Oecologia (2003) 137:10–21
DOI 10.1007/s00442-003-1316-2

ECOPHYSIOLOGY

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Stem respiratory potential in six softwood and four hardwood tree species in the central cascades of Oregon

Received: 29 October 2002 / Accepted: 5 May 2003 / Published online: 3 July 2003

Abstract Mature and old growth trees of varying sapwood thickness were compared with regard to stem respiration. An increment core-based, laboratory method under controlled temperature was used to measure tissue-level respiration (termed respiratory potential) of ten different tree species. Bark (dead outer and live inner combined), sapwood, and heartwood thickness measurements were used to predict sapwood volume from stem diameter (including bark) for four of the ten species. These predictions of sapwood volume were used to scale respiratory potential to the main-bole level (excluding all branches). On the core level, species that maintained narrow sapwood (8–16% of bole radius) such as *Pseudotusga menziesii*, *Taxus brevifolia*, and *Thuja plicata*, had sapwood respiratory potentials in the lower bole that were 50% higher ($P<0.05$) than species with wide sapwood (>16% of bole radius), such as *Abies amabilis*, *Pinus monticola*, and *Tsuga heterophylla*. This pattern was not observed for inner bark respiratory potential, or for sapwood respiratory potential within the crown. On the main-bole level, respiratory potential per unit volume was inversely correlated to the live bole volumetric fraction (inner bark plus sapwood divided by whole bole volume) (Adj. $R^2=0.6$). Specifically, tree species with 18–20% of the main bole alive potentially respired 1.3–3 times more per unit live bole volume than species with over 40%, suggesting that the live bole was less metabolically active in tree species that maintained large volumes of sapwood.

Keywords Stem respiration · Sapwood volume · Inner bark (phloem and cambium) · Xylem · Scaling-up

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Introduction

Stem respiration is an important flux in ecosystem respiration, but difficult to measure directly at the whole tree or ecosystem level. Scaling tree stem respiration measurements to the ecosystem level has received much attention over the last 25 years (e.g., Linder and Troeng 1981; Ryan and Waring 1992; Lavigne and Ryan 1997). Stem respiration's contribution to total autotrophic respiration of forests has been reported to range from 12% (sub-alpine *Pinus contorta* ssp. *latifolia*, Ryan and Waring 1992 and Australian *Pinus radiata* D. Don, Ryan et al. 1996) to 42% (temperate forests, Waring and Schlesinger 1985). Sample respiration measurements, acquired using infrared gas analysis (IRGA) chambers at one or two positions on tree stems, are scaled up to predict whole-stem and stand level respiration rates (e.g., Kinerson 1975; Ryan et al. 1995; Edwards and Hanson 1996). Uncertainty in scaling to the whole-stem level may arise if respiration is assumed to be uniform throughout stems (Stockfors 2000). Small-scale, tissue-based, measurements have indicated significant variation in respiration within stems, with tissue in close proximity to apical (treetop) and/or cambial (inner bark) meristems respiring at higher rates than other areas in the stem. However, given the greater volume of respiring tissue at the tree base versus the treetop (as a result of larger basal stem diameter), tissue-level respiration rates at the tree base have greater influence on whole stem respiration than tissue-level rates near the top (Pruyn et al. 2002a).

Other uncertainties that exist in scaling to the whole-stem level are associated with predicting the tree's inner bark and sapwood volume. Although Pacific Northwest, species-specific values of inner bark thickness are available in the literature (Smith and Kozak 1971), as are equations for predicting sapwood thickness (Lassen and Okkonen 1969) and bole volume (Brown 1962; Chambers and Foltz 1979), they are primarily based on measurements near breast height. Allometric relations for sapwood volume versus stem diameter were developed for *Pinus* spp., *Populus* spp. and *Picea mariana* (Gower et al.

1993, 1997) by destructively sampling stems, measuring sapwood cross-sectional area and stem lengths, and using frustum equations to calculate volume (Husch et al. 1972). However, because of the intensive nature of this work, these studies only measured 18–40 trees on 2–3 different sites, thus limiting the scope of inference for the equations.

Further, the relationship between whole-stem sapwood volume and stem respiration is not well understood. Strong, positive relationships have been developed between the volume of sapwood under an IRGA chamber and the efflux of CO_2 from the bole (nmol s^{-1}) (R^2=0.72, *Abies amabilis*, Sprugel 1990; R^2=0.85, *Pinus ponderosa*, Ryan et al. 1995). Thus, trees with large sapwood volume likely have high values of net CO_2 efflux (nmol s^{-1}), as compared to trees with small sapwood volume. However, stems with larger proportions of live bole do not necessarily have higher respiration rates per unit volume than stems with lower proportions. One hypothesis is that there is an inverse relationship between stem respiration rate (per unit volume) and the live bole volumetric fraction (inner bark plus sapwood divided by whole bole volume). Thus, trees of a given size/age class may have high stem respiration rates (per unit volume), or a large live bole volumetric fraction, but not both. Conversely, trees may have a positive relationship between these two variables. Alternatively, stem respiration may not be related to live bole volume and may instead be regulated by variables such as leaf area / sapwood area ratio, tree size, or tree age.

In the current study, we asked whether small-scale differences in respiration within stems and among species of varying sapwood width were evident at the main-bole level (excluding all branches). The first objective was to quantify potential stem respiration on the tissue level in six softwood and four hardwood tree species of the Pacific Northwest. Second, a series of equations were developed to predict inner bark and sapwood volume of individual trees from stem diameter at breast height to enable scaling tissue-based respiration rates to the main-bole level. Finally, the relationship between species-specific stem respiratory potential and live bole volume (inner bark plus sapwood) was analyzed and discussed in terms of its significance to stem physiology and ecosystem function.

Materials and methods

Study areas

Respiration measurements were conducted on trees sampled from various sites in the H.J. Andrews Experimental Forest, located in the central Cascade Range, Oregon, USA (N 44°, W 122°, elevation 410–1,630 m). Sapwood thickness and tree volume measurements were obtained from the Oregon State University's Department of Forest Science Databank (FSDB, http://www.fsl.orst.edu/lter/). Sapwood thickness measurements were conducted in and near the H.J. Andrews Experimental Forest in study areas dominated primarily by Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] (Dyrness et al. 1974). Tree volume measurements were conducted on trees sampled from reference stands of mature and old growth forests throughout the Pacific Northwest region (Acker et al. 1998).

The H.J. Andrews Experimental Forest is in the 6,400 ha drainage basin of Lookout Creek, a tributary of the Blue River and the McKenzie River. Generally representative of the mountainous landscape of the Pacific Northwest, the Andrews Forest contains extensive examples of the region's conifer forests (including old-growth stands ~500 years old) and associated wildlife and stream ecosystems. Forest communities in the central portion of Oregon's western Cascades vary according to moisture and temperature gradients. For example, the *T. heterophylla* zone occupies an elevational range of 300–1050 m, whereas the *A. amabilis* zone ranges from 1,050–1,550 m (Dyrness et al. 1974).

