Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*

MICHAEL G. RYAN[1]

Department of Forest Science, Oregon State University, Corvallis, OR 97331, U.S.A.

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Stem maintenance respiration was linearly related to live-cell volume for lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) from 4 to 36 cm dbh and for Engelmann spruce (*Picea engelmannii* Parry) from 0 to 20 cm dbh. Sapwood contained greater than 80% of the total live-cell volume in stems. Bole surface area, commonly used to estimate tree respiration costs, poorly estimated stem maintenance respiration. At 15°C, maintenance costs for lodgepole pine were 6.6×10^{-5} kg C·(kg C sapwood)$^{-1}$·d^{-1}. Stem respiration during the growing season, both corrected and uncorrected for maintenance, correlated well with annual stemwood growth. Annual stem maintenance respiration for trees and stands can be estimated using sapwood volume, sapwood temperature, and knowledge of respiratory behavior. Total respiration (construction plus maintenance) estimated using stem growth and a model of maintenance respiration was compared with actual respiration measurements integrated over a 100-d growing season. Estimated respiration agreed with the integrated measurements for Engelmann spruce, but overestimated the integrated measurements by 73% in lodgepole pine. These results suggest that estimates of stem respiration made during the growing season may be affected by transpiration.

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La respiration nécessaire au fonctionnement du tronc était directement fonction du volume de cellules vivantes pour les Pins de Murray (*Pinus contorta* var. *latifolia* Engelm.) de 4 à 36 cm au dhp et pour les Épinettes d'Engelmann (*Picea engelmannii* Parry) de 0 à 20 cm au dhp. Le bois d'aubier contenait plus de 80% du volume total de cellules vivantes dans le tronc. La surface de la tige, généralement utilisée pour évaluer la respiration chez les arbres, n'est pas une méthode fiable pour évaluer la respiration nécessaire au fonctionnement du tronc. A 15°C, $6{,}6 \times 10^{-5}$ kg de C·(kg de C dans le bois d'aubier)$^{-1}$·jour^{-1} était nécessaire au fonctionnement du tronc chez le Pin de Murray. La respiration dans le tronc pendant la saison de croissance, tant corrigée que non-corrigée pour le fonctionnement, était corrélée avec la croissance annuelle du tronc. La respiration annuelle nécessaire au fonctionnement des arbres et des peuplements peut être estimée à partir du volume et de la température du bois d'aubier si on connaît le comportement de la respiration. La respiration totale (croissance et fonctionnement), estimée à partir de la croissance de la tige et d'un modèle dans le cas de la respiration nécessaire au fonctionnement, a été comparée à des mesures de la respiration intégrées sur une saison de croissance de 100 jours. La respiration estimée concordait avec la respiration mesurée pour l'Épinette d'Engelmann mais la surestimait de 73% pour le Pin de Murray. Ces résultats suggèrent que les estimés de la respiration obtenus pendant la saison de croissance peuvent être affectés par la transpiration.

[Traduit par la revue]

Introduction

Sapwood in stems and branches conducts water from roots to leaves, but also acts as an important storage organ. Sapwood can store water, nutrients, and carbohydrates that help trees survive in a fluctuating environment. Sapwood water storage helps conifers avoid drought (Waring and Running 1978; Waring and Franklin 1979) and maintain stomatal function (Waring et al. 1979). Carbohydrate reserves in the ray parenchyma cells of sapwood build new roots and leaves (McLaughlin et al. 1980) and help trees survive insect outbreaks (Waring and Pitman 1985). Carbohydrate storage in conifers exceeds annual stemwood production (calculated from information in Kramer and Kozlowski 1979).

Maintaining the living ray parenchyma cells in sapwood is a cost that balances the benefits of sapwood storage. Sapwood in conifers contains 6–10% living ray cells (Panshin and de Zeeuw 1970) and the energy required to support these cells can be considerable. Stem and branch respiration is an important component in the carbon balance of trees and forests (Kinerson 1975; Sprugel and Benecke 1990; Benecke and Nordmeyer 1982), but has received little attention (Landsberg 1986).

To understand the role of respiration in whole plants and the response of respiration to the environment, we partition respiration into two functional components: construction respiration (R_c) and maintenance respiration (McCree 1970). Construction respiration refers to CO_2 evolution from processes generating energy for the synthesis of plant dry matter. Maintenance respiration (R_m) is the CO_2 evolution from maintenance processes within the cell including protein turnover, the maintenance of ion and metabolite gradients, and physiological adaptation to a changing environment (Penning de Vries 1975). Although the two processes may produce distinct end products, the carbon dioxide evolved is not biochemically distinct. Energy used for transport of sugars is not included in this dichotomy, but can be assigned to growth.

Construction respiration is proportional to the growth increment (adjusted for chemical composition (Chung and Barnes 1977; Williams et al. 1987)), whereas maintenance respiration varies with the amount of living tissue, adjusted

[1]Present address: Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, U.S.A.

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for protein type and protein content. Total respiration (R_t) may then be expressed as

$$[1] \quad R_t = a\frac{dW}{dt} + bW$$

where W is living biomass and a and b are partitioning coefficients (Landsberg 1986). Total R_c for a growing season is independent of temperature (except where temperature affects biomass production), whereas annual R_m costs increase exponentially with temperature (Landsberg 1986). Maintenance respiration may be very important for trees because of the large amount of respiring biomass in the stem, roots, and branches, and the sensitivity of this process to temperature. Despite the potential importance of R_m for trees, little work has been done in this area (Sprugel and Benecke 1990).

Several methods have been used to isolate construction and maintenance respiration in crop plants (Amthor 1984; Lambers et al. 1983). However, most of these methods involve manipulations of photosynthesis and respiration that would be extremely difficult to apply to large trees in the field. Generally, maintenance respiration for woody tissues of trees has been estimated from respiration while the tree is not growing (Butler and Landsberg 1981). Dormant season estimates of R_m may underestimate R_m that occurs during the growing season (McCree 1982); however, they remain the only direct estimate of R_m for large trees (Sprugel and Benecke 1990).

Stem respiration is usually expressed as flux per unit of stem surface area (Landsberg 1986), apparently because of the high respiratory rates of the cambium and phloem. Goodwin and Goddard (1940) showed that oxygen consumption of excised tissue was highest in differentiating xylem cells adjacent to the cambium, less in the cambium and phloem, and lowest in the xylem. A low respiration rate in the xylem is a consequence of the low density of parenchyma ray cells, the only living cells. However, in large stems, the volume of living cells in the sapwood may surpass that of the cambium and phloem. Therefore, in large stems, maintenance respiration may be more closely related to sapwood volume than to surface area.

