or wood) and tree age (old or young) were the two classes used in the ANOVA.

RESULTS

Tree age differed by >150 yr and tree height by >10 m for the young vs. old samples at each site (Table 1). Stand wood growth was 78% lower (37 g m^{-2} y^{-1} vs. 168 g m^{-2} y^{-1}) in the old lodgepole pine stand compared to the young stand. Because old and young trees grew together at the ponderosa pine site, we did not measure stand wood production at that site, but estimated growth efficiency (wood growth/leaf area) of old trees averaged 41% less than the growth efficiency of younger trees (Table 1). There was no significant difference in foliar nitrogen content between needles from young and old trees at either site (Table 1).

Net photosynthesis averaged 14–30% lower (per unit leaf area) in foliage from old trees (Table 2); differences were statistically significant ($P < 0.01$) for all but one lodgepole pine sample. The mean differences in net photosynthesis were more pronounced at the ponderosa pine site. Because the specific leaf area (total leaf surface area/leaf dry weight) was slightly lower for needles from older trees

TABLE 1.

Characteristics of old and young trees at the lodgepole and ponderosa pine sites. Data for the lodgepole site are stand-level means; although the average age of the older stand at this site was 250 yr, the average age of sampled trees was slightly older, as noted. Data for the ponderosa site are means for the six trees used for physiological measurements on 7/1/91. Two younger trees (<40 yr) were included in the 1990 data set.

	Lodgepole site		Ponderosa site	
	Young	Old	Young	Old
Tree age (yr)	45	275	54	229
Diameter at 1.37 m (cm)	13	34	23	76
Tree height (m)	12	21	10	32
Specific leaf area (total surface)/leaf weight (m^2 kg^{-1})	9.1	8.9	7.3	6.6
Leaf nitrogen (% dry weight)	0.94	0.91	1.20	1.22
Estimated growth efficiency (m^3 wood y^{-1} m^{-2} leaf area* 10^{-5})	9.7	3.4	13.9	8.3

TABLE 2.

Photosynthesis (μmol CO_2 m^{-2} s^{-1}) of 1-yr-old foliage from young and old trees. Standard errors are in parentheses; significant differences ($P < 0.01$) are indicated with an *.

Lodgepole site	Young stand	Old stand	% reduction
6/12/91 (N = 8)	2.49 (0.39)	2.02 (0.18)	19
6/28/91 (N = 23)	4.51 (0.16)	3.89 (0.20)	14 *
7/29/91 (N = 15)	3.61 (0.23)	2.95 (0.28)	18 *
8/29/91 (N = 12)	4.60 (0.16)	3.94 (0.22)	14 *
Ponderosa site	**Young trees**	**Old trees**	**% reduction**
7/24/90 (N = 16)	5.38 (0.27)	3.77 (0.22)	30 *
7/1/91 (N = 6)	5.22 (0.20)	3.81 (0.26)	27 *

(Table 1), the difference in CO_2 assimilation was even greater when evaluated on a weight basis (16–34% lower for older trees; data not shown). Stomatal conductance followed a pattern similar to photosynthesis, and the percent reductions between young and old trees were also similar (data not shown).

Net photosynthesis and stomatal conductance tended to decrease during the morning (Figures 1 and 2), and differences with tree age were most pronounced in midmorning at both sites. Integration under the diurnal curves for ponderosa pine (Figure 2) revealed that the foliage samples from old trees averaged 28% lower carbon gain over the 10-hr measurement period. Seasonally there was no apparent trend in net photosynthesis at the lodgepole pine site. Lower photosynthetic rates on 6/12 corresponded with very low atmospheric humidity on that day (just over 30% when initial measurements were made in the morning, compared with 50%–70% on the other measurement days). In general, larger average differences between foliage from young and old trees occurred when average net photosynthesis and stomatal conductance were lower.