Respiratory measurements—field methods

Respiratory potential was estimated from 12 mm increment cores extracted from breast height of standing stems (1 m from ground) of mature trees of ten species (Table 1). Unless indicated otherwise,

Table 1 Ranges of age and diameter for the ten tree species sampled at 1 m, and ranges of height measurements for the four tree species sampled at two additional stem positions within the crown, all from the H.J. Andrews Experimental Forest in the central Cascades, Oregon. Acronyms listed are used in Tables and Figures to follow

Species sampled at 1 m (n=8)	Acronym	Age (years)	Diameter (cm)
Abies amabilis (Dougl.) Forbes	ABAM	170–370	43–80
Acer macrophyllum (Pursh.)	ACMA	15–47	26–49
Alnus rubra (Bong.)	ALRU	12–31	13–35
Castanopsis chrysophylla (Dougl.)	CACH	37–58	8–26
Pinus monticola (Dougl.)	PIMO	105–120	55–60
Populus trichocarpa (Torr. & Gray)[a]	POTR	25–40	37–75
Pseudotsuga menziesii (old) (Mirb.) Franco	PSMEo	300–600	115–157
Pseudotsuga menziesii (young)	PSMEy	13–23	18–28
Taxus brevifola (Nutt.)	TABR	51–81	14–41
Thuja plicata (Donn. ex. D. Donn)	THPL	100–500	68–142
Tsuga heterophylla (old) (Raf.) Sarg.	TSHEo	107–220	53–100
Tsuga heterophylla (young suppressed)	TSHEy	26–100	11–29
Species sampled within the crown (n=4)	Total height (m)	Height to base of live crown (m)	Height to 80% of total tree height (m)
Abies amabilis (Dougl.) Forbes	40–46	16–20	33–41
Pseudotsuga menziesii (old) (Mirb.) Franco	40–53	20–32	35 –42
Thuja plicata (Donn. ex. D. Donn)	21–36	8–14	17–26
Tsuga heterophylla (old) (Raf.) Sarg.	38–45	17–26	28–40

[a] Sample size (n) equaled 4 because of low species abundance

samples were collected in the dormant season: early March of 1999 and 2000, and late September of 2000 and 2001. All sampled trees were free of major stem deformities, or obvious signs of disease. Sampling dates were selected to capture maintenance respiration and avoid growth respiration (McCree 1970; Thornley 1970). Three (March 1999)—four (March, September 2000 and September 2001) trees of each species were selected randomly within the H.J. Andrews Experimental Forest from sites where they grew. Different individuals were selected on each sampling date, except for species that were not abundant in the forest (e.g. *Pinus monticola*), for which the same individuals were sampled each time. Also, three–four younger trees (same number per date as older trees) were selected from each of the two species, *Pseudotsuga menziesii* and *T. heterophylla*. Because the younger *T. heterophylla* were growing in the understorey of mature/old-growth stands, they were considered suppressed, unlike the younger *P. menziesii*, which grew on the edges or in canopy gaps.

In four of the ten species (*A. amabilis*, *P. menziesii*, *Thuja plicata*, and *T. heterophylla*) sampled in September of both years, respiratory potential was measured at two additional stem heights (n=3 trees per species, 2000 and n=4, 2001). In these trees, increment cores were extracted at the base of the live crown and at 80% of maximum tree height in addition to breast height. Because of tree climbing restrictions, the same trees were sampled in both years. Tree age and stem diameter were recorded on trees sampled in March and September of 2000. Tree age was determined from cores taken at 1 m stem height and stem diameter including bark was measured at each stem height of core extraction. Stem heights to the crown samples and treetops (Table 1) were measured using a Forest Pro hypsometer (Laser Technology, 7070 Tucson Way, Englewood, CO 90112, USA).

Sapwood thickness—field measurements

Sapwood thickness was used to calculate sapwood volume in four of the ten tree species (*A. amabilis*, *P. menziesii*, *T. plicata*, and *T. hetrophylla*). Approximately ten trees per stand were measured for a representative sample of the diameter classes present. For *A. amabilis* (n=24 trees) sapwood thickness data were taken from Harmon (1992). For *P. menziesii* (n=600), *T. plicata* (n=50), and *T. heterophylla* (n=200) data were taken from FSDB: TV0404, TV0504, and TV0524. For each tree, sapwood thickness was estimated from two increment cores taken at breast height (Means et al. 1999). The sapwood boundary was identified by eye and defined according to Hillis (1987) as the woody tissue extending from the first growth ring after the inner bark (living phloem and cambium) to the last sapwood ring prior to the transition zone (one or two, lighter-colored growth rings adjacent to the heartwood). The heartwood in these four species was clearly indicated by a lighter color and/or higher moisture content as compared to the neighboring, darker and/or drier heartwood.

Sapwood volume—field measurements

Sapwood volume was calculated for the same four species as for sapwood thickness. To enable these calculations, the outside dimensions of individual standing trees were determined using an optical dendrometer (FP15, Barr and Stroud, Anniesland, Glasgow, W.3, Scotland). It was used to determine the diameter and length of 5–6 segments along each tree's stem. Bark thickness (including both the dead outer bark and the living inner bark) was determined at breast height (1.25 m), and by assuming the bark to wood ratio was constant along the bole, the diameter of wood (without bark) was calculated. Approximately 30 trees per stand were measured for a representative sample of the diameter classes present. These stem diameter data for *A. amabilis* (n=140 trees), *P. menziesii* (n=220), *T. plicata* (n=50), and *T. heterophylla* (n=350) were taken from FSDB TV0096.

Respiratory measurements—laboratory methods

All extracted cores were analyzed within 1 week of sampling. Twenty-four hours prior to measurement, cores were divided into three segments: inner bark and outer and inner sapwood. Any green tissue (i.e., photosynthetic) that was visible just underneath the outer surface of the inner bark samples was carefully removed with a razor blade. Outer and inner sapwood samples were obtained by dividing sapwood into two equal radial lengths. A visible sapwood/heartwood boundary (evidenced by color and/or moisture change in the wood) was not apparent in *Acer macrophyllum*, *Alnus rubra* or *Populus trichocarpa*. Because these trees were young in age (<30 years old on average), the assumption was made that there was no heartwood present. However, because *A. rubra* and *P. trichocarpa* are known to have an indistinct sapwood/heartwood boundary (Panshin and de Zeeuw 1980), there was a possibility that heartwood rings were present in the respiring inner sapwood samples. To justify the heartwood/sapwood separation, respiratory potential was measured in heartwood samples (5–10 growth rings in length, proximal to the transition zone) from all species from the March 2000 sampling, except the three without visible heartwood mentioned previously. Data revealed almost no CO_2 evolution from heartwood (<0.01 nmol CO_2 cm^{-3} s^{-1}, M.L. Pruyn, unpublished data). Although *Castanopsis chrysophylla* was described by Panshin and de Zeeuw (1980) as not having a distinct sapwood/heartwood boundary, in the current study this species showed a distinct color change to darker pink in the several growth rings closest to the pith, and these pinkish rings had no significant respiratory potential.

Segmented core samples were weighed, wrapped tightly in plastic, and then stored at 25°C overnight to allow metabolic activity to stabilize (Goodwin and Goddard 1940). Immediately prior to measurement, core segments were re-weighed and placed in 25 ml vials, which were then sealed with gas-tight rubber septa. Respiration of core samples was measured using a previously developed protocol, which was proven reliable and repeatable (Pruyn et al. 2002b), and free of potential artifacts from measurement conditions (e.g. oxygen depletion in the vials, or non-sapwood parenchyma cell sources of CO_2 production). To determine a rate of CO_2 production, CO_2 concentration within vials was measured with a Hewlett-Packard (5700A) gas chromatograph (GC, Hewlett Packard, Rt. 41, Avondale, PA 19311, USA) immediately after closing the vials and again after an incubation period of 6 h at 25°C. Details of GC analysis, calculation of respiratory potential (nmol CO_2 cm^{-3} s^{-1}), and comparisons to other methods of measuring respiration (e.g. infra red gas analysis) were reported in Pruyn et al. (2002a, 2002b). Immediately following the GC analysis, core segments were weighed a third time. Changes in the three successive wet masses verified that water loss was low (1–3%) between sampling and measurement. Fresh volume of core segments was estimated as the water displaced when samples were submerged (D2395, ASTM 2001). From this point onward, the reported values are referred to as respiratory potential, rather than respiration rate, because measurement conditions of these excised samples were probably different from those in the tree.