The objectives of this study were (*i*) to estimate the contribution of R_c and R_m to total respiration for stems of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and Engelmann spruce (*Picea engelmannii* Parry), (*ii*) to determine the source of the respiratory CO_2 in the maintenance phase, i.e., sapwood or phloem–cambium, (*iii*) to determine whether instantaneous and seasonal growth respiration is related to annual stemwood growth, (*iv*) to determine whether stem respiration rates vary with tree age, and (v) to develop simple equations to estimate the annual cost of stem maintenance respiration.

Methods

Study area

The study was conducted at the Fraser Experimental Forest near Fraser, Colorado, United States (39°54′N, 105°52′W). Long, cold winters and short, cool summers characterize the climate at the experimental forest. An average of 740 mm precipitation falls each year, with about two-thirds as snow. The average monthly temperatures for January and July are −10° and 13°C; annual average temperature is 2°C (Alexander et al. 1985). Frost may limit photosynthetic activity during the spring and autumn, but summer rain storms and cool temperatures keep soil moisture high during the growing season so that stomatal closure associated with moisture stress is rare (Kaufmann 1982*b*). However, nitrogen is low in the soil solution for lodgepole pine forests (Fahey and Knight 1986) and may limit photosynthetic capacity and aboveground growth. Soils are Typic Cryochrepts derived from mixed gneiss and schist.

For each species, I selected 12 trees varying in size from about 4 cm to greater than 40 cm diameter at 1.4 m (dbh) for measurements of stem respiration. These trees differed in age, growth rate, fraction of basal area in sapwood, and ratio of sapwood volume to stem surface area. The lodgepole pine trees grew in three adjacent even-aged stands (40, 62, and 233 years old) at 2800 m elevation. Engelmann spruce trees were selected from an uneven-aged, mixed-species stand at 2750 m elevation. Selected trees had uniform crowns, were dominant or co-dominant, and had no defect or rot in the lower 4-m section.

Gas-exchange measurements

Two chamber types were used for gas-exchange analysis, one type for trees with dbh less than 10 cm and one for larger trees. For the smaller trees, two closed-cell neoprene foam collars surrounded the stem and a split Plexiglas chamber sealed the stem segment from the surrounding air. An aluminum chamber plate (10 × 25 cm) with neoprene facing was attached to each larger tree using rope caulk. A Plexiglas chamber placed over the neoprene seal on the chamber plate isolated the interior from the outside air. A small fan stirred the air inside of the chamber for the larger trees, and a copper–constantan thermocouple measured chamber temperature. Chamber volumes were 280–450 mL.

Chamber plates and foam collars were attached to the east side of the trees in May and June 1987 and remained attached until the trees were harvested in October. All trees had plates or collars attached at 1.8 m, and three trees (approximately 8, 24, and 36 cm dbh) had additional collars or plates attached at 3.5 m. I inserted a copper–constantan thermocouple 2 cm into the sapwood of each tree near the chamber plate or foam collar to measure sapwood temperature. Surface area covered by the chambers was 264 cm^2 for trees greater than 8 cm dbh, 246–291 cm^2 for the small spruces, and 267–377 cm^2 for the small pines.

Carbon dioxide efflux from stems was measured using one of two procedures: an open system with an infrared gas analyzer or a closed system using stored samples analyzed with a gas chromatograph. Midsummer and fall respiration were measured with an open system (Long and Hallgren 1985) with airflow between 5 and 6.7 $mL \cdot s^{-1}$ (Analytical Development Company ADC ASUM) and an infrared gas analyzer (Analytical Development Company ADC LCA2) operating in differential mode. The LCA2 was calibrated daily with a primary standard CO_2 mixture (Matheson). Stem respiration elevated CO_2 concentration 35–250 $\mu mol \cdot mol^{-1}$ for growth measurements and 10–40 $\mu mol \cdot mol^{-1}$ for maintenance measurements.

The remaining respiration measurements were taken using a closed system. I purged the chamber with ambient air at 70 $mL \cdot s^{-1}$ for 120–180 s after the chamber was attached to the tree. The chamber was then sealed from the outside air, and a sample of chamber air (15–20 mL) was withdrawn

and placed into laboratory-evacuated (>99% of air removed) glass tubes. After a measured period of time (3–5 min), a second sample was removed and stored. Carbon dioxide concentration was measured by gas chromatography with an ultrasonic detector using a system designed by Mosier and Mack (1980). Typical precision for this system determined from replicate air blanks was ±2 ppm CO_2. Carbon dioxide flux was calculated from the difference between initial and final concentrations and closure time and adjusted for barometric pressure and chamber temperature. Well-mixed air at the sampling site (354 μmol $CO_2 \cdot mol^{-1}$, SD = 5.6) was used as a standard. The two methods produced comparable respiration estimates. R_m is expressed as $mol \cdot s^{-1} \cdot cm^{-3}$ wet sapwood volume or live-cell volume. R_c and total respiration were expressed as $mol \cdot s^{-1} \cdot cm^{-2}$ chamber surface area.

Respiration was sampled on May 12, June 18, July 3, 4, and 26, August 19, September 15, 17, and 21, and October 6 for the pine, and on June 18, July 5 and 28, August 18, September 16 and 22, and October 5 for the spruce. Maintenance respiration was estimated as CO_2 efflux when trees were not actively growing. To determine the cessation of growth, stainless steel pins were inserted into the trees during the August and September sample periods. The pins wounded the cambium, and when the trees were actively growing, caused wound parenchyma to form and disrupt the normal growth pattern of the xylem (Wolter 1968). Therefore, wound parenchyma and disrupted xylem growth were visible in microtome sections of actively growing trees, but were absent where growth had ceased for the season. Based on these results, active growth had ceased for most trees by August 19. On most sampling dates, all lower chambers were sampled twice (morning and afternoon), and three chambers per species (lower chambers on trees 12, 24, and 36) were sampled five times to estimate the respiration–temperature relationship. Occasionally, weather forced modification of this sampling scheme.

