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MAINTENANCE RESPIRATION AND STAND DEVELOPMENT IN A SUBALPINE LODGEPOLE PINE FOREST[1]

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Abstract. We examined a chronosequence of subalpine lodgepole pine stands to test the hypothesis that low net primary production in older forest stands is caused by higher maintenance respiration costs of woody tissues. We predicted that respiration of woody tissues (particularly stem sapwood) would be greater in older stands and that the higher maintenance costs would account for observed low wood production. For a unit of ground surface, the carbon flux involved in wood production and associated construction respiration was 210 $g \cdot m^{-2} \cdot yr^{-1}$ in a 40-yr-old stand, but declined to 46 $g \cdot m^{-2} \cdot yr^{-1}$ in a 245-yr-old stand. However, maintenance respiration of woody tissues in stems and branches consumed only 61 $g \cdot m^{-2} \cdot yr^{-1}$ in the 40-yr-old stand and 79 $g \cdot m^{-2} \cdot yr^{-1}$ in the 245-yr-old stand. The slight, nonsignificant increase in maintenance respiration of woody tissues could not explain the dramatic decline in aboveground wood production in the old-growth stand.

Key words: carbon budgets; carbon metabolism; Colorado, USA; maintenance respiration; old-growth forests; Pinus contorta; *sapwood; stem respiration; subalpine.*

INTRODUCTION

After a forest is established, net primary production (NPP) increases rapidly until the canopy closes, then decreases as the stand ages and woody biomass accumulates (Whittaker and Woodwell 1968, O'Neill and DeAngelis 1981, Jarvis and Leverenz 1983, Waring and Schlesinger 1985, Pearson et al. 1987). The decrease in NPP after canopy closure is thought to result from changes in the balance between photosynthesis and respiration caused by increased respiration of woody tissues (Yoda et al. 1965, Kira and Shidei 1967, Kramer and Kozlowski 1979). This hypothesis has been widely accepted (Whittaker and Woodwell 1967, Kramer and Kozlowski 1979, Waring and Schlesinger 1985), yet never adequately tested (Jarvis and Leverenz 1983, Sprugel 1984, Landsberg 1986, Sprugel and Benecke 1991).

Why might the balance between photosynthesis and respiration change with stand development? After the canopy closes, leaf area remains constant or declines slowly until mortality of dominant stems increases late in a stand's life (Waring and Schlesinger 1985). Because carbon fixation varies with leaf area, gross production will peak at canopy closure and likely remain the same or decline as the stand ages. In contrast, woody biomass and the surface area of boles and branches increase as stands develop. If woody tissue respiration varies with surface area (Woodwell and Botkin 1970, Kinerson 1975), then respiration will increase with stand age. Therefore, the ratio of respiration to gross production should be larger in older stands, and increased respiration would decrease the carbon available for the production of woody biomass.

Recent advances in the understanding of woody tissue respiration (Havrenek 1981, Ryan 1990, Sprugel 1990) allow better estimation of annual carbon costs of maintenance and construction respiration. Previously, annual respiration costs have been calculated by multiplying average measurements of CO_2 efflux from stems by estimates of the total woody surface area of a forest stand, and correcting for temperature (Woodwell and Botkin 1970, Harris et al. 1975, Kinerson 1975, Linder and Troeng 1981). However, this approach has two flaws: (1) respiration rates vary greatly within and among trees, but much of this variability can be attributed to sapwood volume or growth rate (Havrenek 1981, Ryan 1990, Sprugel 1990), and (2) temperature-corrected respiration rates vary seasonally, because of differential contributions from growth and maintenance respiration (Butler and Landsberg 1981, Linder and Troeng 1981, Lavigne 1988, Ryan 1990, Sprugel 1990).

Partitioning respiration between the components construction and maintenance (Amthor 1986), and the use of sapwood volume, rather than surface area, to estimate woody tissue respiration may greatly affect estimates of total respiration for stands (Ryan 1990). Use of these concepts may also affect the hypothesis that increased respiration lowers NPP in older stands. For example, construction respiration varies linearly with wood production (Ryan 1990, Sprugel 1990), and

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therefore must decrease if NPP decreases. Also, sapwood volume might not increase as much as bole surface area increases in a developing stand. Because leaf area is linearly related to sapwood cross-sectional area (Waring and Schlesinger 1985), if leaf area is static, sapwood volume can only increase if tree height increases. Because most height growth occurs early in stand development, sapwood volume and maintenance respiration may not increase greatly between intermediate and old-growth stands.

In this study, we tested the hypothesis that higher maintenance respiration for woody tissues would reduce net primary production in older stands. We estimated maintenance respiration (R_m) for woody tissues from sapwood volume (Ryan 1990), sapwood temperature (Ryan 1989), and a correction for diurnal temperature amplitude (Ågren and Axelsson 1980). We then compared estimates of R_m with measured changes in aboveground wood production for a chronosequence of subalpine lodgepole pine (*Pinus contorta* ssp. *latifolia*) stands in Colorado.

Study Area

We sampled trees from even-aged stands of lodgepole pine at the Fraser Experimental Forest near Winter Park, Colorado, USA (39°54′ N, 105°52′ W). The subalpine forests at Fraser experience short growing seasons and cool night temperatures, and have abundant moisture throughout the growing season (Alexander et al. 1985). The experimental forest receives an average of 740 mm precipitation each year, with two-thirds falling as snow; the annual average temperature is 2°C. Frost limits photosynthetic activity during the spring and autumn, but summer rain storms keep soil moisture high during the growing season, so that stomatal closure associated with drought is rare (Kaufmann 1982). However, nitrogen levels in the soil are low for lodgepole pine forests (Fahey and Knight 1986) and poor nitrogen availability may limit photosynthetic capacity and growth. Soils are Typic Cryochrepts derived from mixed gneiss and schist. At Fraser, lodgepole pine stands occur from 2600 to 3100 m; stands for this study were at an elevation of 2800 m.