Estimating sapwood and inner bark volumes on the main-bole level

The following series of equations were used to scale core-based respiration to the main-bole level. Branches were excluded from the calculations because resources were not available to estimate their respiration or allometrics for trees in this region. These equations were only performed on the four species for which we had respiratory measurements at multiple heights (i.e. *A. amabilis*, *P. menziesii*, *T. plicata*, and *T. heterophylla*).

Sapwood thickness

Mean sapwood thickness (S_T) was calculated for each stem diameter class, including bark at breast height, according to Lassen and Okkonen (1969). For stem diameters including bark at breast

height (D_B) that were less than 76.2 cm, diameter classes were every 2.54 cm; and for D_B greater than 76.2 cm, diameter classes were every 12.7 cm. The D_B and S_T were then averaged for each D_B class and the following two equations were applied to the data:

$$S_T = \beta_0 + (\beta_1 \cdot D_B^{-1}) \quad (1)$$

$$S_T = \beta_0 \cdot (1 - e^{-\beta 1 \cdot D_B}) \quad (2)$$

After determining that Eq. 2 was better suited for the data, it was applied to trees from the sapwood volume database to calculate sapwood thickness along stems for three of the four species (*P. menziesii*, *T. plicata*, and *T. heterophylla*).

The parameters for Eq. 2 were estimated for *A. amabilis* because there was no available data for S_T versus D_B for this species. Mean sapwood thickness for *A. amabilis* was estimated from logs that were approximately 50 cm in diameter (Harmon 1992). This estimate was assumed to be the maximum sapwood thickness (β_0) for this species (the relationship between S_T and D_B for the three other species from the current study suggested that maximum S_T was reached at a D_B of <50 cm). For the rate of increase of sapwood thickness (β_1) in *A. amabilis*, the same value was used as for *T. heterophylla*.

Sapwood volume

To calculate the sapwood volume in trees, S_T was estimated at various heights along stems. Two different assumptions were used to estimate S_T along stem heights of the four species: (1) S_T was constant along stems and equal to S_T at D_B, and where S_T > stem diameter, heartwood thickness equaled zero; (2) S_T tapered along stems and was a function of stem diameter at the point of estimation. For each assumption of S_T along stem heights, S_T was subtracted from the wood radius (without bark) from both ends of each log (measured via the optical dendrometer) to obtain heartwood radius. Using heartwood radius, total wood radius, and log length (measured via the optical dendrometer) in the formula for the frustum of a right circular cone, heartwood volume and total wood volume for a series of logs along each stem were then calculated. Near treetops, heartwood radius approaches zero, and thus a cone formula was used to calculate heartwood volume for the top log (closest to treetop) from the series of logs along stems. However, because there were no data for the true height of the heartwood within the top log, it was assumed that the height for the heartwood cone was equal to top log's length. Heartwood volume was subtracted from wood volume to calculate sapwood volume for each log, and sapwood volume of each log along stem lengths was summed to calculate sapwood volume for entire trees. Sapwood volumes calculated from each assumption of S_T along stem heights were compared to determine if / how much they differed from one another. Sapwood volume (S_V) was regressed on stem diameter including bark at breast height (D_B) using the following equation:

$$\ln S_V = \beta_0 + \beta_1 \cdot \ln D_B + \beta_2 \cdot (\ln D_B)^2 \quad (3)$$

Cumulative relative sapwood volume and relative stem height

To associate the core respiratory potential measured at each stem height with a portion of the stem's sapwood volume specific to each height, relative cumulative sapwood volume (S_{VC}, sapwood volume below a given height / total sapwood volume) was plotted against relative stem height (H_C, given height / total tree height) for each of the four tree species. From the sapwood volume database (FSDB, cited above), a height from each stem was randomly selected and then cumulative sapwood volume was calculated as the sum of each log's sapwood volume from the tree base up to the selected height. Relative cumulative sapwood volume (S_{VC}) was then regressed on relative stem height (H_C) using the following equation:

$$S_{VC} = \beta_0 + \beta_1 \cdot H_C + \beta_2 \cdot H_C^2 \quad (4)$$

Inner bark thickness and volume

Equation 2 was also used to determine inner bark thickness for trees of varying stem diameter including bark at breast height (D_B) for these four species. However, because there were no data to estimate the parameters for this curve using regression, the average inner bark thickness for each species was taken from Smith and Kozak (1971) and used for β_0 (i.e. *A. amabilis*, 0.33 cm; *P. menziesii*, 0.60 cm; *T. plicata*, 0.33 cm; *T. heterophylla*, 0.35). The species-specific coefficients generated from the sapwood thickness curves were used for the rate of increase of inner bark thickness (β_1).

Then, using the same tree data and methods used for estimating sapwood volume (Eq. 3), inner bark volume was calculated. However, in this case, inner bark thickness was added to the stem wood radius. Next, bole volume (including inner bark, sapwood and heartwood) was calculated for each log along the stem's height. Subtracting sapwood and heartwood volume from bole volume, an estimate for inner bark volume was obtained. Relative cumulative inner bark volume (B_{VC}) was predicted from relative stem height (H_C) using the same methods as for sapwood (Eq. 4).

Scaling core-based respiratory potential to the main-bole level

Using Eq. 3, total inner bark volume and sapwood volume were calculated for each tree from which we took respiratory measurements. Then, using Eq. 4, cumulative relative volume (for both inner bark and sapwood) was calculated to the base of the live crown, to 80% of maximum tree height (near treetop), and to the treetop. Using the results from Eqs. 3 and 4, inner bark and sapwood volume was calculated for each stem segment between core extraction points (i.e. tree base to base of the live crown, base of live crown to near treetop, and near treetop to treetop). To see whether the relative proportion of these three stem segments affected the estimates of whole tree respiratory potential, the tree stems were also proportioned as follows: (1) each segment was 1/3 of the tree height, (2) the bottom stem segment was 1/2 the tree height and the top two segments 1/4, and (3) the bottom two stem segments were 1/4 the tree height and the top segment 1/2.

To determine the proportion of outer sapwood to inner sapwood, the total wood and heartwood volumes were calculated for each height position using the same methods as for total sapwood from above. The volume of inner sapwood and heartwood was calculated using heartwood radius plus half the sapwood thickness. Inner sapwood and outer sapwood volumes were each calculated by subtracting out the adjacent, interior wood volume. The ratio of outer sapwood to inner sapwood volume was then calculated for each vertical position of each species. These ratios ranged from 1.0 to 1.4, with the larger ratios linked to trees of wider sapwood thickness and/or higher stem heights. The ratios were then used to estimate outer sapwood and inner sapwood volumes for each height position of each tree.

To calculate weighted respiratory potential for the entire tree, the core-based measurements were first multiplied by the corresponding volume of tissue (inner bark, outer sapwood, or inner sapwood) for each height position on stems. The potential amount of CO_2 produced by each tissue radial position was then summed from each stem segment along the tree's height. To calculate a weighted respiratory potential per unit volume for each species, the total potential CO_2 was divided by total live bole volume (inner bark plus sapwood) of the tree. Data from the sapwood volume database (FSDB, cited above) were used to calculate the species-specific, live bole volumetric fraction (i.e. inner bark plus sapwood volume divided by total bole volume), which was then regressed on stem diameter including bark at breast height. An equation of the same form as Eq. 3 was fit to the data for each of the four species, and then used to estimate the live bole volumetric fraction for the trees from which we took the respiratory measurements. Weighted respiratory potential per unit volume was also calculated for *P. menziesii* (young) and *T. heterophylla* (young, suppressed) using the breast height measurements of core respiratory potentials to scale to the main-bole level. Respiratory measurements of these

young trees were scaled to the main-bole level using the predictive volume equations of their older, species equivalents. Respiratory potential per unit volume for mature *Pinus ponderosa* (220 years old) was obtained from Pruyn et al. (2002a) and scaled to the main-bole level as in the other species (n=50 trees for predictive volume equations and n=6 trees for live bole respiratory potential). The weighted respiratory potential per unit volume was then plotted against the live bole volumetric fraction for each species. For young *P. menziesii* and *T. heterophylla*, the live bole volumetric fraction was estimated from trees of 20–25 cm stem diameter including bark at breast height.

