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Effects of temperature and tissue nitrogen on dormant season stem and branch maintenance respiration in a young loblolly pine (*Pinus taeda*) plantation

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Summary We measured dormant season (November through February) maintenance respiration rates (R_m) in stems and branches of 9-year-old loblolly pine (*Pinus taeda* L.) growing in plots under conditions of controlled nutrient and water supply in an effort to determine the relationships between R_m and tissue size (surface area, sapwood volume, sapwood dry weight), tissue nitrogen content and temperature. Dormant season R_m per unit size (i.e., surface area, μmol m^{-2} s^{-1}; sapwood volume, μmol m^{-3} s^{-1}; or sapwood dry weight, nmol g^{-1} s^{-1}) varied with tissue size, but was constant with respect to tissue nitrogen content (μmol mol^{-1} N s^{-1}). Cambium temperature accounted for 61 and 77% of the variation in stem and branch respiration, respectively. The basal respiration rate (respiration at 0 °C) increased with tissue nitrogen content, however, the Q_{10} did not. Improved nutrition more than doubled stem basal respiration rate and increased branch basal respiration by 38%. Exponential equations were developed to model stem and branch respiration as a function of cambium temperature and tissue nitrogen content. We conclude that failure to account for tissue nitrogen effects on respiration rates will result in serious errors when estimating annual maintenance costs.

Keywords: carbon balance, productivity, temperature–nitrogen model of maintenance respiration, tissue nutrition, woody tissue.

Introduction

Net carbon gain of a tree or stand is a function of the rate of photosynthesis per unit area of foliage, the respiration rate of photosynthetic tissue, leaf area, and the surface area and respiration rates of woody tissue (Teskey et al. 1987). Environment may affect productivity by altering the balance between photosynthesis and respiration, because these processes respond differently to changes in temperature and soil nutrition. A substantial body of literature exists describing the photosynthetic characteristics of loblolly pine (see Teskey et al. 1987) and the relationship between tissue nutrition, leaf area and stemwood production (Vose and Allen 1988), but very little is known about the effects of woody tissue respiration on productivity and the impacts of nutrition on construction and maintenance costs in this species. Maintenance respiration (R_m) is important to the carbon balance of a forest stand because of its relationship to stand biomass and its sensitivity to environmental conditions. In southern pine ecosystems, R_m can account for 45 to 80% of the total carbon fixed (Kinerson et al. 1977, Waring and Schlesinger 1985, Cropper and Gholz 1993). Because R_m consumes a large portion of carbon in trees, accurate measurements of maintenance respiration from all parts of the forest stand are critical for constructing quantitative carbon budgets and for predicting carbon allocation patterns under different climate and nutrient regimes.

An issue of continuing debate is whether R_m is a function of tissue surface area, sapwood volume or weight (Ryan 1990, Sprugel and Benecke 1990). This is important because the base chosen will affect the interpretation of results. For example, Kinerson (1975) related respiration in loblolly pine stems to tissue surface area on the assumption that the most actively respiring tissue was located in the cambial sheath and the recently formed phloem and xylem tissues. In contrast, Sprugel et al. (1995) reviewed several studies relating R_m to tissue size and concluded that, in woody tissue, R_m is primarily a function of the amount of living tissue in the xylem and should be best correlated with sapwood volume or weight. Sprugel et al. (1995) also showed that respiration rates per unit volume are relatively constant across many coniferous species.

What is not well understood is how woody tissue R_m per unit size is affected by tissue nutrition. Brix (1971) reported that nitrogen fertilization increased dark respiration per unit surface area in new shoots of large Douglas-fir trees. Ryan (1991) showed that R_m in several plant tissues increased linearly with tissue nitrogen concentration ranging from 0.04 to 0.6% of tissue dry weight. Most of the nitrogen in plant tissue is in protein and it is thought that the close relationship between R_m and nitrogen is due to increases in protein content (Amthor 1994) or protein turnover rates (Penning de Vries 1975). If R_m per unit size varies with tissue nutrition, then serious errors may result when estimating R_m of stands growing under differ-

ent nutrient regimes. If this is so, then some other method of estimating stand R_m is needed. Ryan and Waring (1992) proposed a nitrogen-based model where R_m is estimated from temperature and tissue nitrogen content. Nitrogen is an integral element for many physiological processes and a nitrogen-based model would link R_m directly to photosynthesis, carbon allocation, fine root turnover and decomposition (Ryan et al. 1995).

We measured maintenance respiration rates of stem and branch tissue of 9-year-old loblolly pine trees. Stand-level soil nutrient and water manipulations produced a wide range of resource availabilities across the study site, providing an opportunity to examine the effects of tissue nitrogen on R_m. Respiration was measured during the dormant season (November through February) to eliminate the confounding effects of growth. The objectives of this study were: (1) to determine the effects of altered nutrition on dormant season R_m in stem and branch tissue; and (2) to develop a model to predict stem and branch R_m from tissue temperature and tissue nitrogen content.

Materials and methods

Site description

The study site is a loblolly pine plantation at the Southeast Tree Research and Education Site (SETRES), 17 km north of Laurinburg, NC (34°48′ N, 79°12′ W). SETRES is a long-term productivity study site where the effects of nutrition, water and elevated CO_2 on tree growth are being evaluated. The soil is classified as a Wakulla series, a sandy, silicious, thermic psammentic hapludult (USDA Soil Classification System), and is characterized as well drained and infertile. The climate is mild. The mean summer and winter temperatures are 26 and 9 °C, respectively. Mean annual rainfall is 1210 mm evenly distributed throughout the year. The stand consists of a mix of 10 improved North Carolina Piedmont loblolly pine families planted in 1985. In December 1994, the mean tree height was 6.04 m, mean dbh was 10.6 cm and stand density was 1161 trees per hectare.

The experimental design was a 2×2 factorial combination of fertilization (no addition and complete nutrition) and irrigation (no addition and well watered) treatments. Treatments were established on 0.25-ha plots and were replicated four times. Here the replicates are referred to as blocks. The objective of the fertilizer treatment was to maintain optimum foliar nutrition (Murthy et al. 1996). Fertilizer treatments were initiated in the winter of 1992 at age eight and irrigation treatments began in the spring of 1993. Irrigation was suspended during the winter months. Additionally, individual trees in each plot were exposed to differing CO_2 concentrations, but those trees were not used in this study.

