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Sapwood temperature gradients between lower stems and the crown do not influence estimates of stand-level stem CO_2 efflux†

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Summary Temperature plays a critical role in the regulation of respiration rates and is often used to scale measurements of respiration to the stand-level and calculate annual respiratory fluxes. Previous studies have indicated that failure to consider temperature gradients between sun-exposed stems and branches in the crown and shaded lower stems may result in errors when deriving stand-level estimates of stem CO_2 efflux. We measured vertical gradients in sapwood temperature in a mature lowland podocarp rain forest in New Zealand to: (1) estimate the effects of within-stem temperature variation on the vertical distribution of stem CO_2 efflux; and (2) use these findings to estimate stand-level stem CO_2 efflux for this forest. Large within-stem gradients in sapwood temperature (1.6 ± 0.1 to 6.0 ± 0.5 °C) were observed. However, these gradients did not significantly influence the stand-level estimate of stem CO_2 efflux in this forest (536 ± 42 mol CO_2 ha^{-1} day^{-1}) or the vertical distribution of stem CO_2 efflux, because of the opposing effects of daytime warming and nighttime cooling on CO_2 efflux in the canopy, and the small fraction of the woody biomass in the crowns of forest trees. Our findings suggest that detailed measurements of within-stand temperature gradients are unlikely to greatly improve the accuracy of tree- or stand-level estimates of stem CO_2 efflux.

Keywords: Dacrydium cupressinum, scaling.

Introduction

In the study of forest ecosystems, field measurements conducted at the organ level (e.g., leaves, stems or roots) are extrapolated to larger spatial and temporal scales (e.g., a forest stand) to determine the ecosystem-level significance of cellular or physiological processes. For example, measurements of CO_2 efflux from woody stems and branches that have been scaled up to the stand level indicate that woody tissue respiration is important in the regulation of forest productivity because it accounts for 7–42% of total plant respiration (Waring and Schlesinger 1985, Ryan and Waring 1992, Ryan et al. 1994) and typically consumes 5–15% of gross primary production (GPP; Meir and Grace 2002). Previous studies have emphasized that estimating annual stand-level stem CO_2 efflux requires the selection of an appropriate scalar (Lavigne et al. 1996), quantification of within-tree variation in CO_2 efflux between lower stems and upper stems or branches (Sprugel 1990, Damesin et al. 2002, Cavaleri et al. 2006), and measurements of seasonal patterns in CO_2 efflux and temperature response coefficients (Linder and Troeng 1981, Stockfors and Linder 1998). It remains to be determined whether failure to account for vertical temperature gradients in forest stands between the canopy and forest floor biases extrapolation of stem CO_2 efflux to the stand level.

Temperature plays a critical role in the regulation of respiration rates in plant tissues because it affects the activity of enzymes, the availability of substrate and adenylates, and the demand for respiratory products by growth, maintenance and transport processes (Atkin and Tjoelker 2003). A review of the temperature response of respiration in woody tissues from 22 tree species, typically described by an exponential response function (Amthor 1989), indicated that respiration rate increases by a factor of 1.0–2.9 in response to a 10 °C increase in temperature (Damesin et al. 2002). Pronounced vertical gradients in air temperature have been observed in forests with the air temperature above the canopy often as much as 4 °C higher than that within 2 m of the forest floor (Motzer 2005). Because of air temperature gradients, variation in stem size and differences in exposure to direct sunlight, large temperature gradients may also be observed between the woody tissues within forest stands. For example, the magnitude of within-stem temperature variation in a Norway spruce (*Picea abies* (L.) Karst.) tree averaged 3.7 °C during 40 days of measurement and was greater than 10 °C for nearly 8% of the time (Stockfors 2000). This study found that failure to account for these temperature

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gradients resulted in large errors, 35% on average, in modeling the respiration rate of stem segments of this tree. Similarly, Edwards and Hanson (1996) reported that differences in sapwood temperature between north- and south-facing stem surfaces could result in variation in stem CO_2 efflux of up to 25%. These studies suggest that failure to account for the large temperature gradients between the sunlit stems and branches in the crown and shaded lower stem may greatly reduce the accuracy of stand-level estimates of stem CO_2 efflux.

