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Relationship between stem CO_2 efflux, stem sap velocity and xylem CO_2 concentration in young loblolly pine trees

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ABSTRACT

We measured diel patterns of stem surface CO_2 efflux (E_s, μmol m^{-2} s^{-1}), sap velocity (v_s, mm s^{-1}) and xylem CO_2 concetration ($[CO_2]$) (X_s, %) in 8-year-old loblolly pine trees during the spring to determine how v_s and X_s influence E_s. All trees showed a strong diel hysteresis between E_s and stem temperature, where at a given temperature, E_s was lower during the day than at night. Diel variations in temperature-independent E_s were correlated with v_s ($R^2 = 0.54$), such that at maximum v_s, E_s was reduced between 18 and 40%. However, this correlation may not represent a cause-and-effect relationship. In a subset of trees, v_s was artificially reduced by progressively removing the tree canopy. Reducing v_s to near zero had no effect on E_s and did not change the diel hysteretic response to temperature. Diel X_s tended to decrease with v_s and increase with E_s, however, in defoliated trees, large increases in X_s, when $v_s \approx 0$, had no effect on E_s. We conclude that at this time of the year, E_s is driven primarily by respiration of cambium and phloem tissues and that sap flow and xylem transport of CO_2 had no direct influence on E_s.

Key-words: chambers; CO_2 microelectrode; Granier sensors; *Pinus taeda*; sap flow; stem respiration.

INTRODUCTION

Respiration of above ground woody tissues (stem and branch) comprises 15–25% of forest ecosystem respiration (Ryan *et al*. 1994, 1996; Xu *et al*. 2001; Maier *et al*. 2004). These estimates are based on empirical data where CO_2 efflux from the stem (or branch) surface into a chamber is measured with an infrared gas analyzer. This approach assumes that CO_2 generated from metabolism of cambium and xylem parenchyma tissues enclosed within the chamber diffuses radially from the stem interior across the cambial sheath to the surface. However, at high transpiration rates, a portion of the respired CO_2 in sapwood may be carried upward by the transpiration stream instead of released horizontally through the bark, so that measured CO_2 efflux underestimate the actual respiration of the sample section.

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A number of studies (Negisi 1975, 1978, 1982; Lavigne 1987; Kabubari 1988) found that on warm sunny days, measured stem CO_2 efflux (E_s) rates were much lower, 25–50%, compared with what would be expected based on temperature alone. Other studies found that the diel relationship between E_s and temperature exhibits a hysteresis, where CO_2 efflux measurements made at a similar temperature is higher in the late afternoon and evening, when transpiration is low, than in the morning, when transpiration is high (Martin, Teskey & Dougherty 1994; Ryan *et al*. 1995; Lavigne 1996; Stockfors 2000; Maier 2001; Bosc, De Grandcourt & Loustau 2003). These studies suggest that stem surface CO_2 efflux in forest ecosystems may be linked to canopy water use.

Stem CO_2 concentrations are high, ranging from 2 to 10% (Hari, Pekka & Korpilahti 1991; Eklund 1993; Teskey & McGuire 2002). Dissolved carbon in the xylem (CO_2, H_2CO_3 and HCO_3^-) is a combination of CO_2 derived from respiration of nearby xylem parenchyma and cambium tissues, CO_2 imported from respiratory activity of stem and roots lower in the xylem stream, and CO_2 taken up in soil water. Given the high xylem CO_2 concentration ($[CO_2]$) (X_s), the aqueous transport of carbon in the xylem stream represents a potentially large and poorly understood carbon flux in forest ecosystems. If transport and storage of CO_2 in the xylem strongly affects E_s under normal field conditions, then the interpretation of stem gas exchange measured with chamber methods becomes equivocal (Martin *et al*. 1994; Teskey & McGuire 2002). A more complete evaluation of these relationships is needed to understand variation in E_s rates.

Recently, there has been a renewed interest in measuring the origin and fate of carbon in the xylem sap and determining what effect this carbon flux may have on the measurement of E_s (Stringer & Kimmerer 1993; Martin *et al*. 1994; Kaipiainen *et al*. 1998; Edwards & Wullschleger 2000; Clinton, Maier & Sullivan 2001; Teskey & McGuire 2002, 2005; McGuire & Teskey 2002, 2004; Bowman *et al*. 2005). Teskey & McGuire (2002) measured sap flow rate and X_s in large trees of several species (*Quercus alba*, *Liriodendron tulipefera* and *Pinus taeda*) and found that diel patterns were opposed, suggesting that transpiration may significantly affect stem $[CO_2]$ and thus the driving force for radial diffusion of CO_2 in stem tissue. Teskey & McGuire (2005) further demonstrated in hardwood

saplings, by artificially manipulating X_s, that stem surface CO_2 efflux was directly related to internal [CO_2]. McGuire & Teskey (2004) proposed a mass balance approach for estimating stem respiration that accounted for the rates of xylem CO_2 inputs, outputs and storage and surface CO_2 efflux. They found that the diel flux of respired CO_2 within the stem followed different pathways dependent on sap flow rate. At night, when sap flow rates were low, stem surface CO_2 efflux accounted for 74–93% of total stem respiration (i.e. the total from all sources); but during the day, when sap flow rates were high, surface CO_2 efflux accounted for only 23–72% of estimated total stem respiration. Bowman *et al*. (2005) found similar results in several *Dacrydium cupressinum* trees. However, a consistent and measurable relationship between E_s and stem sap flow is far from universal. Clinton *et al*. (2001) found a negative relationship between apparent stem respiration and sap velocity (v_s) in large yellow poplar trees, while others found either no relationship (Carey, Delucia & Ball 1996; unpublished observations, Edwards & Wullschleger 2000) or a positive correlation (Levy *et al*. 1999). In the Levy *et al*. (1999) study, increases in apparent stem respiration with v_s were attributed to transport of CO_2 from the roots, which were assumed to be in equilibrium with high soil pCO_2.

