

Wood CO₂ efflux and foliar respiration for *Eucalyptus* in Hawaii and Brazil

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Summary We measured CO₂ efflux from wood for *Eucalyptus* in Hawaii for 7 years and compared these measurements with those on three- and four-and-a-half-year-old *Eucalyptus* in Brazil. In Hawaii, CO₂ efflux from wood per unit biomass declined $\sim 10\times$ from age two to age five, twice as much as the decline in tree growth. The CO₂ efflux from wood in Brazil was 8–10 $\times$ lower than that for comparable Hawaii trees with similar growth rates. Growth and maintenance respiration coefficients calculated from Hawaii wood CO₂ efflux declined with tree age and size (the growth coefficient declined from 0.4 mol C efflux mol C⁻¹ wood growth at age one to 0.1 mol C efflux mol C⁻¹ wood growth at age six; the maintenance coefficient from 0.006 to 0.001 $\mu\text{mol C (mol C biomass)}^{-1} \text{ s}^{-1}$ at 20 °C over the same time period). These results suggest interference with CO₂ efflux through bark that decouples CO₂ efflux from respiration. We also compared the biomass fractions and wood CO₂ efflux for the aboveground woody parts for 3- and 7-year-old trees in Hawaii to estimate how focusing measurements near the ground might bias the stand-level estimates of wood CO₂ efflux. Three-year-old *Eucalyptus* in Hawaii had a higher proportion of branches < 0.5 cm in diameter and a lower proportion of stem biomass than did 7-year-old trees. Biomass-specific CO₂ efflux measured at 1.4 m extrapolated to the tree could bias tree level estimates by $\sim 50\%$, assuming no refixation from bark photosynthesis. However, the bias did not differ for the two tree sizes. Foliar respiration was identical per unit nitrogen for comparable treatments in Brazil and Hawaii (4.2 $\mu\text{mol C mol N}^{-1} \text{ s}^{-1}$ at 20 °C).

Keywords: carbon allocation, carbon cycling, forest production, modeling, nutrition, productivity, wood respiration.

Introduction

Autotrophic respiration supplies energy for metabolism and growth, and consumes 30–70% of the carbon fixed in photosynthesis (Ryan et al. 1997, Litton et al. 2007). However, the role of autotrophic respiration in the whole tree carbon balance remains poorly identified. Is autotrophic respiration a constant fraction of photosynthesis (Waring et al. 1998, Litton et al. 2007)? If it is a constant fraction, why do black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg, Ryan et al. 1997) and wet primary tropical forests (Chambers et al. 2004) consume $\sim 70\%$ of photosynthesis compared to the commonly reported and assumed 50% (Waring et al. 1998)? Does autotrophic respiration as a fraction of photosynthesis increase with tree size (Yoda 1967, DeLucia et al. 2007) or is it constant (Ryan and Waring 1992, Ryan et al. 2004)? Will increased temperatures change the ratio of photosynthesis to respiration (Ryan 1991)? We will only answer these questions by measuring the autotrophic respiration for studies where we have all of the other components of the carbon budget (Litton et al. 2007), developing robust sampling and extrapolation protocols (Cavaleri et al. 2006, 2008), and by placing autotrophic respiration in the context of a complete carbon balance (Ryan et al. 2004).

This study focuses on some of the sampling issues that are needed to estimate autotrophic respiration for forests to enable answering the above questions. Specifically, we were interested in determining whether wood CO₂ efflux was related to wood growth (Lavigne 1988, Ryan 1990, Ryan et al. 1994, 1996), if wood CO₂ efflux was similar for two closely related species of *Eucalyptus*, if foliar respiration was related to foliar nitrogen (Ryan 1991, 1995, Reich et al. 1996, 2008), if sampling wood CO₂ efflux only near the ground would bias stand-level estimates (Cavaleri et al. 2006) and if wood CO₂ efflux was decoupled from wood respiration by transport of CO₂ to or from the efflux location by sapflow (Teskey and McGuire 2002) or by resistance to CO₂ efflux (Steppe et al. 2007). This study is part of two larger studies where we attempted to measure a complete carbon budget, the Brazil Eucalyptus Potential Productivity (BEPP) Project and the Hawaii growth decline study (Ryan et al. 2004). Our hypotheses were that (1) differences in wood growth explain the variability in wood respiration rates among sites, trees, treatments, position on tree and through time and (2) differences in foliar N explain the variation in foliar respiration among sites, treatments, stand ages and canopy positions. Our objectives were to determine if (1) woody CO₂ efflux for a rapidly growing plantation varies with fertility, tree density, position on stem or tree size or age and if any variations are related to growth or sapwood volume; (2) rates of CO₂ efflux from wood are similar for *Eucalyptus saligna* Sm. in Hawaii and for *E. urophylla* S.T. Blake $\times$ *grandis* Hill ex Maiden in Brazil; (3) measurements of wood CO₂ efflux taken from the ground are biased because of under sampling twig and branch respiration; if so, if that bias varies with tree size; and (4) the foliar respiration per unit nitrogen and the ratio of foliar respiration: photosynthesis are similar for *E. saligna* in Hawaii and for *E. urophylla* $\times$ *grandis* in Brazil.

Methods

Site description

Hawaii The Hawaii study site (19°50'28.1" N and 155°7'28.3" W) is a 4-ha experimental forest of *E. saligna*, located 13 km northeast of Hilo, Hawaii at 350-m elevation (Ryan et al. 2004). Mean annual temperature is 21 °C with an average annual rainfall of about 4000 mm (Binkley et al. 1992). There is no dry season, but winter months tend to be wetter, cloudier and have shorter days. For the years of this study, 1995–2000, when the trees were one to 7 years old, rainfall averaged 3500 mm year⁻¹. The slope is < 5%, and soils are > 2 m deep, acidic (pH 5–6 in water), and are classified as thixotropic, isothermic Typic Hydrudands in the Kaiwika series (Binkley and Resh 1999). Sugarcane was cropped on the site for more than 80 years, with the last crop harvested about 1 year before planting the *Eucalyptus* seedlings. In February 1994, the site was plowed

to turn under the developing vegetation and 3 months later, new regrowth was prevented with glyphosate herbicide (Roundup®, Monsanto Company Agricultural Products, St. Louis, MO). The site was planted in May 1994 using seedlings from a single seed source selected for uniform size.