At the lodgepole pine site, soil water content to a depth of 1 m was significantly greater in the old stand in late June and through most of July (Figure 3, $P < 0.01$); by August soil water content was the same in both stands. Ψ_{leaf} was lower in the older stand for both predawn and midday samples at this site (Figure 4, $P < 0.01$). Overall, the mean difference between lodgepole pine stands for predawn Ψ_{leaf} was 0.11 MPa, about the difference expected due to the additional gravitational potential from 10 m greater height of the older canopy. During the middle of the day, Ψ_{leaf} was generally lower in the older stand at the lodgepole pine site (Figure 4). The difference in midday Ψ_{leaf} between lodgepole pine stands averaged 0.04 MPa throughout the measurement period, somewhat less than the difference expected due to gravity, although at times the midday difference was much greater than the potential difference due to gravity.

No significant differences between the predawn Ψ_{leaf} of old and young trees

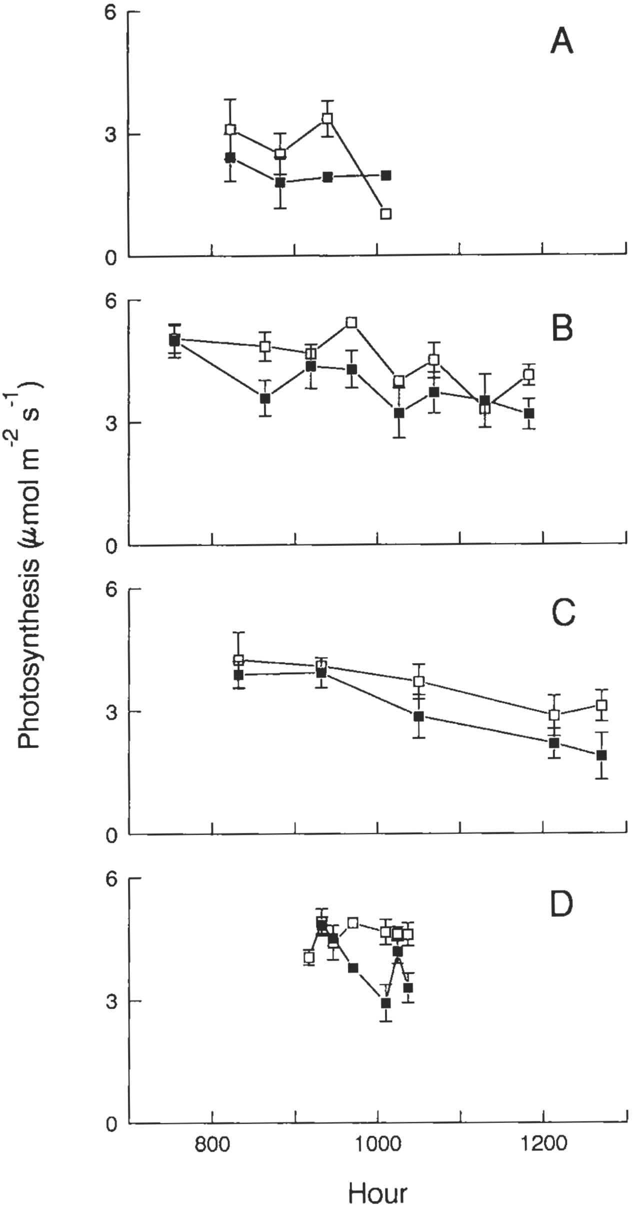

FIGURE 1. Diurnal course of CO_2 assimilation at the LP site for young (open symbols) and old (closed symbols) trees (A = 6/12; B = 6/28; C = 7/29; D = 8/29). Bars represent standard errors.

were measured at the ponderosa pine site. In September, 1990, mean values were −1.17 MPa (n = 5; s.e. = 0.08) and −1.02 MPa (n = 5; s.e. = 0.07) for old and young trees respectively, and in August, 1991, respective mean values for old and young trees were −0.90 MPa (n = 4; s.e. = 0.04) and −0.92 MPa (n = 4; s.e. = 0.04). Expected gravitational differences were not noted, a common observation when there is dew on the foliage (Waring, unpublished data).