For each sample period, average basal respiration rate (R_0: respiration normalized to a temperature of 0°C) and average daily total respiration (R_d) were calculated. R_0 was calculated as

$$[2] \quad R_0 = \frac{R_t}{\exp(T \ln(Q_{10})/10)}$$

where Q_{10} was the average increase of respiration with a 10°C change in temperature for the three intensively sampled chambers (2.04 for pine, 2.84 for spruce), and T was sapwood temperature for R_t. R_d was calculated as

$$[3] \quad R_d = R_0 \sum_{day} \exp(T \ln(Q_{10})/10)$$

where T was sapwood temperature from a continuously monitored tree (see below for details). Average Q_{10} values for the intensively sampled trees were obtained by fitting the model $R_t = \beta_1 e^{\beta_2 T}$ with nonlinear regression separately for each tree for pooled measurements in July, June and August, and September and October, and averaging the nine values. Q_{10} is $\exp(10\beta_2)$.

Independent variables

Trees were harvested, and 1.5-cm slices were removed from the stem at the top and the bottom of the chamber. Sapwood and heartwood radii were measured to the nearest

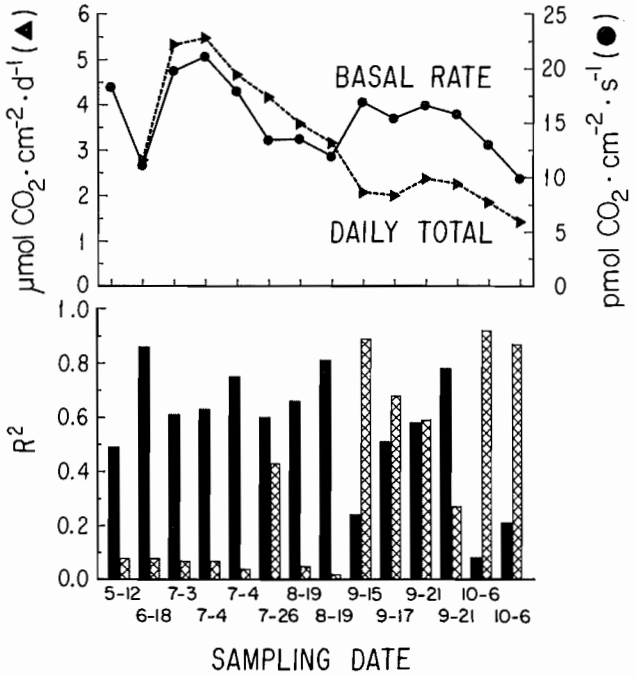

FIG. 1. Average basal respiration rate (R_0, right axis) and daily total respiration (R_d, left axis) for the chamber for pine (CV < 15%), and R^2 for independent regressions of instantaneous respiration and annual dry-weight production (solid) or live-cell volume (hatched) for all sample periods. Number of samples was 9–15; at n = 12, critical value for R^2 is 0.28 at α = 0.05. Sampling dates are given as month-day.

1 mm at four locations for each slice: either side of a diameter through the center of the tree and intersecting the chamber, and either side of a diameter normal to the first. Phloem and 1-year radial growth were measured to 0.1 mm for three cores extracted from the top, middle, and bottom of the chamber locations. I calculated areas using the ellipse formula and sapwood volume for the chamber section using average area and chamber height. Sapwood volume was assigned to the chamber by multiplying the sapwood volume for the cylinder underneath the chamber by the ratio of the chamber arc to the total circumference. Growth and phloem volumes were determined by multiplying average radial growth or phloem thickness in chamber by chamber surface area. Short (25–60 mm) cores of recent sapwood (three per chamber) represent several years of recent growth. These cores were dried and weighed to estimate density of newly produced wood.

The volume of parenchyma ray cells in the sapwood and phloem was estimated for the three trees per species monitored intensively for CO_2. After the final respiration measurement in October, three 5 mm diameter cores were taken from the top, middle, and bottom of each chamber location and placed immediately into a 1% aqueous triphenyl tetrazolium chloride solution. Dehydrogenase in the cytoplasm of living cells reacts with the tetrazolium solution to form a red insoluble compound (Feist et al. 1971). I estimated ray-cell area of thin, freehand tangential sections taken from the outside, middle, and inside of the sapwood radius (three fields per section) using an equal-area dot grid at 150×. Ray-cell area of 25-μm microtome sections was used to check the freehand sections. Live-cell volume is equal

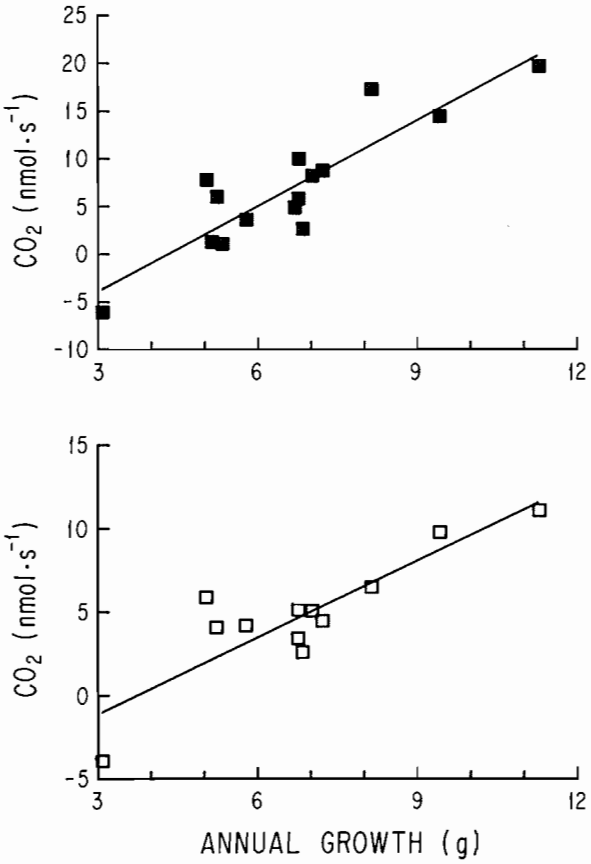

FIG. 2. Instantaneous construction respiration (R_c) for lodgepole pine on July 4 versus annual dry-matter production. Open boxes are morning readings (average temperature = 10.8°C, $R_c = -5.71 + 1.53 \times$ annual growth, $R^2 = 0.76$), filled boxes are afternoon readings (average temperature = 21.3°C, $R_c = -12.9 + 2.99 \times$ annual growth, $R^2 = 0.79$); values are corrected for maintenance respiration.

to sapwood volume times sapwood live-cell fraction plus phloem volume times phloem live-cell fraction.