In this study, we examined the relationship between stem surface CO_2 efflux rate (i.e. apparent stem respiration), v_s and X_s in stems of 8-year-old loblolly pine trees over a 2 week period. Half of the experimental trees had received optimum nutrition from annual fertilization since planting, while the other half grew in the native nutrient-poor soil. Fertilization had significantly increased tree height, diameter and leaf area relative to non-fertilized controls. Fertilized trees are likely to have a different wood hydraulic architecture (Tyree & Ewers 1991), as well as differing patterns of water uptake (Ewers, Oren & Sperry 2000), canopy conductance, stand transpiration (Ewers *et al*. 2001) and rates of maintenance respiration (Maier *et al*. 1998). In some of the trees, we artificially altered v_s through a stepwise reduction in canopy leaf area (Pataki, Oren & Phillips 1998). The objectives were to: (1) determine if there is a diel relationship between stem v_s and stem surface CO_2 efflux; (2) determine if there is a diel relationship between stem v_s and X_s; and (3) determine if there is a relationship between X_s and stem surface CO_2 efflux.

MATERIALS AND METHODS

Site description

The study was conducted in an 8-year-old loblolly pine plantation located at the SETRES II GxE-QTL study site in Scotland County, NC, U.S.A (McKeand *et al*. 2000). The soil is a Wakulla series characterized as a sandy, siliceous, thermic Psammentic Hapludult (sand to >43 m), which is very infertile, somewhat excessively drained, with a water holding capacity of 10–12 cm in a 2 m profile. The site receives an average annual precipitation of 1200 mm distributed evenly throughout the year. Annual temperature averaged 17 °C, with a seasonal average of 26 °C in summer and 9 °C in winter. Greenhouse-grown seedlings were planted in November 1993 after the removal of the existing 10-year-old loblolly pine. Five full-sib families of Atlantic coastal plain and Texas origin were planted in 100 tree plots. Our measurements were confined to a non-fertilized and fertilized plot of one Atlantic coastal plain family (9–1046). The site average leaf area index for the non-fertilized and fertilized plots were 1.19 and 2.91 $m^2\ m^{-2}$, respectively, in October 2000 (Francisco Flores, North Carolina State University, personal communication).

Measurements

We selected six trees in the non-fertilized and fertilized plots (12 trees total). Tree height, stem diameter and number of branches were measured (Table 1). Branch and canopy foliage biomass was estimated using site-specific regression equations (Tim Albaugh, North Carolina State University, personal communication). Average (± SE) stem diameter and estimated canopy biomass were 8.2 ± 0.5 cm and 1725 ± 704 kg in non-fertilized trees and 10.6 ± 0.2 cm and 2658 ± 129 kg in fertilized trees. E_s, stem temperature and v_s were monitored continuously for 11 d. On the last 3 d, X_s was measured in a subset of trees. Instantaneous photosynthesis and stomatal conductance (Licor 6400, Li-Cor, Inc., Lincoln, NE, USA) were measured at the beginning, middle and end of the experiments on upper canopy 1-year-old foliage on all trees during the morning hours (0900–1100 h).

E_s (μmol $CO_2\ m^{-2}\ s^{-1}$) measurements were made using an automated, multichamber sampling system (Butnor, Johnsen & Maier 2005) that consisted of stem chambers, an infrared gas analyzer (EGM-2, PP Systems, Amesbury, MA, USA) and a series of solenoids that sequentially measured stem chambers. The system had an open flow-through design where CO_2 efflux was estimated as the difference between the CO_2 concentration entering and exiting the chamber. Chambers were constructed of Teflon film that surrounded the tree stem 1 m above the ground. The Teflon film was fastened to the stem using collars of closed-cell foam and double-sided tape. Air was distributed to and sampled from the chamber using diffuser rings positioned at the top and bottom of the chamber. Chamber lengths were 25 cm and chamber volume ranged from 0.00179 to 0.00269 m^3, depending on stem diameter. All chambers were leak tested prior to use. Airflow to the chambers was fixed at 0.00225 $m^3\ min^{-1}$. Each chamber was measured for 6 min to assure stable CO_2 measurements. The last minute of each cycle was retained for calculation of surface CO_2 efflux rates. A complete cycle through all of the chambers, including a null chamber, was completed in 42 min, which equals approximately 34 observations for each chamber per day. All chambers were continuously flushed with ambient air (0.00225 $m^3\ min^{-1}$) when chambers were not measured. Simultaneous measurements of chamber air and stem cambium temperature (3 mm) were made using copper/

Table 1. Tree characteristics in April 2001 for the non-fertilized (NF) and fertilized (F) trees located at SETRES II, Scotland County, NC, USA