The plantation contained eighteen 30 by 30 m plots, with two levels of tree spacing [1 by 1 m or 3 by 3 m, equal to 10⁴ (high density – HD) or 1111 trees ha⁻¹ at planting (low density – LD)] and three levels of fertilization (control – C, high fertilization – HF or restore fertility – RF), organized in three randomized blocks. The two spacings were designed to vary the ratio of leaf area:woody tissues and to vary the timing of canopy closure. The three fertilization regimes were designed to test the role of changes in nutrient limitation over time in the decline of wood production (Ryan et al. 2004). Further details about fertilization regimes and plantation management are given in Ryan et al. (2004).

In 1997, we planted a new block of trees from the same seedstock, using the same methods as those used for the original 18 plots. All plots received the HF fertility treatment, and three were LD and three were HD.

Brazil The Brazil study site was part of the BEPP Project (Binkley et al. 2009), located (19°49' S and 40°05' W) near Aracruz, Espírito Santo State, Brazil. Mean annual temperature is 23.5 °C with an average annual rainfall of about 1430 mm, 17 MJ m⁻² day⁻¹ global radiation and 0.8 kPa average daylight vapor pressure deficit. Soils are > 2 m deep, clay loam and classified as a Typic Kandudult. We measured wood CO₂ efflux and foliage respiration once (March 2004) on 3-year-old trees in the BEPP site and on four-and-a-half-year-old trees from the same clone < 500 m from the BEPP site. Trees were planted at a 3 $\times$ 3 m spacing, and we measured the wood CO₂ efflux and foliar respiration in four treatments in the BEPP site (FIU, FNU, FIH and TNU) and in two treatments at the older plantation (FIU and FNU). Treatments carried out were T = operational fertilization, F = potential fertilization with intensive macro- and micro-nutrient fertilization every 6 months to eliminate any soil nutrient restriction to growth; I = irrigated to eliminate any soil moisture deficit; N = rainfed; U = uniform, all trees planted on the same date; and H = heterogeneous, one-third of the trees planted every 2 months. For further details about these treatments, see Binkley et al. (2009).

Ecophysiological measurements

Wood CO₂ efflux Woody tissue CO₂ efflux through bark comprises the sum of three terms: woody tissue respiration (+flux), bark photosynthesis (–flux) and flux from CO₂ dissolved in the xylem sap (+ or –, Cernusak and Marshall 2000, McGuire and Teskey 2004, Bowman et al. 2005, Teskey et al. 2008). We measured wood CO₂ efflux through bark using clear Plexiglas mixing chambers that allowed

bark photosynthesis to estimate the sum of the three terms. Chambers were fitted with neoprene gaskets to create a leak proof seal and attached to a PP Systems CIRAS-1 (PP Systems International, Amesbury, MA) infrared CO₂ analyzer (Hawaii) or to an LCA3 or LCA4 (ADC BioScientific, Herts, UK) infrared CO₂ analyzer (Brazil). Air-flow rates through the chambers ranged from 220 to 300 $\mu\text{mol s}^{-1}$, and chamber seals were checked with a flowmeter. Stable reference air CO₂ concentrations were maintained by drawing air through a 19-l mixing chamber. We measured CO₂ efflux twice on each stem and branch, with measurements $\sim 90^\circ$ from one another, and averaged the replicates before analysis. Diameter was measured at the center point of chamber attachment, and surface wood temperature was taken with a thermocouple thermometer. Measurements were made between 07:00 and 16:00 local time, and all fluxes were corrected to a reference temperature of 20 °C using a Q_{10} of 2.0 (Ryan et al. 1994).

Wood CO₂ efflux was compared with growth, sapwood biomass and total biomass (Hawaii) and growth and biomass (Brazil). To estimate growth occurring during the measurement period, we measured the diameter to be 0.05 cm 30–50 days before and after the respiration measurement (Hawaii) or used growth for the quarter encompassing the measurements (Brazil). We expressed respiration measurements on the basis of biomass by scaling respiration to a cylinder with height equal to chamber height and multiplying that volume by specific gravity of wood from trees harvested for the tree allometric equation (Ryan et al. 2004). Wood growth for the same cylinder was estimated from the diameter change and specific gravity. We estimated growth and maintenance coefficients by assuming that wood CO₂ efflux represented wood respiration, and regressing wood respiration per unit biomass versus growth per unit biomass, where growth respiration is the slope and maintenance respiration is the intercept (Amthor 1989).

In Hawaii, measurements were made 4–5 times per year in 1996 and 1997, and in March 1999, July 2000 and May 2001, when the trees were 2–7 years old. From 1995 to 1999 (1–5 years old), measurements were made in one C and HF plot in each planting density (4 plots total) on 10 trees per plot at 1.4 m and on 4 trees per plot at 3 and 6 m above the ground. In 2000 and 2001 (6–7 years old), we measured 5–10 trees per plot at 1.37 m in all 18 plots and at 10 and 20 m on 18 trees on six plots. In Brazil, measurements were made for both tree ages once in March 2004 at 1.3 m on 20–25 trees in one plot in each treatment and at ~ 5 , 9, 13 and 17 m on 4 trees per plot in each treatment.

Foliar respiration Foliar dark respiration was measured as CO₂ efflux from leaves at night. The CO₂ efflux was measured between 21:00 and 03:00 h on several fully expanded leaves at each of four canopy positions: 4–5 leaves in from

the terminal bud of the upper, middle and lower crown thirds, and 4–5 leaves out from the point of branch attachment in the lower third of the crown. The CO₂ efflux was measured at an ambient CO₂ concentration in large Plexiglas chambers using the procedures and analyzers described above for wood CO₂ efflux.