Statistical analysis

Linear regression was used to relate instantaneous stem respiration rate to the independent variables annual growth and sapwood or live-cell volume. R^2 for these two independent regressions is an index of the contribution of R_c and R_m to total respiration during the measurement period. Because the respiration for each data point is a function of both biomass and temperature, and because temperature was not controlled, I fit separate linear regressions for each species and sample period. Analysis of covariance (SPSS MANOVA, Nie and Hull 1981) was used to test for differences between species in the slope of CO_2 flux with growth or sapwood volume. Separate tests were run for the most stable growth and maintenance measurements.

A nonlinear model was fit to selected R_m measurements using a Levenberg–Marquardt nonlinear algorithm (NLR, SPSS/PC+, Norusis 1988)

$$[4] \quad R_m = \beta_1 V e^{\beta_2 T}$$

where, R_m is maintenance respiration (nmol $CO_2 \cdot s^{-1}$), V is sapwood or live-cell volume (cm^3), and T is temperature (°C). R^2 for the nonlinear regression was calculated as (Kvalseth 1985)

$$[5] \quad R^2 = 1 - \frac{\sum_{i=1}^{n} (Y_i - \hat{Y}_i)^2}{\sum_{i=1}^{n} (Y_i - \overline{Y})^2}$$

Differences in live-cell content between species and wood density among trees were assessed with analysis of variance. Significance level for all tests and regressions was $\alpha = 0.05$.

Temperature modeling

Daily respiration can be estimated using mean biomass temperature and temperature amplitude (Ågren and Axelsson 1980). Because daily midrange air temperature ((max + min)/2) and amplitude are widely available, I compared temperature and amplitude of air with that of sapwood. Sapwood temperature of two large lodgepole pine trees (one tree near the trees measured for respiration, and one in a similar stand at 3200 m elevation) was intensively monitored. I installed copper–constantan thermocouples 3 cm into the sapwood of each tree at 1, 5, 9, and 13 m aboveground. Doubly shielded thermocouples measured air temperature at the same heights. Thermocouples were connected to a data logger (Campbell CR21X) in a standard weather shelter near the monitored trees. Instrument height in the shelter was 1.7 m, and the logger read sapwood, air, and shelter temperatures each minute and recorded the average every 15 min. Trees were monitored June to October 1987; I recorded 92 days of temperature information at the high elevation site and 125 days at the lower elevation site.

Respiration estimated using mean sapwood temperature and amplitude (themselves estimated from air temperature) was compared with respiration estimated using the 15-min sapwood temperatures. Ågren and Axelsson (1980) give daily respiration as

$$[6] \quad R_d = \tau R_0 \exp(\beta T_d) I_0(\beta A)$$

where T_d is mean sapwood temperature, τ is a scaling factor, A is sapwood temperature amplitude, β is $\ln(Q_{10}/10)$, and $I_0(\beta A)$ is a modified Bessel function of zero order. An approximation of $I_0(x)$ with $x < 2$ with error less than 1% (Ågren and Axelsson 1980) is

$$[7] \quad I_0(x) = 1 + 0.25x^2 + 0.016x^4 + 0.0004x^6$$

The R_d estimated with [6] was compared with

$$[8] \quad R_d^{\bullet} = 900 R_0 \sum_{i=1}^{96} e^{\beta T_i}$$

where T_i is the 15-min temperature for time period i. For this comparison, R_0 was 1 and β was 0.072.

Seasonal estimates

To check the consistency of measurements of R_t, I estimated total respiration for a 100-d growing season for the tissue under the lower chambers of the intensively sampled trees. The growing season was partitioned into periods centered around the respiration samples. Respiration for each period was estimated using average R_0 for all measurements within the period to compute R_d in [3], with a separate temperature sum for each day in the period. Q_{10} for the model was 2.04 for pine and 2.84 for spruce. I compared this seasonal estimate with R_m estimated from pine sapwood volume [4] and daily temperature sum, and con-

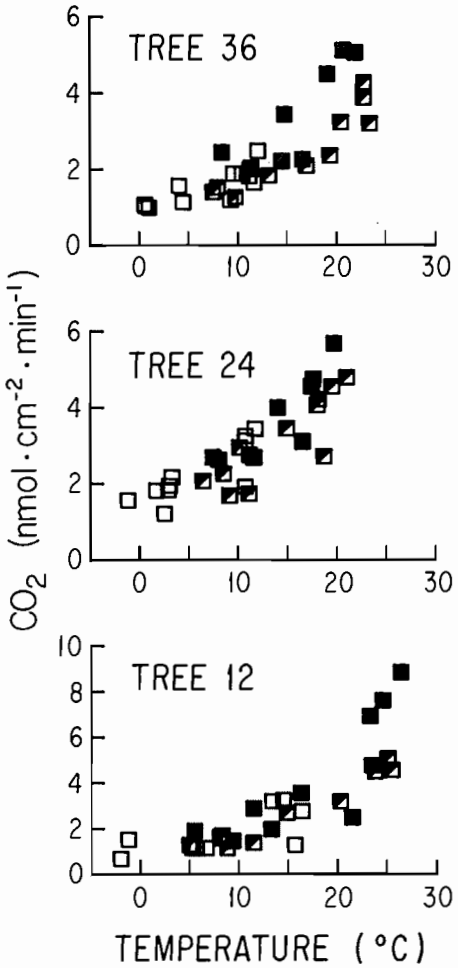

FIG. 3. Unadjusted total respiration (R_t) for intensively sampled lodgepole pine: fall, open boxes, Q_{10} = 2.3; June or August, half-filled boxes, Q_{10} = 1.8; July, filled boxes, Q_{10} = 2.0.

struction respiration (R_{c*}) estimated as a constant fraction of annual dry matter growth (0.25 g C/g C constructed, Chung and Barnes 1977).

Results

Live-cell volume

Average volume of living ray parenchyma cells in xylem differed significantly among species (5.0% for pine, 5.7% for spruce, $p < 0.01$) and among trees within species ($p = 0.03$). Differences among trees within species were not substantial and were greater for pine than for spruce. Volume of living parenchyma in phloem was 7.4% for pine and 8.4% for spruce; these means were not significantly different ($p = 0.10$). Live-cell content of phloem represented 13% of total living cells in sapwood plus phloem for pine and 19% for spruce.