Statistical analysis

All data were analyzed in Statistical Analysis Systems software, release 7.0 (SAS Institute 1998). The Shapiro-Wilk W-test was used to determine whether the response variables were distributed normally. A transformation (square-root or natural log) was performed when necessary to meet assumptions of normality and constant variance. Means were reported ± standard error (SE), except transformed means, for which confidence intervals were used. Within a specific table or figure, if confidence intervals were required for one variable (because of transformations), they were presented for all. Sample size (n) in methods, tables, and figures was reported as number of trees per species.

To compare core respiratory potential among the three tissue radial positions of the ten tree species from the current study, least squares means (LSMEANS) were generated using PROC MIXED analysis, with randomized block design and strip-plot (split-block) treatments (Little and Hills 1978; Milliken and Johnson 1984). For the breast-height comparisons, trees were blocks and the effects of tissue radial position, species, and their interaction were tested for each sampling date separately. The same block design was used for the multiple stem height comparisons, except that tissue vertical position was added as both a main effect and interaction terms. Multiple pair-wise comparisons (t-tests) among stem tissue radial and/or vertical positions and species were conducted using Fisher's protected least significant difference (FPLSD) procedure (Fisher 1966).

Non-linear regression analysis in Sigma Plot, release 6.0 (SPSS, 1986–2000) was used to describe the relationship between sapwood thickness and stem diameter including bark at breast height. Linear regression analysis in SAS-Assist was used to describe the relationships between (1) sapwood volume and stem diameter including bark at breast height, (2) relative cumulative sapwood volume and relative stem height, and (3) live bole volumetric fraction and stem diameter including bark at breast height. Linear regression analysis was also used to describe the relationship between main-bole net CO_2 efflux and live bole volume and between main-bole respiratory potential and live bole volumetric fraction.

Results

Comparison of core respiratory potential among species

At breast height the trends in core respiratory potential (nmol CO_2 cm^{-3} s^{-1}) among tissue radial positions and among species were repeatable with respect to year and date sampled, with consistent, significant differences among species for all dates tested (Table 2, P<0.0001). For the species examined, inner bark respiratory potential was 2–11 times higher than that of outer sapwood, and outer sapwood respiratory potential was 1.3–2 times higher than inner sapwood (Table 2). There were no significant differences between the respiratory potential for old versus young trees of either *Pseudotusga menziesii* or *T. heterophylla*.

The effects of tissue radial position and the interaction between species and tissue were significant for year 2 of March and both years of September (P<0.03). *A. rubra* and *A. macrophyllum* had the highest inner bark respiratory potential of the ten species sampled (30–60% higher than the other species, Table 2). Inner bark respiratory potentials were also notably higher in *Pinus monticola*, *Populus trichocarpa* (September, year 2) and *C. chrysophylla* (September, year 2) than that of the other species. This pattern among species was not repeated in outer sapwood, where the respiratory potentials of *T. plicata* and *Taxus brevifola* were 20–80% higher than the other species. Older *P. menziesii* and the hardwoods, *A. macrophyllum*, *A. rubra*, and *C. chrysophylla* also had notably higher outer sapwood respiratory potentials than the other species (Table 2).

There were no consistent, significant trends in respiratory potential among the three stem heights in any of the four species *A. amabilis*, *Pseudotusga menziesii*, *T. plicata*, and *T. heterophylla*. The effect of vertical position and the interaction of species, vertical position, and tissue were significant in year 1 (P=0.002), but not year 2 (P=0.3). However, the interaction between species and vertical position was significant for both years (P<0.02). The most evident trend (although not significant for all four species) was of increasing respiratory potential from tree base to treetop in the outer sapwood (Table 3). At each vertical position, *T. plicata* outer sapwood respiratory potential was 20–50% higher than the other species with the exception of near treetop, year 2 (Table 3).

Estimating sapwood and inner bark volumes on the main-bole level

Sapwood and inner bark thickness

Many of the Eq. 1 parameters were not significant and did not describe the relationship between sapwood thickness (S_T) and diameter including bark at breast height (D_B) for *P. menziesii*, *T. plicata*, and *T. heterophylla* (P>0.05, data not shown). In contrast, for Eq. 2 the parameters were all significant (Table 4) and the adjusted R^2 values were higher [i.e. *P. menziesii* (Eq. 1) 0.72, (Eq. 2) 0.76; *T. plicata* (1) 0.26, (2) 0.34; *T. heterophylla* (1) 0.53, (2) 0.62]. Sapwood thickness increased with stem diameter including bark at breast height until a certain stem diameter was reached, after which point sapwood thickness remained relatively constant (Fig. 1).

Sapwood and inner bark volume

Sapwood volume (S_V), calculated using stem diameter from breast height (assumption one of S_T along stem heights), was significantly higher than S_V calculated using

Table 2 Breast height respiratory potential (nmol CO_2 cm^{-3} s^{-1} at 25ºC; except March, year 1 at 15°C) of cores for the tree species sampled from the H.J. Andrews Experimental Forest in the central Cascades, Oregon. LSMEANS and 95% confidence intervals from Strip plot analysis in PROC MIXED (n=4 trees; except March, year 1n=3). Different trees of each species were sampled for 2 consecutive years for both March and September samplings. Significant differences among means from Fisher's protected least squares differences (P<0.05). For all comparisons, each season (March or September) and each year (1 or 2) were analyzed separately. Different lowercase letters represent differences among tissue radial positions within each row. Different uppercase letters represent differences among species within each column

