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Stem growth and respiration in loblolly pine plantations differing in soil resource availability

CHRIS A. MAIER

USDA Forest Service, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA

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Summary Stem respiration and growth in 10-year-old loblolly pine (*Pinus taeda* L.) plantations were measured monthly during the third year of fertilization and irrigation treatments to determine whether soil resource availability differentially altered growth and respiration in stem tissue. Fertilized trees had significantly greater stem biomass, stem nitrogen concentration ([N]) and growth rate than unfertilized trees. Stem respiration (R_t) was significantly greater in fertilized trees when expressed on a per unit surface area ($R_{t,a}$, μmol CO_2 m^{-2} s^{-1}), sapwood volume ($R_{t,v}$, μmol CO_2 m^{-3} s^{-1}), or mass ($R_{t,w}$, nmol CO_2 g^{-1} s^{-1}) basis; however, there was no difference between treatments when expressed as a function of stem N content ($R_{t,n}$, μmol CO_2 $(mol\ N)^{-1}$ s^{-1}). Irrigation had no significant effect on R_t or annual stem growth. Daily total respiration (R_d, mol CO_2 m^{-2} day^{-1}) and stem diameter growth both had a seasonal bimodal pattern with peaks in early spring and midsummer. Stem [N] declined significantly during the growing season. Stem growth rate and [N] explained 75% of the seasonal variation in temperature-normalized $R_{t,a}$.

The mature tissue method was used to partition total stem respiration (R_t) into maintenance (R_m) and growth (R_g) components. There was a linear correlation between winter $R_{t,v}$, a measure of basal R_m, and sapwood N content; however, $R_{t,v}$ per unit N was greater in January before diameter growth started than in the following December after growth ceased, indicating that $R_{t,v}$ declined as stem diameter increased. Consequently, estimates of annual maintenance respiration (R_M) based on January data were 44% higher than estimates based on December data. Growth respiration was correlated with stem growth rate ($r^2 = 0.55$). The growth respiration coefficient (r_g)—the slope of the relationship between R_g and stem growth rate—was 0.24. Respiration accounted for 37% of annual stem carbon budget. Stem carbon-use efficiency (CUE)—the ratio of stem growth to stem growth plus respiration—averaged 0.63 and was unaffected by fertilization.

Keywords: carbon allocation, carbon balance, forest ecosystem, growth respiration, maintenance respiration, stem respiration.

Introduction

Factors that regulate carbon use in stem growth and respiration are of interest to forest managers and ecologists, not only because stem wood represents an economic output, but because stems represent a long-term carbon sink, capable of removing and storing a large amount of atmospheric carbon (Ryan et al. 1994, 1996). Carbon allocated to stems to support growth and respiration accounts for a significant portion (10 to 42%) of the autotrophic carbon budget over the life of a forest (Waring and Schlesinger 1985, Landsberg and Gower 1997). Changes in environment (e.g., climate change) or management regimes (e.g., fertilization) that alter stem carbon-use efficiency (CUE), i.e., the ratio of carbon allocated to growth to total carbon allocated to growth and respiration, may affect stem production (Ryan et al. 1994, 1995, 1996). Understanding how environmental changes affect the relationship between stem growth, respiration and nutrition is essential for developing and validating forest productivity models (Ryan et al. 1994).

The functional model of respiration (McCree 1970, Amthor 1989, 2000), applied to stems, provides a means for assessing the role of respiration in the stem carbon budget. The model partitions respiration into growth and maintenance components:

$$R_t = r_g(dW/dt) + r_m W, \quad (1)$$

where R_t is total stem respiration rate, W is stem biomass, dW/dt is stem growth rate, r_g is the growth respiration coefficient and r_m is the maintenance respiration coefficient. Growth respiration rate (R_g) is the product of $r_g(dW/dt)$ and maintenance respiration rate (R_m) is the product of $r_m W$. Equation 1 provides a useful framework for understanding responses to environmental change in field-grown trees. The model is also the basis for carbon partitioning in some process-based forest productivity models (Sprugel et al. 1995). Estimating r_g and r_m for woody tissue under field conditions is difficult because of the combined activities of mature (mostly maintenance respiration) and growing (a combination of growth and maintenance respiration) tissues (Ryan et al. 1994). The most widely used approach for stems is the mature tissue method (Amthor 1989, 2000), where R_t measured during the dormant season (i.e., no growth) represents basal R_m (corrected for temperature) throughout the year (Ryan 1990, Sprugel and Benecke 1991, Lavigne 1996, Lavigne and Ryan 1997, Stockfors and Linder 1998*a*). The difference between R_t and R_m during

growth represents R_g. The ratio of R_g and stem growth rate is an estimate of r_g (Chiariello et al. 1989, Amthor 1994).

Nutrient availability strongly affects stem productivity, carbon allocation and respiration under most conditions. Woody tissue R_m is often correlated with tissue nitrogen (N) content (Ryan 1991, Ryan et al. 1994) probably because protein turnover and other processes related to protein metabolism make a significant contribution to maintenance costs (Penning de Vries 1975*a*). Because of this, the maintenance term in Equation 1 can be written as a function of N content rather than dry mass (Barnes and Hole 1978, Amthor 2000). However, a relationship between R_m and N is not always observed in field-grown trees. Lavigne and Ryan (1997) found no relationship between R_m and sapwood nitrogen concentration ([N]) in several boreal tree species. In contrast, winter stem R_m per unit mass was correlated with stem [N] in eastern white pine (*Pinus strobus* L.) trees (Vose and Ryan 2001). Experimental data examining effects of artificially altering soil N availability on stem respiration is limited. Increases in soil nutrient availability will likely affect stem respiration by increasing tissue [N] and the associated protein maintenance and construction costs. Maier et al. (1998) reported that fertilized loblolly pine (*Pinus taeda* L.) trees had increased sapwood [N] and winter R_m per unit sapwood volume compared with controls. In their study, total CO_2 efflux from a section of stem wood was linearly correlated with tissue N content. In contrast, Stockfors and Linder (1998*a*) measured no effect of stem [N] on R_m per unit live cell volume in fertilized Norway spruce (*Picea abies* (L.) Karst.) trees, although R_t correlated well with stem N content. Ryan et al. (1996) also found little effect of fertilization on stem R_m per unit sapwood volume in *Pinus radiata* D. Don.

Growth respiration should increase with N availability, if only because growth rate increases with N supply. However, the effect of nutrient availability on r_g is not well understood. Stockfors and Linder (1998*a*) found no effect of increased nutrient availability on r_g in *P. abies*. Because r_g is a function of tissue chemical composition, it should only change if the substrates (e.g., NO_3^- or NH_4^+) or products of respiratory and biosynthetic metabolism are altered by changes in nutrient availability (Amthor 2000).