In Hawaii, measurements were made in January, May, September and December 1995, October 1996 and February 1998. In Brazil, measurements were made in March 2004. Sample foliage was harvested, measured for leaf area, dried at 70 °C for 48 h, weighed and analyzed for N content using a LECO CHN analyzer (LECO, St. Joseph, MI). We corrected respiration rates to 20 °C using a Q_{10} of 2.

Photosynthesis In Brazil and Hawaii, we measured the photosynthesis of fully expanded leaves in the upper canopy under conditions of saturating light (photosynthetically active radiation $> 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$) and ambient CO₂. In Hawaii, photosynthesis measurements were taken under conditions of high humidity (vapor pressure deficit < 1 kPa) with a PP Systems CIRAS-1 photosynthesis system. Photosynthesis was measured periodically throughout the experiment on several trees per treatment accessed by scaffolding towers (Ryan et al. 2004). In Brazil, we measured the photosynthesis of fully expanded leaves for the same four canopy positions as for respiration, under ambient humidity (vapor pressure deficit 1–3.5 kPa) with a Li-Cor LI-6400 photosynthesis system (Li-Cor Biosciences, Lincoln, NE). Photosynthesis was measured on two leaves per position for four trees per treatment on 2 separate days.

Twig, branch and bole biomass and CO₂ efflux for 3- and 7-year-old trees

In 2000, we sampled three each of 3- and 7-year-old trees in Hawaii to estimate wood CO₂ efflux for branches and twigs (not measured in earlier samples) and to compare the wood CO₂ efflux budgets for trees at peak growth (~ 3 years old) with those where wood growth had declined (7 years old). We measured CO₂ efflux on 6–12 branches (> 0.5 cm diameter) and 4–8 twigs (< 0.5 cm diameter) per tree using the same analyzer and procedures described above under the section ‘Wood CO₂ efflux’, except that the branches and the twigs were measured in the dark. We estimated dry weight of the main stem, branches 0.5–1.0 cm, branches > 1 cm and twigs (branches < 0.5 cm diameter) by harvesting and weighing each component and by drying a subsample to constant weight at 70 °C.

Statistical analysis

Differences in CO₂ efflux per unit biomass carbon or sapwood biomass were assessed using repeated-measures analysis of variance (ANOVA) with year as the repeated measure. We used analysis of covariance to determine if

Table 1. Coefficients for a linear regression between wood CO₂ efflux ($\mu\text{mol C mol C}^{-1} \text{ s}^{-1}$) and relative growth ($\mu\text{mol C mol C}^{-1}$). If wood CO₂ efflux approximates wood respiration, the slope is the growth respiration coefficient and the intercept is the maintenance coefficient. SEE is standard error of the estimate, and the slopes and the intercepts are plotted versus tree age in Figure 2B and C.

Tree age (year)	Slope ($\mu\text{mol C mol C}^{-1}$)	Intercept ($\mu\text{mol C mol C}^{-1} \text{ s}^{-1}$)	<i>n</i>	<i>r</i> ²	SEE
1	0.411	0.00644	56	0.96	0.0013
2	0.279	0.00459	80	0.44	0.0039
3	0.222	0.00388	80	0.35	0.0024
5	0.152	0.00054	58	0.12	0.0013
6	0.076	0.00119	88	0.15	0.0007
7	0.249	0.00047	92	0.51	0.0007

wood CO₂ efflux varied with tree age, fertility and tree density treatments or position on stem (1.4, 3, 6, 10 and 20 m) using relative growth as a covariate. This analysis tests for differences in CO₂ efflux with treatment, age or position on tree that are not related to differences in stem growth. Linear regressions of wood CO₂ efflux ($\mu\text{mol C mol}^{-1} \text{ s}^{-1}$) versus relative growth ($\mu\text{mol C mol C}^{-1} \text{ s}^{-1}$) were used to estimate the growth and maintenance respiration coefficients for each year. In this regression, the growth coefficient is the slope and the maintenance coefficient is the intercept (Table 1). We used linear regression to assess the trend in growth and maintenance coefficients with tree age in Hawaii and the relationship between respiration and photosynthesis in Brazil. Analysis of variance was used to evaluate differences in component biomass proportions and wood CO₂ efflux between 3- and 7-year-old trees in Hawaii; among treatments, stem position and tree age for wood CO₂ efflux in Brazil; and among leaf position and tree age for foliar respiration and for foliar respiration/foliar N in Brazil. Analyses were performed using SPSS (SPSS, Chicago, IL).

Results

Hawaii wood CO₂ efflux

Wood CO₂ efflux per unit biomass carbon at 20 °C differed with tree density and fertility, but the largest effect was a substantial decline with tree age (repeated measures ANOVA, Figure 1A, $P < 0.01$). Wood CO₂ efflux per unit sapwood biomass (Ryan 1990) also declined with tree age (Figure 1B, $P < 0.01$). Within a year, differences in wood CO₂ efflux among fertility and density treatments and position on tree were mostly not significant after accounting for relative growth.

The decline in wood CO₂ efflux per unit biomass as the trees became older and larger was substantial, and the percentage decline exceeded the decline in stand wood growth (Ryan et al. 2004) and in individual tree growth. For all treatments, wood CO₂ efflux per unit biomass at age five declined to 9–14% of that at age two. At the stand level, wood growth ($\text{kg C m}^{-2} \text{ year}^{-1}$) at age five dropped to 26–52% of that at age two (Ryan et al. 2004). Individual

tree relative wood growth ($\text{kg C kg C}^{-1} \text{ year}^{-1}$) at age five declined to 18–92% of that at age two, stand relative growth at age six declined to 14–18% of that at age two (Figure 1C) and individual tree absolute growth (diameter increment) at age five declined to 19–24% of that at age two.