Plot	Tree	Treatment	d.b.h. (cm)	Height (cm)	Number of branches	Foliage biomass (g)	
						Predicted	Measured
NF	1	UC	9.6	560	44	2017	–
	2	C	8.3	541	43	2006	1984
	3	UC	6.6	476	37	1239	–
	4	C	7.1	459	47	1531	1185
	5	C	8.3	516	39	1661	1299
	6	UC	9.1	546	45	1898	–
F	1	C	10.8	767	37	3063	2781
	2	C	11.2	709	42	2491	2912
	3	C	10.4	701	38	2387	2758
	4	UC	10.7	714	32	2913	–
	5	UC	10.9	691	36	2820	–
	6	UC	9.8	755	34	2278	–

The column labelled 'Treatment' refers to whether the canopies of trees were removed [cut (C)] or left intact [uncut (UC)]. d.b.h., diameter at breast height.

constantan thermocouples. Immediately after the experiments were completed, stem diameter at the top and bottom of the chambers were measured with digital calipers. Stem surface area inside the chamber was estimated from the average of the two diameter measurements and includes the bark.

Stem v_s (mm s^{-1}) was measured using custom-made 30-mm-long thermal dissipation sap velocity probes (Granier 1985, 1987). Briefly, paired probes were inserted radially into the tree such that the probes were approximately 5 cm apart vertically. For each tree, two probes were installed on opposite sides (north and south) of the stem just below the stem chamber. v_s was measured every 10 s and these values were averaged every 15 min. In our trees, essentially all of the xylem was hydroactive; however, while we only measured the outer 3 cm, the probes measured the previous 2 years of growth and captured the majority of stem sap flow in these trees (Ewers & Oren 2000).

X_s (%) was measured *in situ* on four trees using CO_2 microelectrodes (Model MI-720; Microelectrodes, Inc., Bedford, NH, USA). We followed methods described by McGuire & Teskey (2002) and Teskey & McGuire (2002). Briefly, electrodes were calibrated with humidified compressed CO_2 gas at 2, 5 and 10% concentrations. Because the electrodes are temperature sensitive, a temperature correction was applied (McGuire & Teskey 2002). To measure X_s, a small hole 10 mm in diameter and 7–10 mm deep was drilled through the bark into the xylem, 20–25 cm below the stem chamber. The tip of a 5-cm-long low-density polyethylene tube was inserted into the hole, and the outside edge sealed to the tree with putty adhesive. A microelectrode was then inserted into the polyethylene tube such that the electrode tip did not make contact with xylem. Adhesive putty was used to seal the body of the microelectrode to the polyethylene tube. Four probes were installed, one each in four trees (two non-fertilized and two fertilized).

Experiments

We examined the relationship between E_s, v_s and X_s using two different approaches. In the first experiment, we compared hourly average measurements of E_s and v_s for three trees in the non-fertilized (trees 1, 3 and 6) and fertilized (trees 4, 5 and 6) plots (Table 1). In young loblolly pine trees, the response of E_s to diel changes in stem temperature typically exhibits a hysteresis, where at a similar temperature E_s is higher at night than during the day (Maier 2001) (Fig. 1). We assumed a *priori* that this diel hysteresis was a function of v_s Therefore, to remove potential effects of v_s, only night-time (2300–0500 h) E_s measurements were

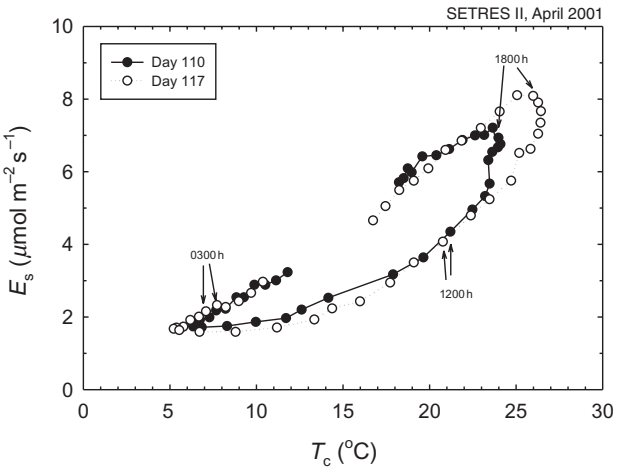

Figure 1. An example of the diel pattern of hysteresis between measured stem surface CO_2 efflux (E_s) and cambium temperature (T_c), where at a given temperature, E_s was lower during the day than at night. Response patterns from a non-fertilized tree are shown for day of year (DOY) 110 near the beginning of the experiment and DOY 117 after >90% of the canopy had been removed. Corresponding measurements for three times are shown.

used to model E_s. v_s during this time was always less than 0.01 mm s^{-1}. Night-time E_s was modelled as a function of temperature by fitting the data to the exponential equation:

$$E_s = \beta_0 e^{(kTc)}, \quad (1)$$

where E_s is measured stem CO_2 efflux (μmol m^{-2} s^{-1}), β_0 is CO_2 efflux at 0 °C, k is the temperature coefficient and T_c is measured cambium temperature. Nonlinear regression (PROC NLIN, SAS Institute, Cary, NC, USA) was used to estimate β_0 and k in Eqn 1. Model performance was examined graphically by comparing predicted and observed values of E_s and by calculating the percent root mean square error (%RMSE), a measure of model precision, and the percent absolute deviation (%AD), an estimate of model accuracy (Maier 2001). A t-statistic was used to test for differences between non-fertilized and fertilized plots. Equation 1 was then used to predict diel patterns of E_s (E_p). Residual E_s (E_r), the difference between E_s and E_p, represents variation assumed to a result of xylem transport of CO_2. We hypothesized that the diel pattern of E_r and the ratio E_r/E_p would be correlated with v_s.