In this study, vertical gradients in sapwood temperature were measured in a mature lowland podocarp rain forest located in South Westland, New Zealand to: (1) estimate the effects of within-stem temperature variation on the vertical distribution of stem CO_2 efflux; and (2) use these findings to develop a stand-level estimate of stem CO_2 efflux for this forest. These primary forests are characterized by large, emergent conifers (*Podocarpaceae*), predominantly 200–400-year-old rimu (*Dacrydium cupressinum* Sol. ex. Lamb) trees, with a dense mixed understory (Ogden and Stewart 1995) dominated by broad-leaved shrubs. We hypothesized that the effects of within-tree variation in temperature on the distribution of stem CO_2 efflux is large in this forest because the relatively open canopy (leaf area index = 3.5, Walcroft et al. 2005) allows large sections of upper stems to be exposed to direct sunlight at midday. We further hypothesized that high temperatures in the forest canopy result in a large contribution of CO_2 efflux from upper stems to the stand-level estimate of stem CO_2 efflux. This study aims to further our understanding of the environmental factors that limit carbon balance and productivity in a native New Zealand forest.

Materials and methods

Site description

The study site was situated within a native lowland forest located in Okarito Forest, South Westland, New Zealand (43°12′ S, 170°18′ E, 50 m a.s.l.) and featured a 25-m-tall tower to access the forest canopy within a 0.25-ha study plot. The site is dominated by *D. cupressinum* trees having a mean canopy height of 20 m and occupying 78% of the basal area (Walcroft et al. 2005). Common tree species in the sub-canopy include kamahi (*Weinmannia racemosa* L.k., 12% of basal area), Westland quintinia (*Quintinia acutifolia* Kirk., 10% of basal area) and southern rata (*Metrosideros umbellata* Cav.).

Mean annual temperature is 11.3 °C, with a small range between winter and summer of 8.6 °C, and low air saturation deficit. Annual rainfall is high, about 3400 mm, and evenly distributed throughout the year. As a result, soils are frequently saturated, highly leached and acidic (pH 3.8–4.4 to a depth of 500 mm). The soil nitrogen concentration at a similar adjacent site was 633 μmol g^{-1} and soil-extractable phosphorus concentration was 12 μmol g^{-1} (Richardson et al. 2004). Soils at the site have a high organic matter content (about 30%), low permeability and low porosity.

CO_2 efflux in D. cupressinum stems

Efflux of CO_2 from stems was measured every 2.2 h for 7 days in January 2002 in nine rimu stems (0.18 to 0.67 m in diameter), as described by Bowman et al. (2005). Only nighttime measurements (from 0000 to 0600 h NZST) were used in this study to eliminate measurement errors caused by the transport of respiratory CO_2 in the xylem stream during daylight hours (McGuire and Teskey 2004, Bowman et al. 2005). Stem CO_2 efflux was expected to result from both growth and maintenance respiration because measurements were made during the austral growing season. Rates of CO_2 efflux were determined with an infrared gas analyzer (Model LI-6262, Li-Cor) installed in an open-flow manifold system with polycarbonate gas-exchange chambers attached to the south-facing (shaded) side of each stem at about 1.3 m above ground. The flow of compressed air (43–47 Pa CO_2 concentration) to the chambers was maintained at 0.5 l min^{-1} by a flow controller (Model SR-10, Sierra Instruments, Monterrey, CA). The gas-exchange chambers were half-cylindrical, enclosed 250 cm^2 of stem surface, and were each equipped with a small 24-V fan to mix the air within the chamber. A gasket of closed-cell neoprene foam was fitted to the edges of the chambers to facilitate attachment to tree stems, and caulking cord (Mortite, Kankakee, IL) was applied over fissures between the chambers and tree stems to create airtight seals. The chambers were secured tightly to the stems with ratchet straps. The sampling duration for each chamber was 12 min with all stems sampled once during each 132-min measurement cycle, which consisted of nine stem sampling periods and tests of the zero and span calibrations of the gas analyzer. Sapwood temperatures were measured with constantan-chromega thermocouples placed 15 mm beneath the bark surface and in close proximity to the sampling chamber.