Wood CO₂ efflux ($\mu\text{mol C mol C}^{-1} \text{ s}^{-1}$) was related to relative growth ($\mu\text{mol C mol C}^{-1} \text{ s}^{-1}$) for plot means for all treatments and tree ages (Figure 2A, $P < 0.01$), with a maintenance coefficient of $0.0006 \mu\text{mol C mol C}^{-1} \text{ s}^{-1}$ and with a growth coefficient of $0.40 \mu\text{mol C mol C}^{-1}$. The analysis of covariance showed that the slope of the covariate (relative growth) varied with tree age ($P < 0.05$). However, the simple linear regression of the growth coefficient with tree age was not significant (Figure 2B, $P = 0.11$). Linear regression of the maintenance coefficient with age showed a decline (Figure 2C, $P < 0.01$).

Brazil wood CO₂ efflux

Wood CO₂ efflux at 1.2 m varied by treatment and stand age (Figure 3A). Wood CO₂ efflux per mass at 1.2 m in four-and-a-half-year-old stands was 57% of that of the 3-year-old stands (the traditional fertilization (T) and the high fertility (F) did not differ in response, so we used both FNU and TNU treatments with the FIU treatment for this comparison, ANOVA, $P < 0.01$). Wood CO₂ efflux at 1.2 m was similar in the rainfed and irrigated stands ($P = 0.92$), but the heterogeneous treatment (FIH) had 36% higher CO₂ efflux than the uniform treatment ($P = 0.05$). Rates at 1.2 m averaged $0.034 \mu\text{mol (kg C)}^{-1} \text{ s}^{-1}$ for the 3-year-old plantation and $0.020 \mu\text{mol (kg C)}^{-1} \text{ s}^{-1}$ for the 4.5-year-old plantation. These rates were substantially lower than those measured for comparable treatments and ages in Hawaii – $0.53 \mu\text{mol (kg C)}^{-1} \text{ s}^{-1}$ for 3-year-old 3×3 HF trees and $0.23 \mu\text{mol (kg C)}^{-1} \text{ s}^{-1}$ for 4.5-year-old 3×3 HF trees. Wood CO₂ efflux was not related to relative growth for the spring quarter of 2004 for 3-year-old trees ($P = 0.46$) or for four-and-a-half-year-old trees ($P = 0.27$).

Wood CO₂ efflux increased exponentially with stem height (two-factor ANOVA – polynomial contrast,

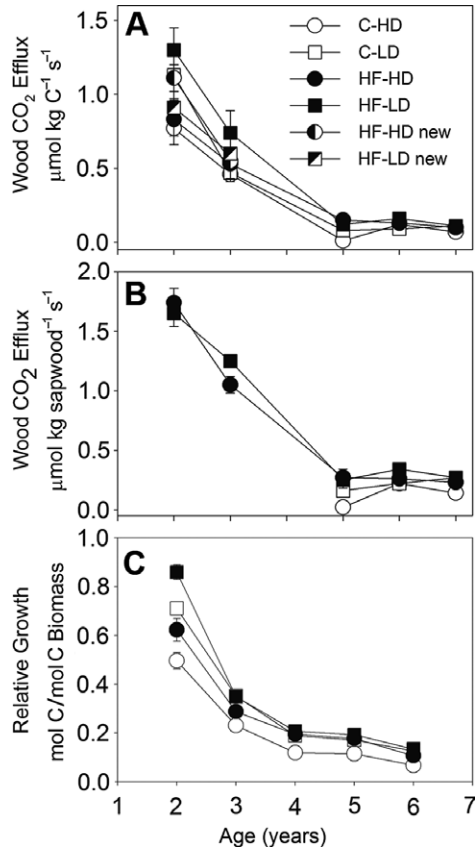


Figure 1. Hawaii site: Wood CO₂ efflux at 20 °C differs among treatments and declines with stand age and tree size. (A) Per unit biomass, (B) per unit sapwood biomass. C = control, HF = high fertility, LD = low density, 3 × 3 m spacing, 1111 trees ha⁻¹, HD = high density, 1 × 1 m spacing, 10⁴ trees ha⁻¹, new = plantation established in 1998, compared to the original establishment in 1994. (C) Stand relative growth rate (growth/biomass) also declines with stand age and tree size, but the decline is about half that of wood CO₂ efflux. Error bars are standard errors. For details about the treatments, see Ryan et al. (2004).

Figure 3B, $P < 0.01$), but was lower for the four-and-a-half-year-old trees at every height class (two-way ANOVA – main effect, Figure 3B, $P < 0.01$) and increased less with height on stem for the four-and-a-half-year-old trees than for the 3-year-old trees (two-way ANOVA – interaction, $P < 0.01$). Stem growth was not measured above 1.2 m, so we could not compare wood CO₂ efflux with growth. However, wood CO₂ efflux ($\mu\text{mol C mol C}^{-1} \text{s}^{-1}$) was negatively related to stem diameter at the measuring point ($r^2 = 0.30$, $P < 0.01$), and the relationship did not vary with tree age (analysis of covariance, $P = 0.52$).

Effects of assuming upper stems and branches are similar to those of lower stem

Most of our measurements of wood CO₂ efflux were made at 1.4-m height. We made intensive measurements