Species	March			September		
	Inner bark	Outer sapwood	Inner sapwood	Inner bark	Outer sapwood	Inner sapwood
ABAM						
Year 1	–	–	–	^{a}1.1 (0.6, 2.1)^{AB}	^{b}0.25 (0.13, 0.46)^{ADE}	^{c}0.06 (0.03, 0.12)^{A}
Year 2	–	–	–	^{a}1.5 (1.0, 2.4)^{A}	^{b}0.24 (0.15, 0.37)^{ABE}	^{b}0.14 (0.08, 0.23)^{A}
ACMA						
Year 1	–	0.15 (0.10, 0.19)^{BC}	–	^{a}2.6 (1.4, 1.8)^{B}	^{b}0.30 (0.16, 0.56)^{ACE}	^{c}0.04 (0.02, 0.07)^{A}
Year 2	^{a}2.5 (1.9, 3.3)^{AB}	^{b}0.50 (0.38, 0.66)^{AC}	^{c}0.29 (0.22, 0.38)^{AB}	^{a}3.0 (1.9, 4.7)^{B}	^{b}0.31 (0.20, 0.48)^{ABD}	^{c}0.10 (0.06, 0.15)^{AC}
ALRU						
Year 1	–	0.10 (0.05, 0.14)^{AB}	–	^{a}2.4 (1.3, 4.5)^{B}	^{b}0.28 (0.15, 0.52)^{ACDE}	^{b}0.19 (0.10, 0.36)^{B}
Year 2	^{a}2.9 (2.2, 3.9)^{A}	^{b}0.49 (0.37, 0.65)^{AC}	^{b}0.41 (0.31, 0.54)^{AF}	^{a}3.1 (2.0, 4.9)^{B}	^{b}0.37 (0.24, 0.58)^{AC}	^{c}0.15 (0.10, 0.23)^{AB}
CASH						
Year 1	–	0.15 (0.11, 0.20)^{BC}	–	^{a}1.4 (0.8, 2.6)^{AB}	^{b}0.39 (0.21, 0.72)^{AC}	^{b}0.22 (0.12, 0.40)^{B}
Year 2	^{a}1.2 (0.9, 1.6)^{C}	^{b}0.52 (0.40, 0.69)^{AC}	^{c}0.27 (0.20, 0.36)^{B}	^{a}2.2 (1.4, 3.4)^{AB}	^{b}0.38 (0.24, 0.59)^{AC}	^{b}0.23 (0.14, 0.35)^{BD}
PIMO						
Year 1	–	–	–	–	–	–
Year 2	^{a}2.6 (2.0, 3.4)^{A}	^{b}0.24 (0.18, 0.31)^{B}	^{c}0.12 (0.09, 0.16)^{D}	^{a}1.9 (1.2, 3.0)^{AB}	^{b}0.19 (0.12, 0.30)^{BE}	^{c}0.08 (0.05, 0.13)^{CE}
POTR						
Year 1	–	0.08 (0.04. 0.13)^{A}	–	^{a}0.3 (0.2, 0.5)^{C}	^{b}0.10 (0.06, 0.19)^{B}	^{b}0.10 (0.06, 0.19)^{A}
Year 2	–	–	–	^{a}2.1 (1.3, 3.3)^{AB}	^{b}0.20 (0.13, 0.31)^{BE}	^{c}0.10 (0.06, 015)^{AC}
PSMEo						
Year 1	–	0.12 (0.07, 0.16)^{AB}	–	^{a}1.9 (0.9, 3.9)^{AB}	^{b}0.41 (0.22, 0.75)^{AC}	^{b}0.21 (0.11, 0.38)^{B}
Year 2	^{a}1.8 (1.3, 2.3)^{BC}	^{b}0.36 (0.28, 0.48)^{A}	^{c}0.18 (0.14, 0.24)^{E}	^{a}1.1 (0.7, 1.7)^{C}	^{b}0.36 (0.23, 0.56)^{A}	^{c}0.17 (0.11, 0.26)^{AB}
PSMEy						
Year 1	–	0.12 (0.08, 0.17)^{AB}	–	–	–	–
Year 2	^{a}1.8 (1.4, 2.4)^{BC}	^{b}0.24 (0.18, 0.32)^{B}	^{c}0.13 (0.10, 0.17)^{DE}	^{a}1.3 (0.8, 2.0)^{AC}	^{b}0.22 (0.14, 0.34)^{ABE}	^{c}0.06 (0.04, 0.09)^{CE}
TABR						
Year 1	–	0.21 (0.17, 0.26)^{CD}	–	^{a}1.4 (0.8, 2.6)^{AB}	^{a}0.66 (0.36, 1.2)^{C}	^{b}0.22 (0.12, 0.40)^{B}
Year 2	^{a}1.8 (1.4, 2.4)^{BC}	^{b}0.46 (0.35, 0.61)^{AC}	–	^{a}1.4 (0.9, 2.1)^{AC}	^{b}0.56 (0.36, 0.87)^{C}	^{c}0.29 (0.19, 0.45)^{D}
THPL						
Year 1	–	0.24 (0.19, 0.28)^{D}	–	^{a}1.6 (0.9, 2.9)^{AB}	^{b}0.48 (0.26, 0.88)^{AC}	^{b}0.33 (0.18, 0.62)^{B}
Year 2	^{a}1.6 (1.2, 2.1)^{C}	^{b}0.67 (0.51, 0.88)^{C}	^{b}0.47 (0.36, 0.62)^{F}	^{a}1.5 (1.0, 2.4)^{AC}	^{b}0.52 (0.33, 0.81)^{CD}	^{b}0.29 (0.19, 0.45)^{D}
TSHEo						
Year 1	–	0.07 (0.06, 0.11)^{A}	–	^{a}0.8 (0.4, 1.5)^{A}	^{b}0.12 (0.07, 0.23)^{BD}	^{b}0.07 (0.04, 0.13)^{A}
Year 2	^{a}1.4 (1.1, 1.9)^{C}	^{b}0.24 (0.18, 0.31)^{B}	^{c}0.14 (0.10, 0.18)^{DE}	^{a}1.1 (0.7, 1.7)^{C}	^{b}0.15 (0.09, 0.23)^{E}	^{c}0.05 (0.03, 0.08)^{E}
TSHEy						
Year 1	–	–	–	^{a}1.2 (0.6, 2.1)^{AB}	^{b}0.13 (0.07, 0.24)^{BE}	^{b}0.10 (0.06, 0.19)^{A}
Year 2	^{a}1.3 (1.0, 1.5)^{C}	^{b}0.19 (0.14, 0.25)^{B}	^{c}0.12 (0.09, 0.15)^{D}	^{a}0.57 (0.4, 0.9)^{D}	^{b}0.14 (0.09, 0.21)^{E}	^{c}0.05 (0.03, 0.08)^{E}

diameter including bark at the point of estimate (assumption 2) (P<0.0001, data not shown). However, when S_V from assumption 1 was plotted against S_V from assumption 2, the slope approximated 1.0 (range: 0.98–1.01, among the four species) and the y-intercept, 0 (range: –0.004 to –0.028), indicating that the bias between the two assumptions was slight and likely not biologically important. Similar results were found for inner bark volume. Thus, sapwood thickness and inner bark thickness at D_B were assumed to be constant along stem heights (assumption 1) when calculating volume estimates for the four species. There was a curvilinear relationship between D_B and sapwood volume (S_v) (Fig. 2), evidenced by the significant squared-term in the equation (Table 4).

Table 3 September measurements of core respiratory potential (nmol CO_2 cm^{-3} s^{-1} at 25°C) at breast height, base of the live crown, and near treetop of four species from the H.J. Andrews Experimental Forest in the central Cascades, Oregon. LSMEANS and 95% confidence intervals from Strip plot analysis in PROC MIXED (n=3 trees in year 1 and 4 trees in year 2). Significant differences among means from Fisher's protected least squares differences (P<0.05). For all comparisons each year (1 or 2) was analyzed separately. Different lowercase letters represent differences among tissue radial positions within each row. Different uppercase letters represent differences among species and vertical positions within each column