Methods

To reduce site differences, we selected three adjacent stands growing within 300 metres. The youngest stand (40-yr, 40 yr old in 1986) was established when a plot had been clear-felled for a regeneration study (Alexander et al. 1985). The 65-yr-old stand (65-yr) was located in an area clear-felled for a fire break. The 245-yr-old (245-yr) was a remnant of the old-growth lodgepole pine stand that had originally covered the area of all three stands. The old-growth stand was likely established after a catastrophic wildfire ≈300 yr ago; most of the trees in the stand were established between 230 and 280 yr ago (W. Moir, *personal communication*). Tree age in the old-growth stand averaged 245 yr in the plots used for this study.

We randomly located three circular plots 100–250 m^2 in size in each stand in 1986; each plot contained ≈30 trees. Stem diameter at 1.4 m height was measured on each tree in the plot and 5-yr radial growth, 5-yr height growth, and sapwood and heartwood radii at 1.4 m were measured on every third tree. Radial growth and sapwood and heartwood radii were measured on two cores per sampled tree to 0.1 mm for growth and 1 mm for sapwood and heartwood. Annual stemwood growth, standing biomass in various components, and sapwood volume were estimated using double sampling (Cochran 1977) and equations given in Pearson et al. (1984) for standing biomass of stems, coarse roots (>2 mm diameter), and branches, Ryan (1989) for sapwood, and Kaufmann and Troendle (1981) for leaf area and canopy biomass. Double sampling equations adjust plot estimates for the intensively measured trees using the difference between the plot mean basal area and intensive sample mean basal area and the relationship between basal area and component biomass.

Temperature data for the period 1981–1985 at a weather station 1600 m distant and 50 m lower in elevation were used to estimate respiration; minimum temperatures were increased by 7°C to offset the effect of cold air drainage at the weather station (Kaufmann 1984). Respiration and aboveground wood production are presented as averages over 1981–1985, the period measured for stem radial growth. Construction respiration for wood growth was estimated as 28% of the carbon in the new growth (Chung and Barnes 1977), and growth is reported as the carbon incorporated into growth plus the respiration needed for construction. Carbon for woody biomass was estimated at 50% of dry mass (Edwards et al. 1981).

Maintenance respiration of stem sapwood was estimated using an equation developed by Ryan (1990):

$$R_m = 0.00486 V_s \exp(0.0663T), \quad (1)$$

where T is temperature (in degrees Celsius), V_s is sapwood volume (in cubic centimetres), and R_m is maintenance respiration (in nanomoles of CO_2 released per second). R_m for branches and coarse roots was estimated using the rate in Eq. 1 and assuming their volume was 100% sapwood. Sapwood temperature was estimated from air temperature using an equation developed from data collected on site (Ryan 1989); daily respiration estimates were corrected for amplitude of diel temperature variation (Ågren and Axelsson 1980). We estimated the error for an annual estimate of maintenance respiration by using the standard deviation of the coefficients in Eq. 1.

We measured standing stocks of soil nutrients and soil N availability in the three stands to check our assumption that productivity should be similar for the three stands. In September 1986, we sampled 0–10 cm

mineral soil in the three stands, and collected four composite samples (10 subsamples each) from each stand. Samples were air-dried and the fraction <2 mm analyzed as follows: organic matter was determined by a modified Walkley-Black procedure (Graham 1959), total nitrogen by Kjeldahl analysis (Bremner and Mulvaney 1982), extractable nitrate plus nitrite-nitrogen and ammonium-nitrogen by analysis (ALPKEM RFA 200, ALPKEM, Clackamas, Oregon, USA) of 2 mol/L KCl extracts (Keeney and Nelson 1982), extractable P by analysis (ALPKEM RFA 200) of 0.5 mol/L $NaHCO_3$ extracts (Olsen and Sommers 1982), and cations by inductively coupled plasma spectroscopy of ammonium acetate extracts (Thomas 1982).

Nutrient availability was estimated using a mixed-bed ion exchange resin in nylon mesh bags placed between the forest floor and mineral soil (Binkley and Matson 1983). We placed five bags in each plot, two on the soil-sample transect, and three on a transect normal to the soil transect. Bags were placed in September 1986 and collected September 1987. Resin bags were frozen after collection, stored at −15°C, thawed, and extracted with 2 mol/L NaCl. Filtered extracts were analyzed for NH_4-N and NO_3-N colorimetrically with an ALPKEM RFA 300 autoanalyzer and for a variety of other elements by inductively coupled plasma spectroscopy.

To check leaf areas estimated from sapwood cross-sectional area (leaf surface area [all sides, in square metres] = 0.44 sapwood area in square centimetres at a height of 1.4 m [Kaufmann and Troendle 1981]), we measured photosynthetically active radiation (PAR) transmitted through the canopy with a LI-COR LI-190SB PAR sensor coupled to a Campbell 21X data logger. We sampled transmitted light at >60 points per plot with points spaced 2 m along a grid with a randomly determined starting location. All plots were sampled between 1000 and 1300 solar time on cloudless days during a 2-wk period in August 1987. Transmittance was calculated as the ratio of PAR in stand to PAR in an adjacent clearing. Leaf areas were then calculated using measured energy transmittance and Beer's Law:

$$L = \frac{\ln(I/I_0)}{-0.5/3.34}, \quad (2)$$

where L is all-sides leaf area (in square metres per square metre), I/I_0 is measured light transmitted, 0.5 is the extinction coefficient, and 3.34 converts projected leaf area to total leaf area for lodgepole pine (Kaufmann et al. 1982). Pierce and Running (1988) found that an extinction coefficient of 0.5 accurately described transmittance for coniferous stands with a projected leaf area index of <5.

Differences in growth, component biomass, soil nutrients, and maintenance respiration among plots were evaluated with a one-factor analysis of variance at α = .05. When the ANOVA factor is a continuous variable (e.g., stand age), orthogonal polynomial contrasts, rather than means tests, are commonly used to describe the response to treatment (Steel and Torrie 1980). However, we had only three levels of stand age and two of the levels were much closer to each other than to the third. Under these conditions, orthogonal polynomial contrasts provide poor estimates of the response to treatment. Therefore, we used an F-protected LSD (Milliken and Johnson 1984) to compare means; where variance was heterogeneous, we used Dunnett's T3 test for multiple comparisons (Dunnett 1980).