Measurements

We estimated stem and branch respiration by measuring CO_2 flux from stem and branch tissue into respiration chambers. The chambers were constructed of PVC pipe that enclosed stem segments near breast height and branch segments at the base of a 2-year-old (1991) branch. The chambers were opaque and excluded all light from reaching the tissue. All chambers were 230 mm in length and varied in diameter (64 to 203 mm) to enclose the tissue segment. A small fan stirred the chamber air. The chambers were installed in late summer and fall 1993 and remained in place throughout the study.

An automated sampling system, set up in an open flow-through design, measured the diurnal CO_2 flux into stem and branch chambers. The system allowed sequential sampling of 16 respiration chambers, with each chamber sampled on an hourly time step. An LI-6262 infrared gas analyzer (Li-Cor, Inc., Lincoln, NE) set up in a differential configuration measured the CO_2 concentration of air entering and exiting the respiration chamber. Air flow to and from the chambers ranged from 1.5 to 3.0 l min^{-1} depending on CO_2 flux rates and were monitored with mass flow meters (Model 820 Flow Monitor, Sierra Instruments, Inc., Monterey, CA). Air flow rates leaving the chambers were slightly less than the supply air flow rates to maintain a positive chamber pressure. All tubing was 6.4-mm-diameter high-density polyethylene. Thermocouples constructed from 24-gauge copper-constantan wire measured chamber air and cambium temperatures. A data logger (Campbell CR21X, Campbell Scientific, Logan, UT) controlled chamber switching, monitored sensors and recorded data.

Tissue surface areas inside the respiration chambers were calculated from measurements of stem diameter (dendrometer bands) and branch diameter (digital caliper) at points just above and below each chamber. In young loblolly pine trees, essentially all of the wood is sapwood, so sapwood volume was estimated from inside bark diameter. Stem and branch biomass were estimated from sapwood volume based on equations developed from 16 trees harvested in January 1993.

We measured tissue nitrogen concentration monthly on five trees in each treatment plot by sampling the outer 2 cm of the stem (increment hammer) near breast height for stem nitrogen and a small secondary branch of a first flush 1991 branch for branch nitrogen. All bark was removed from the samples. The tissue was dried at 60 °C for 3 days then ground through 0.2-mm mesh in a Wiley Mill. Tissue nitrogen concentration was assessed with a Carlo-Erba elemental analyzer (Model NA 1500, Fisons Instruments, Danvers, MA) following the manufacturer's protocol with standards from the National Bureau of Standards (Rochester, NY). Tissue nitrogen content in the sample sections inside the respiration cuvette was calculated as the product of nitrogen concentration and sapwood biomass. Respiration per unit surface area (μmol m^{-2} s^{-1}), per unit sapwood volume (μmol m^{-3} s^{-1}), per unit sapwood weight (nmol g^{-1} s^{-1}) and per unit nitrogen (μmol mol^{-1} N s^{-1}) was calculated based on the difference in CO_2 concentration entering and exiting the chamber using a modified photosynthesis equation (Long and Hallgren 1985).

Because of time and labor constraints, only three of the four experimental blocks (Blocks 1, 2 and 4) were used in the study. Four average-sized trees in each irrigated, fertilized, and irrigated + fertilized treatment plot were selected for respiration measurements. Three trees were measured in each control plot and one sampling line was used as a blank and served as a system check. A total of 45 trees were used for respiration

measurements in the study. Maintenance respiration was measured in stems on 7 days (November 2, 16, 1993, January 26, February 2, 8, 15, and 27, 1994) and in branches on 5 days (January 27, February 3, 9, 16, and 24, 1994). On each day either stem or branch tissues from all treatments within one block were measured. Because the number of days exceeded the number of blocks, most blocks were used more than once during the study. Measurements normally began at 0700 h and ran continuously for 23 h. This sampling approach allowed respiration measurements over a wide range of temperatures. Treatment mean respiration rates and cambium temperature were calculated for each hour of each day by averaging the rates for all trees in each treatment plot. All data analyses were performed on treatment means.

Analysis of treatment effects

We used analysis of variance to test for effects of fertilization and irrigation on dormant season stem and branch maintenance respiration. A replication was defined as the measurements made in a block within one day, because only one block could be measured per day and temperatures typically varied widely between measurement days. Replicating by block and day reduced variation caused by temperature and nitrogen content because these parameters were relatively constant within a block on any given day. The statistical analysis was based on a randomized block design where the replication as defined by block and day constituted blocks in the statistical sense.

Modeling

We developed models to describe stem and branch R_m as a function of cambium temperature and tissue nitrogen content using a two-stage process. In Stage 1, respiration in each treatment plot was modeled only as a function of daily cambium temperature assuming that nitrogen content was constant throughout a day. In Stage 2, the daily model parameter estimates from Stage 1 were modeled as a function of tissue nitrogen content measured over the study period.

Modeling daily respiration (Stage 1) Respiration was modeled as a function of cambium temperature using the model:

$$R_{m,flux\,(i)} = \beta_0 \exp(\beta_1 T_i) + e_i \qquad E(e_i) \tilde{} N(0,\delta^2), \tag{1}$$

where $R_{m,flux\,(i)}$ is the CO_2 flux from the tissue in the cuvette per unit time (μmol CO_2 s^{-1}), T_i is cambium temperature (°C) at hour i (i = 1, 2, ..., 23), β_0 and β_1 are parameters to be estimated, and e_i is the current residual. However, because measurements on any one day were diurnal courses from the same set of trees in each plot, the hourly measurements are autocorrelated, that is, the value of $R_{m,flux\,(i)}$ at time i is influenced by $R_{m,flux\,(i-1)}$ at time i – 1. When autocorrelation is present, the ordinary least squares parameter estimates are still unbiased but inefficient and no longer have minimum variance (Neter et al. 1985). Autocorrelation was accounted for by imposing a structure on the residuals using the autoregressive model:

$$R_{m,flux\,(i)} = \beta_0 \exp(\beta_1 T_i) + u_i, \tag{2}$$

where $u_i = e_i + \rho(e_{i-1})$.