Species	Inner bark	Outer sapwood	Inner sapwood
	Breast height		
ABAM			
Year 1	^{a}1.5 (1.1, 1.8)^{AB}	^{b}0.4 (0.2, 0.7)^{AB}	^{b}0.2 (0.1, 0.3)^{AC}
Year 2	^{a}1.5 (0.9, 2.5)^{AB}	^{b}0.2 (0.1, 0.4)^{A}	^{b}0.1 (0.1, 0.2)^{AE}
PSME			
Year 1	^{a}1.9 (1.4, 2.4)^{B}	^{b}0.4 (0.3, 0.7)^{AB}	^{b}0.2 (0.1, 0.4)^{AB}
Year 2	^{a}1.1 (0.7, 1.9)^{AB}	^{b}0.4 (0.2, 0.6)^{AB}	^{c}0.2 (0.1, 0.3)^{AB}
THPL			
Year 1	^{a}1.7 (1.3, 2.1)^{AB}	^{b}0.8 (0.5, 1.1)^{BE}	^{b}0.4 (0.2, 0.7)^{BD}
Year 2	^{a}1.5 (0.9, 2.5)^{AB}	^{b}0.5 (0.3, 0.9)^{BC}	^{b}0.3 (0.2, 0.5)^{BD}
TSHE			
Year 1	^{a}1.2 (0.9, 1.6)^{AB}	^{b}0.2 (0.1, 0.4)^{A}	^{b}0.1 (0.04, 0.3)^{A}
Year 2	^{a}1.1 (0.6, 1.8)^{AB}	^{b}0.15 (0.1, 0.2)^{A}	^{c}0.05 (0.03, 0.09)^{C}
	Base of the live crown		
ABAM			
Year 1	^{a}1.5 (1.1, 1.9)^{AB}	^{b}0.4 (0.3, 0.7)^{AB}	^{c}0.1 (0.05, 0.3)^{A}
Year 2	^{a}1.9 (1.1, 3.1)^{AB}	^{b}0.3 (0.2, 0.5)^{AB}	^{b}0.2 (0.1, 0.3)^{AB}
PSME			
Year 1	^{a}1.8 (1.4, 2.4)^{B}	^{b}0.6 (0.4, 0.9)^{B}	^{b}0.3 (0.2, 0.6)^{BC}
Year 2	^{a}1.0 (0.6, 1.6)^{AB}	^{b}0.4 (0.3, 0.7)^{B}	^{b}0.3 (0.2, 0.5)^{BD}
THPL			
Year 1	^{a}1.9 (0.8, 1.5)^{B}	^{b}1.1 (0.8, 1.5)^{C}	^{c}0.6 (0.4, 0.9)^{D}
Year 2	^{a}1.3 (0.7, 2.4)^{AB}	^{a}0.7 (0.4, 1.3)^{BC}	^{b}0.2 (0.1, 0.4)^{AB}
TSHE			
Year 1	^{a}0.6 (0.4, 1.0)^{C}	^{b}0.2 (0.1, 0.4)^{A}	^{b}0.1 (0.04, 0.3)^{A}
Year 2	^{a}0.9 (0.5, 1.5)^{B}	^{b}0.2 (0.1, 0.3)^{A}	^{c}0.1 (0.05, 0.13)^{AE}
	Near treetop		
ABAM			
Year 1	^{a}1.8 (1.4, 2.3)^{B}	^{b}0.6 (0.4, 0.8)^{B}	^{c}0.2 (0.1, 0.4)^{AB}
Year 2	^{a}1.7 (1.0, 2.8)^{AB}	^{b}0.5 (0.3, 0.8)^{BC}	^{c}0.1 (0.08, 0.2)^{AE}
PSME			
Year 1	^{a}1.0 (0.7, 1.4)^{A}	^{a}0.9 (0.7, 1.3)^{CE}	^{b}0.4 (0.2, 0.7)^{BD}
Year 2	^{a}1.4 (0.8, 2.3)^{AB}	^{ab}1.0 (0.6, 1.7)^{C}	^{b}0.5 (0.3, 0.9)^{D}
THPL			
Year 1	^{a}2.5 (2.1, 3.1)^{D}	^{a}2.1 (1.6, 2.5)^{D}	^{b}0.5 (0.3, 0.7)^{BD}
Year 2	^{a}1.4 (0.8, 2.3)^{AB}	^{b}0.3 (0.2, 0.6)^{AB}	^{b}0.3 (0.2, 0.4)^{BE}
TSHE			
Year 1	^{a}1.2 (0.9, 1.5)^{A}	^{b}0.4 (0.2, 0.6)^{A}	^{b}0.2 (0.1, 0.3)^{AC}
Year 2	^{a}1.0 (0.6, 1.7)^{AB}	^{b}0.4 (0.2, 0.6)^{AB}	^{c}0.2 (0.1, 0.3)^{AB}

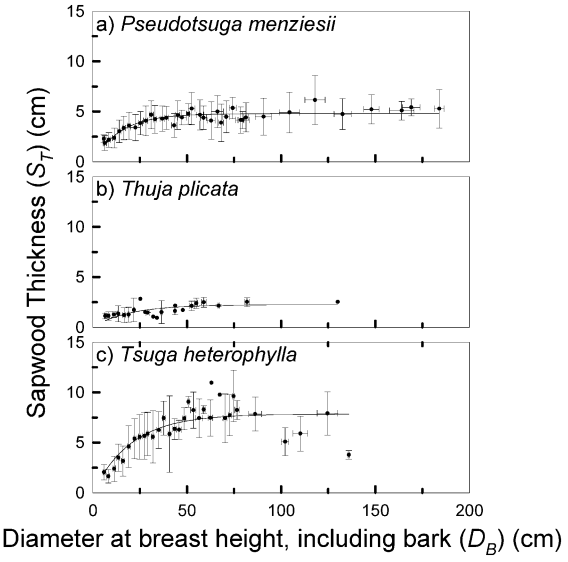

Fig. 1 The relationship of sapwood thickness (cm) to stem diameter including bark at breast height (cm) for three tree species from the Pacific Northwest. Sample sizes and equation parameters with standard errors and their significance listed in Table 4

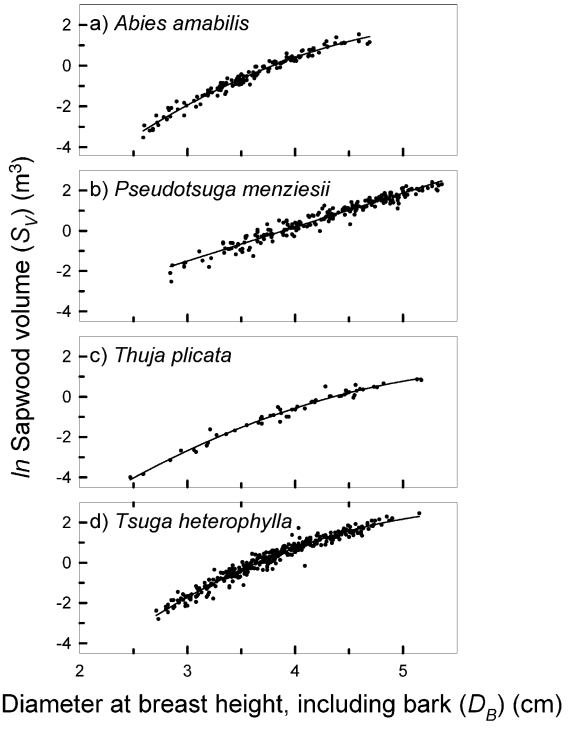

Fig. 2 The relationship of sapwood volume (m^3) to diameter including bark at breast height (cm) of four species from the Pacific Northwest. Sample sizes and equation parameters with standard errors and their significance listed in Table 4

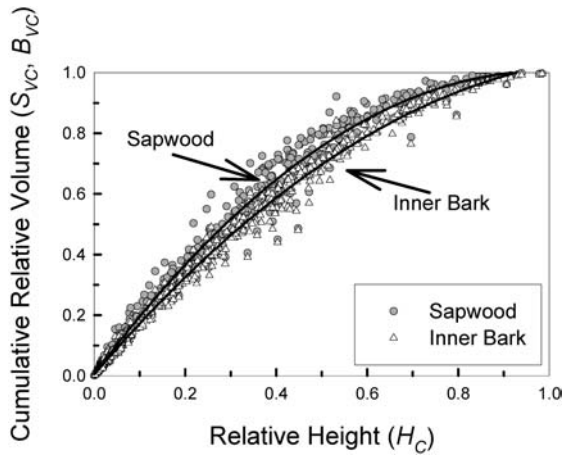

Fig. 3 The relationship between relative cumulative inner bark and sapwood volume and relative height for four Pacific Northwest species, *Abies amabilis*, *Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla*. Sample sizes and equation parameters with standard errors and their significance listed in Table 4

Cumulative relative sapwood and inner bark volume and relative height

For the regression of cumulative relative sapwood volume (S_{VC}) on relative stem height (H_C), the values at 0 and 100% relative height were defined because of the nature of the function. The convex shape of the curve of relative cumulative sapwood volume versus relative stem height (Fig. 3) showed that most of the sapwood volume was within the lower portions of the stem. As the curve tapered off at higher stem heights, less sapwood volume accumulated with each height increment. Sapwood volume accumulated at a higher rate at stem bases because volume increases as the square of stem radius. To test whether the relationship between S_{VC} and H_C was similar for all four species, the effects of species and the interaction of species by H_C, were included in the regression model (Eq. 4). The effects of species and the interaction term were not significant (P>0.2) and were systematically dropped. At this point, the y-intercept (β_0) was no longer significant (P>0.1), leaving H_C and H_C^2 as the main effects (Table 4). The results from the regression of cumulative relative inner bark volume (B_{VC}) on H_C were similar to those from S_{VC} versus H_C (Table 4).