Loblolly pine is a major tree species in natural and plantation forests in the southeastern United States. Presently, over 18 million hectares of loblolly pine forests in the region are maintained under a range of management regimes (Schultz 1997). Fertilization is increasingly used as a management option to increase productivity on nutrient-poor sites (Allen and Albaugh 1999). Nitrogen and carbon resources are tightly linked; although it is not well understood how N fertilization affects the long-term carbon cycle. Fertilization may decrease the time for a regenerating loblolly pine stand to switch from being a net carbon source to a net carbon sink (Maier and Kress 2000). This study examined seasonal changes in stem growth and respiration in 10-year-old loblolly pine plantations during the third year of a fertilization and irrigation experiment. At the time of the study, improved resource availability had increased stem growth and doubled standing biomass (Albaugh et al. 1998). The objectives were to: (1) examine effects of irrigation and fertilization treatments on seasonal and annual stem growth and respiration; (2) partition stem respiration into growth and maintenance components and determine if respiration parameters varied with growth rate and tissue N content; and (3) determine effects of resource availability on stem carbon-use efficiency.

Materials and methods

Site description

The study site was a loblolly pine plantation located at the Southeast Tree Research and Education Site (SETRES), 17-km north of Laurinburg, NC (34°48′ N, 79°12′ W). Mean annual air temperature is 17 °C with minimum temperatures in January (0.5 °C) and maximum temperatures in July (33 °C). Mean annual precipitation is 1210 mm evenly distributed throughout the year, but extended droughts often occur during the growing season. The soil is an excessively well-drained, deep loamy sand classified as a sandy, siliceous, thermic psammentic hapludult (Wakulla series, USDA Soil Classification System). The stand is a mixture of 10 improved North Carolina Piedmont loblolly pine families planted in 1985 after harvesting of the previous natural longleaf pine (*Pinus palustris* Mill.) stand.

Treatments consisted of a 2 × 2 factorial combination of nutrition (no addition and optimum nutrition) and water (no addition and well watered) replicated four times. Treatment plots were 50 × 50 m with interior sampling plots of 30 × 30 m. Treatment objectives were to maintain foliage in fertilized treatments at optimum nutrition (foliar [N] of 1.3% with other macronutrient concentrations held in balance) and soil in the irrigated treatments at a minimum of 40% available soil water content. Nutrient treatments began in March 1992 and irrigation began in April 1993. Through 1994, 419 kg ha^{-1} N, 106 kg ha^{-1} P, 225 kg ha^{-1} K, 135 kg ha^{-1} Ca, 112 kg ha^{-1} Mg, 107 kg ha^{-1} and 1.5 kg ha^{-1} B were added to the fertilized treatments (T. Albaugh, North Carolina State University, personal communication). Irrigation was suspended during the dormant season (approximately late November–February). Albaugh et al. (1998) provides a detailed description of treatment objectives, application, monitoring and efficacy. All non-pine vegetation was controlled with a combination of chemical (glyphosate) and mechanical methods. In December 1994, stand density was 1161 trees ha^{-1}. Mean tree height, diameter at breast height (1.3 m) and height to live crown in the control stand were: 9.2 m, 5.6 cm and 1.2 m, respectively. The corresponding values for the irrigated stand were: 9.4 m, 5.7 cm and 1.3 m, respectively; those for the fertilized stand were: 11.6 m, 6.3 cm and 1.2 m, respectively; and those for the fertilized and irrigated stand were: 12.2 m, 6.6 cm and 1.3 m, respectively (Albaugh et al. 1998).

Measurements

Beginning in January 1994, stem CO_2 efflux measurements were made monthly with an automated, multi-chambered sampling system and an infrared gas analyzer (LI-6262, Li-

Cor, Inc., Lincoln, NE) as described by Maier et al. (1998). Briefly, the system had an open flow-through design, where CO_2 efflux was measured as the difference between CO_2 concentration entering and exiting the chamber. Respiration chambers were constructed of PVC pipe and completely enclosed a segment of the tree stem near 1.3 m above ground. Chamber volume ranged from 0.00746 to 0.0117 m^3 depending on stem diameter (7.0 to 12.8 cm). Airflow rates through the chamber ranged from 1.5 to 3.0 l min^{-1}. Sixteen chambers were sampled sequentially at an hourly time-step. Twenty-four-gauge wire copper-constantan thermocouples measured chamber air and stem temperatures (5 mm below bark).

Three (control plots) or four (irrigated, fertilized and irrigated + fertilized plots) trees in each treatment plot were selected for respiration measurements (45 trees total); only three of the experimental blocks were used in the study (Maier et al. 1998). The same trees were sampled throughout the study. Each block was measured on a separate day. Measurements normally began between 0700 and 0900 h and ran continuously for 17 to 23 h. Each block-plot was measured once a month.

Diameter measurements were made every 2 weeks during the growing season and monthly during the winter with dendrometer bands positioned above and below the respiration chamber. Stem surface area was calculated from stem diameter and included bark. In young loblolly pine, nearly all the wood is sapwood (Schultz 1997); therefore, sapwood volume and dry mass estimates were based on inside-bark diameters. Sapwood density was calculated from a relationship between stem mass and sapwood volume developed from 16 trees harvested in January 1993 (sapwood density = 0.49 g cm^{-3}).

Tissue [N] and carbon concentration ([C]) were measured monthly on five trees per treatment plot and averaged. An increment hammer was used to sample the outer 2 cm of sapwood (minus bark) near 1.3-m stem height in a spiral around the stem. Tissue was dried at 60 °C and ground in a Wiley Mill to pass a 0.2-mm mesh screen. Tissue [N] was measured with a Carlo-Erba elemental analyzer (Model NA 1500, Fisons Instruments, Danvers, MA). Tissue N and carbon (C) content in the sapwood covered by the respiration chamber was calculated as [N] or [C] × sapwood dry mass.

Analysis of seasonal and annual responses

Annual means for the physical characteristics of stem segments within the respiration chamber (diameter, surface area, sapwood volume, sapwood dry mass and [N]) and instantaneous stem respiration rates were calculated from the monthly observations. Instantaneous stem respiration was expressed as a function of surface area ($R_{t,a}$, μmol CO_2 m^{-2} s^{-1}), sapwood volume ($R_{t,v}$, μmol CO_2 m^{-3} s^{-1}), sapwood dry mass ($R_{t,w}$, nmol CO_2 g^{-1} s^{-1}) or sapwood N content ($R_{t,n}$, μmol CO_2 (mol $N)^{-1}$ s^{-1}).

For each sample period, respiration at 20 °C (R_{20}), the temperature coefficient (k) and daily respiration rate were calculated for each tree. Values of R_{20} and k were estimated as:

$$R_{t,a} = R_{20} e^{[k(T-20)]}, \quad (2)$$

where $R_{t,a}$ is stem respiration rate per unit stem area (μmol CO_2 m^{-2} s^{-1}), R_{20} is stem respiration rate at 20 °C, k is the temperature coefficient ($Q_{10} = e^{(k10)}$), and T is stem temperature. Nonlinear regression was used to estimate parameters in Equation 2. The diurnal response of stem respiration to temperature typically exhibited a hysteresis with $R_{t,a}$ having a higher rate at night than during the day at a similar stem temperature (Ryan et al. 1995). To account for this hysteresis, $R_{t,a}$ was matched with stem temperature measured from 0 to 4 h earlier. The appropriate lag time for each tree was determined from the best fit to Equation 2.