This equation differs from Equation 1 in the definition of the error term. The model error term (u_i) consists of the current residual (e_i) and part of the previous residual (e_{i-1}). The autocorrelation parameter, ρ, is the correlation between adjacent residuals (Neter et al. 1985). This model is a first-order autoregressive model and the errors at time i are related only to errors at time i − 1. Equation 2 was fitted by the nonlinear autoregression technique described by Gallant (1987) to estimate the model parameters β_0 and β_1 for each treatment on

Table 1. Mean dormant season maintenance respiration per unit surface area, $R_{m,a}$, per unit volume, $R_{m,v}$, per unit dry weight, $R_{m,g}$, and per mole nitrogen, $R_{m,n}$, tissue size characteristics, tissue nitrogen concentration (%N) and tissue temperature in stems (November–February) and branches (January–February) in 9-year-old loblolly pine trees.[1]

Treatment	Surface area (m^2)	Sapwood volume (cm^3)	Sapwood weight (g)	Cambial tissue °C[3]	%N	Maintenance respiration[2]				*n*
						$R_{m,a}$	$R_{m,v}$	$R_{m,g}$	$R_{m,n}$	
Stem										
Control	0.061 a	879.5 a	303.3 a	9.6 a	0.10 a	0.64 a	44.4 a	0.13 a	1.91 a	7
Irrigated	0.062 a	917.0 a	316.2 a	9.8 a	0.09 a	0.80 a	55.3 a	0.16 a	2.43 b	7
Fertilized	0.069 b	1126.0 b	388.0 b	9.5 a	0.15 b	1.39 b	86.5 b	0.25 b	2.25 b	7
Irr. + Fert.	0.071 b	1233.9 b	425.1 b	9.5 a	0.16 b	1.47 b	86.3 b	0.25 b	2.13 b	7
Branch										
Control	0.012 a	38.8 a	7.99 a	9.7 a	0.27 a	0.36 a	112.0 a	0.54 a	2.84 a	5
Irrigated	0.012 a	41.6 a	8.44 ab	9.5 a	0.28 a	0.43 ab	129.9 a	0.63 ab	3.24 ab	5
Fertilized	0.014 b	51.8 b	10.07 bc	9.7 a	0.35 b	0.52 bc	137.0 ab	0.70 bc	2.82 a	5
Irr. + Fert.	0.014 b	54.4 b	10.47 c	9.8 a	0.35 b	0.60 c	162.3 b	0.83 c	3.37 b	5

[1] Within each tissue and column, means sharing a common letter do not differ significantly at α = 0.05 according to Tukey's studentized range test and based on a randomized block design analysis of variance.

[2] $R_{m,a}$ = μmol m^{-2} s^{-1}; $R_{m,v}$ = μmol m^{-3} s^{-1}; $R_{m,g}$ = nmol g^{-1} s^{-1}; and $R_{m,n}$ = μmol mol^{-1} N s^{-1}.

[3] Mean temperature of stem or branch cambium tissue during respiration measurements.

each day of measurement. All nonlinear regression procedures were performed with PROC NLIN in the SAS software package (1988; SAS Institute Inc., Cary, NC).

Model development (Stage 2) The parameter estimates for each day and treatment plot from Equation 2 provided a data set consisting of 28 and 20 observations for stem and branch respiration, respectively. The relationship of these parameters with tissue nitrogen content was investigated in an attempt to develop models of $\beta_0 = f_0(N)$ and $\beta_1 = f_1(N)$ over the study period. Significant relationships between β_0 and β_1 and tissue nitrogen content were used to modify Equation 1 giving a temperature–nitrogen model:

$$R_{m,flux\ (i)} = f_0(N)\ \exp(f_1(N)T). \quad (3)$$

The performance of the models was examined graphically by plotting the predicted versus observed values based on the pooled data set from all days and treatments. Several fit statistics and measures of accuracy and precision were also used to evaluate the models (Buford 1991, Dougherty et al. 1995). Finally, the utility of each model was assessed on an independent validation data set of maintenance respiration measurements collected the following year on the same trees (November 1994).

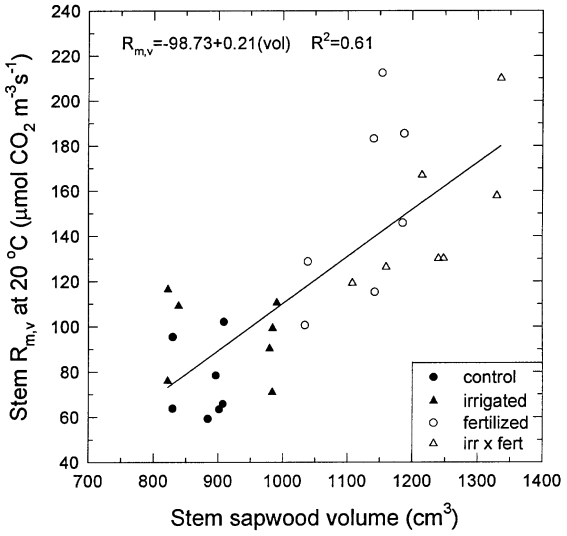

Figure 2. Stem maintenance respiration rate per unit sapwood volume corrected to 20 °C (Q_{10} = 2) versus stem sapwood volume in 9 year-old loblolly pine trees. Points are means for the dormant season (November 1993–February 1994).