In the second experiment, we examined how artificially reducing v_s, through a progressive removal of canopy leaf area, affected the diel patterns E_s and X_s. In trees with low leaf area, transpiration is proportional to leaf area (Cienciala & Lindroth 1995; Sala, Smith & Devitt 1996), and abrupt reductions in leaf area can reduce canopy transpiration and v_s (Oren *et al*. 1999). In this experiment, the canopies of three of the six trees in the non-fertilized (trees 2, 4 and 5) and fertilized (trees 1, 2 and 3) plots (Table 1) were removed in thirds (Cut treatment). The canopy of the cut tree was divided vertically into three levels based on an equal number of branches. Canopy removal was done equally from each level based on branch foliage biomass (Table 1). After an initial period, to establish individual tree E_s and v_s behaviour (≈ 48 h), one-third of the canopy leaf area in the cut trees was removed by removing branches. Measurements continued for 3 d, and then another third of foliage biomass was removed followed by another 4 d of measurements after which the remaining foliage was removed except for a single 1-year-old branch at the top of the canopy. Branch removal was completed by 1000 h on the day of treatment.

Diel patterns of v_s and E_s were compared graphically between uncut and cut trees. To facilitate comparisons, maximum daily rates of v_s and E_s data were normalized to the maximum rates measured on DOY (day of year) 109 before the cutting treatments began. Changes in the normalized maximum rates of v_s and E_s resulting from the cutting treatment were compared using repeated measures analysis of variance (ANOVA) (PROC MIXED, SAS Institute, Cary, NC, USA), utilizing an autoregressive covariance structure. We hypothesized that during the daylight hours maximum v_s would decrease and maximum E_s would increase in cut trees relative to uncut trees. On the last 2 d of the experiment, we compared diel patterns of v_s, E_s and X_s. We hypothesized that X_s would increase in cut trees relative to uncut trees because respired CO_2 in the xylem would accumulate when v_s is low in cut trees, and that increases in X_s in cut trees would cause a concomitant increase in E_s.

RESULTS

Diel patterns

Stem cambium temperatures ranged from 0–30 °C over the 11 d of measurements (Fig. 2a). Stem temperatures peaked in early afternoon on most days. E_s had a strong diel pattern that was well correlated with cambium temperature (Fig. 2b), however, maximum daily E_s always occurred after maximum stem temperature (35–210 min) (Fig. 2a & b) creating a diel hysteresis. For example on DOY 110, E_s was lower during the morning and early afternoon than at night when measured at a similar temperature (Fig. 1). The magnitude of the daily hysteretic response varied among trees and within a tree over time.

Stem v_s increased rapidly during the morning and reached maximum values between 1000 and 1200 h then rapidly declined in the afternoon (Fig. 2c and inset). An exception to this pattern was observed on DOY 115, which was rainy and cool, when maximum v_s was measured in late afternoon. During the night, v_s was less than 0.01 mm s^{-1}. Peak sap velocity generally occurred 5–8 h before maximum E_s.

Experiment 1

To remove potential effects of v_s on E_s, temperature response curves were developed using only nighttime measurements when v_s was less than 0.01 mm s^{-1}. Night-time E_s was well correlated ($R^2 = 0.90$–0.96, Eqn 1) with stem cambium temperature (Table 2). Predictions based on the equation showed good agreement with observed values. The %RMSE averaged 12.3% of mean night-time E_s. All of the models exhibited a mean %AD of less than 14% and indicates that the models accurately predicted night-time E_s over the time period measured. There was no significant difference between non-fertilized and fertilized trees in basal CO_2 efflux rate (β_0; non-fertilized: 1.22 ± 0.08SE; fertilized: 1.37 ± 0.04; $P = 0.12$) or the temperature coefficient (k; non-fertilized: 0.073 ± 0.001; fertilized: 0.071 ± 0.001; $P = 0.77$).

Using the parameters in Table 2 with Eqn 1, we compared predicted E_p with observed E_s (Fig. 2b and inset). During the day, E_p was always greater than measured E_s, with the largest differences occurring around midday during periods of rapid change in stem temperature and v_s. E_r, the difference between E_p and E_s, generally decreased with increasing v_s (Fig. 2b and inset). The negative ratio of E_r/E_p, a relative measure of reduced E_s, was negatively correlated with v_s (Fig. 3) and there was no difference between non-fertilized and fertilized trees in the slope of this relationship. These data suggest that during the day high v_s could potentially reduce E_s up to 40% of that predicted on temperature alone.