Monthly values of k were used to normalize measured $R_{t,a}$ to 20 °C. Daily stem respiration rate (R_d, either as mol CO_2 m^{-2} day^{-1}, mol CO_2 m^{-3} day^{-1} or mol CO_2 kg^{-1} day^{-1}) was calculated by summing hourly diurnal measurements assuming hourly measurements reflected mean stem respiration rate during that period.

Statistical analysis was based on a randomized block design using treatment plot means, i.e., the average of the three or four trees in each plot. Analysis of variance was used to test for treatment effects on annual observations for stem physical characteristics, $R_{t,a}$, $R_{t,v}$, $R_{t,m}$ and $R_{t,n}$ and monthly observations of R_{20}, k, stem [N], stem growth and stem respiration. Mean separation of treatment effects was performed with Tukey's studentized range test. All significance levels were at the $\alpha < 0.05$ (two-tailed) unless otherwise indicated. Regression procedures were used to examine the relationship between temperature-normalized $R_{t,a}$ and growth and sapwood N content.

Partitioning stem respiration into maintenance and growth components

The mature tissue method was used to partition stem respiration into maintenance and growth components. This method assumes that stem CO_2 efflux during the winter, when stem diameter growth was negligible, represents maintenance respiration. In this study, maintenance respiration (R_m) was estimated from measurements made for periods with no observed diameter growth (January and December). Stem CO_2 efflux from stem segments within the respiration chamber was modeled as a function of temperature and N content as described by Maier et al. (1998):

$$R_{m,f} = (b_0 + b_1 N) e^{(kT)}, \quad (3)$$

where subscript f denotes CO_2 efflux rate (μmol CO_2 s^{-1}) of the stem segment within the chamber and N is sapwood N content (moles), calculated as the product of sapwood biomass within the respiration chamber and mean plot stem [N]. Parameter k is the temperature coefficient as in Equation 2 and T is stem temperature lagged 2 h. Because [N] was available only at the treatment plot level, treatment plot means (mean of the three or four measured trees) for $R_{m,f}$ were used to fit Equation 3. Equation 3 was solved by nonlinear regression proce-

dures. Model fit statistics for accuracy and precision were performed as outlined by Buford (1991).

Maintenance respiration rate during the rest of the year (February–November) was estimated from Equation 3 using monthly measurements of stem temperature and N content (based on stem dry mass corrected for diameter growth). Growth respiration rate ($R_{g,f}$, μmol CO_2 s^{-1}) for each measurement period was estimated as the difference between measured stem CO_2 efflux rate ($R_{t,f}$, μmol CO_2 s^{-1}) and calculated $R_{m,f}$. Linear regression was used to estimate the growth respiration coefficient (r_g), the slope of the relationship between $R_{g,f}$ and stem growth rate. For this analysis, monthly estimates of $R_{g,f}$ for each treatment plot was regressed against stem diameter growth for that period. Analysis of covariance test for heterogeneity of slopes was used to test for treatment differences in r_g.

Annual respiration estimates and stem carbon-use efficiency

Annual carbon use in growth and respiration was estimated for stem tissue enclosed within the respiration chambers. Daily stem growth rate and R_d (dry mass basis) were estimated as the linearly interpolated value between measured rates. Daily growth respiration was the product of r_g and stem growth rate. Daily stem maintenance respiration was estimated with Equation 3 and daily mean temperature and stem sapwood N content. Continuous measurement of plot stem temperature was part of the site environmental monitoring. Daily values were summed to obtain annual stem growth rate (G), total stem (R_T), growth (R_G) and maintenance (R_M) respiration rates. Values of G, R_T, R_G and R_M were expressed in mol C $chamber^{-1}$ $year^{-1}$. The fraction of carbon used in stem metabolism that was incorporated into new stem structure, i.e., stem carbon-use efficiency (CUE), was estimated as the ratio of carbon contained in new stem growth to total carbon used for growth plus respiration ($CUE = G/(G + R_T)$) (Ryan et al. 1995, 1996).

Results

Annual and seasonal responses

Three years of fertilization significantly increased stem diameter compared with control trees. Because of increased diameter, fertilized trees (fertilized and fertilized + irrigated treatments) had 14% more respiring surface area and 27% more sapwood volume and biomass than unfertilized trees (control and irrigated treatments) (Table 1). Stem diameter growth in 1994 was 11.7 and 20.1 mm in unfertilized and fertilized trees, respectively. Fertilization also significantly increased stem [N]. Mean stem [N] in fertilized trees for the year was 1.45 mg g^{-1} compared with 0.90 mg g^{-1} in unfertilized trees. The fertilization-induced increases in stem diameter and [N] were paralleled by enhanced stem respiration rates. Stem respiration rates expressed per unit stem area ($R_{t,a}$), per unit sapwood volume ($R_{t,v}$) or dry mass ($R_{t,w}$) were significantly higher (36–49%) in fertilized trees than in unfertilized trees (Table 1); however, there was no significant difference between unfertilized and fertilized trees in R_t expressed on a per unit N basis ($R_{t,n}$). Irrigation had no significant effect on stem physical characteristics or respiration rates. Therefore, data were combined across irrigation treatments in all subsequent analyses.

Stem cambium temperature ranged from 3 °C in January to about 25 °C in June, July and August (Figure 1a). There were no significant differences in stem temperature between treatments. Stem [N] was always greater in fertilized trees than in unfertilized trees and winter [N] was 30–35% greater than summer [N] (Figure 1b). Stem [N] reflected concentrations in the outer 2 cm of sapwood and probably overestimated total stem [N] by 10–20% (author's unpublished data). There was no treatment effect on sapwood [C], which ranged from 46 to 52% (48.7 ± 0.21 SE). Stem diameter growth (mm day^{-1}) had a seasonal bimodal pattern with high growth rates in midspring and again during the summer (Figure 1c). In unfertilized trees, maximum growth rate occurred in April with a smaller peak in July, whereas in fertilized trees, growth rates were similar in April, July and August. Stem growth rates were significantly greater in fertilized trees than in unfertilized trees from April through October.