Results

Treatment effects

Mean values for dormant season maintenance respiration, tissue size characteristics, tissue nitrogen concentration and cambium temperature are presented in Table 1. Fertilization resulted in an increase in tissue nitrogen concentration and

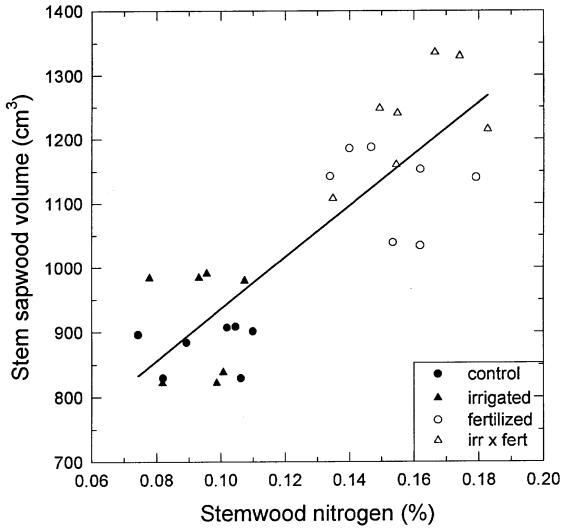

Figure 1. Sapwood volume of stems versus stem nitrogen concentration (% of dry weight) in 9-year-old loblolly pine trees. Each point is the mean for the dormant season (November 1993–February 1994).

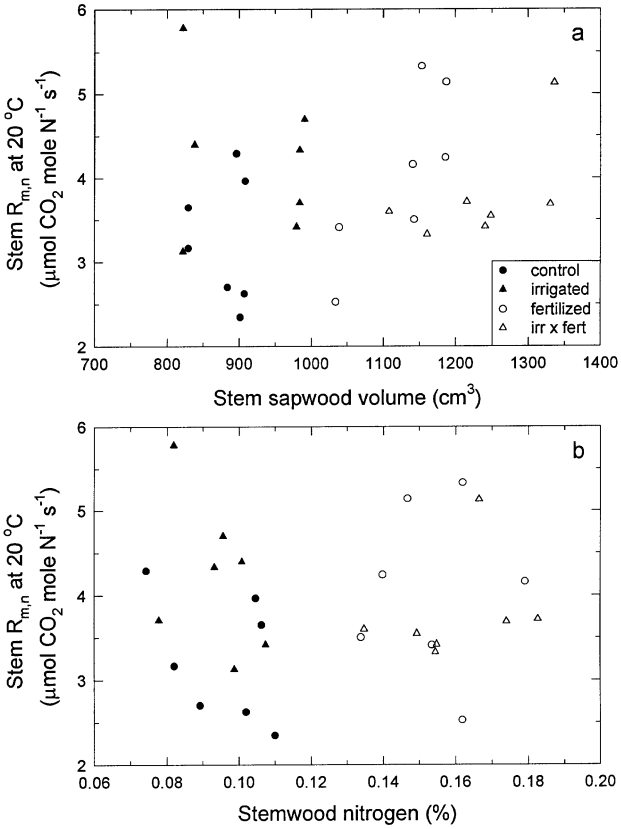

Figure 3. Stem maintenance respiration rate per mole nitrogen corrected to 20 °C (Q_{10} = 2) versus (a) stem sapwood volume and (b) stem sapwood nitrogen concentration (% of dry weight). Points are means for the dormant season (November 1993–October 1994).

tissue growth. Stem tissue nitrogen concentrations were low and averaged 0.09% in the nonfertilized plots and 0.16% in the fertilized plots, whereas branch nitrogen concentrations were higher and averaged 0.27 and 0.35% in the nonfertilized and fertilized treatments, respectively. Stem and branch surface areas, sapwood volumes and weights were significantly enhanced in the fertilized treatments. Stem and branch respiration rates per unit surface area ($R_{m,a}$), per unit sapwood volume ($R_{m,v}$), and per unit weight ($R_{m,g}$) were significantly increased in the fertilized treatments, whereas there was no clear fertilization treatment effect on respiration rate per mole nitrogen ($R_{m,n}$) (Table 1). Because fertilization increased both tissue size and tissue nitrogen concentration, tissue size (e.g., sapwood volume) was well correlated with nitrogen concentration (Figure 1). Therefore, tissue respiration per unit size ($R_{m,v}$, $R_{m,a}$, $R_{m,g}$) was variable with respect to tissue size. For example, stem $R_{m,v}$ increased linearly with sapwood volume (Figure 2). Almost identical relationships were observed for $R_{m,a}$ and tissue surface area (R^2 = 0.72) and for $R_{m,g}$ and tissue biomass (R^2 = 0.60). Because tissue size and tissue nitrogen concentration were correlated and R_m per unit size varied among treatments, we were unable to determine the cause of increased R_m per unit size in the fertilized treatments. However, $R_{m,n}$ was relatively constant across treatments (Table 1) and $R_{m,n}$ appeared to be constant with respect to sapwood volume (Figure 3a) and tissue nitrogen concentration (Figure 3b). The variability in R_m with tissue size and the constancy of R_m with tissue nitrogen content suggest that R_m is not just a function of tissue size or tissue nitrogen concentration, but a function of the total amount of nitrogen (nitrogen content) in the tissue.

Table 2. Stem cambium temperature, tissue N content (moles in tissue within the respiration chamber), autocorrelation statistics and parameter estimates for Equation 2.