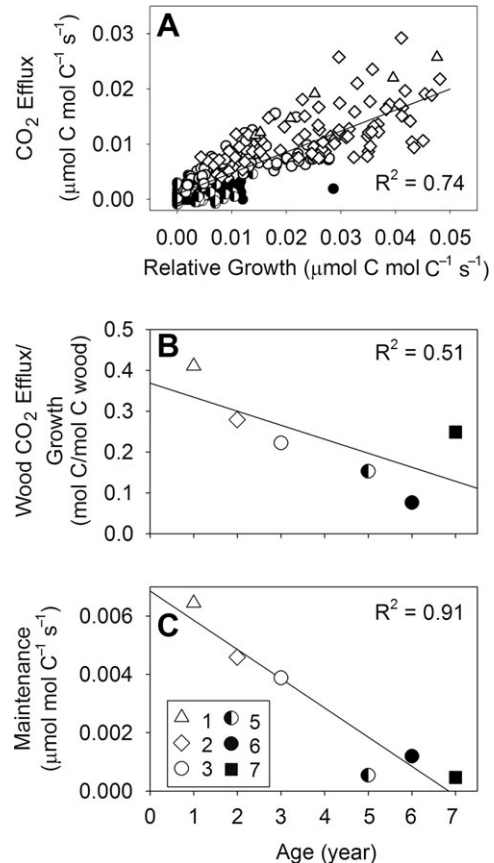


Figure 2. Hawaii site: (A) Wood CO₂ efflux per unit biomass carbon versus growth per unit of biomass carbon for all samples. Plotting these variables yields the growth coefficient (slope) and the maintenance coefficient (intercept), $y = 0.0006 + 0.40x$. (B) Slope of the regression of wood CO₂ efflux per unit biomass carbon versus growth per unit of biomass carbon for each sample year (the growth coefficient) declines with tree age or size. (C) Intercept of the regression of wood CO₂ efflux per unit biomass carbon versus growth per unit of biomass carbon for each sample year (the maintenance coefficient) declines with tree age or size.

on three 3-year-old and three 7-year-old trees to determine if assuming branches and twigs had the same CO₂ efflux as lower stem biomass would bias whole tree CO₂ efflux estimates. The smaller 3-year-old trees had a greater proportion of their biomass in branches < 0.5 cm and in foliage than did the larger 7-year-old trees, while the 7-year-old trees had a larger proportion of stemwood biomass (ANOVA, Figure 4A, $P < 0.05$). Wood CO₂ efflux per tree did not differ between the 3- and 7-year-old trees for the branch or the stem component, or for the total (Figure 4B, ANOVA, branch > 0.5 cm, $P = 0.13$; branch < 0.5 cm, $P = 0.54$; stem, $P = 0.61$; total, $P = 0.52$). Total wood CO₂ efflux including branches (Total A) was 50% greater than total CO₂ efflux estimated from the measurements at 1.4 m (Total C, paired t test, Figure 4B, $P = 0.04$), because CO₂ efflux for branches was

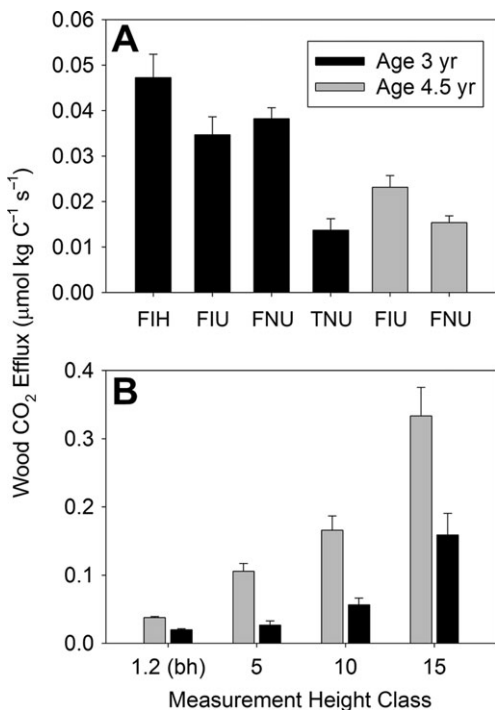


Figure 3. Brazil site: Brazil wood CO₂ efflux (A) at 1.2 m by treatment and age. The CO₂ efflux from wood was lower for the four-and-a-half-year-old plantation, (B) by stem height class and plantation age. The CO₂ efflux increased exponentially with height on stem and was lower at a given height for the older trees. For the treatments, T = operational fertilization, F = high fertility, I = irrigated, N = rainfed, U = uniform planting date and plantation, H = planting date offset for planting thirds to yield heterogeneous plantation. See text for further details on treatments. Error bars are standard errors.

2.0 μmol kg C⁻¹ s⁻¹ (> 0.5 cm) and 3.2 μmol kg C⁻¹ s⁻¹ (< 0.5 cm), compared to 0.64 μmol kg C⁻¹ s⁻¹ for stemwood of 3-year-old trees and 0.13 μmol kg C⁻¹ s⁻¹ for stemwood of 7-year-old trees, respectively. Small branches had obvious chlorophyll and their photosynthesis may reduce CO₂ efflux. If branch photosynthesis reduces CO₂ efflux during the day to zero for branches < 1 cm, then calculating total woody CO₂ efflux from stem measurements alone had a negligible impact on the total CO₂ efflux (Figure 4B, Totals B and C, $P = 0.50$).

Foliar respiration in Hawaii and Brazil

Foliar respiration in Hawaii *E. saligna* at 20 °C increased linearly with foliar N content (Figure 6 in Ryan et al. 2004), but the slope differed for the HF and C treatments: 4.2 μmol mol N⁻¹ s⁻¹ for the HF treatment ($r^2 = 0.21$) and 5.2 μmol mol N⁻¹ s⁻¹ for the C treatment ($r^2 = 0.37$). For *E. urophylla* × *grandis* in Brazil, foliar respiration at 20 °C also increased linearly with foliar N ($r^2 = 0.19$, $P < 0.01$). As the regression explained such a low amount of the variance, we estimated mean respiration