Respiration per unit stem surface area ($R_{t,a}$) increased predictably with temperature (Table 2), although occasionally because of either low stem temperatures (< 4 °C) or a small range in diurnal temperatures (< 10 °C), $R_{t,a}$ was not significantly correlated with stem temperature ($P > 0.05$). The temperature dependence of $R_{t,a}$ varied seasonally; being less sensitive to temperature during summer than at other times of the year. The temperature coefficient (k) varied from 0.02 in July to 0.09 in February, with an annual mean of 0.053. There were no treatment differences in k except in the fall (September–November) when k was higher in fertilized trees than in unfertilized trees. Values of R_{20} were always significantly greater in fertilized trees than in unfertilized trees except in January (Table 2). The $R_{t,a}$ normalized to 20 °C increased rapidly in late winter and early spring to an annual maximum in April in unfertilized and fertilized trees (Figure 1d). In unfertilized trees, normalized $R_{t,a}$ declined by 50% from April to June and remained stable until late fall, then declined further to an annual low in December. A similar decline in normalized $R_{t,a}$ in late spring occurred in fertilized trees, but $R_{t,a}$ increased again in the summer and remained relatively high until late fall. The seasonal pattern of normalized $R_{t,a}$ was related to seasonal changes in stem growth and stem [N]. Stem growth rate and stem [N] explained 51 and 24%, respectively, of the seasonal variation in $R_{t,a}$. The observed seasonal patterns for $R_{t,a}$, R_{20} and k were similar when analyzed on a per unit sapwood volume or mass basis.

Daily stem respiration per unit area (R_d) had a similar seasonal bimodal pattern as stem growth rate in both fertilized and unfertilized trees (Figure 1e). In the fertilized stands, peak R_d in April and August coincided with increases in stem growth rate. In unfertilized stands, a similar peak in R_d and stem growth occurred in April, but the increase in R_d in August lagged behind stem growth. Peak R_d during the growing season was seven to eight times greater than winter R_d (December), and R_d was significantly greater in fertilized trees than in unfertilized trees ($P < 0.10$) in every month except January.

Table 1. Physical characteristics of stem tissue within respiration chambers and total stem respiration rates normalized to 20 °C[1] expressed per unit surface area ($R_{t,a}$), volume ($R_{t,v}$), mass ($R_{t,w}$) and mole nitrogen ($R_{t,n}$) in 10-year-old loblolly pine trees. Values are annual means calculated from monthly observations except for stem growth, which is the mean annual diameter growth. The standard error of the mean is in parentheses.

Treatment	Stem diameter (cm)	Stem growth (cm)	Surface area (cm^2)	Sapwood volume (cm^3)	Sapwood biomass (g)	N ($g\ kg^{-1}$)	$R_{t,a}$[2]	$R_{t,v}$[2]	$R_{t,w}$[2]	$R_{t,n}$[2]
Control	9.35	1.04	643	1023	501	0.90	1.62	102.4	0.21	3.16
	(0.13)	(0.03)	(89)	(31)	(15)	(0.03)	(0.14)	(8.8)	(0.02)	(0.28)
Irrigated	9.82	1.29	665	1112	545	0.90	1.88	114.6	0.23	3.54
	(0.29)	(0.08)	(11)	(40)	(19)	(0.03)	(0.15)	(9.2)	(0.02)	(0.29)
Fertilized	11.29	1.91	739	1400	686	1.40	3.26	173.1	0.35	3.57
	(0.26)	(0.08)	(16)	(64)	(31)	(0.04)	(0.24)	(12.7)	(0.03)	(0.27)
Irr. + Fert.	11.98	2.10	781	1570	769	1.50	3.59	179.5	0.37	3.43
	(0.21)	(0.08)	(18)	(76)	(37)	(0.04)	(0.25)	(12.8)	(0.03)	(0.23)

[1] Respiration values were normalized to 20 °C based on $Q_{10} = 1.7$.
[2] Units: $R_{t,a}$ = μmol CO_2 m^{-2} s^{-1}; $R_{t,v}$ = μmol CO_2 $m^{-3}_{sapwood}$ s^{-1}; $R_{t,w}$ = nmol CO_2 $g_{dw}^{-1}{}_{sapwood}$ s^{-1}; and $R_{t,n}$ = μmol CO_2 $(mol\ N_{sapwood})^{-1}$ s^{-1}.

Maintenance respiration

Stem maintenance respiration rate per unit volume of sapwood ($R_{m,v}$) was correlated with stem N content (N content = sapwood dry mass × [N]) (Figure 2). However, $R_{m,v}$ per unit N was greater in January before the initiation of stem diameter growth than in December after stem diameter growth had ceased. Because the relationship between $R_{t,v}$ and N content varied, Equation 3 was parameterized separately for the January and December data:

$$R_{m,\text{f-Jan}} = (-0.000109 + 0.59N)e^{(0.069T)}, \quad (4)$$

for January, and

$$R_{m,\text{f-Dec}} = (0.000071 + 0.27N)e^{(0.079T)}, \quad (5)$$

for December. Predictions based on the above models showed good agreement with observed values (Table 3). The percent absolute deviation (%AD) between modeled and observed data, a measure of model accuracy, was less than 20% and the percent root mean square error (%RMSE) between modeled and measured $R_{m,f}$, a measure of precision, was less than 3% of the mean flux.

The seasonal pattern of $R_{m,f}$, estimated from seasonal changes in stem cambium temperature and sapwood N content, and measured stem efflux ($R_{t,f}$) is shown in Figure 3. Equation 3 parameterized with January data ($R_{m,f\text{-Jan}}$) predicted 20 to 70% more maintenance respiration than did the December data ($R_{m,f\text{-Dec}}$). During the period of observed diameter growth (March–November), $R_{m,f\text{-Jan}}$ accounted for 20 to 90% of $R_{t,f}$. In contrast, $R_{m,f\text{-Dec}}$ was always less than 50% of $R_{t,f}$ during the same period.

An assumption of the mature tissue method for estimating seasonal $R_{m,f}$ is that winter $R_{m,f}$ corrected for temperature and N content should be constant. The relationships shown in Figure 2 suggest that this is not the case for these stands. For example, $R_{m,f\text{-Dec}}$ predicted less $R_{m,f}$ than measured $R_{t,f}$ for the previous January (Figure 3). Thus, by subtraction, there was substantial growth respiration in January at a time of no dimensional growth. Conversely, $R_{m,f\text{-Jan}}$ predicted more maintenance respiration than was measured in December. The difference in maintenance respiration between January and the following December may be associated with the relatively large change in sapwood volume (diameter growth between January and December increased sapwood volume within the chambers by 20 to 65%). A chamber by chamber comparison of $R_{t,v}$ normalized to 20 °C between January and the following December showed that $R_{t,v}$ measured in December was always lower, by 48% on average, than $R_{t,v}$ measured in the previous January (Figure 4a). The difference in $R_{t,v}$ between January and December was correlated with the difference in volume growth over the same period (Figure 4b).

Growth respiration

Growth respiration ($R_{g,f}$) for each measurement period was calculated as the difference between measured $R_{t,f}$ and predicted $R_{m,f\text{-Jan}}$ or as the difference between $R_{t,f}$ and predicted $R_{m,f\text{-Dec}}$. There was a significant correlation between $R_{g,f}$ and stem growth rate (Figure 5). Lagging $R_{g,f}$ and stem growth by one month did not improve the correlation. The growth respiration coefficient (r_g) was 0.21 based on $R_{m,f\text{-Jan}}$ (Figure 5a) and 0.27 based on $R_{m,f\text{-Dec}}$ (Figure 5b). In neither case was there a significant fertilizer treatment effect on r_g. Data shown in Figure 5 were combined to test if r_g differed depending on whether $R_{m,f}$ was estimated from $R_{m,f\text{-Jan}}$ or $R_{m,f\text{-Dec}}$. In this case, there was no significant interaction between growth rate and measurement period ($P = 0.40$); overall, r_g was 0.24 ($r^2 = 0.55$). However, the intercept was significantly greater than zero ($P = 0.049$) when the December data were used to estimate $R_{m,f}$.