Annual growth and sapwood volume were not correlated for the chambers ($r = 0.07$, $p = 0.80$ for pine; $r = 0.11$, $p = 0.69$ for spruce), but sapwood volume was correlated with phloem volume ($r = 0.53$, $p = 0.04$ for pine; $r = 0.81$, $p < 0.01$ for spruce).

Respiration: pine

R_t was highly correlated with annual wood production during growth, and with sapwood, phloem, and live-cell

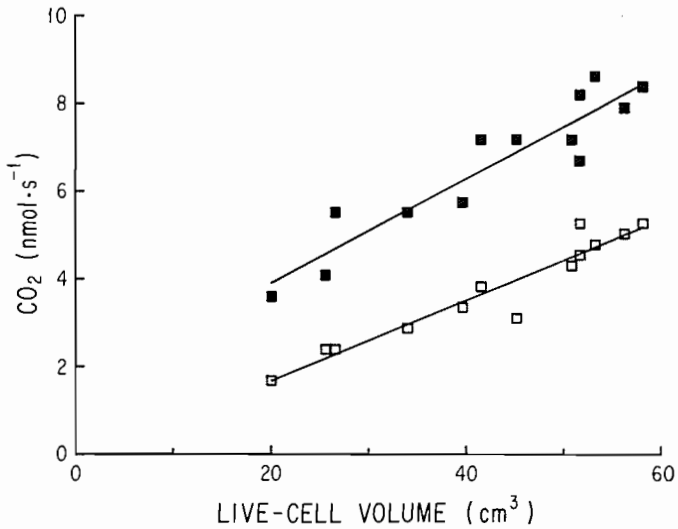

FIG. 4. Maintenance respiration (R_m) for lodgepole pine on October 6 at an average temperature of 0.5°C (open boxes, $R_m = -0.16 + 0.0918 \times$ live-cell volume, $R^2 = 0.92$, standard error of the estimate (SEE) = 0.36) and at an average temperature of 13.0°C (filled boxes, $R_m = 1.52 + 0.119 \times$ live-cell volume, $R^2 = 0.87$, SEE = 0.60).

volumes after the end of active cell division (Fig. 1). For this period, sapwood volume accounted for most of the variability in R_t; with sapwood entered in a multiple linear regression, phloem volume never accounted for significant additional variation. R^2 for regressions of R_t and live-cell volume were always about 2% greater than R^2 for regressions of R_t and sapwood volume.

When corrected for sapwood maintenance, instantaneous CO_2 flux from growing lodgepole pine stems estimates R_c. For all samples taken during active cell division, R_c was linearly related to annual dry-matter production ($p < 0.05$, Fig. 2). Negative R_t do not indicate stem photosynthesis, because these stems had sufficient bark to block light. R_m from living cells in sapwood and phloem appeared to have little effect on R_t during active growth. Specific gravity of sapwood differed among trees within species ($p < 0.01$), and correction of volume growth for actual specific gravity increased R^2 for the regressions estimating R_c from annual stem growth by about 0.06. After cell division ceased, R_c appeared to remain an important component of R_t until the October sample.

R_0 varied from 0.010 to 0.022 nmol $CO_2 \cdot cm^{-2} \cdot s^{-1}$, and R_d peaked at 5.5 μmol $CO_2 \cdot cm^{-2} \cdot d^{-1}$ in early July and declined to 2.0 μmol $CO_2 \cdot cm^{-2} \cdot d^{-1}$ by October (Fig. 1). For pine, R_0 was comparable for periods during and after active cell division. Total respiration increased predictably with temperature (Fig. 3).

R_m for the main stem of lodgepole pine was a linear function of live cell volume (Fig. 4). Sapwood, not phloem or cambium, accounted for the differences in R_m because (*i*) surface area was constant among chambers (except for the two smallest trees), (*ii*) phloem live-cell volume was a small proportion of the total, and (*iii*) phloem volume by itself estimated R_m with R^2 20% less than sapwood volume. Two trees (28 and 40 cm dbh) had consistently low (0.5*x*) respiration for their sapwood volume. These trees were the only study trees infected with mistletoe, and I eliminated them from the analysis of R_m for the October sample.

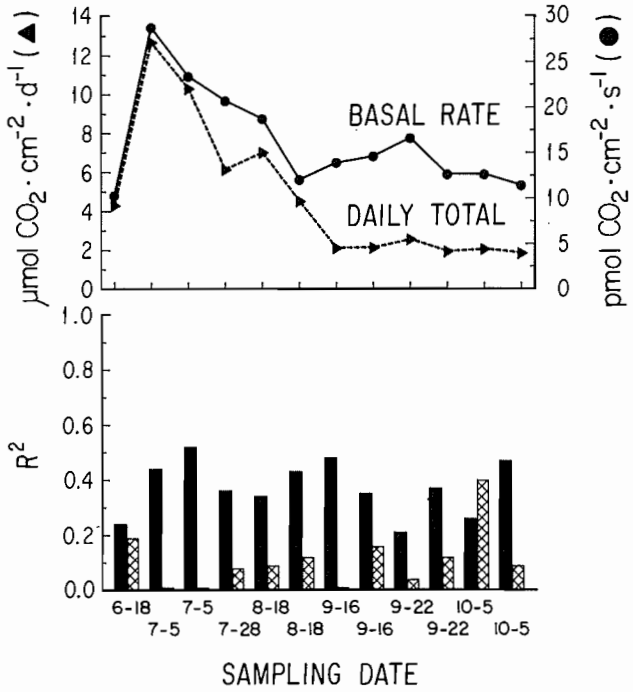

FIG. 5. Average basal respiration rate (R_0, right axis) and daily total respiration (R_d, left axis) for the chamber for spruce (CV < 12%), and R^2 for independent regressions of instantaneous respiration and annual dry-weight production (solid) or live-cell volume (hatched) for all sample periods. Number of samples was 9–15; at $n = 12$, critical value for R^2 is 0.28 at $\alpha = 0.05$. Sampling date is given as month-day.