The temperature response of stem CO_2 efflux (E_A) was determined by a modified Arrhenius function as adopted by Turnbull et al. (2003):

$$E_A = E_o e^{\frac{A_o}{R_g}\left(\frac{1}{T_o}-\frac{1}{T_a}\right)} \quad (1)$$

where E_o is CO_2 efflux at the base temperature T_o (here 15 °C), T_a is stem sapwood temperature (K), R_g is the gas constant (8.314 J mol^{-1} K^{-1}), and A_o is a parameter related to the activation energy of respiratory enzymes which describes the magnitude of the temperature response. Nonlinear curve fitting for temperature response curves was conducted with SigmaPlot 2001 (SPSS, Chicago, IL).

Within-tree temperature gradients and stem CO_2 efflux

Sapwood temperature was measured at four locations in three *D. cupressinum* trees in the austral summer from January 17 to March 6, 2002. Measurement positions were located at 1.3 m height (lower stem), 1 m above the lowest crown branch (mid stem), halfway between the lowest crown branch and the tree apex (lower crown), and 1–2 m below the tree apex (upper crown). The three trees differed in diameter at 1.3 m (0.18,

0.31 and 0.63 m) and in height (17.1, 24.1 and 28 m), and thus, measurement positions along the stems differed in absolute height. Constantan-chromega thermocouples were inserted at each measurement position, about 15 mm below the bark surface, in small holes drilled into the stem and held in place with caulking cord. All thermocouples were installed on the south side of the tree stems. Temperatures were measured every 30 min and recorded with a Campbell CR10 data logger and AM25T thermocouple multiplexer (Campbell Scientific, Logan, UT). Differences in daily maximum, daily minimum and mean sapwood temperature between the stem positions of a tree were assessed by a two-way mixed model analysis of variance and considered statistically significant at $P < 0.05$.

The potential for within-tree gradients in temperature to influence the spatial distribution of stem CO_2 efflux was assessed by calculating instantaneous rates of stem CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) and daily CO_2 fluxes (μmol CO_2 m^{-2} day^{-1}) for each stem section (lower stem, mid stem, lower crown and upper crown). Instantaneous stem CO_2 efflux and daily CO_2 fluxes for each stem section were estimated from the hourly stem temperature for that stem section. To isolate the effects of temperature gradients on CO_2 fluxes, we assumed no variation in E_o or A_o with stem height.

Stem surface area and stand-level stem CO_2 efflux

To estimate the stem surface area of the *D. cupressinum* trees at the study site, a taper function, based on the three trees used to assess within-stem temperature gradients, was derived to estimate stem diameter at any tree height and applied to all trees on the study site. Stem diameter and height were measured in these three trees at the three upper positions (mid stem, lower crown and upper crown) used to assess within-stem temperature gradients. Relative stem diameter and height based on diameter at 1.3 m and absolute tree height, respectively, were then calculated from these data to correct for the large variation in size among trees. A third-degree polynomial was fit to the relative diameter and height data ($n = 9$), along with relative diameter measurements at 1.3 m, and used to describe stem taper:

$$d = b_0 + b_1 h + b_2 h^2 + b_3 h^3 \quad (2)$$

where d is relative diameter (ratio of the diameter at a given point to the diameter at 1.3 m), h is relative height (ratio of the height at a given point to the tree's maximum height) and b_0 through b_3 are polynomial parameters. Derivation of polynomial parameters and fit statistics from relative diameter and height measurements was conducted by nonlinear curve fitting with Sigma Plot 2001.

With Equation 2 and an inventory of the diameter and height of each tree in the study plot (W.S.F. Schuster, unpublished data), stem diameter was estimated for all *D. cupressinum* trees at 0.5-m intervals from the ground to the stem apex. Each 0.5-m stem segment was assumed to approximate the shape of the frustrum of a circular cone. The surface area of each 0.5-m stem segment of each tree was then calculated, and each segment was assigned to one of the four stem sections (lower stem, mid stem, lower crown and upper crown) based on mensurational data on canopy height (i.e., the height of the lowest canopy branch) for each tree in the study plot (W.S.F. Schuster, unpublished data). The surface area estimates for each 0.5-m stem segment were summed to estimate total stem surface area and the vertical distribution of stem surface area for each tree and at the stand level. Because of the large variation in tree size in the study plot, the absolute heights of the stem sections varied among trees. As a result, the upper crowns of the smaller *D. cupressinum* trees are in the lower or middle portions of the forest canopy.