TABLE 1. Stand characteristics for a lodgepole pine chronosequence. Means with different superscript letters differ significantly (one-way ANOVA, $P < .05$).

Stand age (yr)	All-sides leaf area (m^2/m^2)	Stand density (trees/ha)	Basal area (m^2/ha)	Average tree height (m)
40	12.3[a]	4376[a]	35.2[a]	10.3[a]
65	12.1[a]	3311[b]	40.4[a,b]	11.9[b]
245	7.7[b]	1067[c]	44.7[b]	17.4[c]

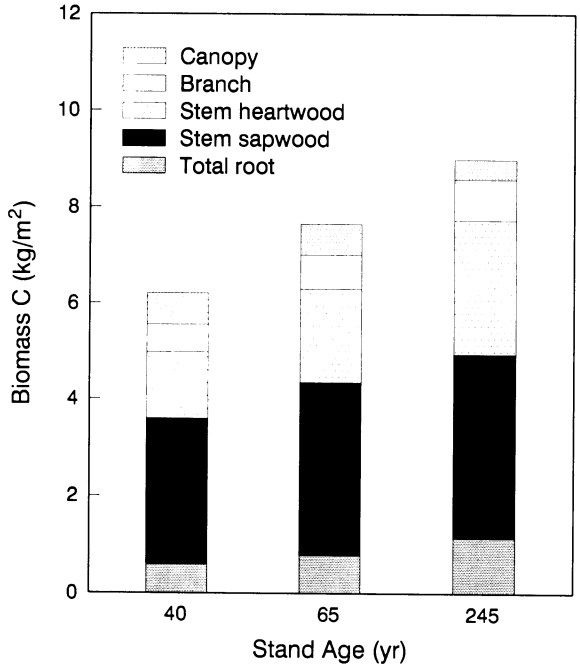

FIG. 1. Biomass carbon for a lodgepole pine chronosequence. Canopy C was estimated from an allometric relationship with sapwood basal area; heartwood and sapwood C were estimated from an allometric relationship with tree height and sapwood basal area; branch and root C were estimated from an allometric relationship with tree basal area.

RESULTS

These stands show a pattern typical for stand development in lodgepole pine. Woody biomass and basal area increased with stand age, while the number of stems and leaf area declined (Fig. 1, Table 1). Total

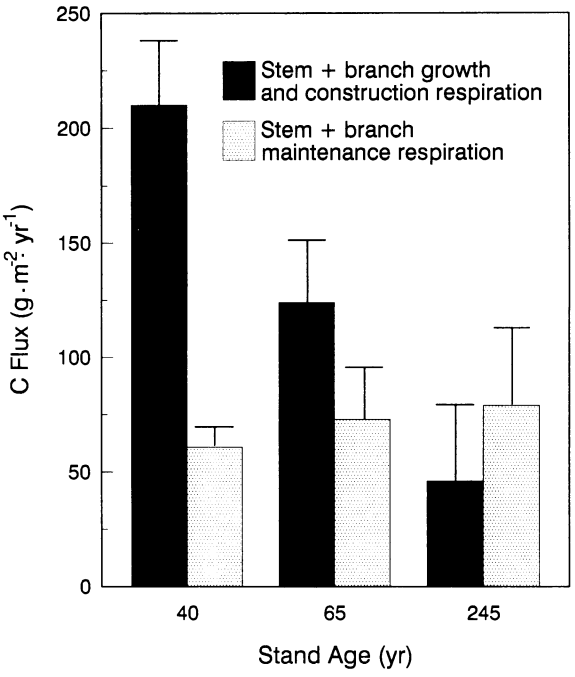

FIG. 2. Annual carbon use for stem and branch growth and for stem and branch maintenance respiration in a lodgepole pine chronosequence. Values are averages for the years 1981–1985, and growth includes construction respiration. Error bars show upper halves of 95% confidence intervals; these intervals include the variability within stands and variability among years.

biomass carbon increased from 6200 g/m^2 in the 40-yr stand to 8970 g/m^2 in the 245-yr stand. Heartwood, branch, and total root biomass were each significantly greater in the oldest stand. Sapwood volume estimates were slightly higher in the 245-yr stand (carbon content 4400 g/m^2) compared with the 40-yr stand (3600 g/m^2), but the difference was not significant ($P = .24$). Leaf biomass carbon was significantly lower in the oldest stand (410 g/m^2 in the 245-yr vs. 650 g/m^2 in the 40-yr stand). Mortality on the study plots was <0.6% of the stems per year; over a 50-yr period, mortality in the 245-yr stand was ≈1% of the stems per year (W. Moir, *personal communication*).

Annual wood production declined dramatically with stand age, but sapwood maintenance respiration increased only slightly (Fig. 2). At age 40 yr, the carbon flux involved in wood production and associated construction respiration was 210 g·m^{-2}·yr^{-1}. Wood production and associated construction respiration declined to 124 g·m^{-2}·yr^{-1} by age 65 and to 46 g·m^{-2}·yr^{-1} by age 245. All differences in wood production among stands were significant ($P < .01$). Branch and root growth were <15% of stem growth for all stands. Annual sapwood maintenance costs, as carbon, were 61 g·m^{-2}·yr^{-1} in the 40-yr stand and 79 g·m^{-2}·yr^{-1} in the 245-yr stand. Because sapwood R_m was estimated from sapwood volume (Eq. 1) sapwood R_m also did not vary significantly with stand age. Based on the standard deviations of the R_m model coefficients, an approximate uncertainty interval for the annual sapwood maintenance estimates was 13%. The coefficient of variation for respiration estimates among years was 4%. Within-stand coefficients of variation for basal area, sapwood volume, and leaf area were <20%.