Treatment	Julian date	Block	T_{min} °C	T_{max} °C	N	DW[1]	ρ[2]	β_0[3]	β_1[4]	r[5]	n
Control	306	1	–0.7	14.7	0.022	0.24	0.88	0.021	0.044	0.42	23
	320	4	13.8	27.4	0.023	0.96	0.52	0.030	0.057	0.75	23
	26	4	5.5	17.9	0.016	0.70	0.65	0.021	0.053	0.63	23
	33	2	–3.2	2.7	0.024	ns[6]	ns	ns	ns	ns	23
	39	1	8.0	16.9	0.017	0.62	0.69	0.011	0.084	0.89	23
	46	4	–1.6	16.5	0.019	0.40	0.80	0.017	0.040	0.26	23
	58	2	4.4	8.3	0.024	0.70	0.65	0.016	0.050	0.93	23
Irrigated	306	1	–0.7	12.5	0.023	0.15	0.92	0.029	0.043	0.51	23
	320	4	14.8	28.2	0.021	1.32	0.34	0.025	0.065	0.89	23
	26	4	4.9	17.4	0.017	0.37	0.82	0.031	0.043	0.69	23
	33	2	–3.2	2.6	0.023	ns	ns	ns	ns	ns	23
	39	1	9.1	17.7	0.019	0.91	0.54	0.012	0.094	0.81	23
	46	4	–0.9	16.3	0.020	0.24	0.88	0.018	0.047	0.48	23
	58	2	4.5	8.4	0.023	0.46	0.77	0.025	0.066	0.95	23
Fertilized	306	1	–0.9	10.0	0.046	0.17	0.92	0.066	0.037	0.46	23
	320	4	14.0	27.3	0.050	0.22	0.89	0.076	0.050	0.84	23
	26	4	5.5	19.7	0.043	0.15	0.92	0.088	0.026	0.76	23
	33	2	–3.3	2.2	0.039	ns	ns	ns	ns	ns	23
	39	1	8.6	17.4	0.038	0.74	0.63	0.020	0.106	0.82	23
	46	4	–1.6	15.8	0.041	0.15	0.93	0.054	0.033	0.40	23
	58	2	4.5	8.1	0.039	0.37	0.82	0.040	0.041	0.95	23
Irr. + Fert.	306	1	–0.9	10.0	0.044	0.18	0.91	0.034	0.066	0.51	23
	320	4	16.2	26.5	0.055	0.56	0.72	0.052	0.068	0.88	23
	26	4	6.9	14.6	0.055	0.34	0.83	0.087	0.048	0.85	23
	33	2	–3.8	2.3	0.046	ns	ns	ns	ns	ns	23
	39	1	8.2	17.5	0.037	0.47	0.76	0.019	0.110	0.86	23
	46	4	0.7	14.0	0.057	0.15	0.93	0.056	0.059	0.70	23
	58	2	4.8	7.7	0.046	0.48	0.76	0.044	0.055	0.96	23

[1] Durbin-Watson statistic: DW < 1.26 indicates positive first-order autocorrelation at α = 0.05. DW > 1.26 but < 1.44 are inconclusive, and DW > 1.44 indicates no autocorrelation.

[2] ρ = Autocorrelation between adjacent error terms in Equation 1.

[3] Parameter estimate correcting for autocorrelation (Equation 2); β_0 is the intercept parameter.

[4] Parameter estimate correcting for autocorrelation (Equation 2); β_1 is the slope.

[5] r = Correlation coefficient between predicted and observed (Equation 2).

[6] ns = Nonsignificant (P > 0.05). There was no significant relationship between $R_{m,flux}$ and cambium temperature.

Modeling

During the study, cambium temperatures ranged from −3.8 to 28.2 °C in stems and −5.1 to 27.3 °C in branches. However, on any measurement day, the temperature range was usually less than 20 °C. Tissue maintenance respiration during any one day, measured as CO_2 flux ($R_{m,flux}$; μmol CO_2 s^{-1}) from the tissue segment within the respiration chamber, was first modeled as a function of temperature ignoring any possible autocorrelation (Equation 1). The Durbin-Watson statistic revealed that autocorrelation was significant on most days for stems (Table 2) and branches (Table 3). Because the degree of autocorrelation (ρ) ranged from 0.01 to 0.93, we used Equation 2 to model daily temperature responses for both tissues. Temperature explained a significant portion ($P < 0.01$) of the variation in $R_{m,flux}$ in both tissues (r ranged from 0.26 to 0.99) on all but one day. The lack of a significant relationship ($P > 0.05$ on Day 33 for stems and Day 27 for branches) was because of low temperatures and a small diurnal range.

Daily estimates of basal respiration (β_0) and the temperature coefficient (β_1) from Equation 2 are presented in Tables 2 and 3 for stem and branch tissues, respectively. These parameter estimates were modeled as linear functions of tissue nitrogen content (moles N in tissue within the respiration chamber). In stems, the basal respiration rate (β_0) showed a linear relationship ($P < 0.001$, $R^2 = 0.62$) with tissue nitrogen content (Figure 4a), whereas the temperature coefficient (β_1) was not correlated with tissue nitrogen content ($P = 0.72$) (Figure 4b). The mean stem temperature coefficient (β_1) was 0.058 and the Q_{10} was 1.79 where $Q_{10} = \exp(\beta_1 \times 10)$. The response for branch tissue was similar to that for stems. The relationship of basal respiration rate (β_0) to branch nitrogen content was also linear ($P = 0.0107$, $R^2 = 0.38$) (Figure 5a), and there was no correlation between the temperature coefficient (β_1) and branch nitrogen content ($P = 0.96$) (Figure 5b). The mean branch temperature coefficient (β_1) was 0.063 ($Q_{10} = 1.88$). These results suggest that elevated tissue nitrogen content increased the basal respiration rate but did not affect the Q_{10} during the dormant season. However, care must be exercised when interpreting these results. By regressing β_0 and β_1 from all treatments across nitrogen we have assumed that the slope of the parameter estimate versus tissue nitrogen content is the same for all treatments, which may not be true. We lacked sufficient data within treatments to establish separate regression equations for each treatment and then test for heterogeneity of slopes. Although the equations presented here may not precisely describe the true response of β_0 and β_1 to tissue nitrogen content, they were developed over a range of nitrogen contents and should be a reasonable approximation.

Table 3. Branch cambium temperature, tissue N content (moles in tissue within the respiration chamber), autocorrelation and parameter estimates for Equation 2.