Stand-level stem CO_2 efflux was estimated for 30 days, beginning January 17, 2002, based on measurements of stem CO_2 efflux from nine *D. cupressinum* trees, stand-level estimates of stem surface area for the four stem sections, and hourly stem temperature for each section (using the mean sapwood temperature for that stem section from the three described *D. cupressinum* trees). The stand-level CO_2 flux attributable to woody stems was estimated as a proportion of the gross primary productivity for the site during January 2002, as determined by a process-based model of canopy carbon uptake (Whitehead et al. 2002).

Results and discussion

Within-tree variation in sapwood temperature

Large gradients in sapwood temperature between the upper and lower stem sections were typically observed in *D. cupressinum* trees (Table 1, Figure 1). During the day, maximum sapwood temperature in the upper crown was significantly greater than in the lower stems because of greater absorption of solar radiation (two-way ANOVA, $P < 0.1$, Table 1). Stem temperatures in the upper crown were between 1.6 ± 0.1 and 6.0 ± 0.5 °C, or 11.6 and 43.7% higher than in the lower stem. At night, the temperature gradient was reversed, with upper crown temperatures between 0.9 ± 0.2 and 1.7 ± 0.3 °C, or 10.7 and 21.5% less than in lower stem positions because of greater radiative cooling in the crown and absorption of long-wave radiation from the soil by the lower stems. Consequently, the high sapwood temperatures in the crown during the day were offset by lower temperatures at night, such that there were no significant gradients in mean daily sapwood temperature between the lower stems and upper crown positions (Table 1).

This finding is broadly consistent with the results of previous measurements of temperature gradients across a wide range of forest ecosystems. For example, Yanez-Espinosa et al. (2003) found that high daytime temperatures in the canopy of a semi-evergreen neotropical forest are balanced by lower temperatures at night resulting in only a small (about 1 °C) enhancement in canopy temperature over several days. In a subalpine coniferous forest in Colorado with a canopy height of 11.3 m (Niwot Ridge LTER, Monson et al. 2002), mean maximum air temperature at 8 m was 3.5 ± 1.8 °C higher than that at 2 m, whereas at night, mean minimum air temperature was 1.7 ± 0.7 °C lower than that at 2 m between June 1 and July 15

in 2000–2002 (R. Monson, unpublished data). These offsetting maximum and minimum temperatures resulted in only a slight increase in air temperature at 8 m of 0.2 ± 1.3 °C over the measurement period. In a temperate deciduous forest in Wisconsin (Willow Creek Flux Tower, Chequamegon Ecosystem-Atmosphere Study, Cook et al. 2004), the air temperature gradient during the day was less pronounced as mean maximum air temperature in the upper canopy (24.3 m) was only 1.5 ± 1.5 °C higher than that at 1 m. At night, mean minimum air temperature at 24.3 m was 1.8 ± 0.5 °C lower than that at 1 m, resulting in a decrease in the mean daily air temperature in the upper canopy by 1.0 ± 1.1 °C from June 1 to July 15 in 2000–2002 (K. Davis and P. Bolstad, unpublished data). In their estimates of annual respiration in a *Pinus sylvestris* L. forest, Ågren and Axelsson (1980) modeled diel temperature variation with a sine function with an amplitude equal to the mean difference between maximum and minimum temperature. Although this method reliably approximated annual respiration, i.e., errors were generally less than 5%, the authors cautioned that diel temperature variation is not entirely symmetric around the mean with daytime temperatures tending to differ more from the mean than nighttime temperatures for aboveground biomass in forests.