All-sides leaf area was 37% lower in the oldest stand (Table 1, $P < .01$), but because of the exponential relationship between leaf area and energy absorption, canopy light absorption decreased only ≈14% between the 40- and 65-yr stands and the 245-yr stand. Measured energy absorption (1 minus transmittance) as a fraction of incident PAR was 0.80 for the 40-yr stand, 0.84 for the 65-yr stand, and 0.71 for the 245-yr stand. However, because the sample size was small (three stands) and coefficients of variation were high (21–41%), PAR absorption did not vary statistically among stands ($P = .12$). All-sides leaf areas estimated from PAR transmitted were 12.0, 14.3, and 9.3 for the 40-yr, 65-yr, and 245-yr stands, respectively. Leaf areas estimated from light absorption are likely greater than actual leaf area (compare to Table 1) because branches and boles also absorb light.

Nutrient concentrations and soil nutrient availability were similar among the stands (Table 2). Of the nutrients sampled, only total nitrogen ($P = .06$) and Na ($P = .04$) varied among the stands; however, these differences were not substantial. Inorganic nitrogen availability assessed with resin bags was uniformly low (4.2 μg/g resin for NH_4-N and 8.4 μg/g resin for NO_3-N) and did not differ among stands ($P = .61$ for NH_4-N;

TABLE 2. Soil nutrients in 0–10 cm mineral soil and N collected on ion exchange resins (IER) in subsurface nylon mesh bags in the field, for a lodgepole pine chronosequence.

Stand age (yr)		Organic matter (%)	Total nitrogen (%)	Soil nutrient concentration (μg/g)						Total N on IER* [μg/(g resin)]
				NH_4-N	NO_3-N	P	Ca	Mg	K	
40	$\bar{X}$	5.1	0.081	9.1	0.95	14	1100	150	260	9.7
	(SD)	(0.4)	(0.013)	(1.0)	(0.53)	(6.6)	(190)	(25)	(33)	(4.6)
65	$\bar{X}$	5.7	0.068	8.0	0.53	22	950	150	230	6.4
	(SD)	(1.4)	(0.010)	(1.3)	(0.05)	(4.6)	(150)	(33)	(33)	(0.4)
245	$\bar{X}$	5.8	0.098	9.9	0.70	16	1000	140	230	13.0
	(SD)	(1.0)	(0.019)	(1.9)	(0.16)	(1.7)	(230)	(34)	(75)	(2.5)

* Values corrected for extractions on nonincubated blanks.

$P = .14$ for NO_3-N). Available Ca, Mg, K, Al, Mn, S, and Mn assessed with ion exchange resin bags also did not vary among stands ($P > .26$). Foliar nitrogen concentrations did not differ between the 40-yr and 245-yr stands, but were lower in the 65-yr stand (A. W. Schoettle, *unpublished manuscript*).

Discussion

As expected, aboveground wood production was substantially lower in the 245-yr stand. However, increased woody tissue respiration fails to account for the low production. These results contradict established hypotheses (Yoda et al. 1965, Kira and Shidei 1967, Whittaker and Woodwell 1967, Kramer and Kozlowski 1979, Waring and Schlesinger 1985) about the effect of woody tissue respiration on net primary production in forests.

The pattern of NPP for the lodgepole pine chronosequence in this study is typical of the species in the central Rocky Mountains. Pearson et al. (1987) examined several subalpine lodgepole forests in Wyoming, and found that net ecosystem production peaked around 40 yr, dropped rapidly from 40 to 80 yr, and slowly declined thereafter. Simulations using a growth-and-yield model (RMYLD, Edminster 1978) with the 40-yr stand as the initial conditions also showed the same pattern. Stem biomass estimated with the equations of Pearson et al. (1984) differed <5% with stem biomass estimated using a local tree volume equation (Myers 1964).

The lower leaf area in the oldest stand complicates interpretation of the results, because wood production and leaf area are linked (Waring 1983). The lower leaf area in the 245-yr stand might cause lower wood production, because carbon fixation varies with leaf area. However, wood production per unit leaf area (growth efficiency, Waring 1983) declined substantially with leaf age (Fig. 3). Therefore, the lower growth in the 65-yr and 245-yr stands was likely caused by some factor other than changing leaf area.

Estimates of sapwood maintenance respiration appear reliable because they were developed from measurements of trees on site, rates are comparable to other estimates, and maintenance rates would need to be substantially greater to invalidate results. The equation used to estimate R_m from sapwood volume (Ryan 1990) was developed using trees growing in stands used for this study; the relationship between R_m and sapwood volume did not vary with tree size or age. Sapwood maintenance rate for lodgepole pine was roughly in the middle of the range of R_m rates found in four other conifers (*Pinus ponderosa, Pinus elliottii, Pinus resinosa, Tsuga heterophylla*), and ≈25% below the highest rate (M. G. Ryan et al., *unpublished manuscript*). Mohren (1987) reports a nearly identical rate for sapwood R_m, calculated using biochemical considerations. In contrast, Sprugel (1990) reports a rate for sapwood R_m in 30-yr-old *Abies amabilis* trees ≈6 times the rate

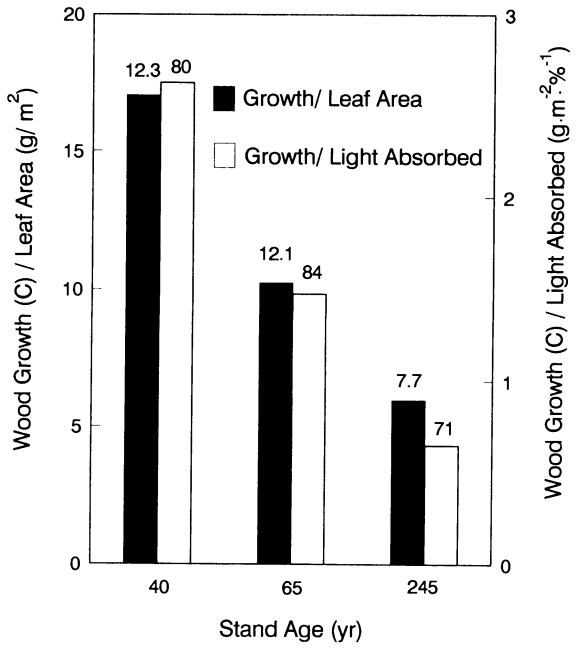

FIG. 3. Annual wood growth (as carbon) per unit of leaf area or per unit of light absorbed for a lodgepole pine chronosequence. All-sides leaf area is listed above the solid bars, and light absorption (percent) is listed above the empty bars. Values for growth include construction respiration.

for lodgepole pine. Sprugel's (1990) higher rate might be partially explained by the higher N content of *Abies* sapwood (Ryan 1991*a*). In this study, rates for sapwood maintenance would need to be 4 times greater than measured to account for the reduction in growth between the 40-yr and 245-yr stands (after adjustment for leaf area differences).