The analysis of variance showed that carbon isotope ratios were significantly different between age classes ($P < 0.01$) and tissue types ($P < 0.01$), with no

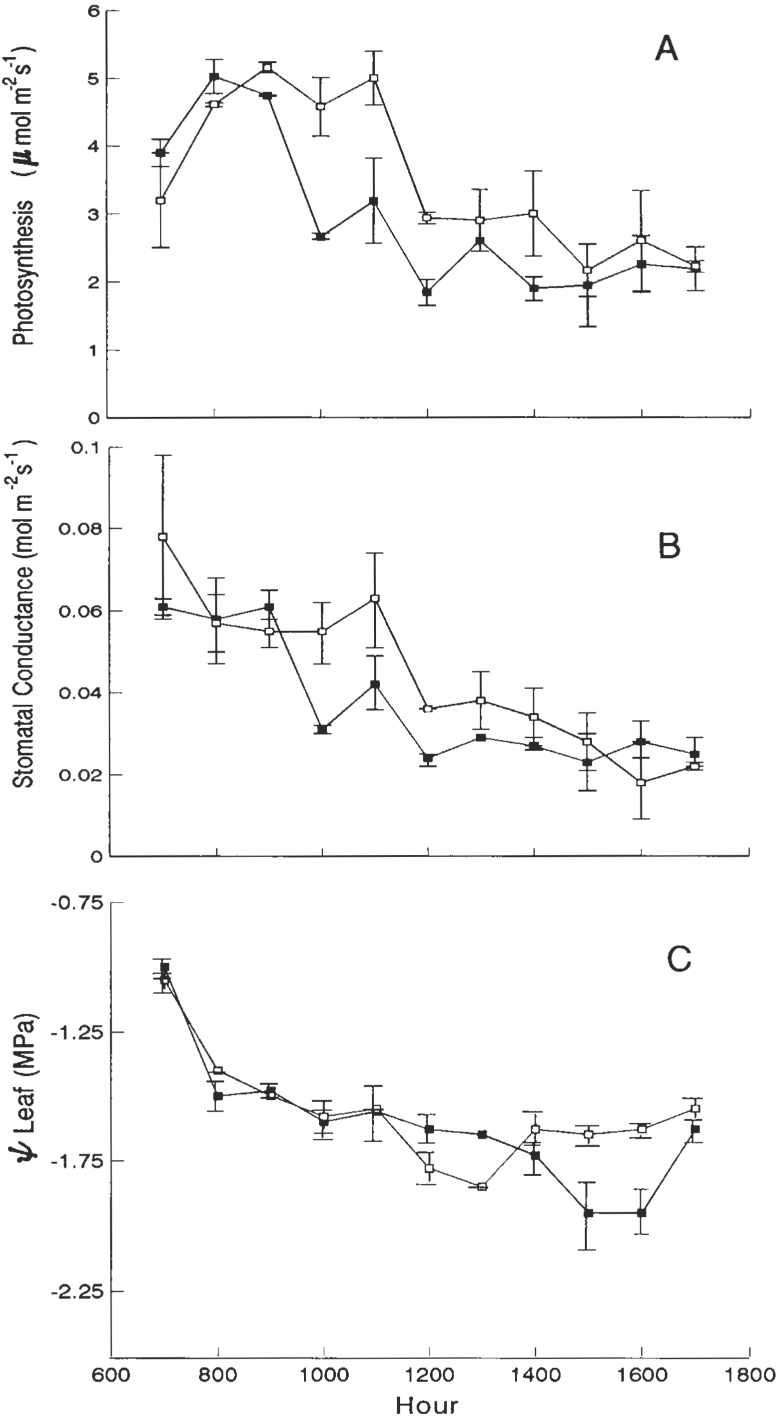

FIGURE 2. Diurnal course of CO_2 assimilation (A), stomatal conductance (B) and leaf water potential (C) for young (open symbols) and old (closed symbols) trees at the PP site on 8/1/91. Each data point represents the mean value of measurements from two trees except for the 13:00 measurement of the old trees, which is a single measurement. Bars represent standard errors.