Stem CO_2 efflux, taper and surface area

Previous research at our research site showed that CO_2 efflux from *D. cupressinum* stems, calculated with Equation 1, ranged from 0.43 to 0.95 μmol CO_2 m^{-2} s^{-1} or from 13.7 to 75.2 μmol CO_2 m^{-3} s^{-1} at 15 °C (r^2 = 0.65–0.87, $P < 0.001$) (Bowman et al. 2005). These rates were similar to those reported for other conifer species and ecosystems. For example, stem CO_2 efflux (at 15 °C) was 0.2–1.0 μmol CO_2 m^{-2} s^{-1} across eight boreal forests stands (Ryan et al. 1997) and 13–55 μmol CO_2 m^{-3} s^{-1} in a temperate *Pinus strobus* L. stand (Vose and Ryan 2002). Variation in stem CO_2 efflux in *D. cupressinum* was unrelated to commonly used scalars including sapwood volume, sapwood area, or nitrogen concentration of the inner bark or sapwood tissues (Bowman et al. 2005). The lack of a strong, scalable relationship between CO_2 efflux and sapwood volume or nitrogen concentration may be caused by between-tree differences in the proportion of respiratory activity occurring in sapwood tissues relative to inner bark tissues, the small range of nitrogen concentrations in the sampled wood (0.26–0.84%), or the small number of trees sampled (n = 9). As a result, mean values for E_o, 0.72 ± 0.02 μmol CO_2 m^{-2} s^{-1}, and the temperature response coefficient A_o, 45.5 ± 1.8 kJ mol^{-1} K^{-1}, were used to estimate stand-level stem CO_2 efflux for this forest.

The stem taper of *D. cupressinum* trees was well described by a third-degree polynomial model (R^2 = 0.97, $P < 0.0001$):

$$d = -2.05h^3 + 2.61h^2 - 1.69h + 1.16 \quad (3)$$

where d is relative diameter calculated as the ratio of diameter at a given height to the diameter at 1.3 m and h is relative height calculated as the ratio of the height at a given point to the tree's maximum height. All model parameters were highly significant ($P < 0.005$). This simple model accurately reflects the common assumption that the form of tree stems approximates that of three linked geometric solids with the shape of the lower bole, middle bole and upper bole assumed to be similar to a neiloid frustrum, a parabolic frustrum and a cone, respectively (Avery and Burkhart 2002).

The total stem surface area of the *D. cupressinum* trees in the study plot and the proportion of stem surface area located in

Table 1. Daily mean, maximum and minimum sapwood temperatures (± SE) for three *Dacrydium cupressinum* trees at four stem positions from January 17 through March 6, 2002. Within a column for each tree, means sharing a common letter do not differ significantly at $P < 0.05$ according to a two-way, mixed model analysis of variance. Statistical comparisons were not made across trees. Height and diameter at breast height, respectively, for the three trees were: Tree 5, 28 and 0.63 m; Tree 18, 24.1 and 0.31 m; and Tree 30, 17.1 and 0.18 m.

	Daily sapwood temperature (°C)		
	Mean	Maximum	Minimum
Tree 5			
Upper crown	14.6 ± 0.3 a	21.0 ± 0.1 a	10.9 ± 0.1 a
Lower crown	14.9 ± 0.3 b	20.3 ± 0.1 b	11.9 ± 0.1 b
Mid stem	14.1 ± 0.2 c	16.3 ± 0.1 c	11.8 ± 0.1 b
Lower stem	13.5 ± 0.2 d	15.0 ± 0.0 d	11.8 ± 0.1 b
Tree 18			
Upper crown	13.6 ± 0.3 a	17.0 ± 0.1 a	10.3 ± 0.3 a
Lower crown	13.7 ± 0.3 bc	16.4 ± 0.1 b	11.3 ± 0.3 b
Mid stem	13.8 ± 0.2 b	15.8 ± 0.1 c	11.9 ± 0.3 c
Lower stem	13.6 ± 0.2 ac	15.4 ± 0.0 d	11.7 ± 0.3 d
Tree 30			
Upper crown	13.9 ± 0.3 a	19.9 ± 0.1 a	9.4 ± 0.3 a
Lower crown	13.8 ± 0.3 b	17.8 ± 0.1 b	9.9 ± 0.3 b
Mid stem	13.7 ± 0.3 b	16.9 ± 0.1 c	10.5 ± 0.3 c
Lower stem	13.8 ± 0.3 ab	16.5 ± 0.1 d	11.1 ± 0.3 d