In our site-specific model (Eq. 1), respiration roughly doubles with each 10°C increase in temperature ($Q_{10} = 1.9$). Other studies have shown a similar temperature response (Butler and Landsberg 1981, Linder and Troeng 1981). In contrast, Paembonan et al. (1991) showed that the temperature response for respiration of wood, foliage, and branches combined varied with monthly mean temperature. In their study, Q_{10} was ≈3 at 5°C and declined linearly to ≈1.5 at 25°C. However, Paembonan et al. (1991) studied a 12-yr-old tree, where foliar respiration likely dominated, and did not separate growth from maintenance respiration. If the temperature response observed by Paembonan et al. (1991) was used to estimate annual maintenance respiration for woody tissues in this study, estimated respiration would increase by 20%.

Why might the hypothesis about maintenance respiration and NPP in forests be in error? Whittaker and Woodwell (1967) reasoned that respiration costs in older stands must consume a larger fraction of gross primary production (GPP) because (1) stem surface area increased dramatically with stand growth, (2) respiration appeared to vary with stem surface area, and (3)

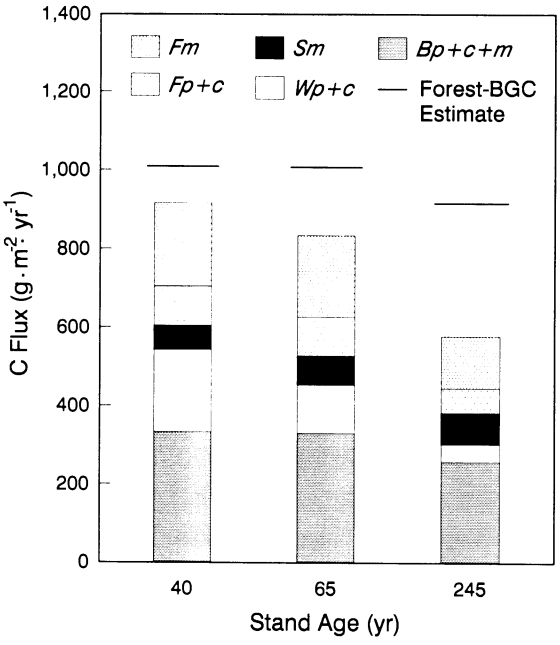

FIG. 4. Annual carbon flux and the annual total of net daytime carbon fixation estimated from the Forest-BGC model for a lodgepole pine chronosequence. Forest-BGC estimates are averaged over the period 1981–1985 (CV = 5%). F_m = maintenance respiration of foliage, F_{p+c} = foliage production and construction respiration, S_m = maintenance respiration of aboveground woody tissue, W_{p+c} = wood production and construction respiration, B_{p+c+m} = total belowground carbon allocation.

leaf area (and presumably GPP) remained relatively constant once the canopy closed. However, much of the respiration associated with stem surface area is likely respiration to support the construction of new cells (Goodwin and Goddard 1940). From this viewpoint, large surface areas and high respiration rates signal stands with high NPP. Maintenance, in contrast, requires fixed carbon, which is then unavailable for growth (Amthor 1986). For woody tissue, maintenance respiration is related to sapwood volume, not surface area (Ryan 1990, Sprugel 1990), and sapwood volume is similar in the young and old stands in this study.

A New Hypothesis

To attempt to explain why growth and growth efficiency were so low in the 245-yr stand, we developed a gross carbon budget (Ryan 1991*b*) for these stands and compared the budget with the annual total of daytime net photosynthesis estimated with the Forest-BGC model (Running 1984, Running and Coughlan 1988). Because results suggest neither sapwood maintenance respiration nor decreased leaf area explained the low growth in the 245-yr stand, we wished to explore two alternative explanations: (1) fine root production was greater in the old stand, or (2) photosynthesis per unit leaf area was lower in the old stand.

We estimated an annual gross carbon budget as the sum of aboveground wood and foliage production and construction respiration, aboveground sapwood and foliage maintenance respiration, and total belowground carbon allocation (Ryan 1991*b*). Aboveground wood production (and associated construction respiration) and aboveground sapwood R_m were from this study. Total belowground allocation, canopy maintenance respiration, and canopy production were estimated as in Ryan (1991*b*): total belowground allocation was estimated from litterfall (Raich and Nadelhoffer 1989); canopy production and litterfall were estimated from canopy turnover (12% of total canopy biomass at this site [Schoettle 1989]), adjusted for the fraction of total fine litter that was leaf litter (Fahey 1983); dark maintenance respiration for foliage was estimated from air temperature and canopy N (using foliar N from Schoettle 1989). Carbon used for root exudation or lost to herbivory was assumed negligible for these stands.

The Forest-BGC model was used to estimate annual net daytime carbon fixation for 1981–1985. The program was run separately for each of the 5 yr with these inputs: leaf biomass in 1986; foliar N from Schoettle (1989); soil water capacity at site; temperature, relative humidity, and precipitation from a nearby weather station with minimum temperatures adjusted to offset the effect of cold air drainage at the weather station (Kaufmann 1984); irradiance estimated with the MTCLIM interpolation program (Running et al. 1987); and snowpack from a nearby Soil Conservation Service snowcourse. Coefficients for foliage, wood, and root respiration were set to 0, so that the program would calculate total net daytime carbon fixation.