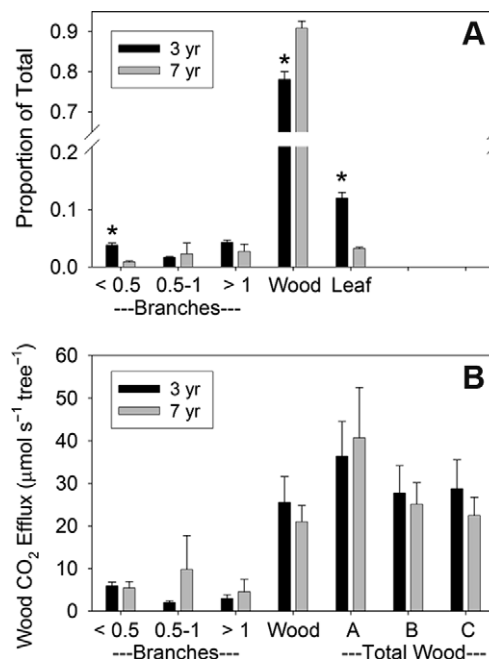


Figure 4. Hawaii site: (A) Foliage and twigs (0–0.5 cm) had a higher proportion of the total biomass in 3-year-old trees and wood had a higher proportion in the 7-year-old trees. (B) Total wood CO₂ efflux for branches was similar for 3- and 7-year-old trees. Neither differences in the total amount of branches and wood in 3-year-old and 7-year-old trees, nor differences in the biomass-specific respiration rates caused differences in total tree wood CO₂ efflux between the two age classes. Total CO₂ efflux per tree was greater when considering the higher CO₂ efflux from branches [compare Total A (including branch-specific rates) with Total C (computed using rates measured at 1.3 m applied to all biomass)]. However, small branches had a considerable amount of chlorophyll, and if the CO₂ efflux during the day was offset by photosynthesis for branches < 0.5 and 0.5–1.0 cm (Total B), then wood CO₂ efflux per tree was similar to that estimated in Ryan et al. (2004) from biomass and rates measured at 1.3 m (Total C). Error bars are standard errors.

per N from mean respiration and mean N per area as 4.2 μmol mol N⁻¹ s⁻¹ at 20 °C. Foliar respiration per unit area and per unit foliar N (Figure 5A and B) varied by leaf position (two-factor ANOVA excluding the FIH and TNU treatments as they were only implemented in the 3-year-old stands, $P < 0.01$); respiration per unit area increased with tree age (two-factor ANOVA excluding the FIH and TNU treatments, $P < 0.01$), but foliar respiration per N did not (two-factor ANOVA excluding the FIH and TNU treatments, $P = 0.32$). In Brazil, foliar respiration increased linearly with light-saturated photosynthesis [$r^2 = 0.64$, Figure 6, respiration (μmol m⁻² s⁻¹) = 0.038 × photosynthesis (μmol m⁻² s⁻¹)]. In Hawaii, both foliar respiration and maximum photosynthesis increased with foliar N (Ryan et al. 2004). The ratio of respiration at 20 °C to maximum photosynthesis (R:P) was 0.030 for Hawaii (data in Ryan et al. 2004).

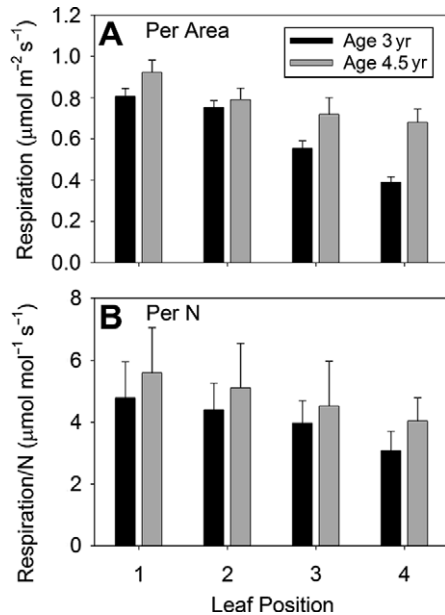


Figure 5. Brazil site: Foliar respiration per unit leaf area (A) and N (B) varied by leaf position (position '1' representing leaves receiving the most light and position '4' the least), but differences between years were not significant. Mean respiration per N was $4.3 \mu\text{mol mol}^{-1} \text{s}^{-1}$ at 20°C , compared to $4.2 \mu\text{mol mol}^{-1} \text{s}^{-1}$ at 20°C for the HF treatment for Hawaii *Eucalyptus* and $5.2 \mu\text{mol mol}^{-1} \text{s}^{-1}$ at 20°C for the C treatment for Hawaii *Eucalyptus*. Error bars are standard errors.

Discussion

Wood CO₂ efflux Brazil and Hawaii

Wood CO₂ efflux per unit biomass in Hawaii *E. saligna* declined dramatically as the trees became older and larger, and the decline was greater than the decline in stand and individual tree growth. Wood CO₂ efflux was related to growth for individual sampling periods and for all data combined, but the relationship changed with the tree age or size. Growth and maintenance coefficients for each sample period, derived by regressing CO₂ efflux per unit biomass ($\mu\text{mol C mol C}^{-1} \text{s}^{-1}$) against relative growth ($\mu\text{mol C mol C}^{-1} \text{s}^{-1}$), also declined with stand age (the linear decline with tree age for the growth coefficient was not significant, $P = 0.11$).

The growth respiration coefficient estimates the energy used to synthesize structural material and varies by compound (Penning de Vries et al. 1974, Williams et al. 1987). Construction of 1 mol C of cellulose requires 1.2 mol C of glucose (0.2 mol is respired), while that of 1 mol C of lignin requires 2.5 mol C of glucose (Williams et al. 1987). The empirical estimates for wood are about 1 mol C wood 1.25 mol^{-1} glucose, where one-quarter of the carbon is respired in construction (Ryan 1991). We did not estimate *Eucalyptus* construction costs using any of the indirect methods available (Ryan 1991). However, we think it unlikely that the composition of new tissue