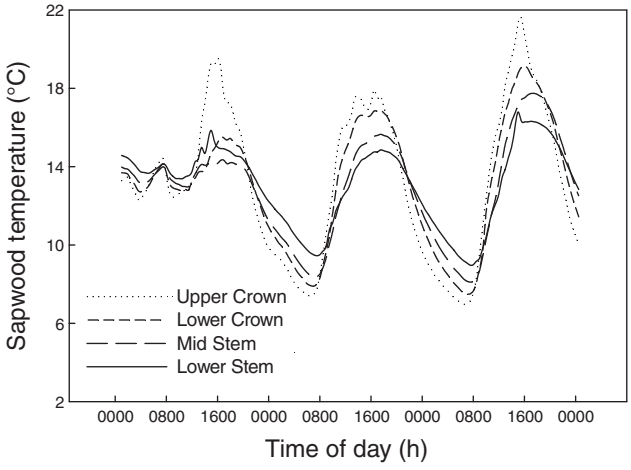

Figure 1. Representative vertical gradient in sapwood temperature observed in a single *Dacrydium cupressinum* tree at four stem heights from February 14 to 16, 2002.

each of the stem sections (lower stem, mid stem, lower crown and upper crown) were estimated with the stem taper model and the results of a mensurative inventory of tree diameter, tree height and canopy height on the study plot (W.S.F. Schuster, unpublished data). Total *D. cupressinum* stem surface area was 7245 $m^2\ ha^{-1}$ and exhibited a strong vertical gradient in distribution with 56.1 ± 3.7% of stem surface area occurring below the lowest crown branch in *D. cupressinum* trees, whereas only 19.1 ± 1.6% of stem surface area was found in the lower or upper crown (Table 2). However, these data likely underestimate the proportion of woody biomass in the canopy of this stand because the lower crowns of smaller *D. cupressinum* trees are generally located in the lower portions of the forest canopy.

Stand-level estimate of stem CO_2 efflux

We determined the amount of CO_2 diffusing from *D. cupressinum* stem surfaces at the stand level based on the estimate of stand-level stem surface area for the four stem sections, the means of E_o and A_o for *D. cupressinum* stems (Bowman et al. 2005), and the hourly sapwood temperature for each section. Estimated CO_2 efflux from *D. cupressinum* stems was 536 ± 42 mol $CO_2\ ha^{-1}\ day^{-1}$ (varying between 474 and 698 mol $CO_2\ ha^{-1}\ day^{-1}$) in this lowland podocarp rain forest during the peak of the austral growing season. The vertical distribution of stem CO_2 efflux through the forest stand is largely a function of the distribution of stem surface area, as shown in Table 2, with 55.4, 24.9, 16.2 and 3.6% of the stand-level CO_2 flux attributable to the lower stem, mid stem, lower crown and upper crown, respectively. The minor differences in the vertical distribution of stem CO_2 efflux and stem surface area shown in Table 2 are attributable to variation in sapwood temperatures among the stem positions.

We assumed that stem CO_2 efflux and the temperature response coefficient did not vary with stem height or between north-facing (sunlit) and south-facing (shaded) surfaces. However, previous studies have shown that CO_2 efflux from woody stems may vary with tree height and between north- and south-facing surfaces. For example, surface-area-based rates of CO_2 efflux were 2–19 times greater in tree crowns compared with lower stems (Damesin et al. 2002, Cavaleri et al. 2006). Higher rates of CO_2 efflux in the upper stems or branches of forest trees may be a result of increased respiratory activity in the underlying tissues (Pruyn et al. 2002*a*, 2002*b*), decreased bark thickness and resistance to CO_2 diffusion in upper stems and branches (Teskey et al. 2008), or transport of respiratory CO_2 in the transpiration stream (Teskey and McGuire 2002, McGuire and Teskey 2004) or a combination of these. In addition, Edwards and Hanson (1996) found that CO_2 efflux may be as much as 25% greater on sunlit stem surfaces than on shaded surfaces. Accordingly, increased values of E_o or A_o, or both, with height in our study trees or increased efflux on the south-facing (shaded) surfaces would result in an underestimate of stand-level CO_2 flux from the woody stems of *D. cupressinum* at the study site.