Carbon fixation estimated by Forest-BGC was greater than carbon fixation estimated by summing carbon fluxes, and the greatest difference occurred in the oldest stand (Fig. 4). Even though leaf area in the 245-yr stand was 37% lower than in the two younger stands, Forest-BGC estimated only a 13% decrease in GPP, because foliar N was similar and light absorption declined by only 14%. Sapwood R_m was a minor component of annual carbon fixation in the carbon budget: 7% of the total budget in the 40-yr stand, and 13% in the 245-yr stand. In contrast, estimated total belowground carbon allocation was 36% of the total budget in the 40-yr stand, but increased to 45% in the 245-yr stand.

Two mechanisms that may explain both the low NPP in the 245-yr stand and the discrepancy between Forest-BGC estimates of carbon fixation and the annual carbon budget will be considered. First, a major carbon sink is missing from the carbon accounting, or second, true carbon fixation was lower than estimated by the Forest-BGC model, or both. We will examine each hypothesis for plausibility.

Carbon used belowground could be greater than estimated, but because nutrition was similar among stands and total belowground carbon was already very large

in the 245-yr stand, we believe this explanation is unlikely. Belowground allocation costs are difficult to measure directly, and there is no agreement on accepted procedures (Singh et al. 1984) or estimates (Raich and Nadelhoffer 1989). The relationship we used to estimate belowground carbon allocation (Raich and Nadelhoffer 1989) appears to be robust for rates of carbon loss as litterfall ranging from 100 to 500 $g \cdot m^{-2} \cdot yr^{-1}$. However, its use for determining local trends has not been tested. Several investigators have hypothesized that changes in available nutrients will promote changes in fine root turnover, with fine root turnover increasing as nutrient availability decreases (Keyes and Grier 1981, Vogt et al. 1983, 1986, Linder and Rook 1984). However, Nadelhoffer et al. (1985) and Aber et al. (1985) suggest that increased nitrogen availability leads to increased fine root turnover. If fine root turnover and nutrient availability are linked, the stable soil nutrient profiles and low but stable available nitrogen in this study should indicate stable fine root production across the chronosequence. However, because we have no direct measurement of belowground carbon costs, we cannot discount this hypothesis.

An alternate hypothesis would also explain the carbon budget for the chronosequence: the model overestimates GPP, particularly in older stands. Simple mechanistic models can generate reasonable estimates of photosynthesis (Ågren et al. 1991), but most of these models were developed from measurements on young, rapidly growing trees. Leaf water potential (Kramer and Kozlowski 1979), nutrition (Grier et al. 1982), canopy light environment, and water conductivity (Tyree 1988) could differ between old and young trees, and potentially affect photosynthesis. Leaf water potential will decrease with height, but the −0.1-MPa difference expected from a 10-m difference in tree height would not likely affect stomatal conductance and photosynthesis. Photosynthesis and foliar N have been linked (Field and Mooney 1986), but foliar N did not differ between the oldest and youngest stands in this study. Canopy light environment may differ among these stands, but we cannot easily assess any impact on productivity.

Because the diameter of the smallest twigs apparently controls water potential gradients within trees (Tyree 1988), changes in hydraulic architecture with age could change either leaf water potential or the capacity to deliver water to an actively transpiring leaf. Also, foliage in the tops of tall, old trees may experience higher water potential gradients (and consequently more negative leaf water potentials) because of increasing resistance from longer branches and longer stems. Because leaf water potential and stomatal conductance are linked (Schulze and Hall 1984), foliage in taller trees may have lower stomatal conductance and photosynthetic rates. For example, Mattson-Djos (1981) found that 16 m tall Scots pine (*Pinus sylvestris*) have stomatal conductances ≈50% of those in 2 m tall saplings. Additionally, Kline et al. (1976) found that total transpiration per unit of sapwood conducting area in a 75-m Douglas-fir (*Pseudotsuga menziesii*) was 30% less than that of trees 18–25 m tall.

GPP (carbon) would need to decline by 160 $g \cdot m^{-2} \cdot yr^{-1}$ between age 40 yr and 245 yr to account for the lower aboveground NPP in the 245-yr stand. This represents 18% of the GPP estimated by Forest-BGC for the 245-yr stand. In 1991, photosynthesis and conductance of 1-yr-old needles were 16–22% lower in the 245-yr stand than in the 40-yr stand; even greater differences in photosynthesis and conductance were found between 10 and 30 m tall ponderosa pine in Oregon (B. Yoder et al., *unpublished manuscript*). These results support the hypothesis that reduced photosynthesis accounts for the low net primary productivity in the oldest stand.

Conclusions

Our results show that the low aboveground wood production in the 245-yr stand of lodgepole pine is not caused by high maintenance respiration of woody tissues. Sapwood maintenance respiration was at most 13% of the annual carbon budget, lower than estimated elsewhere (Waring and Schlesinger 1985, Landsberg 1986). Carbon budgets for other forests should be examined to determine whether these results apply generally. Of the two hypotheses advanced to explain low wood production in the 245-yr stand (high belowground allocation or low photosynthesis), low photosynthesis seems more plausible.

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Literature Cited

Aber, J. D., J. M. Melillo, K. J. Nadelhoffer, C. A. McClaugherty, and J. Pastor. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. Oecologia (Berlin) **66**:317–321.

Ågren, G. I., and B. Axelsson. 1980. Population respiration: a theoretical approach. Ecological Modelling **11**:39–54.

Ågren, G. I., R. McMurtrie, W. J. Parton, and J. Pastor. 1991. State-of-the-art models of production-decomposition linkages in conifer and grassland ecosystems. Ecological Applications **1**:118–138.

Alexander, R. R., C. A. Troendle, M. R. Kaufmann, W. D. Shepperd, G. L. Crouch, and R. K. Watkins. 1985. The Fraser Experimental Forest, Colorado: research program and published research 1937–1985. United States Department of Agriculture Forest Service General Technical Report **RM-118**.