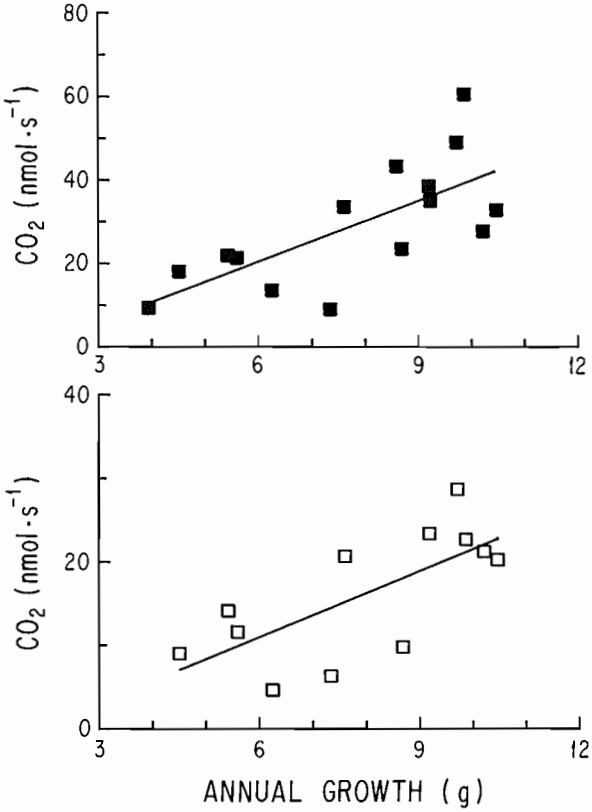

FIG. 6. Instantaneous construction respiration (R_c) for Engelmann spruce on July 5 versus annual dry-matter production. Open boxes are morning (average temperature 11.3°C, $R_c = -4.84 + 2.63 \times$ annual growth, $R^2 = 0.50$), filled boxes are afternoon readings (average temperature = 18.5°C, $R_c = -8.66 + 4.85 \times$ annual growth, $R^2 = 0.51$); values are corrected for maintenance respiration.

Because both growth and maintenance appeared to influence respiration measurements for all but the October sample, I fit eq. 4 to the October sample only. For live-cell volume (cm^3), $\beta_1 = 0.0852$ (SE = 0.0036), $\beta_2 = 0.0669$ (SE = 0.0061), $R^2 = 0.92$, and $n = 26$. For sapwood volume (cm^3), $\beta_1 = 0.00486$ (SE = 0.00025), $\beta_2 = 0.0663$ (SE = 0.0073), and $R^2 = 0.89$. The sapwood volume model predicts sapwood will respire 6.6×10^{-5} kg C · (kg C sapwood)$^{-1}$ · d^{-1} at 15°C.

Respiration: spruce

For Engelmann spruce, R^2 for the regressions of R_t with annual growth or live-cell volume were substantially lower than for pine (Fig. 5). Growth appeared to influence R_t evenly throughout the study, and live-cell volume was significant only for the morning October sample. For most samples taken during active growth, R_c was linearly related to annual dry-matter production (Fig. 6). In midsummer (July 3–5), Engelmann spruce trees had higher R_c per unit of annual growth than did lodgepole pine, and this species difference was weakly significant ($p = 0.06$).

R_0 varied from 0.01 to 0.029 nmol $CO_2 \cdot cm^{-2} \cdot s^{-1}$, and R_d peaked at 12.7 μmol $CO_2 \cdot cm^{-2} \cdot d^{-1}$ in early July and declined to 2.0 μmol $CO_2 \cdot cm^{-2} \cdot d^{-1}$ by October (Fig. 5). During active cell division, R_d was substantially greater for spruce than for pine, whereas rates were similar between species after active cell division ceased. R_t increased with temperature (Fig. 7), but Q_{10} values were much greater than 2.

R_t measured after active cell division ceased was poorly correlated with live-cell volume. For the October sample, respiration measured for larger trees appeared to be unrelated to live-cell volume and responded very slowly to an increase in sapwood temperature (Fig. 8). Trees less than 20 cm in diameter generally responded to temperature increases predictably. R^2 for a linear regression of R_t and live-cell volume was greater than 0.75 for trees less than 20 cm dbh for four of the six fall sample periods ($p < 0.05$). Annual dry-matter production explained some of the variability in R_t in the fall (Fig. 5), but a regression of R_t and phloem volume was never significant. Because of the large variability in the spruce respiration measurements, I did not fit the data to eq. 4. Regression slopes for the relationship between R_m and sapwood volume were not significantly different between Engelmann spruce and lodgepole pine for the October morning samples ($p = 0.89$).

Seasonal estimates

Measured respiration integrated over a 100-d growing season was roughly equal to the sum of R_m estimated from sapwood volume and construction respiration (R_{c*}) estimated as a constant fraction of annual dry-matter growth (0.25 g C/g C constructed) for Engelmann spruce (Table 1). However, integrated measured respiration was substantially lower than $R_{c*} + R_m$ for lodgepole pine. For either species, R_m for the 100-d growing season was about 40% of the sum of R_m and R_{c*} for 12-cm trees and about 65% for 36 cm dbh trees.

Temperature modeling

Sapwood temperatures differed substantially from air temperatures (Fig. 9), probably because of the large heat

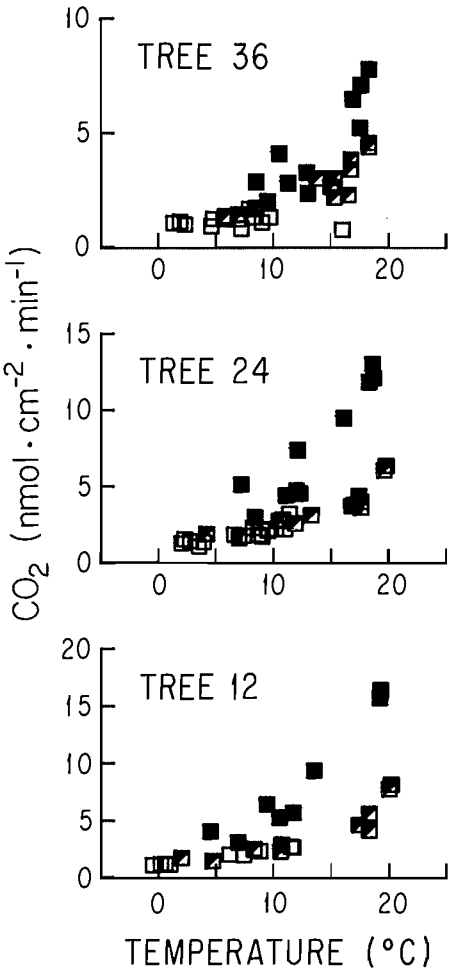

FIG. 7. Unadjusted respiration (R_t) for intensively sampled Engelmann spruce: fall, open boxes, Q_{10} = 3.3; June or August, half-filled boxes, Q_{10} = 2.3; July, filled boxes, Q_{10} = 2.8.