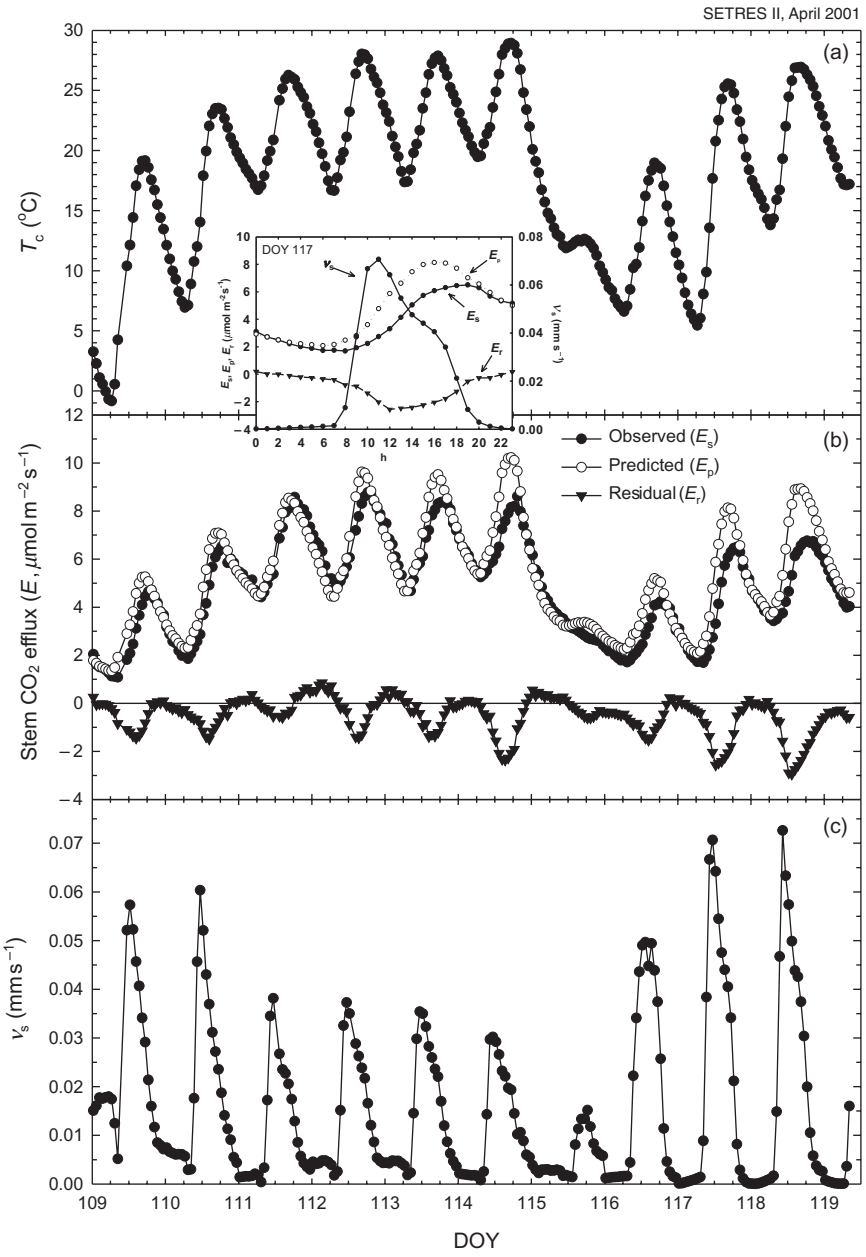

Figure 2. An example of the diel response patterns of (a) cambium temperature (T_c), (b) measured (E_s), predicted (E_p) and residual (E_r) stem surface CO_2 efflux, and (c) sap velocity (v_s) for a fertilized uncut tree. Residual respiration is the difference between E_s and E_p. Predicted stem surface CO_2 efflux (E_p) was estimated using temperature response curves developed from nighttime E_s measurements when $v_s < 0.01$ mm s^{-1}. Inset: Diel patterns of the parameters for 1 d. DOY, day of year.

Experiment 2

In this experiment, we examined how artificially changing v_s through a progressive removal of canopy leaf area affected E_s. Foliage was removed in thirds on DOY 110, 113 and 117 (arrows, Fig. 4). To aid in making comparisons between cut and uncut trees, v_s and E_s were normalized to the maximum rates measured on DOY 109 before the branch removal treatment began (Fig. 5). There were no significant differences in v_s or E_s between non-fertilized and fertilized trees (Table 3). Removal of one-third to two-thirds of the canopy leaf area had only small effects on v_s and E_s; and non-fertilized and fertilized trees behaved differently (Figs 4 & 5, Table 3). In the non-fertilized trees, maximum daily v_s was reduced ≈20% following the first cutting (DOY 110) when roughly one-third of the canopy was removed (Fig. 5). Removal of the second third of the canopy (DOY 113) had no further effect on the magnitude of this response. In fertilized trees, the first cutting treatment had no effect on v_s, but v_s was significantly less in the cut trees 3 d following the second cutting treatment (Fig. 5). After removal of most of the canopy (DOY 117), v_s was reduced 80–90% of that in uncut trees in both non-fertilized and fertilized trees. The lack of a large decrease in v_s following abrupt changes in leaf area was likely due to stomatal compensation. Stomatal conductance significantly increased in foliage of cut trees after the second cutting treatment (Table 4). Net photosynthesis tended to increase in cut trees following branch removal, but this difference was only significant for DOY 114.