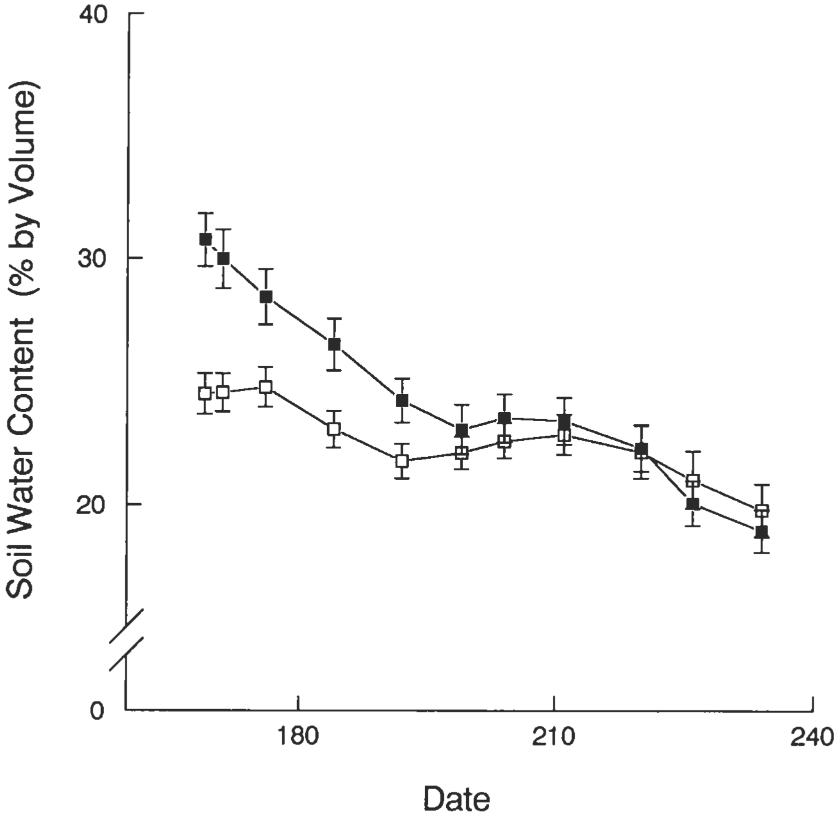

FIGURE 3. Seasonal course of soil water content for the young stand (open symbols) and old stand (closed symbols) at the LP site determined from time domain reflectometry. Error bars are standard errors ($N = 10$).

significant interaction. Mean $\delta^{13}C$ for 1-yr-old foliage from young and old trees was -27.2 and -26.0, respectively; mean $\delta^{13}C$ for wood from young and old trees was -25.8 and -24.5, respectively. Carbon isotope ratios of both tissue types increased linearly with total tree height (regression, $P < 0.01$; Figure 5). With increasing tree height, the relative abundance of ^{13}C increased both in earlywood at 1.3 m and in 1-yr-old foliage from the midcrown. The slopes of both regression equations were significantly different from zero ($P < 0.01$ for both tissue types), but the slopes of the two lines were not significantly different from one another. On the average, $\delta^{13}C$ increased by a little more than 0.5 per mil for each 10 m total height. Ages were not available for all of these trees, so the regression could not be performed as a function of age; however, the age classes in Table 1 correspond with the size distributions in Figure 5.