Treatment	Julian date	Block	T_{min} °C	T_{max} °C	N	DW[1]	ρ[2]	β_0[3]	β_1[4]	r[5]	n
Control	27	4	4.0	7.8	0.0012	ns[6]	ns	ns	ns	ns	23
	34	2	−2.8	16.3	0.0021	0.57	0.72	0.0025	0.047	0.80	23
	40	1	11.8	26.6	0.0014	1.18	0.41	0.0019	0.060	0.93	22
	47	4	5.1	21.9	0.0012	0.97	0.52	0.0018	0.052	0.86	23
	55	2	−2.8	19.3	0.0016	1.78	0.11	0.0036	0.052	0.98	23
Irrigated	27	4	4.6	9.9	0.0018	ns	ns	ns	ns	ns	23
	34	2	−3.2	14.9	0.0018	0.65	0.68	0.0029	0.049	0.84	22
	40	1	8.1	27.3	0.0013	1.22	0.39	0.0011	0.090	0.95	22
	47	4	−5.3	22.6	0.0018	0.64	0.68	0.0024	0.067	0.90	23
	55	2	−2.7	20.8	0.0016	0.72	0.64	0.0034	0.063	0.98	23
Fertilized	27	4	4.4	9.4	0.0030	ns	ns	ns	ns	ns	23
	34	2	−1.0	15.2	0.0025	0.74	0.63	0.0035	0.063	0.88	22
	40	1	9.4	27.0	0.0024	1.38	0.31	0.0023	0.074	0.98	22
	47	4	−4.6	22.4	0.0030	0.53	0.74	0.0035	0.055	0.86	23
	55	2	−1.2	19.0	0.0023	1.28	0.36	0.0039	0.071	0.99	23
Irr. + Fert.	27	4	4.4	9.1	0.0031	ns	ns	ns	ns	ns	23
	34	2	−2.9	16.2	0.0024	0.55	0.72	0.0036	0.064	0.81	22
	40	1	10.3	27.2	0.0022	2.07	0.01	0.0023	0.080	0.99	22
	47	4	−3.9	20.5	0.0031	0.34	0.83	0.0043	0.062	0.86	23
	55	2	−1.8	20.4	0.0024	0.58	0.71	0.0055	0.062	0.97	23

[1] Durbin-Watson statistic: DW < 1.26 indicates positive first-order autocorrelation at $\alpha = 0.05$. DW > 1.26 but < 1.44 are inconclusive, and DW > 1.44 indicates no autocorrelation.

[2] ρ = Autocorrelation between adjacent error terms in Equation 1.

[3] Parameter estimate correcting for autocorrelation (Equation 2); β_0 is the intercept parameter.

[4] Parameter estimate correcting for autocorrelation (Equation 2); β_1 is the slope.

[5] r = Correlation coefficient between predicted and observed (Equation 2).

[6] ns = Nonsignificant ($P > 0.05$). There was no significant relationship between $R_{m,flux}$ and cambium temperature.

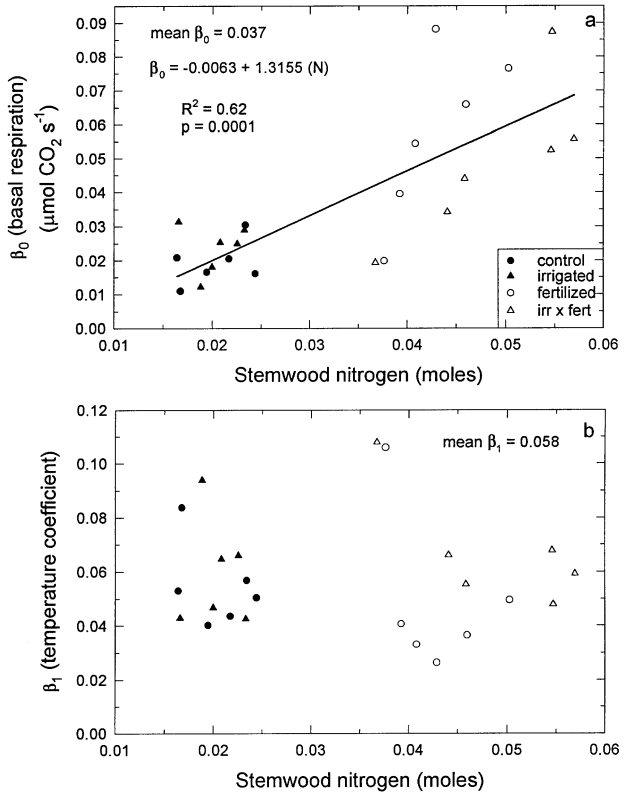

Figure 4. Relationship of (a) stemwood basal respiration rate (β_0) and (b) the temperature coefficient (β_1) with stem sapwood nitrogen content. Each point is the parameter estimate for Equation 2 for each day of measurement.

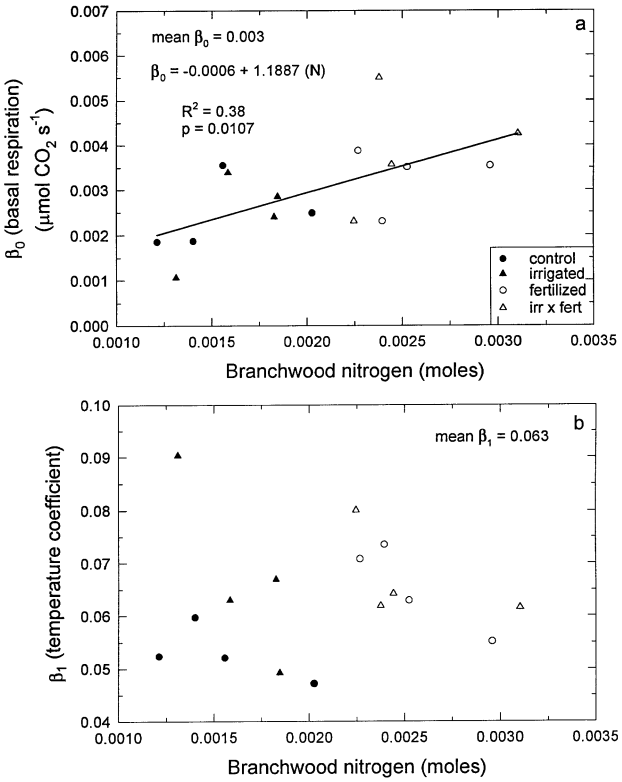

Figure 5. Relationship of (a) branchwood basal respiration rate (β_0) and (b) the temperature coefficient (β_1) with branch sapwood nitrogen content. Each point is the parameter estimate for Equation 2 for each day of measurement.