Table 2. Parameter estimates and fit statistics for Equation 1

	Tree	a	k	r^2	n^a	%RMSE[b]	%AD[c]
Non-fertilized	1	1.53	0.075	0.94	209	12.6	9.5
	2	1.35	0.074	0.93	209	13.9	11.0
	3	1.06	0.070	0.96	206	12.2	8.9
	4	1.14	0.072	0.92	208	14.4	11.9
	5	1.05	0.073	0.94	202	12.8	10.4
	6	1.18	0.070	0.96	206	9.9	7.6
Fertilized	1	1.39	0.070	0.88	208	15.2	12.5
	2	1.50	0.072	0.87	209	16.2	13.5
	3	1.25	0.073	0.95	208	11.3	8.7
	4	1.37	0.072	0.95	206	10.9	7.9
	5	1.25	0.073	0.96	207	8.4	6.8
	6	1.43	0.068	0.96	208	9.6	7.3

Equation 1 was fitted to stem surface CO_2 efflux (E_s) measured at night, between 2300 and 0500 h, when sap velocity (v_s) was less than 0.01 mm s^{-1}.

[a]n is the number of observations.

[b]Percent root mean square error. $$\%\mathrm{RMSE} = \left[\frac{1}{n}\sum_{i=1}^{n}\left(\frac{\hat{y}_i - y_i}{y_i}\right)^2\right]^{1/2} \times 100$$

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

In contrast, cutting treatment had little effect on the diel patterns of E_s (Fig. 4). There was no significant fertilizer or fertilizer-by-cutting treatment interaction on normalized E_s (Table 3). However, in the fertilized trees E_s declined 7–15% two days following the first cutting treatment (Fig. 5). This difference was maintained throughout the experiment. There was no apparent response of E_s to large changes in v_s The pattern of E_s in fertilized and non-fertilized trees was similar throughout the experiment even after the final removal of branches when v_s in cut trees was ≈10% of that in uncut trees (Figs 4 & 5). Furthermore, large reductions in v_s following the final cutting treatment had little effect on the diel E_s-temperature hysteresis. For example, the magnitude of the hysteresis was similar on days having a similar range in temperature, but a large difference in maximum v_s (compare DOY 110 and 117, Fig. 1).

We measured X_s in four trees over the last 2.5 d of the experiment. During this time, X_s ranged from 1 to 8%. X_s changed diurnally reaching a maximum at night and a minimum near noon (Fig. 6). In uncut trees, X_s generally decreased during the day when v_s was high and increased at night when v_s was low suggesting that sap flow had a strong influence over X_s. A similar pattern was observed in cut trees; however, X_s increased more relative to uncut trees when v_s was reduced following the final cutting treatment. Large diel changes in X_s appeared to have little

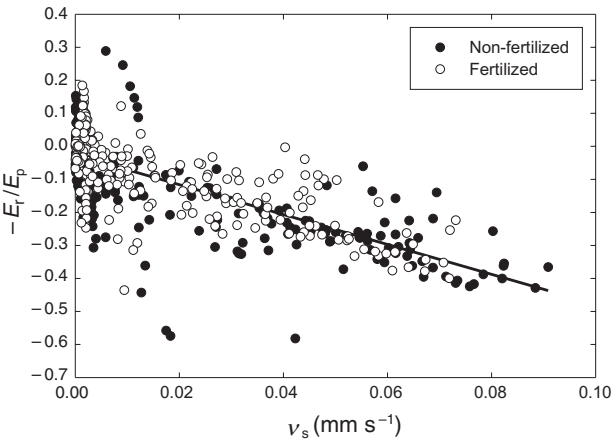

Figure 3. The relationship between the negative ratio of residual and predicted stem surface CO_2 efflux (E_r/E_p) and sap velocity (v_s). Predicted stem surface CO_2 efflux (E_p) was estimated using temperature response curves developed from nighttime E_s measurements when $v_s < 0.01$ mm s^{-1}. Residual respiration is the difference between E_s and E_p. E_r/E_p is expressed as a negative ratio to illustrate the potential reduction in E_s at high v_s Each point is the average of three trees. y = –0.026 – 4.526x $R^2 = 0.54$.

Table 3. Probability values for the effect of fertilization, cutting treatment and time and their interactions on the normalized maximum daily sap velocity (v_s) and stem surface CO_2 efflux (E_s)

Effect	v_s	E_s
Fertilization (F)	0.3964	0.4608
Cut (C)	<0.0001	0.0914
F × C	0.2556	0.1258
Day (D)	<0.0001	<0.0001
F × D	0.2127	<0.0001
C × D	<0.0001	0.1538
F × C × D	0.1709	0.4096