DISCUSSION

Understanding the cause of the decline in wood production as stands age is important for developing and improving mechanistic models of forest growth. Ryan and Waring (1992) showed from an analysis of stand carbon balance that

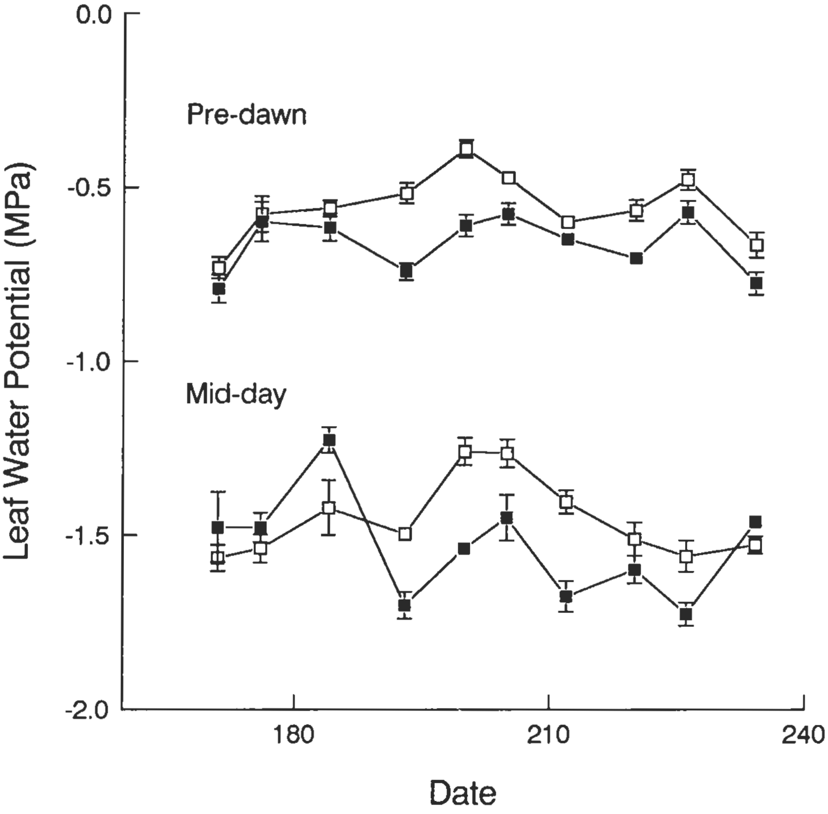

FIGURE 4. Seasonal course of predawn and midday leaf water potential for the young stand (open symbols) and old stand (closed symbols) at the LP site. Error bars are standard errors ($N = 9$).

much of the difference in wood production observed between a young and an aging lodgepole pine stand could be explained by a reduction in unit-leaf photosynthesis rates of about 18%. In this study, net photosynthesis of 1-yr-old foliage from old and young ponderosa and lodgepole pine trees differed by about this amount. That is, the lower net photosynthetic rates we measures in 1-yr-old foliage could explain the lower wood production and growth efficiency if the foliage of the entire canopies had the same average differences in photosynthetic activity.

These results do not prove that lower net photosynthetic rates cause lower growth efficiency in old trees. It is conceivable that causality may be in the opposite direction: growth reductions due to any other reason could lower net photosynthesis due to a smaller carbon sink. This possibility deserves investigation. For the present, it is appropriate to view these results as a critical test that "fails to disprove" the hypothesis that photosynthetic reductions are an important cause of growth decline with age. Much work remains to be done.