TABLE 1. Integrated measured total stem respiration (R_T) and maintenance respiration estimated from eq. 4 (R_m) for May 20 to August 28 and growth respiration estimated from annual stem growth ($R_{c\cdot}$) for lodgepole pine and Engelmann spruce

Nominal diam. (cm)	R_T	R_m	$R_{c\cdot}$	$R_T-(R_m+R_{c\cdot})$
		Lodgepole pine		
12	0.091	0.066	0.088	−0.062
24	0.116	0.115	0.080	−0.078
36	0.084	0.102	0.055	−0.073
		Engelmann spruce		
12	0.232	0.071	0.098	0.063
24	0.189	0.106	0.089	−0.006
36	0.141	0.126	0.054	−0.040

NOTE: Respiration units are moles CO_2 for the chambers.

capacity of stems. Mean daily temperature was statistically identical for all four thermocouple locations within a tree (ANOVA, p = 0.72, lower tree), so sapwood temperatures within a tree were averaged. Sapwood daily mean temperature was significantly higher than shelter midrange temperature (1.13°C (SE = 0.07) for low-elevation tree, 1.99°C (SE = 0.11) for high-elevation tree), and the two trees differed ($p < 0.01$). Sapwood amplitude was identical for the two trees (mean = 4.21, SE = 0.11, p = 0.40), despite a 1.8°C difference in amplitude of air temperature.

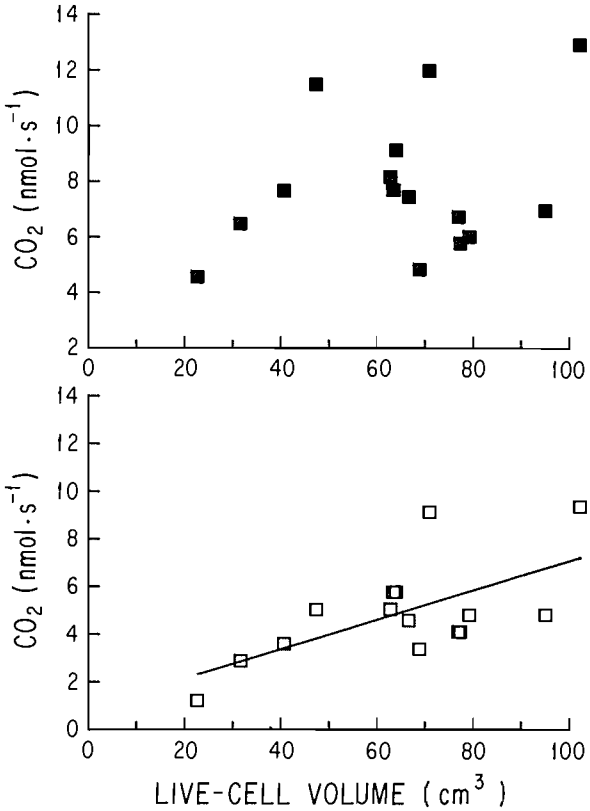

FIG. 8. Maintenance respiration for Engelmann spruce on October 5 at an average temperature of 0.6°C (open boxes, R_m = 0.90 + 0.0616 × live-cell volume, R^2 = 0.41, SEE = 1.69) and at an average temperature of 13.0°C (filled boxes, regression not significant).

Linear regressions efficiently estimated sapwood daily mean temperature (T_s) from shelter midrange temperature (T_a) (T_s = 0.26 + 1.115T_a, R^2 = 0.94 for the lower tree; T_s = 0.007 + 1.137T_a, R^2 = 0.94 for the upper tree). Use of the appropriate T_s and average amplitude in [6] and [7] yields estimates that are unbiased with respect to values calculated using 15-min sapwood temperature in [8] (bias less than 1.5% for the season). Although T_s differed between trees, the use of either equation produced respiration estimates biased less than 7.0% when compared with [8]. In contrast, use of shelter midrange temperature and amplitude in [6] and [7] underestimated [8] by 13.4% for the high-elevation trees and 5.1% for the low-elevation trees for the season.

Discussion

Maintenance respiration is the ecologically interesting component of stem respiration, because annual total maintenance will vary exponentially with temperature. Growth respiration is a fixed cost per unit dry matter built (assuming chemical constituency is the same (Penning de Vries 1975; Chung and Barnes 1977)); therefore, environmental differences will not affect this component. Knowledge of maintenance respiration costs will allow prediction of carbon allocation patterns for species growing in different physiographic locations, as forest stands develop, and in response to global warming.

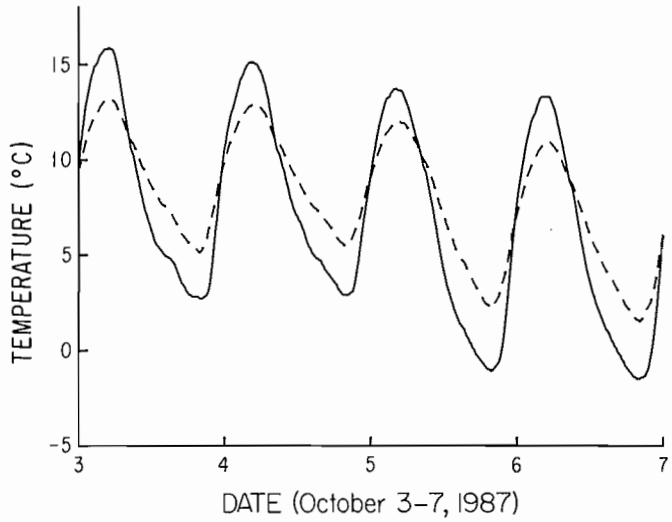

FIG. 9. Average sapwood temperature (broken line) and shelter air temperature (solid line) for lodgepole pine at 2800 m.