Scaling respiratory potential to the main-bole level

Upon scaling to the main-bole level, inner bark potential CO_2 efflux (mmol s^{-1}) was 15–50% of the main-bole potential CO_2 efflux for all four species (Fig. 4a). There was a positive relationship between main-bole potential CO_2 efflux and live bole volume (Fig. 4a). A log/log equation described the inverse relationship between live bole volumetric fraction and stem diameter including bark at breast height (Table 4). Trees with higher live bole volumetric fractions (*A. amabilis*, *T. heterophylla*) had

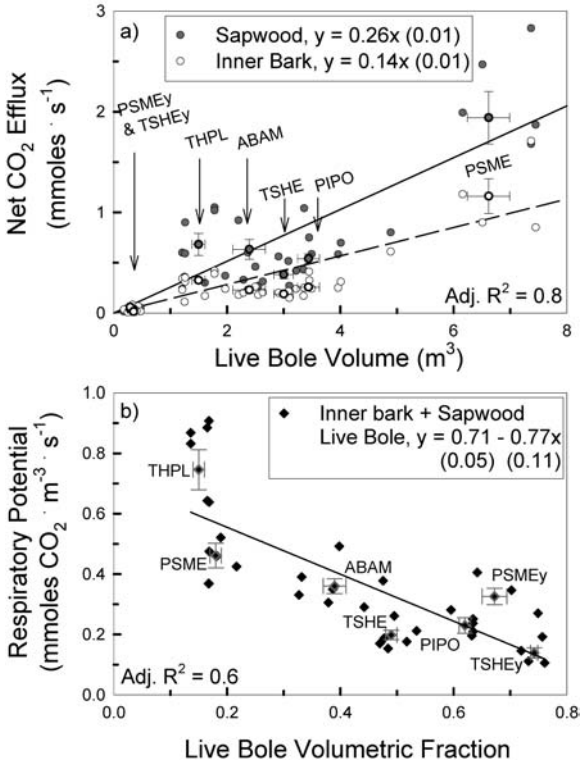

Fig. 4 **a** The relationship between net CO_2 efflux from the live bole (inner bark plus sapwood) and live bole volume, and **b** between respiratory potential of live boles and live bole volumetric fraction (inner bark plus sapwood divided by whole bole volume) for five species. *Abies amabilis*, *Pseudotsuga menziesii*, *Thuja hetrophylla*, and *Tsuga heterophylla* (n=7 mature trees and n=4 young trees) were from the H.J. Andrews Forest in the central Cascades and *Pinus ponderosa* (n=6 trees) from Gilchrist in the Eastern Cascades, Oregon. Means ± standard error for each species are shown in bold. Regression equations were fit to individual trees and not means. Equation parameter estimates significant (P<0.0001) and standard errors in parentheses. *Panel a* regressions were fit separately for inner bark and sapwood

lower main-bole respiratory potentials per unit volume than trees with lower live bole volumetric fractions (Fig. 4b). Estimates of main-bole respiratory potential were not affected by the way the stems were segmented vertically (i.e. bole segment volumes calculated using height to core extraction point versus arbitrary proportions of the bole height), as the means derived from each method were within 5–10% of one another and their standard errors overlapped (data not shown). Also, young *P. menziesii* and young (suppressed) *T. heterophylla*, with live bole volumetric fractions 3–4 times higher than older trees of the same species, had respiratory potentials that were 30% lower than the older trees (Fig. 4b).

Table 4 Equation parameters for the tree species, *Abies amabilis*, *Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla*, to predict thickness, volume, and relative cumulative volume of sapwood and inner bark, and live bole volumetric fraction. Parameter estimates ± SE, significant at $P<0.05$. (n sample size, S_T sapwood thickness, B_T inner bark thickness, S_V sapwood volume, B_v inner bark volume, D_B stem diameter including bark at breast height, S_{VC} relative cumulative sapwood volume, B_{VC} relative cumulative inner bark volume, H_C relative height, L_{BF} live bole volumetric fraction)

Sapwood (n)	Sapwood thickness versus breast height diameter $S_T=\beta_0 \cdot (1-e^{\beta 1 \cdot D_B})$			
	Adjusted R^2	β_0	β_1	
ABAM (24)	–	5.9±0	−0.05±0.01	
PSME (600)	0.76	4.8±0.1	−0.07±0.01	
THPL (50)	0.34	2.2±0.2	−0.05±0.05	
TSHE (200)	0.62	7.8±0.5	−0.05±0.01	
Inner bark (n)	Inner bark thickness versus breast height diameter $B_T=\beta_0 \cdot (1-e^{\beta 1 \cdot D_B})$			
	Adjusted R^2	β_0	β_1	
ABAM (24)	–	0.33±0	−0.05±0.01	
PSME (600)	–	0.60±0	−0.07±0.01	
THPL (50)	–	0.33±0	−0.05±0.05	
TSHE (200)	–	0.35±0	−0.05±0.01	
Sapwood (n)	Sapwood volume versus breast height diameter $\ln S_V=\beta_0\pm(\beta_1 \cdot \ln D_B)\pm(\beta_2 \cdot \ln D_B^2)$			
	Adjusted R^2	β_0	β_1	β_2
ABAM (140)	0.97	−15.2±0.7	6.0±0.4	−0.52±0.05
PSME (220)	0.95	−9.5±0.7	3.1±0.3	−0.17±0.04
THPL (50)	0.97	−13.7±0.8	4.8±0.4	−0.38±0.06
TSHE (350)	0.96	−15.2±0.6	6.0±0.3	−0.51±0.04
Inner bark (n)	Inner bark volume versus breast height diameter $\ln B_V=\beta_0\pm(\beta_1 \cdot \ln D_B)\pm(\beta_2 \cdot \ln D_B^2)$			
	Adjusted R^2	β_0	β_1	β_2
ABAM (140)	0.97	−17.2±0.7	5.7±0.4	−0.50±0.05
PSME (220)	0.95	−11.4±0.7	2.8±0.3	−0.15±0.04
THPL (50)	0.98	−16.4±0.8	4.9±0.4	−0.40±0.06
TSHE (350)	0.96	−17.7±0.6	5.5±0.3	−0.47±0.04
All species (n)	Relative cumulative sapwood volume versus relative height $S_{VC}=\beta_0\pm(\beta_1 \cdot H_C)\pm(\beta_2 \cdot H_C^2)$			
	Adjusted R^2	β_0	β_1	β_2
Sapwood (760)	0.99	0	2.02±0.02	−1.02±0.02
All species (n)	Relative cumulative inner bark volume versus relative height $B_{VC}=\beta_0\pm(\beta_1 \cdot H_C)\pm(\beta_2 \cdot H_C^2)$			
	Adjusted R^2	β_0	β_1	β_2
Inner bark (760)	0.99	0.004±0.002	1.75±0.01	−0.73±0.02
Live bole (n)	Live bole volumetric fraction versus breast height diameter $\ln L_{BF}=\beta_0\pm(\beta_1 \cdot \ln D_B)\pm(\beta_2 \cdot \ln D_B^2)$			
	Adjusted R^2	β_0	β_1	β_2
ABAM (140)	0.95	−1.0±0.2	0.6±0.1	−0.2±0.01
PIPO (50)	0.78	−2.2±0.5	1.0±0.3	−0.1±0.03
PSME (220)	0.97	0.3±0.2	0.1±0.1	−0.1±0.01
THPL (50)	0.97	−1.6±0.3	0.6±0.1	−0.2±0.01
TSHE (350)	0.93	−1.4±0.1	0.9±0.1	−0.2±0.01