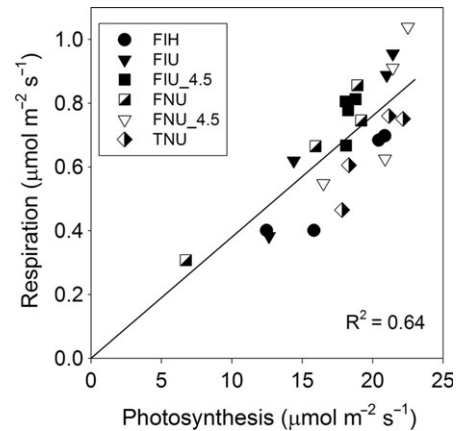


Figure 6. Brazil site: Foliar dark respiration is related to light-saturated photosynthesis across treatments ($y = 0.038x$). Points are means of dark respiration and photosynthesis by treatment and canopy position. For the treatments, T = operational fertilization, F = high fertility, I = irrigated, N = rainfed, U = uniform planting date and plantation, H = planting date offset for planting thirds to yield heterogeneous plantation (see text for further details on treatments). Treatments not labeled '4.5' were 3 years old.

changed very much that the actual construction costs dropped from $0.4 \text{ mol C respired mol C}^{-1}$ wood constructed at age one to $0.1 \text{ mol C respired mol C}^{-1}$ wood constructed at age six, because a construction cost of $0.1 \text{ mol C respired mol C}^{-1}$ wood constructed is lower than that of pure cellulose.

Maintenance respiration per unit of biomass carbon could decline as the proportion of sapwood to total woody biomass declines, because the only living cells (ray parenchyma) are in the sapwood, cambium and phloem (Ryan 1989). However, wood CO₂ efflux per unit sapwood volume also declined by about the same proportion as did CO₂ efflux per unit biomass (Figure 1B). Maintenance respiration per unit sapwood volume (calculated assuming CO₂ efflux equaled respiration) did not vary with tree size/age (Ryan 1990) for *Picea engelmannii* (Parry ex Engelm.) and *Pinus contorta* (Douglas ex Loudon), but maintenance respiration did vary with relative growth rate for two conifers (*P. mariana* and *Pinus banksiana* Lamb) and aspen (*Populus tremuloides* Michx.) at six different sites in Canada (Lavigne and Ryan 1997).

Wood CO₂ efflux for Brazil *E. urophylla* $\times$ *grandis* was 6–10% of similar size *E. saligna* in Hawaii, and this difference was not related to differences in growth. For example, at age three, trees in comparable treatments in Brazil (LD and high fertility) and Hawaii (LD and high fertility) were 13–15 cm in diameter with annual diameter growth rates of 1.3–1.7 cm. We suspect that the differences in CO₂ diffusion through the bark (Steppe et al. 2007) caused these differences (see below).

Wood CO₂ efflux rates for the Hawaii *Eucalyptus* were substantially larger than those found in an old-growth

tropical rainforest for similar diameters. Cavaleri et al. (2006) reported wood CO₂ efflux for 10-cm diameter stems at 0.08 and 0.02 $\mu\text{mol kg C}^{-1} \text{s}^{-1}$ for 40-cm diameter stems at 20 °C. Hawaii *Eucalyptus* had a diameter of 10 cm by age two, when respiration rates were 1.1–1.3 $\mu\text{mol kg C}^{-1} \text{s}^{-1}$ at 20 °C. The Brazil wood CO₂ efflux rates were comparable to those in the old-growth forest, but almost certainly the Brazil trees were growing substantially faster. Boreal trees had rates of 0.1–0.7 $\mu\text{mol kg C}^{-1} \text{s}^{-1}$ at 20 °C with lower rates for the larger, older trees (Lavigne and Ryan 1997).

The decline in wood CO₂ efflux with tree size that substantially exceeds the decline in growth and the large difference in Brazil and Hawaii CO₂ efflux rates suggest that some mechanism other than growth or maintenance processes is altering wood CO₂ efflux and that this process changes with tree age and size. We suggest four potential mechanisms to explain a decline in wood CO₂ efflux that is greater than the decline in growth: (1) *decreased diffusion through bark*: more transport of CO₂ produced by respiration away from the respiring region (Teskey and McGuire 2002, Teskey et al. 2008), perhaps because CO₂ diffusion through bark decreases as trees grow larger; (2) *higher sapflow*: more sapflow per unit of bark surface area would remove more CO₂ from the respiring region as trees grow larger; (3) *decreasing contribution from root zone CO₂*: wood CO₂ efflux may comprise some dissolved CO₂ transported from the root zone (Teskey and McGuire 2007), perhaps this transport decreases with tree size; or (4) *increasing bark photosynthesis*: bark photosynthesis (Cernusak and Marshall 2000) increases as trees grow larger.

Decreased diffusion through bark Radial growth slows as trees increase in size, and this slower radial growth could promote bark with more resistance. Decreased diffusion should – all else being equal – raise CO₂ concentration inside larger stems. However, CO₂ concentration inside 6-year-old stems in Hawaii was 3.5%, compared to 9.5% in 1-year-old stems (Ryan, unpublished data), but likely respiration inside the stem was greater in the 1-year-old stems as well.

Higher sapflow in larger trees Water flux through the xylem was similar in 1- and 5-year-old trees at the same site (Barnard and Ryan 2003). However, water flux relative to the area available for diffusion could increase. For example, sapwood thickness remains about 2 cm for these trees, regardless of tree size (Barnard and Ryan 2003). So, as the tree diameter increases, the ratio of sapwood volume to bark surface area will decrease as the tree diameter increases. Hence, sapflow increases relative to the area available for diffusion. For example, a 1-year-old tree in the Hawaii high fertility, LD treatment had an average diameter of 6.6 cm and a ratio of sapwood volume to surface area of 1.4. The average

6-year-old tree in the same treatment had an average diameter of 17.4 cm and a ratio of sapwood volume to surface area of 1.8, yielding 22% less diffusion area for the same amount of water flow.

Decreasing contribution from root zone CO₂ Soil respiration did decline as the plantation aged (Ryan et al. 2004) – age one to age six declines ranged from 8% for the high fertility, LD treatment to 34% for the control, LD treatment. If soil diffusion to CO₂ remained constant, the lower soil respiration indicates a lower CO₂ concentration in the soil profile and less available for root water uptake. The $\delta^{13}\text{C}$ of wood CO₂ efflux was 2.2‰ more negative for 1-year-old trees compared to 5-year-old trees in Hawaii eucalyptus (Ryan, unpublished data), suggesting that the CO₂ efflux in the smaller trees came from a more depleted source such as soil heterotrophs.