Stand-level stem respiration costs and stem carbon-use efficiency

Annual stem maintenance respiration (R_M) was estimated sep-

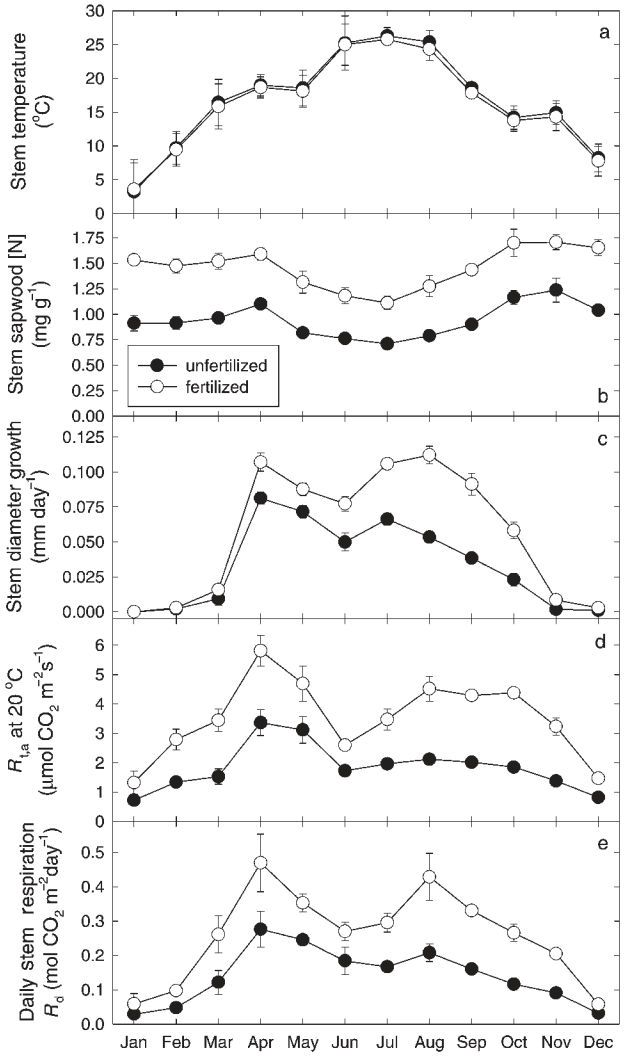

Figure 1. Seasonal trends in (a) stem temperature measured at 5-mm depth, (b) stem sapwood nitrogen concentration, (c) stem growth rate, (d) instantaneous total stem respiration normalized to 20 °C, and (e) daily stem respiration (R_d) in unfertilized and fertilized loblolly pine trees. Values are means (± 1 SE) of $n = 3$ observations.

arately based on the January and December equations (Equation 3). Maintenance respiration based on the January equation yielded R_M values that were 44% higher than those derived from the December measurements (Table 4). Based on the January equation, the sum of R_M and R_G was 3.62 and 7.61 mol C chamber^{-1} year^{-1} for unfertilized and fertilized trees, respectively. These values are within 9% of integrated total R_T. In contrast, based on the December equation, $R_M + R_G$ underestimated R_T by 20% in both treatments.

Annual stem growth rate (G) was 5.98 and 12.02 mol C chamber^{-1} in the unfertilized and fertilized stands, respectively (Table 4). Annual stem respiration (R_T), calculated from integrated measured daily rates, was 3.32 and 7.13 mol C chamber^{-1} in the unfertilized and fertilized stands, respectively. Fertilization had no effect on stem carbon-use efficiency (CUE), which averaged 0.63.

Table 2. Temperature responses of stem respiration per unit stem area ($R_{t,a}$) in unfertilized (UF) and fertilized (F) loblolly pine trees (Equation 2). Abbreviations: R_{20} is stem respiration (µmol m^{-2} s^{-1}) at 20 °C; k is the temperature coefficient ($Q_{10} = e^{(k10)}$); and n is number of trees. Values within a month and column followed by a different letter are significantly different at $\alpha = 0.05$.

Month	Treatment	R_{20}	k	n
Jan	UF	0.82 a	0.052 a	8
	F	2.01 a	0.048 a	7
Feb	UF	1.39 a	0.085 a	21
	F	2.65 b	0.091 a	23
Mar	UF	1.44 a	0.045 a	18
	F	3.53 b	0.046 a	23
Apr	UF	3.37 a	0.061 a	21
	F	5.78 b	0.059 a	24
May	UF	2.89 a	0.057 a	19
	F	4.37 b	0.065 a	22
Jun	UF	1.80 a	0.034 a	12
	F	2.53 b	0.040 a	11
Jul	UF	1.72 a	0.019 a	16
	F	3.34 b	0.022 a	19
Aug	UF	2.04 a	0.022 a	15
	F	4.53 b	0.029 a	19
Sep	UF	1.99 a	0.044 a	21
	F	4.20 b	0.051 b	24
Oct	UF	1.86 a	0.057 a	21
	F	4.52 b	0.064 b	24
Nov	UF	1.39 a	0.051 a	21
	F	3.39 b	0.059 b	24
Dec	UF	0.75 a	0.065 a	21
	F	1.49 b	0.072 a	24

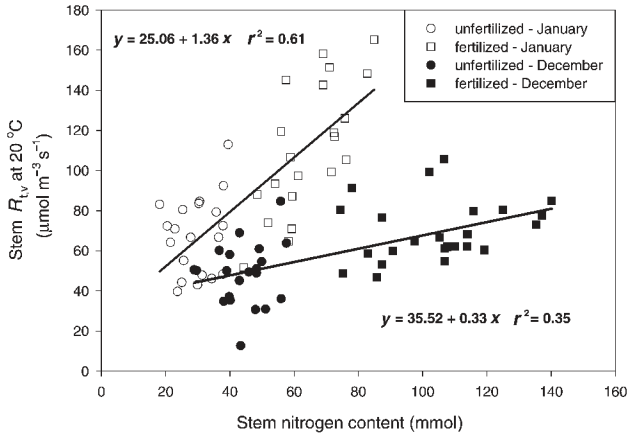

Figure 2. Relationships between stem respiration per unit sapwood volume ($R_{t,v}$) and sapwood N content ([N] × sapwood dry mass) of tissue within the respiration chamber measured in January before the initiation of stem diameter growth and in December after diameter growth had ceased. Each value is an individual tree observation.

Table 3. Fit statistics for winter maintenance respiration equations (Equation 3) based on January and December stem respiration measurements.