The parameter means for β_1 and nitrogen functions for β_0 were inserted directly into Equation 4, giving

$$R_{m,flux} = (-0.0063 + 1.3155\,N)\exp(0.058\,T)$$

for stems, and

$$R_{m,flux} = (-0.0006 + 1.1887\,N)\exp(0.063\,T)$$

for branches. Predictions from the temperature–nitrogen model containing β_0 as a function of nitrogen content showed good agreement with observed values in stems (Figure 6a and Table 4). The correlation (r) between observed and predicted values was 0.95. There was more variability between observed and predicted values for branches, but the correlation was still highly significant (r = 0.89, P < 0.0001) (Figure 6b and Table 4).

Each model was validated with an independent set of respiration measurements made in November 1994 on the same trees. Figures 6c and 6d show the predicted versus observed $R_{m,flux}$ for stems and branches, respectively. A similar pattern of response to the modeled data was seen in stems. The temperature–nitrogen model slightly overpredicted the minimum, maximum and mean respiration rates (Table 4). Also, the variability increased at high $R_{m,flux}$ values possibly because of autocorrelation. The fit statistics revealed that the model predicted stem $R_{m,flux}$ the following year with similar accuracy (percent absolute deviation, %AD), but was slightly less precise (percent root mean square error, %RMSE) than in 1993, possibly because of yearly variation in tree and environmental factors (Table 4). In contrast to stems, branch $R_{m,flux}$ was much lower in the fall of 1994 than in the previous year. As a result, the model overpredicted branch $R_{m,flux}$. These results suggest that there are other important factors affecting branch and possibly stem physiology that have not been accounted for in these models.

Discussion

Dormant season stem $R_{m,a}$ at 25 °C ranged from 1.7 in the nonfertilized treatment to 3.3 μmol m^{-2} s^{-1} in the fertilized treatment. These rates were substantially higher than those reported by Kinerson (1975) for 12- to 16-year-old loblolly pine trees (0.6 μmol m^{-2} s^{-1} at 25 °C), but similar to stem respiration rates in loblolly pine seedlings (1.0–3.25 μmol m^{-2} s^{-1}) (Martin et al. 1994). On a sapwood volume basis, stem $R_{m,v}$ (44–86 μmol m^{-3} s^{-1}) was higher than that reported for other conifers such as *Pinus elliottii* var. *elliottii* Engelm. (8.3 μmol m^{-3} s^{-1} at 10 °C) and *Pinus ponderosa* Dougl. ex Laws. (8.0 μmol m^{-3} s^{-1} at 10 °C) (Ryan et al. 1995), but was

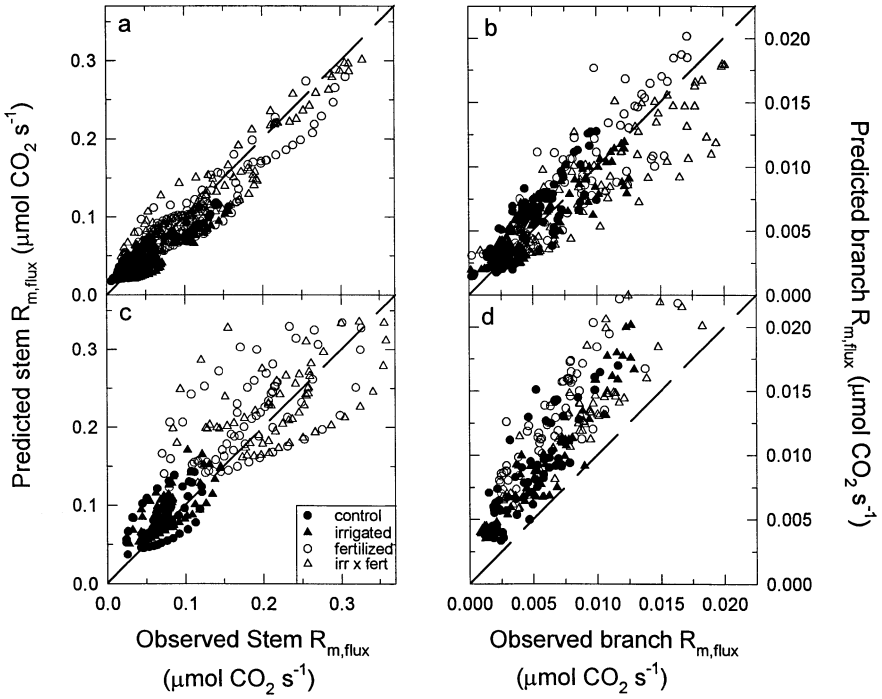

Figure 6. Predicted stem and branch maintenance respiration rates based on Equation 2 versus the observed rates based on the modeled (a and b) and validation (c and d) data sets.

Table 4. Fit statistics for dormant season stem and branch maintenance respiration models based on the modeled and validation data.

	Modeled data						Validation data					
	Mean $R_{m,flux}$	Min. $R_{m,flux}$	Max. $R_{m,flux}$	r[1]	%RMSE[2]	%AD[3]	Mean $R_{m,flux}$	Min. $R_{m,flux}$	Max. $R_{m,flux}$	r	%RMSE	%AD
Stem												
Model	0.072	0.018	0.301	0.95	30.68	−12.44	0.156	0.037	0.393	0.87	30.50	−22.19
Observed data	0.074	0.006	0.328	–	–	–	0.138	0.024	0.358	–	–	–
Branch												
Model	0.006	0.002	0.020	0.89	39.44	−23.51	0.012	0.003	0.032	0.92	93.3	−93.30
Observed data	0.006	0.001	0.020	–	–	–	0.007	0.001	0.022	–	–	–

[1] Correlation coefficient between predicted and observed values.