Table 2. Stem surface area and daily stem CO_2 efflux for four stem sections at the forest stand level and the proportion of the stand total contributed by each stem section based on measurements of three *Dacrydium cupressinum* trees.

Stem section	Surface area		CO_2 efflux	
	($m^2\ ha^{-1}$)	(%)	(mol $ha^{-1}\ day^{-1}$)	(%)
Upper crown	249	3.4	19	3.6
Lower crown	1139	15.7	87	16.2
Mid stem	1791	24.7	133	24.9
Lower stem	4068	56.1	297	55.4
Total	7245	100	536	100

A process-based model of canopy carbon uptake applied to data from our field site (Whitehead et al. 2002) indicated that canopy carbon uptake or GPP, during the same measurement period (January 2002), was 5010 mol C $ha^{-1}\ day^{-1}$ (A.S. Walcroft and Whitehead, unpublished data). Therefore, stem CO_2 efflux in the forest stand results in the release to the atmosphere of 10.7% of the carbon fixed by photosynthesis in the canopy. This estimate is consistent with the majority of recent estimates of the proportion of annual GPP consumed by woody tissue respiration, which typically range between 5 and 15% of GPP (Meir and Grace 2002). Old forests, such as this 200–400-year-old podocarp stand, are important carbon pools because of their abundance of standing biomass. However, only a few previous studies have estimated stand-level stem CO_2 efflux (i.e., wood respiration) for primary or old-growth forests (Law et al. 2001, Harmon et al. 2004, Cavaleri et al. 2006). Therefore, the stand-level estimate of stem CO_2 efflux provided by this study contributes to our understanding of the relative magnitude of carbon fluxes in primary forests and the effects of temperature and stand structure on these fluxes.

Effects of temperature on CO_2 efflux at the stand-level

We observed large vertical gradients in sapwood temperature in the forest stand—the maximum difference in sapwood temperature between the upper crown and lower stem was typically between 1.6 and 6.0 °C. Similarly, Stockfors (2000) observed large within-tree variation in sapwood temperature and concluded that these gradients may significantly affect the accuracy of scaled-up estimates of stem respiration for trees and whole stands. Our study confirmed that the high temperatures typical of the upper crown of forests have the potential to increase CO_2 efflux in upper stems and branches. For example, in response solely to within-tree variation in temperature, upper-crown positions exhibited a 14.6–29.9% increase in CO_2 efflux (Figure 2a). However, these high rates of CO_2 efflux during the day were offset by 5.3–18.6% lower efflux, relative to lower stem positions at night (Figure 2a). The maximum differences in CO_2 efflux between the upper crown and lower stem observed during the 30-day period were 45.3% during the day and 21.5% during the night. As a result, over the 30 days in which within-tree temperature gradients were measured and used to model CO_2 efflux, mean daily CO_2 flux per unit stem surface area was estimated to be only 4.9 ± 0.1, 4.5 ± 0.1, and 2.2 ± 0.1% greater in the upper crown, lower crown

and mid stem, respectively, relative to the lower stem (Figure 2b). Furthermore, because of the vertical distribution of stem biomass (Table 2), daily CO_2 flux at the stand level attributable to the lower stem sections of *D. cupressinum* trees greatly exceeded that from the upper-crown, lower-crown and mid-stem sections (Figure 2c). Therefore, although large within-tree temperature gradients are likely to be common in forest stands, these gradients are unlikely to be important for estimating stand-level stem CO_2 efflux because of (1) the opposing effects of daytime warming and nighttime cooling on stem CO_2 efflux in the forest canopy, and (2) the small fraction of woody biomass located in the crowns of forest trees. Our findings suggest that detailed measurements of within-stand temperature gradients are unlikely to greatly improve the accuracy of tree- or stand-level estimates of wood CO_2 efflux, particularly for time periods longer than a few days.