	Mean $R_{m,f}$	Minimum $R_{m,f}$	Maximum $R_{m,f}$	r[1]	%RMSE[2]	%AD[3]	n[4]
January							
Model	0.047	0.015	0.135	0.98	2.3	17.1	168
Observed	0.046	0.013	0.130				
December							
Model	0.041	0.011	0.094	0.95	1.6	13.8	252
Observed	0.041	0.012	0.104				

[1] Correlation coefficient between predicted and observed values.

[2] Percent root mean square error (%RMSE); $\%\mathrm{RMSE} = \left(\frac{100}{n} \sum_{i=1}^{n} \left(\frac{\hat{y}_i - y_i}{y_i} \right)^2 \right)^{\frac{1}{2}}$.

[3] Percent absolute deviation (%AD); $\%\mathrm{AD} = \frac{100}{n} \sum_{i=1}^{n} \left| \frac{\hat{y}_i - y_i}{y_i} \right|$.

[4] The value of n is the number of observations (treatment plot mean).

Discussion

Seasonal respiration

Stem respiration rates measured in this study were comparable with those reported for other conifers across wide ranges of age classes and environments (Ryan 1990, Ryan et al. 1994, Sprugel et al. 1995, Lavigne and Ryan 1997, Stockfors and Linder 1998*a*, Vose and Ryan 2001). Daily respiration (R_d) varied seasonally in a bimodal pattern with the highest rates measured in April and again in August with a significant decline during late spring and early summer. Although much of the seasonal variation in R_d was caused by changes in stem temperature, the rapid increase and then decline in R_d during the growing season was associated with changes in stem diameter growth and possibly [N]. Increases in R_d coincided with increases in stem diameter growth except for control stands in August, when the increase in R_d occurred after maximum growth measured in July. Edwards and Hanson (1996) and Stockfors and Linder (1998*a*) reported that stem respiration occurred 10 to 40 days after peak diameter growth rate in several tree species most likely because wood synthesis occurs after cell expansion (Sprugel and Benecke 1991). In this study, averaging stem growth over 15- to 20-day periods may have masked any lag between R_d and stem growth.

The decline in stem [N] during the early growing season coincided with reductions in stem growth and respiration. Stem growth rate and [N] explained 51 and 24%, respectively, of the seasonal variation in temperature-corrected $R_{t,a}$. Because of the importance of N in growth and maintenance processes of living tissues (Amthor 1989), temporal variations in tissue [N] may have influenced the seasonal pattern of stem respiration independently of temperature.

Partitioning total respiration into maintenance and growth components

A critical assumption of the mature tissue method is that R_m measured when growth is absent represents R_m during active growth varying only with changes in temperature (Sprugel and Benecke 1991). That is, respiration rates should be similar before and after the growing season (correcting for temperature and changes in sapwood volume or N content). In these stands, at a given temperature, $R_{t,v}$ (and $R_{t,n}$) measured in January before the initiation of diameter growth was much larger than in December after diameter growth had ceased. Consequently, annual R_M derived from $R_{m,f\text{-}Jan}$ predicted 44% more R_M than $R_{m,f\text{-}Dec}$. A within-tree comparison showed that temperature-normalized $R_{t,v}$ measured in December was 48% lower than in the previous January, indicating that R_m per unit sapwood volume (or N content) declined as stem diameter increased (i.e., $R_{t,v}$ was inversely related to sapwood volume). Ryan et al. (1994) and Sprugel et al. (1995) suggested that R_m per unit sapwood volume should be relatively constant for similar types of tissue within a stand and advocated use of sapwood volume as a basis for extrapolating chamber measurements to the stand-level. Numerous studies in both plantations and natural mixed-age forests, where within-stand stem diameters varied tenfold, have found that temperature-corrected R_m per unit sapwood volume is relatively constant (Ryan 1990, Sprugel 1990, Ryan and Waring 1992, Ryan et al. 1995, 1996, Law et al. 1999). However, in other studies, stem respiration rates expressed on a volume or area basis were dependent on stem diameter (Yoda et al. 1965, Rakonczay 1997, Levy and Jarvis 1998). Lavigne et al. (1996) and Lavigne and Ryan (1997) reported a negative relationship between R_m per unit sapwood volume and the ratio of stem sapwood volume to surface area (V/A) for three boreal tree species. This is probably because stem sapwood CO_2 efflux is a combination of respiration of the physiologically active, but relatively thin layer of newly formed phloem and xylem tissue (correlated with surface area), and the less physiologically active ray parenchyma in the xylem (correlated with sapwood volume). As stems grow, the ratio of the amount of less physiologically active sapwood tissue to the more active phloem increases (Kramer

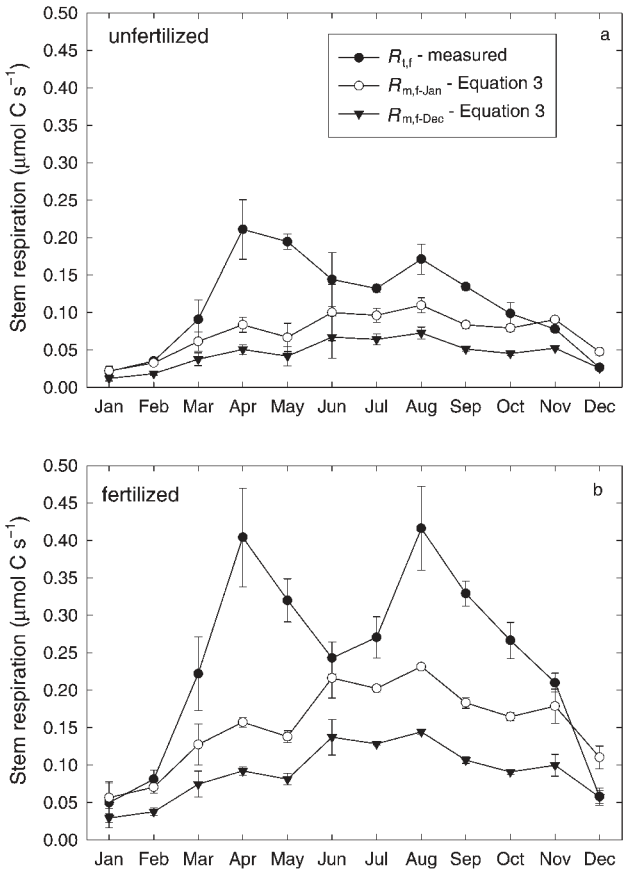

Figure 3. Seasonal trends in measured stem CO_2 efflux ($R_{t,f}$) and predicted maintenance CO_2 efflux ($R_{m,f}$) in (a) unfertilized and (b) fertilized stands. Maintenance CO_2 efflux was calculated with Equation 3 parameterized with either January ($R_{m,f\text{-}Jan}$) or December ($R_{m,f\text{-}Dec}$) measurements. Values are means (± 1 SE) of $n = 3$ observations.