Amthor, J. S. 1986. Evolution and applicability of a whole plant respiration model. Journal of Theoretical Biology **122**: 473–490.

Binkley, D., and P. Matson. 1983. Ion exchange resin bag method for assessing forest soil N availability. Soil Science Society of America Journal **47**:1050–1052.

Bremner, J. M., and C. S. Mulvaney. 1982. Nitrogen—total. Pages 595–624 *in* A. L. Page, R. H. Miller, and D. R.

Keeney, editors. Methods of soil analysis. Part II. Chemical and microbiological properties. American Society of Agronomy, Madison, Wisconsin, USA.

Butler, D. R., and J. J. Landsberg. 1981. Respiration rates of apple trees, estimated by CO_2-efflux measurements. Plant, Cell and Environment **4**:153–159.

Chung, H-H., and R. L. Barnes. 1977. Photosynthate allocation in *Pinus taeda*. I. Substrate requirements for synthesis of shoot biomass. Canadian Journal of Forest Research **7**:106–111.

Cochran, W. G. 1977. Sampling techniques. Third edition. John Wiley & Sons, New York, New York, USA.

Dunnett, C. W. 1980. Pairwise multiple comparisons in the unequal variance case. Journal of the American Statistical Association **75**:796–800.

Edminster, C. B. 1978. RMYLD: computation of yield tables for even-aged and two-storied stands. United States Department of Agriculture Forest Service Research Paper **RM-199**.

Edwards, N. T., H. H. Shugart, Jr., S. B. McLaughlin, W. F. Harris, and D. E. Reichle. 1981. Carbon metabolism in terrestrial ecosystems. Pages 499–536 *in* D. E. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, England.

Fahey, T. J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. Ecological Monographs **53**:51–72.

Fahey, T. J., and D. H. Knight. 1986. Lodgepole pine ecosystems. BioScience **36**:610–617.

Field, C., and H. A. Mooney. 1986. The photosynthesis–nitrogen relationship in wild plants. Pages 25–55 *in* T. J. Givnish, editor. On the economy of plant form and function. Cambridge University Press, Cambridge, England.

Goodwin, R. H., and D. R. Goddard. 1940. The oxygen consumption of isolated woody tissues. American Journal of Botany **27**:234–237.

Graham, E. R. 1959. An explanation of theory and methods of soil testing. University of Missouri Agricultural Experiment Station Bulletin **734**.

Grier, C. C., K. A. Vogt, and R. O. Teskey. 1982. Carbon uptake and allocation in subalpine ecosystems. Pages 64–69 *in* R. H. Waring, editor. Carbon uptake and allocation in subalpine ecosystems as a key to management. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.

Harris, W. F., P. Sollins, N. T. Edwards, B. E. Dinger, and H. H. Shugart. 1975. Analysis of carbon flow and productivity in a temperate deciduous forest ecosystem. Pages 116–122 *in* D. E. Reichle, J. F. Franklin, and D. W. Goodall, editors. Productivity of world ecosystems. National Academy of Sciences, Washington, D.C., USA.

Havrenek, W. M. 1981. Stem respiration, radial growth, and photosynthesis of a cembran pine tree (*Pinus cembra* L.) at the timberline. Mitteilungen der Forstlichen Bundesversuchsanstalt Wein **142**:443–467.

Jarvis, P. G., and J. W. Leverenz. 1983. Productivity of temperate, deciduous and evergreen forests. Pages 233–280 *in* O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, editors. Encyclopedia of plant physiology. New Series. Volume 12D. Physiological plant ecology IV. Ecosystem processes: mineral cycling, productivity and man's influence. Springer-Verlag, Berlin, Germany.

Kaufmann, M. R. 1982. Evaluation of season, temperature and water stress effects on stomata using a leaf conductance model. Plant Physiology **69**:1023–1026.

———. 1984. Effects of weather and physiographic conditions on temperature and humidity in subalpine watersheds of the Fraser Experimental Forest. United States Department of Agriculture Forest Service Research Paper **RM-251**.

Kaufmann, M. R., C. B. Edminster, and C. A. Troendle. 1982. Leaf area determinations for subalpine tree species in the central Rocky Mountains. United States Department of Agriculture Forest Service Research Paper **RM-238**.

Kaufmann, M. R., and C. A. Troendle. 1981. The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species. Forest Science **27**:477–482.

Keeney, D. R., and D. W. Nelson. 1982. Nitrogen—inorganic forms. Pages 643–693 *in* A. L. Page, R. H. Miller, and D. R. Keeney, editors. Methods of soil analysis. Part II. Chemical and microbiological properties. American Society of Agronomy, Madison, Wisconsin, USA.

Keyes, M. R., and C. C. Grier. 1981. Above- and belowground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Canadian Journal of Forest Research **11**:599–605.

Kinerson, R. S. 1975. Relationships between plant surface area and respiration in loblolly pine. Journal of Allied Ecology **12**:965–971.

Kira, T., and T. Shidei. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Japanese Journal of Ecology **17**:70–87.

Kline, J. R., K. L. Reed, R. H. Waring, and M. L. Stewart. 1976. Field measurement of transpiration in Douglas-fir. Journal of Applied Ecology **13**:273–283.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York, New York, USA.

Landsberg, J. J. 1986. Physiological ecology of forest production. Academic Press, London, England.

Lavigne, M. B. 1988. Stem growth and respiration of young balsam fir trees in thinned and unthinned stands. Canadian Journal of Forest Research **18**:483–489.

Linder, S., and D. A. Rook. 1984. Effects of mineral nutrition on carbon dioxide exchange and partitioning of carbon in trees. Pages 211–236 *in* G. D. Bowen and E. K. S. Nambiar, editors. Nutrition of forest trees in plantations. Academic Press, New York, New York, USA.

Linder, S., and E. Troeng. 1981. The seasonal variation in stem and coarse root respiration of a 20-year-old Scots pine (*Pinus sylvestris* L.). Mitteilungen der Forstlichen Bundesversuchsanstalt Wein **142**:125–139.