Increasing bark photosynthesis as trees grow larger This explanation is unlikely because the thicker bark of larger trees reduces light to photosynthetic tissue and would act to reduce the contribution of bark photosynthesis with tree size. The bark of larger trees might also have a lower photosynthetic photon flux density, as the trees grow and the canopy closes.

Differences between the decline in wood CO₂ efflux and the decline in growth, the decline in growth and maintenance coefficients and the large difference between Hawaii and Brazil wood CO₂ efflux rates for similar-sized trees growing at similar rates suggest that wood CO₂ efflux is decoupled from wood respiration. We know that transport of CO₂ can decouple CO₂ efflux from wood respiration (Teskey and McGuire 2002, Teskey et al. 2008). This study shows that potential changes in bark resistance to CO₂ diffusion, sapflow or CO₂ supplied to the xylem stream from the soil may change with tree age or size and further complicate linking CO₂ efflux from wood with woody respiration. Measurements at zero sapflow (Teskey and McGuire 2007) would help distinguish between interference from CO₂ transport in the xylem stream and changing resistance to diffusion.

Effects of assuming upper stems and branches are similar to those of lower stem

Cavaleri et al. (2006) found that small diameter branches in an old-growth tropical forest had high rates of wood CO₂ efflux, similar to what we found in Hawaii and Brazil.

However, because branch biomass is low in *Eucalyptus*, wood CO₂ efflux for the primary stem accounted for the majority of total wood CO₂ efflux for our Hawaii *Eucalyptus*, unlike Cavaleri et al. (2006) where smaller branches accounted for the majority of total wood CO₂ efflux. Both Hawaii and Brazil measurements showed that wood CO₂ efflux rates were greater for upper stems and branches than

for lower stems, although some of the differences may be related to the differences in wood growth at the measuring point. Branch photosynthesis for branches < 1 cm could offset some or most of the wood CO₂ efflux during the day and change the estimate of total wood CO₂ efflux by as much as 50%. For estimating ecosystem level wood CO₂ efflux, this study suggests more focus on the upper stem and branches, and estimating the offset from photosynthesis, because ignoring these could cause large errors in stand-level estimates of wood CO₂ efflux.

Foliar respiration

Foliar respiration rates were identical in Hawaii and Brazil for similar treatments (4.2 $\mu\text{mol mol N}^{-1} \text{s}^{-1}$ at 20 °C for the LD, high fertility treatments and 5.2 $\mu\text{mol mol N}^{-1} \text{s}^{-1}$ at 20 °C for the Hawaii control treatment – not available in Brazil). The rate is close to that reported for a variety of trees grown in a wet old-growth tropical forest (3.1 $\mu\text{mol mol N}^{-1} \text{s}^{-1}$ at 20 °C, using a measured Q_{10} of 2.3 and the reported regression slope of 0.34 $\mu\text{mol g N}^{-1} \text{s}^{-1}$ for the population, Cavaleri et al. 2008). This rate is also similar to those found for boreal and subalpine trees and shrubs (5.2 $\mu\text{mol mol N}^{-1} \text{s}^{-1}$ at 20 °C, Ryan 1995), but is lower than that found in temperate white pine (9.6 $\mu\text{mol mol N}^{-1} \text{s}^{-1}$ at 20 °C, Vose and Ryan 2002). Reich et al. (2008) found respiration:N rates in a large survey varying from 0.3 to 2.0 $\mu\text{mol mol N}^{-1} \text{s}^{-1}$ at 20 °C for 0.5–2% N by weight.

The ratio of respiration at 20 °C to maximum photosynthesis (R:P) was similar for Hawaii and Brazil *Eucalyptus* (0.038 for Brazil and 0.030 for Hawaii). However, the relationship between respiration and photosynthesis differed for *Eucalyptus* and a Costa Rica native old-growth tropical forest. In Costa Rica, R:P (Cavaleri et al. 2008) was greater than that for *Eucalyptus* (0.083 at 40 m height and 0.055 at 10 m height). One intriguing explanation for this difference might be a difference in sink strength between these two ecosystems. The *Eucalypt* ecosystems have a wood growth of 0.5–1.5 kg C m⁻² year⁻¹ (Ryan et al. 2004), compared with about 0.2 kg C m⁻² year⁻¹ for a typical wet tropical old-growth forest ecosystem (Clark et al. 2001), even though leaf area in the *Eucalyptus* (leaf area index of 3–5, Ryan et al. 2004) is lower than that in the Costa Rican forest (leaf area index = 6, Clark et al. 2008). Perhaps, the higher R:P for the slow growing tropical wet forest is simply luxury consumption of excess carbon fixed in photosynthesis.

In conclusion, CO₂ efflux from wood per unit biomass was related to growth for Hawaii *E. saligna*, but declined ~ 10× from age two to age five, twice as much as the decline in tree growth. The CO₂ efflux from wood in Brazil was 8–10× lower than that comparable for Hawaii trees with similar growth rates, but it also declined with tree age. Hawaii *Eucalyptus* growth and maintenance coefficients calculated for each sample year declined with tree

age and size, with the growth coefficient at age six lower than that estimated for pure cellulose. These results suggest a decoupling of CO₂ efflux through bark from wood respiration. Future measurements of wood CO₂ efflux should measure upper stems and branches and wood photosynthesis, and evaluate different bark types of *Eucalyptus* clones about their diffusivity to CO₂ efflux. Foliar respiration was identical per unit nitrogen for comparable treatments in Brazil and Hawaii. Our results suggest that obtaining stand-level estimates of foliage respiration for *Eucalyptus* can be fairly simple, but stand-level estimates of wood CO₂ efflux and a link to wood respiration remain problematic.

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