Although our study was not designed to provide explanations for the observed differences in photosynthetic rates, we gathered sufficient information to address some possibilities. Microclimatic variation was definitely not a contributing factor. Our sampling was restricted to foliage near the ends of branches, fully exposed to direct sunlight. The open nature of the ponderosa pine stand assured an aerody-

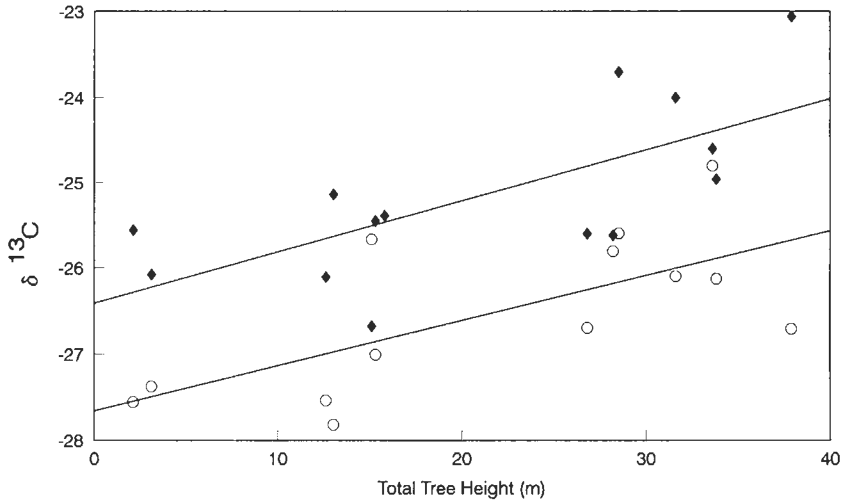

FIGURE 5. Changes in $\delta^{13}C$ ratios of whole needle (open circles) and earlywood (closed diamonds) tissue with tree height. For wood, the best fir linear regression model is $\delta^{13}C = 0.060 * (ht) - 26.41$ ($R^2 = 0.49$); for needles the best fit regression line is $\delta^{13}C = 0.052 * (ht) - 27.66$ ($R^2 = 0.68$).

namically well-mixed atmosphere with little likelihood of significant CO_2 gradients with height. In the two lodgepole pine stands, we obtained direct access by scaffolding to the canopies and confirmed that no significant difference in microclimate existed between the young and old stands.

Restrictions in the availability of soil nitrogen or water could not explain the reduction in stomatal conductance and photosynthesis by older trees. Leaf nitrogen concentrations were similar, regardless of tree age, and predawn Ψ differed little among ponderosa pine trees or lodgepole pine stands.

Kull and Koppel (1987) showed that maximum photosynthetic capacity (the rate of photosynthesis when CO_2 is ambient and all other environmental conditions are optimal) of Scots pine was reduced as trees aged. Although we did not measure photosynthetic capacity directly, we noted similar high rates of net photosynthesis early in morning on samples collected from both young or old trees. Also, the lack of difference in leaf nitrogen concentrations argues against significant variation in photosynthetic capacity among young and old trees (Field and Mooney 1983, Schoettle 1990).

If the maximum capacity for photosynthesis was the same in leaves of old and young trees, the reduced net photosynthesis in old trees should have been due to lower stomatal conductance. One way to evaluate the relative effects of stomatal conductance and enzymatic carboxylation on total net photosynthesis is to determine the ratios of stable isotopes of carbon (^{13}C and ^{12}C) in plant tissue (as long as the isotopic composition CO_2 in the atmosphere is constant). Carboxylating enzymes discriminate against the heavier isotope, but the degree of discrimination decreases when the concentration of CO_2 in the leaf mesophyll decreases (e.g., Farquhar et al. 1982). Mesophyll CO_2 decreases when stomatal conductance becomes more limiting to photosynthesis than the activity of carboxylating enzymes, because the rate of CO_2 supply is lower than the rate of consumption.

Therefore, a relatively high proportion of ^{13}C (i.e., a high value $\delta^{13}C$) indicates that during the time the carbon for that tissue was fixed, stomata were relatively more limiting to photosynthesis than the enzyme-mediated activity of carboxylation.