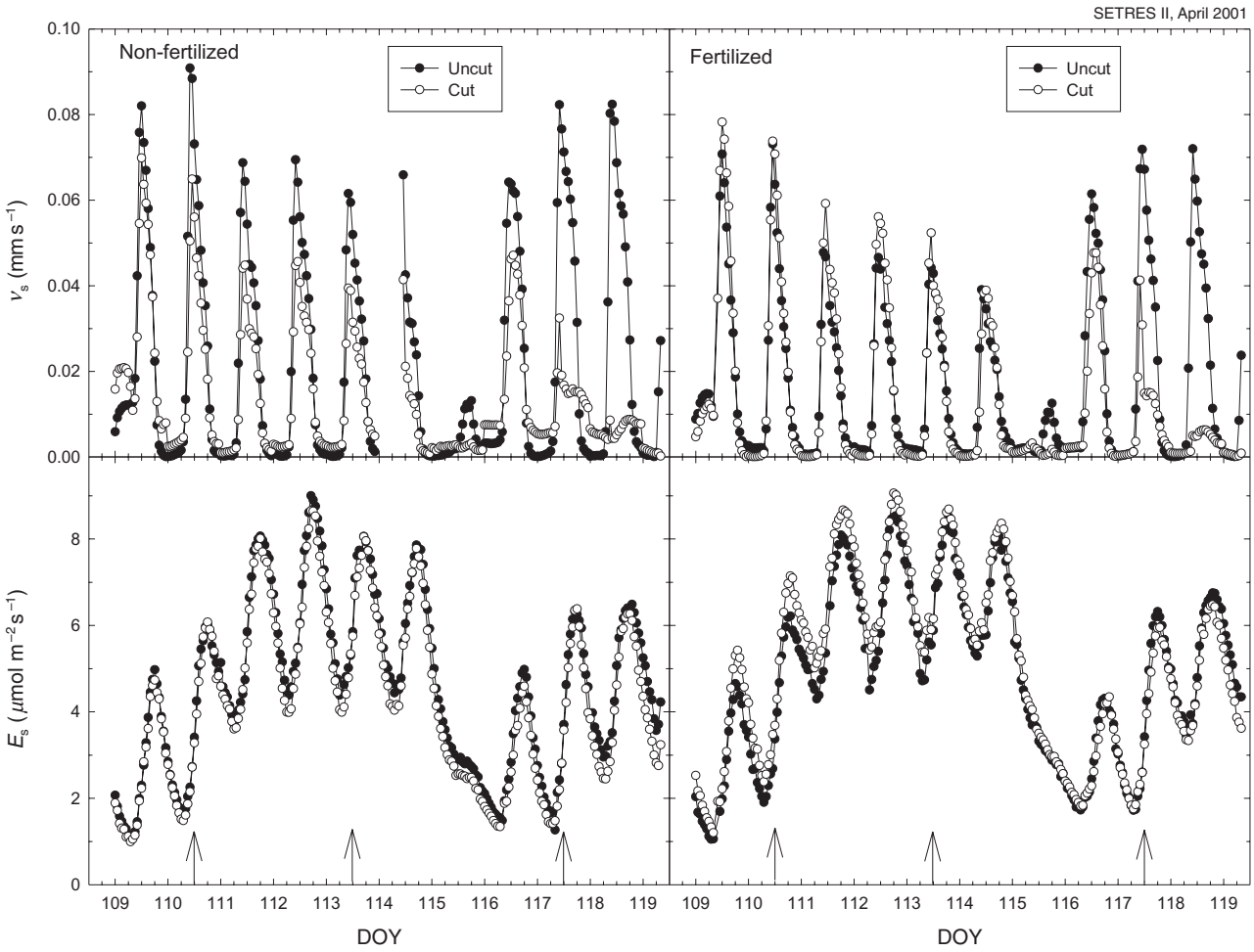

Figure 4. Diel patterns of hourly sap velocity (v_s) and stem surface CO_2 efflux (E_s) for non-fertilized and fertilized trees with intact canopies (uncut) and those where the canopy was progressively removed (cut) in thirds (arrows) over the course of the study. Each point is the average of three trees. DOY, day of year.

effect on E_s. For example in the fertilized trees, X_s in cut trees increased twofold after trees received the last canopy removal (DOY 117), but there was no apparent change in E_s. In the non-fertilized trees, E_s was similar between uncut and cut trees on day 118 despite a fourfold difference in X_s. These data suggest that E_s in these trees was not influenced by CO_2 transported in the xylem stream.

DISCUSSION

Our trees showed the typical diel counterclockwise hysteresis between E_s and stem temperature (Fig. 1) reported for trees in other studies (Ryan *et al*. 1995; Lavigne 1996; Stockfors 2000; Maier 2001; Damesin *et al*. 2002; Bosc *et al*. 2003). We used two different approaches to determine whether or not xylem transport and storage of CO_2 was responsible for this hysteresis. These two approaches produced seemingly contradictory results. The first experiment assumed *a priori* that the diel hysteresis was a function xylem CO_2 transport. Therefore, night-time E_s temperature response functions, when $v_s \approx 0$, were used to predict daytime rates (E_p). Predicted daytime rates were always greater than observed. The difference between observed and predicted stem CO_2 efflux ($E_r = E_p - E_s$) was correlated with v_s and suggest that during the day high v_s could reduce E_s by up to 40% below that measured when v_s is low. These data support the idea that midday suppression of stem respiration measured in other studies (Negisi 1975, 1978, 1982; Lavigne 1987; Kabubari 1988) is a function of transpiration rate. Negisi (1979) artificially alter v_s in detached *Pinus densiflora* stems and found that E_s was reduced by 70% at a v_s rate of 0.15 mm s^{-1}, a value that corresponds well with our data (Fig. 3). Levy *et al*. (1999) also found a correspondence between E_r and v_s; however, in their study, residual efflux was positively correlated with v_s. They concluded that imported CO_2 in the xylem stream contributed up to 12% of E_s.