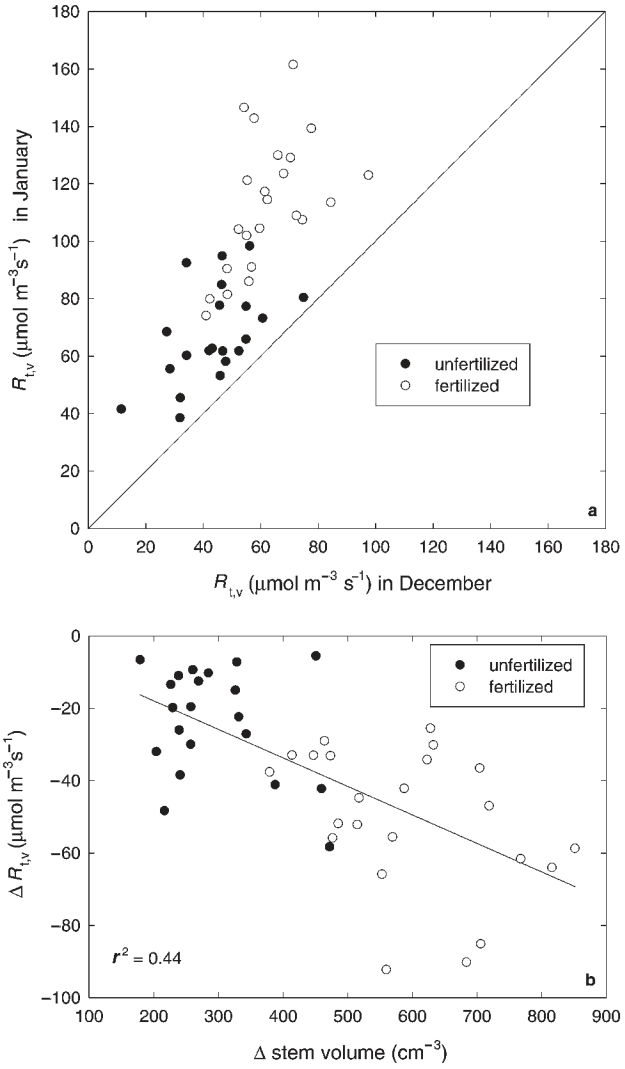

Figure 4. (a) Relationships between stem respiration per unit sapwood volume ($R_{t,v}$) normalized to 20 °C measured in January versus that measured in December, (b) the difference between $R_{t,v}$ measured in December and January versus the change in stem sapwood volume. Each value represents an individual tree.

and Kozlowski 1979) and R_m per unit sapwood volume should decline.

On the other hand, differences in $R_{t,v}$ may be an artifact from inadequately defining sapwood volume because some wood was heartwood (metabolically inactive) or not all sapwood was functional. If sapwood volume and consequently N content is overestimated in December then the base by which stem CO_2 efflux is divided is too large and $R_{m,f\text{-}Dec}$ underestimates R_m for all other months. Although loblolly pine typically does not develop heartwood until Age 17 to 25 (Schultz 1997), and there was no visible heartwood development in these stands (Mann 1999), it cannot be stated with confidence that all the wood was functioning sapwood. However, the stands did not have closed canopies, and leaf area index (LAI) and sapwood cross-sectional area and volume (within the chambers) at the base of the live crowns were still increasing. In addition, the ratio of canopy leaf area (LA, m^2 ha^{-1}) and basal area (BA, cm^2 ha^{-1}) were similar in January and December (LA/BA = 0.1) (T. Albaugh, personal communication) indicating that most of the wood was probably functional sapwood. These results suggest that caution is necessary when comparing volume (or N) based R_m in dissimilar stands (Lavigne et al. 1996) and within fast-growing stands where large changes in stem sapwood volume occur over a relatively short period of time (< 1 year).

Winter R_m expressed as a function of stem size ($R_{t,v}$, $R_{t,a}$ or $R_{t,m}$) increased with increased tissue N content, but R_t per mole N ($R_{t,n}$) was relatively constant (Maier et al. 1998). The relationship between stem R_m and N varies for other species. Stem $R_{t,v}$ (live cell volume) was unrelated to [N] in *P. abies* (Stockfors and Linder 1998) and Lavigne and Ryan (1997) observed no significant relationship between $R_{t,v}$ and [N] in several boreal species. However, Vose and Ryan (2001) found that $R_{t,m}$ increased with [N] in *P. strobus*. A correlation between R_m and [N] or N content has been reported for both fine roots (Ryan et al. 1996, Zogg et al. 1996, Vose and Ryan 2001) and foliage (Ryan 1995, Ryan et al. 1996, Stockfors and Linder 1998*a*, Vose and Ryan 2001). If cellular [N] is indicative of protein

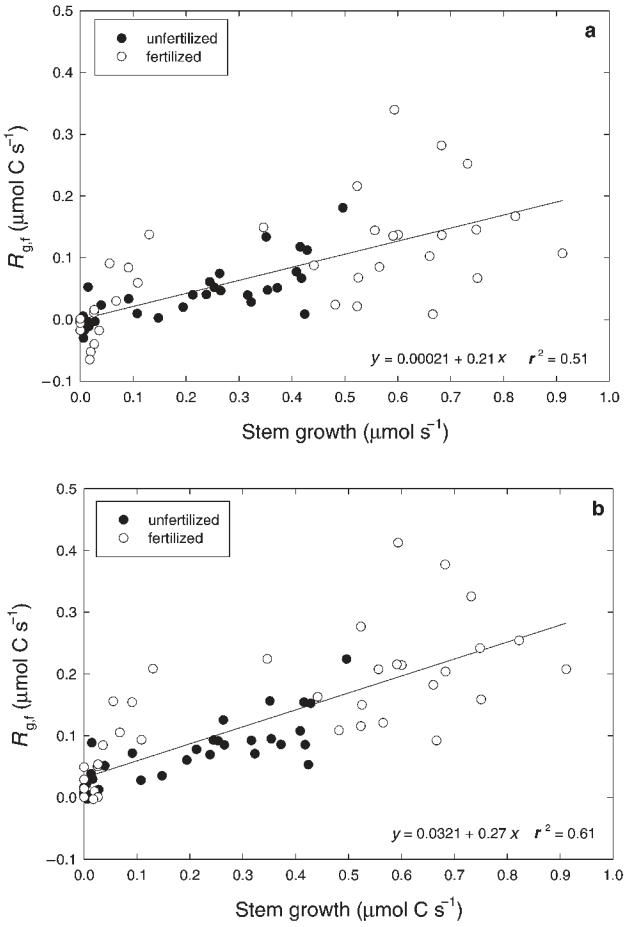

Figure 5. Relationships between growth respiration ($R_{g,f}$) calculated as the difference between measured ($R_{t,f}$) and predicted maintenance ($R_{m,f}$) respiration, and stem growth rate. The slope defines the growth respiration coefficient (r_g). In (a) $R_{g,f}$ is the difference between $R_{t,f}$ and $R_{m,f\text{-}Jan}$ and in (b) $R_{g,f}$ is the difference between $R_{t,f}$ and $R_{m,f\text{-}Dec}$. Each value represents a treatment plot mean.

content (Penning de Vries 1975*a*) and protein metabolism consumes the largest portion of R_m in woody tissues (Amthor 1994), then seasonal changes in [N] may result in significant changes in maintenance respiration rate. For example, sapwood [N] varied by 35% seasonally with a significant decline during the growing season. Because of this decline, particularly from May through August, N-based estimates of R_m were 26 to 37% less than a similar estimate base solely on sapwood volume.