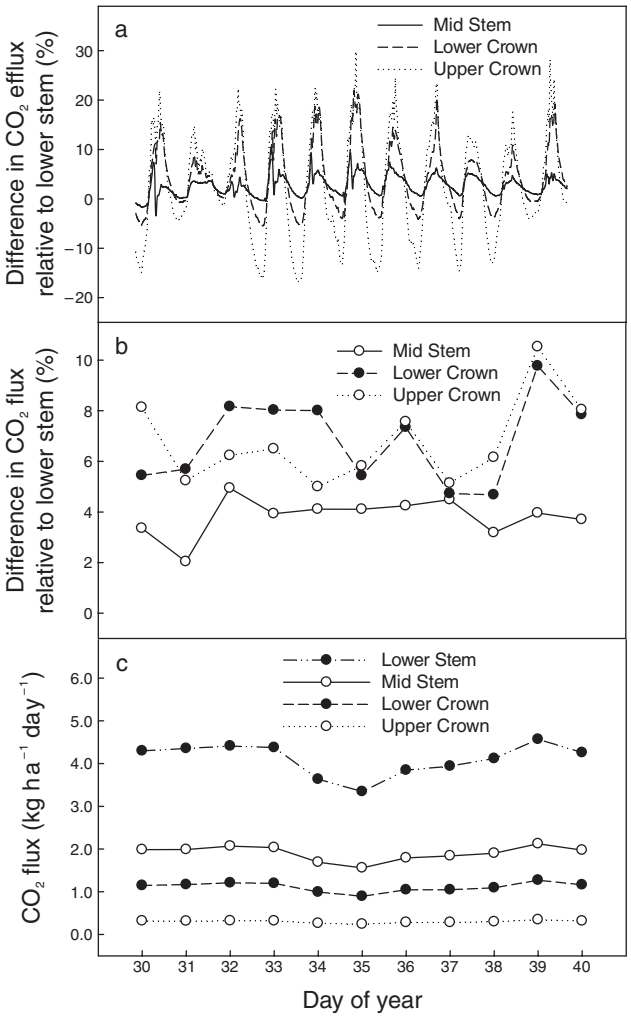

Figure 2. (a) Diel variation in the ratio of the difference between the estimated rates of stem CO_2 efflux from upper-crown, lower-crown and mid-stem positions and the lower-stem positions relative to the estimated rates of respiration from the lower-stem positions from January 30 to February 9, 2002. Values are means for three *Dacrydium cupressinum* trees. (b) Ratio of the difference between daily CO_2 flux (per unit surface area) in upper-crown, lower-crown, mid-stem and lower-stem positions relative to the daily CO_2 flux in the lower-stem positions. Values are means of three *D. cupressinum* trees. (c) The daily CO_2 flux, at the stand level, attributable to respiration in each of the four stem sections (lower stem, mid stem, lower crown and upper crown).

Within-canopy variation in temperature is also of little importance when scaling certain leaf physiological processes to the canopy level. Despite the importance of leaf temperature in regulating enzymatic rates of carboxylation, electron transport and respiration, studies have reported good results in modeling canopy carbon exchange with big-leaf models that ignore vertical gradients in leaf physiological parameters and microclimatic characteristics within canopies (Amthor 1994, Lloyd et al. 1995). Furthermore, incorporation of canopy gradients in temperature and other micrometerological characteristics had little (< 3%) influence on modeled net canopy carbon uptake in a temperate deciduous forest (Baldocchi and Wilson 2001).

The lowland podocarp rain forest that we investigated has a relatively low leaf area index (LAI) of 3.5 (Walcroft et al. 2005) and, consequently, high exposure of stems at all heights to direct sunlight. Within-tree differences in temperature may be greater in forest stands with more closed canopies and higher LAI values where upper stems and branches may be exposed to the sun but lower stems receive little direct sunlight. However, large within-stand temperature gradients are also absent in tropical, temperate deciduous and subalpine forests, further indicating the broad applicability of our findings. In conclusion, we have confirmed that stem CO_2 efflux is an important component of the carbon balance of temperate primary forests, accounting for 10.7% of GPP during the growing season. Although we still have much to learn about scaling CO_2 efflux measurements to the tree and stand level, our results indicate that assessing the magnitude of vertical gradients in sapwood temperature is not necessary to accurately estimate stem CO_2 efflux at the forest stand level.

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