For pine, live-cell volume (Havrenek 1981) was the best estimator of stem R_m, and when lodgepole pine was in its maintenance phase (October samples), neither annual growth nor phloem volume explained significant additional variation. Sapwood appeared to be the major contributor to R_m, since phloem contained less than 20% of the living cells in the tree stems and did not significantly decrease variability in R_t. However, R_m per unit live cell may be greater in phloem if the phloem cells contain higher levels of enzymes. D. Sprugel (to be published)[2] also found that R_m for stemwood of young *Abies amabilis* was related to sapwood volume.

R_m of pine sapwood did not vary with tree age or growth rate, and R_m by sapwood was likely the reason Kinerson (1975) reported a poor correlation between stem surface area and respiration of dormant stems. Increased R_m in *Abies balsamea* with thinning found by Lavigne (1988) may result from larger sapwood volumes in trees from thinned stands, rather than increased tissue rates. Two lodgepole pine trees infected with mistletoe had very low maintenance rates for their sapwood volume, but respiration measurements during growth were unaffected. Wanner and Tinnin (1986) found that dark respiration rates (presumably mostly maintenance) of twigs infected with mistletoe were significantly lower than uninfected twigs. Lower maintenance rates probably occur in mistletoe-infected trees because mistletoe lowers carbohydrate reserves and lessens the need for enzymes used to convert starches to sugars. Infected trees expend less carbon, but low R_m rates may only indicate a carbohydrate-deficient tree.

Annual budgets of stem maintenance respiration constructed using surface area rather than sapwood or live-cell volume will produce poor estimates of R_m. The error in estimates of R_m will depend on the sapwood volume and surface area of both the segments measured for respiration and for the entire tree. For example, I estimated daily respiration for 15 lodgepole pine trees for which I had detailed information about sapwood volume and surface area (Ryan 1989). Using the mean rate per unit surface area for the chambers in this study, the ratio of R_m estimated from surface area to R_m estimated from sapwood volume varied from 0.7 to 1.8. If an investigator had monitored only small or large trees to estimate the respiration rate per unit surface area, estimates of R_m using surface area could be as much as 0.4 to 3.2 times R_m estimated from sapwood volume. Sapwood volume can be estimated from tree height, sapwood area, and diameter (Ryan 1989). Using sapwood volume is especially important when estimating R_m for larger trees.

Annual respiration budgets must be constructed with care, since the pattern of temperature in stems differs substantially (but predictably) from air temperature (Saxton and McCaughey 1988), and because respiration responds exponentially to temperature. Estimating daily respiration using the model of Ågren and Axelsson (1980) with estimates of sapwood temperature and amplitude derived from air temperature appeared to produce unbiased estimates.

The apparently low values of integrated measured respiration for pine (Table 1) and the lack of correlation of spruce R_t with live-cell volume in the fall represent anomalous behavior. I believe that removal of CO_2 by the transpiration stream of actively transpiring trees may explain both anomalies.

Pine and spruce differ in their stomatal response to humidity gradients (Kaufmann 1982*a*). Stomatal conductance is high for lodgepole pine, and it is relatively insensitive to changes in the leaf to air humidity gradient (Kaufmann 1982*a*). In contrast, stomatal conductance is lower for Engelmann spruce and it is more sensitive to changes in the leaf to air humidity gradient. In summer, transpiration by pine remains high and fairly constant, whereas transpiration by spruce can be greatly reduced by stomatal closure induced by a midday high leaf to air humidity gradient. With transpiration following this behavior, respiration measurements for pine in summer will be consistently low, and those for spruce will be low in the morning and higher when transpiration ceases in the afternoon. Q_{10} values for the intensively sampled trees were about 2 for pine, a typical value (Sprugel and Benecke 1990). However, Q_{10} for spruce averaged 2.8, indicating afternoon rates were much greater than expected from temperature alone.

Stomatal conductance for both pine and spruce is reduced when air temperature of the previous night goes below 0°C (Kaufmann 1982*b*). For the October 6 pine sample, previous night minimum was −1.8°C and for the October 5 spruce sample, previous night minimum was 3.1°C (Fig. 9). Therefore, transpiration should have been reduced for pine (allowing respired CO_2 to reach the chamber), whereas spruce should have had transpiration that was normal for the daily weather conditions. The lower leaf to air humidity gradient in the fall should promote midday transpiration by spruce (removing CO_2 before it reached the chamber).

Respiration from cell-wall thickening also appeared to complicate the October 5 spruce measurements. Thick spruce bark of the larger trees might also have slowed diffusion of CO_2 and uncoupled measurement from the tissue rates. The lack of increase in R_m for Engelmann spruce (>20 cm dbh) with increasing sapwood volume is likely caused by interference with CO_2 evolution, not changes in the fundamental relationship between R_m and sapwood volume.

[2]D. Sprugel. 1990. Components of woody respiration in young *Abies amabilis* trees. In review.

Negisi (1979) working with excised stems observed apparent changes in stem respiration that varied with the xylem water flux. Removal of CO_2 by the transpiration stream may also account for the lower stem respiration rates found in water-stressed *Pinus densiflora* trees by Negisi (1978), and may explain temperature-independent diurnal variation in stem respiration found by Negisi (1972, 1975) and Edwards and McLaughlin (1978).

Correlation of R_t with seasonal production of wood is not surprising because wood production is the seasonal integral of instantaneous growth. However, in both spruce and pine, R_t was correlated with annual growth well beyond the end of active cell division. Cell-wall thickening can occur for as much as a month beyond active cell division (Sprugel and Benecke 1990), consuming energy for growth. The high correlations of R_t with annual growth indicate that cell-wall thickening is an important component of R_t in early fall for both species. Zabuga and Zabuga (1985), Lavigne (1988) and D. Sprugel (to be published)[2] also found that R_t was correlated with annual wood production. Variation in seasonal growth respiration corrected for temperature was found by Linder and Rook (1984), but not by Lavigne (1987). Lavigne (1987) attributes differences between respiration rates in thinned and unthinned stands to differences in temperature regime, but these differences are probably caused by higher growth rates in thinned stands.

Conclusions

Stem R_m is linearly related to sapwood and live-cell volume for lodgepole pine for trees from 4 to 36 cm dbh, ages of 40 to 230 years, and radial growth rates of 0.4 to 1.4 mm·year^{-1}. Sapwood or live-cell volume, not bole surface area, should be used to estimate stem maintenance respiration. Instantaneous stem R_c is linearly related to annual dry-matter production for both species. Instantaneous R_t may underestimate actual respiratory activity in stems, perhaps because of removal of CO_2 in the transpiration stream.

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