Discussion

Core-based respiratory potential

The patterns of increasing respiratory potential from the sapwood/heartwood boundary to the inner bark identified within the ten different tree species from the central Cascades, Oregon were similar to those in *Pinus ponderosa* and *Pseudotusga menziesii* (Pruyn et al. 2002a, 2002b). Increased respiratory activity of the inner bark and outer sapwood rings of stems may be related to their ray parenchyma cells being more involved in supporting growth and secondary wall formation in the cambial zone (Goodwin and Goddard 1940) as compared to the inner rings where the roles of parenchyma may be more storage oriented (Dickson 1991). Another possibility is that outer sapwood rings may be more involved in adjusting concentrations of materials in the xylem stream

(Sauter et al. 1973; Van Bel 1990) since the outer xylem has been reported to be more conductive in the outer versus the inner sapwood rings (Comstock 1965; Spicer and Gartner 2001; Domec and Gartner 2003). Enhanced activity in the outer growth rings may be linked to nitrogen and nonstructural carbohydrate concentrations (e.g. sugars and starches) within parenchyma cells, which would provide greater enzyme and substrate levels for respiration. For example, increased amounts of nitrogen (*Fraxinus nigra* L., Goodwin and Goddard 1940) and soluble carbohydrates (*Pinus taeda*, Saranpää and Höll 1989) were detected in the inner bark and outer sapwood as compared to the inner sapwood and heartwood. Reduced activity in middle and inner sapwood may also be explained by age-related changes (Frey-Wyssling and Bossard 1959; Yang 1993; Gartner et al. 2000), dormant metabolic activity in sapwood parenchyma (Shain and Mackay 1973), and/or the onset of heartwood formation (Bamber 1976).

Trends between stem diameter and sapwood/inner bark amounts

The stem diameter at which maximum sapwood thickness occurred differed among *Pseudotusga menziesii*, *T. plicata*, and *T. heterophylla*. Sapwood thickness increased rapidly with stem diameter where stem diameters were smaller (0–25 cm) and increased more slowly at larger stem diameters. This trend was similar to a previous study on six western coniferous species, including inland and coastal *P. menziesii* and *T. plicata*, with sapwood thickness generally increasing most rapidly during the first 15–20 years of growth (Lassen and Okkonen 1969). The log/log relationship between sapwood volume and stem diameter was also recorded for two different *Pinus* species in contrasting environments (Gower et al. 1993). However, no curvature was detected in the relationship, likely because the stem diameters ranged from 19–24 cm. The curvature in the log/log relationship in the current study indicated that sapwood volume increased at a slower rate with larger stem diameters. This curvature is similar to the theoretical result for a hollow, right-circular cone (sapwood minus heartwood) with sapwood reaching a maximum thickness at the base and tapering to zero at the top of the cone.

Inter-species comparisons on the main-bole level

The lower main-bole respiratory potential per unit volume in young trees versus old trees in the current study contrasted the results of a previous study in which young *Pinus ponderosa* trees (30 years old) respired at rates that were three times higher than older trees (220 years old, Pruyn et al. 2002a). However, in the previous study there was no difference in the live bole volumetric fraction between the young and old pines (0.80 for both age classes), whereas in the current study the live bole volumetric fraction of younger trees was 1.5–2 times higher than older trees of the same species. Another possible explanation was that the young *T. heterophylla* in the current study were suppressed and had lower net photosynthesis, which resulted in lower respiration rates of the live bole.

The inverse relationship between main-bole respiratory potential and live bole volumetric fraction indicated that species maintaining larger proportions of live bole tissue respire at lower rates, which may be the result of lower concentrations of ray parenchyma, and/or respiratory enzymes (nitrogen) and substrates (nonstructural carbohydrates) in the live bole. Literature values do not suggest a correlation between main-bole respiratory potential and the volumetric proportion of parenchyma cells in the sapwood. According to Panshin and de Zeeuw (1980), sapwood parenchyma volume was fairly constant among *T. plicata* (ray volume, 6.9%), *Pseudotusga menziesii* (7.4%), *T. heterophylla* (8.8%), and *Pinus ponderosa* (6.8%), which contrasted the decreasing trend in their main-bole respiratory potentials from the current study. However, the literature estimates of ray volume are not an indication of ray vitality and further investigation is needed to clarify the potential relationship between respiratory potential and live rays. It may be that ray parenchyma cells in species with higher main-bole respiratory potentials are more concentrated in nitrogen or total nonstructural carbohydrates than in species with lower respiratory potentials. For example, maintenance respiration (on a mass, volume, or surface area basis) in the sapwood of *P. taeda* increased with stem wood nitrogen concentration (Maier et al. 1998). Additionally, differences in total nonstructural carbohydrate utilization in two hardwoods were explained by estimations of their differential needs for winter maintenance and spring growth respiration (Barbaroux et al. 2003).

Further research is necessary to better understand carbon partitioning and balance at the tree level. If carbon reserve materials in the conifers from the current study were limiting, and set amounts were allocated for winter maintenance and spring growth respiration, it may have been advantageous for the trees with larger live bole volumes to respire at lower rates. If respiration increased with sapwood amount, then trees potentially risk depleting sapwood reserves (via respiration) during the dormant season, and thus limiting reserves available for wound repair, or growth during the early stages of the following growing season. Some studies have suggested that carbon reserves may be limiting in trees, for example, measured carbon reserve amounts (total nonstructural carbohydrates) were 38% below in *Fagus sylvatica* and 8% above in *Quercus petraea* their estimated carbon reserve requirements (Barbaroux et al. 2003). Further research is needed to ascertain whether the inverse relationship between main-bole respiratory potential and the live bole volumetric fraction is robust among other species, age classes, and sites. It would also be interesting to determine why some young tree species (*Pinus ponderosa)* respire at much higher rates than older trees of the

same species, whereas others do not follow this pattern (*Pseudotusga menziesii*), especially in light of the fact that these two species maintain contrasting amounts of sapwood.

Acknowledgements The authors express thanks to H.J. Andrews Experimental Forest staff for permitting the extraction of increment cores from the trees. Also, thanks to Nicky DeVeny, Jeff Langlois, and Nathan Poage who assisted in core extraction and respiratory analysis with the gas chromatograph. Further, thanks to the tree climbers, Scott Hyde, Andre Mallot, and Nathan Poage, for scaling trees to seemingly impossible heights to extract cores. This research was funded by USDA CSREES 96-35103-3832 and 97-35103-5052 and NSF DEB 9632921. Data sets provided by the Forest Science Data Bank are from a partnership between the Department of Forest Science, OSU, and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, Oregon, funded by NSF-LTER grants, BSR-90-11663 and DEB 9632921.

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