[2] %RMSE (Percent root mean square error):

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

[3] %AD (Percent absolute deviation):

$$\%\mathrm{AD} = \frac{100}{n}\sum_{i=1}^{n}\left|\frac{\hat{y}_i - y_i}{y_i}\right|.$$

similar to that of *Pinus radiata* D. Don (15–39 μmol m^{-3} s^{-1}) (Ryan et al. 1996) and *Abies amablis* (Dougl.) Forbes (86 μmol m^{-3} s^{-1} at 15 °C) (Sprugel 1990). On a sapwood dry weight basis, stem $R_{m,g}$ was also higher than that reported for other conifers (Sprugel et al. 1995). Ryan (1995) observed that foliage R_m per unit weight increased with tissue nitrogen content in several species, but found no differences in stem and branch R_m per unit sapwood volume in *P. radiata* grown under different nutrient regimes (Ryan et al. 1996). The differences between our results and those in the other studies are probably associated with differences in tree size, age and tissue chemistry. Our trees were small (dbh: 8–15 cm) and the proportion of newly laid down sapwood to older sapwood was high. As trees grow, the proportion of young physiologically active tissue to older, less active tissue decreases (Kramer and Kozlowski 1979).

Our data show that respiration rate ($R_{m,a}$, $R_{m,v}$, and $R_{m,g}$) increased as tissue size or nitrogen concentration increased, but respiration rate per mole nitrogen ($R_{m,n}$) was relatively constant. Increased $R_{m,a}$ with size could be the result of more

respiring tissue per unit surface area in larger diameter stems, which consisted entirely of sapwood in this study. Increased $R_{m,v}$ and $R_{m,g}$ with size could be the result of increased cellular nitrogen concentration, more respiring cells per volume (or gram) of wood, or increased activity of the ray parenchyma cells (Ryan et al. 1996). Cropper and Gholz (1991) and Ryan et al. (1996) showed that root maintenance respiration per unit volume or weight varied with tissue size. Maintenance respiration was also much greater in branch tissue than in stem tissue when expressed on a per unit volume or dry weight basis, but was lower when expressed per unit surface area. These results suggest that comparisons of size-based maintenance respiration rates among different tissues and different age stands will be difficult and extrapolating respiration measurements made in chambers to the stand based on tissue volume or weight may lead to serious errors. It is interesting that there was less variation in maintenance respiration among treatments when expressed per unit nitrogen ($R_{m,n}$) than when expressed per unit area, volume or dry weight. Also, there appeared to be less variation in $R_{m,n}$ than in the size-based measurements among tissue types. Stem and branch $R_{m,n}$ reported here were similar to nitrogen-based foliage respiration measurements made in several woody species (1.5–3.4 μmol CO_2 mol^{-1} N s^{-1}, Ryan 1995) even though foliage often has 10 times the nitrogen concentrations of woody tissues. Expressing maintenance respiration per unit nitrogen content rather than size may offer a means for comparing respiration rates between tissues of different type, age, and chemical composition.

We modeled tissue R_m flux (μmol CO_2 s^{-1}) as a function of temperature and nitrogen content. Cambium temperature explained most of the variation in dormant season stem and branch R_m. Wood has a high resistance to CO_2 diffusion and R_m is sometimes better correlated with previous temperatures than with current tissue temperature (Negisi 1982, Ryan et al. 1995). We tested for a lagged respiration response to cambium temperature by lagging cambium temperature 1 to 3 h and found that respiration in the treatment plots was always better correlated with current cambium temperature than with the lagged cambium temperatures, perhaps reflecting the small size of our trees (< 15 cm in dbh). Basal respiration flux (β_0, μmol s^{-1} at 0 °C) increased with tissue nitrogen content by 112 and 37% in stems and branches, respectively; however, nitrogen content had no effect on the temperature coefficient (β_1). The Q_{10} ($Q_{10} = \exp(\beta_1 \times 10)$) for stem and branch tissues was about 1.8, which is similar to that reported for dormant woody tissue in other tree species (Sprugel and Benecke 1990, Ryan et al. 1995). Other nutrients may also influence maintenance respiration rates. Phosphorus, like nitrogen, is an important element in the biochemistry of photosynthesis and respiration and is known to affect foliage gas exchange. For example, Reich and Schoettle (1988) found that needle phosphorus and nitrogen limited photosynthesis in *Pinus strobus* L. seedlings and that the P:N ratio appeared to control the maximum photosynthetic rate. Also, low tissue phosphorus concentration may reduce dark respiration rates by limiting ATP production (Amthor 1989). Because our fertilization treatments involved a complete application of macro- and micronutrients such that other nutrients were kept in balance with foliar nitrogen (Murthy et al. 1996), increased R_m may be in response to a combination of nutritional factors and not just to nitrogen.

Use of the regression equations to predict woody tissue maintenance costs requires that the relationships with temperature and tissue nitrogen be stable over time. Stem maintenance respiration rates appeared to be stable from one dormant season to the next. This was not so for branches. Branch maintenance respiration in November 1994 was much lower than in January 1994 and may reflect a shift in branch metabolic activity (i.e., growth and maintenance) reducing the need for respiration products (Amthor 1994). Another explanation for the reduced branch R_m is the elimination of photosynthetic tissue. The study branches still contained corticular chlorophyll and probably maintained some photosynthetic ability; however, the permanently installed chambers prevented sunlight from reaching the enclosed tissue, and most of the chlorophyll may have disappeared in these branch segments by the end of the study. Thus, reduced R_m might be an artifact caused by eliminating the need to maintain costly photosynthetic enzymes. The year-to-year variability in branch R_m suggests that R_m may vary within the canopy as has been shown by Sprugel (1990) and Ryan et al. (1996). Therefore, estimates of stand-level maintenance respiration based on scaled-up measurements at one level would produce errors.

In conclusion, dormant season woody tissue R_m per unit size varied with tissue size in young loblolly pine. This variability may be the result of differences in tissue nitrogen content. Temperature accounted for most of the variation in dormant season stem and branch $R_{m,flux}$, although tissue nitrogen content was also an important factor. Increased nitrogen content was correlated with increased basal respiration rates in stems and branches, but not Q_{10} values. In stems, an exponential model including temperature and nitrogen content as independent variables accurately predicts stem R_m during the dormant season. Branch respiration was more variable and thus more difficult to model. Branch age, canopy position and some estimate of corticular photosynthesis may be needed to predict R_m accurately in this tissue. We conclude that failure to account for tissue nitrogen will result in serious errors when estimating tree or stand annual maintenance costs. Knowledge of the relationship between R_m and tissue nitrogen will aid in comparing maintenance respiration costs between stands and ecosystems.

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