A weakness of the mature tissue method that was not considered in this study is the potential acclimation of sapwood R_m to seasonal changes in temperature. Because respiration at any particular temperature may be linked to recent temperature history through acclimation, the short-term response of R_m to temperature measured in the winter may not reflect the actual temperature response of R_m during the summer (Amthor 1994). It is difficult to assess seasonal temperature acclimation of R_m because R_m and R_g occur simultaneously in growing stems. However, the relationship between $R_{t,a}$ and temperature varied seasonally with lower k values during the growing season than during the winter. Stockfors and Linder (1998*b*) also observed a seasonal shift in the temperature dependence of respiration with a lower value for k during the summer; however, others have found no seasonal variation in k (Linder and Troeng 1981, Lavigne and Ryan 1997). Generally, plants grown at high temperatures have a lower specific respiration rate at a given temperature than plants grown at a low temperature (Jones 1986). For example, Teskey and Will (1999) measured 44% lower foliar respiration rates in loblolly pine seedlings grown at 35 °C than at 25 °C when both were measured at 35 °C. Acclimation of physiological processes to seasonal temperature changes is less clear, although seasonal shifts in the temperature response of photosynthesis and respiration do occur in field-grown trees (Strain et al. 1976, Paembonan et al. 1991). If temperature acclimation occurs, dormant season R_m equations would likely overestimate R_m for most of the growing season.

Stem growth respiration (R_g) was significantly correlated with stem growth rate. The growth coefficient ($r_g = 0.24$) was comparable with that reported in other studies that used the mature tissue approach to estimate R_m. Sprugel et al. (1995) gave values for woody tissue r_g between 0.25 and 0.42. Lavigne and Ryan (1997) reported a similar range for r_g (0.24 and 0.39) in young jack pine (*Pinus banksiana* Lamb.) trees, although Stockfors and Linder (1998) found that r_g was

Table 4. Annual estimates of carbon used for stem growth and respiration, and stem carbon-use efficiency (CUE = $G/(G + R_T)$) for unfertilized and fertilized stands of 10-year-old loblolly pine. Annual stem growth (G, mol C chamber^{-1} year^{-1}) and total stem respiration rate (R_T, mol C chamber^{-1} year^{-1}) are the sum of estimated daily values. Annual stem maintenance respiration (R_M, mol C chamber^{-1} year^{-1}) was calculated from Equation 3 parameterized with either January or December respiration measurements. Annual growth respiration (R_G, mol C chamber^{-1} year^{-1}) is the product of the respiration coefficient (r_g; 0.24) and G. Values in parentheses are standard errors of the mean.

Treatment	G	R_G	January		December		R_T	CUE
			R_M	$R_M + R_G$	R_M	$R_M + R_G$		
Unfertilized	5.98 (0.43)	1.43 (0.10)	2.19 (0.09)	3.62	1.23 (0.05)	2.66	3.32 (0.23)	0.64
Fertilized	12.02 (0.60)	2.89 (0.14)	4.72 (0.33)	7.61	2.64 (0.19)	5.53	7.13 (0.28)	0.63

lower in *P. abies* (0.11 to 0.20). Penning de Vries (1975*b*) calculated a theoretical value of 0.21 for generic wood. However, other theoretical estimates were lower: 0.17 for ponderosa pine (*Pinus ponderosa* Laws.; Carey et al. 1996), 0.15 for slash pine (*Pinus elliotti* Engelm.; Chung and Barnes 1977), and 0.12 for loblolly pine seedlings (Griffin 1994). Sprugel et al. (1995) suggested that theoretical estimates are generally lower than measurement-based estimates because they do not include energy costs associated with phloem transport.

The increase in R_g in fertilized trees was a result of increased stem growth rather than increased cost of tissue production (i.e., r_g). A shift in r_g in the fertilized trees would only occur if the substrate or products or both of respiration or biosynthesis changed (Amthor 2000). Griffin et al. (1993) estimated an increase in needle construction cost with increased [N] in loblolly pine seedlings. However, for the stands in this study, Warren et al. (1999) found that stems of fertilized trees had 10–20% more phenolics and proanthocyanidins than stems of unfertilized trees. Increased concentrations of secondary compounds and proteins might increase r_g, depending on the balance of other changes in composition. It may be that the regression approach used in this study lacked the sensitivity to detect small changes in r_g.

Stem carbon-use efficiency

Total carbon used for stem growth plus respiration in fertilized stands was 19.2 mol C chamber^{-1} year^{-1}, more than twice that in unfertilized stands (9.3 mol C chamber^{-1} year^{-1}). Despite this large difference, there was no treatment difference in CUE, presumably because fertilization had no effect on r_g. Stem CUE (0.63) was higher than that reported for three boreal tree species (0.37 to 0.59 Lavigne and Ryan 1997), but was similar to that reported by Ryan et al. (1996) for 20-year-old *P. radiata* stands (0.66). According to Ryan et al. (1996), improved nutrition also did not change stem CUE.

Conclusions

Fertilization of these mid-rotation loblolly pine stands increased stem growth rate and stem respiration per unit surface area, sapwood volume or sapwood mass, but had no effect on stem respiration expressed as a function of tissue N content. Stem growth rate explained most of the seasonal variation in temperature-normalized stem respiration rate, although seasonal changes in stem [N] were also significant.

The functional model of respiration is currently the best approach for understanding stand-level respiration dynamics and for extrapolating small-scale, periodic chamber measurements to annual, stand-level estimates of respiration. The success of this approach requires accurate estimates of growth and maintenance respiration and their associated coefficients. Increased tissue N content had no effect on the growth coefficient (r_g) in these trees; therefore, changes in R_g were strictly a function of changes in growth. On the other hand, R_m was responsive to environmental and physiological factors and therefore was spatially and temporally variable. Winter $R_{t,v}$ was significantly correlated with tissue N content. Because N content varied seasonally, expressing R_m as a function of N content may better reflect the actual maintenance costs. There was evidence that R_m declined over the course of the study, which may be attributed to an increase in sapwood volume to area ratio. If this trend is general, it limits the ability to predict respiration of stands that differ in age or stem size using a single set of model parameter values. Annually, R_T consumed 37% of the carbon allocated to stems. Fertilization had no effect on CUE, thus an increase in tissue [N] does not appear to alter carbon partitioning between growth and respiration in stem tissue of 10-year-old loblolly pine.

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