The positive slope in Figure 5 demonstrates that as ponderosa pine trees became larger, the relative amount of ^{13}C in both needles and wood increased. The isotope discrimination shows that stomatal conductance was relatively more limiting to time-integrated photosynthesis in old, large trees than in younger, smaller trees. The fact that the same trend occurred in wood as in leaf tissue suggests that the net photosynthetic activity of the entire canopies for each age class was similarly constrained by stomatal conductance.

From this point on, our discussion becomes more speculative; our data suggest preliminary inferences that we hope will inspire further work. The diurnal curves in Figure 2 show that stomata of older trees began closing about 2 hr earlier in the day compared with younger trees, but the leaf water potentials for young and old trees were nearly identical at this time. How could this happen if other environmental conditions, such as vapor pressure deficit, were the same? If stomatal conductance (and therefore evaporative flux) of old and young trees is different, and the water potential gradient is the same, it means that the hydraulic conductance of the old trees was lower.[2]

Differences in the hydraulic conductance are, we believe, a likely reason for the observed differences in stomatal conductance and photosynthesis. More rapid closure and delayed opening of stomata have been demonstrated previously on trees with reduced hydraulic conductance (Borghetti et al. 1989, Sperry et al. 1993), exactly the diurnal observations made at the ponderosa pine site (Figure 2D). Similarly, Mattson-Djos (1981) showed that stomatal conductance of 16 m tall Scots pine was 50% lower than that of 2 m tall trees, and Kline et al. (1976) found in Douglas-fir that the transpiration rate per unit of sapwood cross-sectional area was 30% less in a 75 m tree compared with 18–25 m trees (see also Running et al. 1975). The mechanism for this response is not known and deserves further investigation. In sugarcane, changes in hydraulic architecture affect chemical signals from roots that induce stomatal closure (Meinzer et al. 1991). However, it takes several days for water to move from the roots to the leaves of a mature conifer (Kline et al. 1976), so such signals cannot explain the diurnal differences in stomatal behavior we observed.

Aside from the effects of gravity, the main stem of a tree contributes little to the total hydraulic conductance compared with branches (Hellkvist et al. 1974, Tyree 1988). Waring and Silvester (1993) found that the hydraulic conductance of short (0.25 m) branches of *Pinus radiata* D. Don was two to five times that of long (7 m) branches. As a result, on clear days, the stomata on foliage of long branches

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[2] Hydraulic conductance (G) for the vascular system of a tree can be calculated from Darcy's Law as $G = Q/\Delta\Psi$, with $\Delta\Psi = \Psi_{leaf} - \Psi_{root}$ and Q = transpiration rate (Heine 1971). For aerodynamically rough canopies, Q for a unit of leaf area can be estimated from the Penman-Monteith equation and will vary only with canopy conductance and the vapor pressure deficit of the atmosphere (Riha and Campbell 1984). Therefore, if Ψ_{root} was nearly equal for young and old trees and stomatal conductance for the sampled needles was proportional to conductance by the whole canopy, then the measured differences in stomatal conductances and diurnal leaf water potentials would indicate lower hydraulic conductance in the older trees.

closed completely by midafternoon; on short branches stomata remained open, and photosynthesis and transpiration continued unconstrained. From an analysis of ratios of ^{13}C to ^{12}C in foliage from different lengths of branches, Waring and Silvester (1993) reasoned that the reduced hydraulic conductance of the longer branches resulted in increased stomatal closure relative to shorter branches. Older trees often support longer branches than younger trees, because when height growth stops, natural pruning also diminishes. As the branches grow in length, the age of the conducting wood also increases (Pothier et al. 1989). Together these factors combine to reduce hydraulic conductance, and indirectly, through stomata control, could explain the observed reduction in photosynthetic rates by foliage from old trees.

We plan further studies to evaluate more critically whether photosynthesis and stomatal conductance are reduced throughout the canopy as a function of lengthening branches and decreasing hydraulic conductance. Further studies are also planned to investigate in more detail the relationships between growth decline and reduced photosynthesis in old trees.

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