Mattson-Djos, E. 1981. The use of pressure-bomb and porometer for describing plant water stress in tree seedlings. Pages 45–57 *in* P. Puttonen, editor. Proceedings of a Nordic symposium on vitality and quality of nursery stock. Department of Silviculture, University of Helsinki, Finland.

Milliken, G. A., and D. E. Johnson. 1984. Analysis of messy data. I. Designed experiments. Lifetime Learning, Belmont, California, USA.

Mohren, G. M. J. 1987. Simulation of forest growth applied to Douglas fir stands in the Netherlands. Dissertation. Landbouwuniversiteit de Wageningen, Wageningen, The Netherlands.

Myers, C. A. 1964. Volume tables and point-sampling factors for lodgepole pine in Colorado and Wyoming. United States Department of Agriculture Forest Service Research Paper **RM-6**.

Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology **66**:1377–1390.

Olsen, S. R., and L. E. Sommers. 1982. Phosphorus. Pages 403–430 *in* A. L. Page, R. H. Miller, and D. R. Keeney, editors. Methods of soil analysis. Part II. Chemical and microbiological properties. American Society of Agronomy, Madison, Wisconsin, USA.

O'Neill, R. V., and D. L. DeAngelis. 1981. Comparative productivity and biomass relationships of forest ecosystems. Pages 411–450 *in* D. E. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, England.

Paembonan, S. A., A. Hagihara, and K. Hozumi. 1991. Long-term measurements of CO_2 release from the aboveground parts of a hinoki forest tree in relation to air temperature. Tree Physiology **8**:399–405.

Pearson, J. A., T. J. Fahey, and D. H. Knight. 1984. Biomass and leaf area in contrasting lodgepole pine forests. Canadian Journal of Forest Research **14**:259–265.

Pearson, J. A., D. H. Knight, and T. J. Fahey. 1987. Biomass and nutrient accumulation during stand development in Wyoming lodgepole pine forests. Ecology **68**:1966–1973.

Pierce, L. L., and S. W. Running. 1988. Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. Ecology **69**:1762–1767.

Raich, J. W., and K. J. Nadelhoffer. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology **70**:1346–1354.

Running, S. W. 1984. Microclimate control of forest productivity: analysis by computer simulation of annual photosynthesis/transpiration balance in different environments. Agricultural and Forest Meteorology **32**:267–288.

Running, S. W., and J. C. Coughlan. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. Ecological Modelling **42**:125–154.

Running, S. W., R. R. Nemani, and R. D. Hungerford. 1987. Extrapolation of synoptic meterological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. Canadian Journal of Forest Research **17**:472–483.

Ryan, M. G. 1989. Sapwood volume for three subalpine conifers: predictive equations and ecological implications. Canadian Journal of Forest Research **19**:1397–1401.

———. 1990. Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. Canadian Journal of Forest Research **20**:48–57.

———. 1991*a*. The effect of climate change on plant respiration. Ecological Applications **1**:157–167.

———. 1991*b*. A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. Tree Physiology **9**:255–266.

Schoettle, A. W. 1989. Potential effect of premature needle loss on the foliar biomass and nutrient retention of lodgepole pine. Pages 443–454 *in* R. K. Olson and A. S. Lefohn, editors. Transactions—effects of air pollution on western forests. Air and Waste Management Association, Pittsburgh, Pennsylvania, USA.

Schulze, E.-D., and A. E. Hall. 1984. Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. Pages 181–230 *in* O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, editors. Encyclopedia of plant physiology. New series. Volume 12B. Physiological plant ecology II. Water relations and carbon assimilation. Springer-Verlag, Berlin, Germany.

Singh, J. S., W. K. Lauenroth, H. W. Hunt, and D. M. Swift. 1984. Bias and random errors in estimation of root production: a simulation approach. Ecology **65**:1760–1764.

Sprugel, D. 1984. Density, biomass, productivity, and nutrient cycling changes during stand development in wave-regenerated balsam fir forests. Ecological Monographs **54**: 165–186.

———. 1990. Components of woody-tissue respiration in young *Abies amabilis* trees. Trees **4**:88–98.

Sprugel, D., and U. Benecke. 1991. Woody tissue respiration and photosynthesis. Pages 329–351 *in* J. P. Lassoie and T. M. Hinckley, editors. Methods and approaches in tree ecophysiology. CRC Press, Cleveland, Ohio, USA.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill, New York, New York, USA.

Thomas, C. W. 1982. Exchangeable cations. Pages 159–165 *in* A. L. Page, R. H. Miller, and D. R. Keeney, editors. Methods of soil analysis. Part II. Chemical and microbiological properties. American Society of Agronomy, Madison, Wisconsin, USA.

Tyree, M. T. 1988. A dynamic model for water flow in a single tree: evidence that models must account for hydraulic architecture. Tree Physiology **4**:195–217.

Vogt, K. A., C. C. Grier, and D. J. Vogt. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Advances in Ecological Research **15**:303–377.

Vogt, K. A., E. A. Moore, D. J. Vogt, M. J. Redlin, and R. L. Edmonds. 1983. Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas-fir stands of different ages and site productivities. Canadian Journal of Forest Research **13**:249–437.

Waring, R. H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Advances in Ecological Research **13**:327–354.

Waring, R. H., and W. H. Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press, Orlando, Florida, USA.

Whittaker, R. H., and G. M. Woodwell. 1967. Surface area relations of woody plants and forest communities. American Journal of Botany **54**:931–939.

Whittaker, R. H., and G. M. Woodwell. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. Journal of Ecology **56**:1–25.

Woodwell, G. M., and D. B. Botkin. 1970. Metabolism of terrestrial ecosystems by gas exchange techniques: the Brookhaven approach. Pages 73–85 *in* D. E. Reichle, editor. Analysis of temperate forest ecosystems. Springer-Verlag, New York, New York, USA.

Yoda, K., K. Shinozaki, H. Ogawa, K. Hozumi, and T. Kira. 1965. Estimation of the total amount of respiration in woody organs of trees and forest communities. Journal of Biology of Osaka City University **16**:15–26.