The second experiment examined how artificially reducing v_s by eliminating canopy leaf area affected E_s. Our attempt to create varying levels of stem v_s by a stepwise defoliation of the canopy was only partially successful. Increased stomatal conductance largely compensated for a

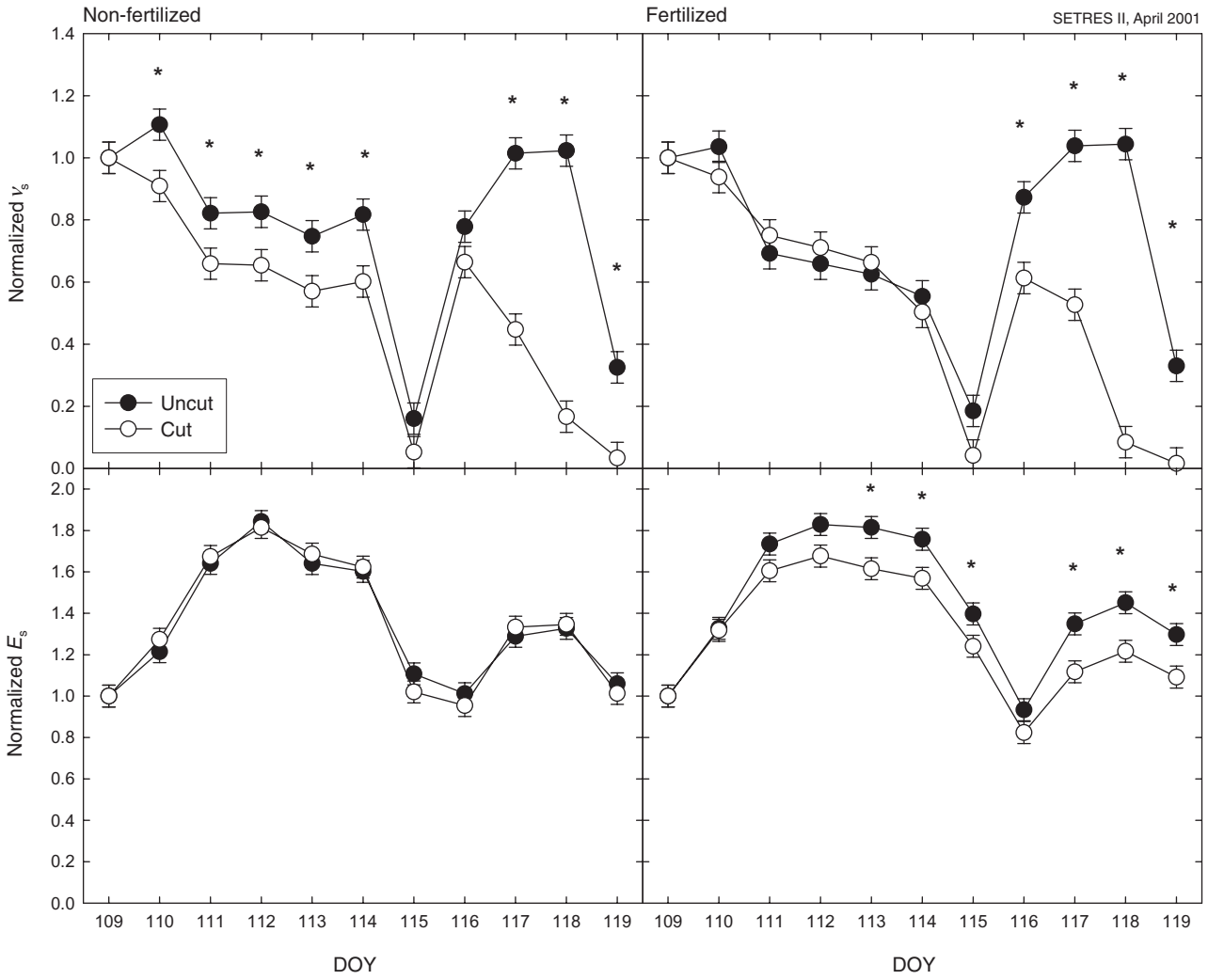

Figure 5. Least squares mean (± SE) of maximum daily sap velocity (v_s) and stem surface CO_2 efflux (E_s) for non-fertilized and fertilized trees. Data are normalized to the maximum values measured on day of year (DOY) 109. Comparisons are made between trees with intact canopies (uncut) and those where the canopy was progressively removed (cut) in thirds over the course of the study. Each point is the average of three trees. An asterisk denotes a significant difference between uncut and cut means at $\alpha = 0.05$.

Table 4. Stomatal conductance (g_L) and net photosynthesis (P_n) of upper canopy foliage in non-fertilized (NF) and fertilized (F) trees with intact canopies [uncut (UC)] and those where the canopies were progressively removed [cut (C)] over the course of the study

		108		114		117	
	Treatment	g_L	P_n	g_L	P_n	g_L	P_n
NF	UC	48.0	3.6	17.0	3.4	30.0	5.6
		(13.0)	(0.8)	(1.8)	(0.2)	(4.4)	(0.4)
	C	39.0	3.9	29.0	5.0	47.6	6.5
		(7.0)	(0.7)	(2.6)	(0.4)	(5.9)	(0.3)
F	UC	37.4	4.3	8.7	2.1	31.0	4.7
		(1.0)	(0.2)	(0.6)	(0.2)	(4.1)	(0.2)
	C	44.3	5.0	32.0	4.9	55.0	5.5
		(4.0)	(0.1)	(1.0)	(0.4)	(9.5)	(0.5)

Measurements on day of year (DOY) 108 represent pre-cutting values whereas values on DOY 114 and 117 are after two-thirds of the canopy was removed in cut trees. Values are the mean of three trees. Numbers within parentheses are the SEs of the mean.

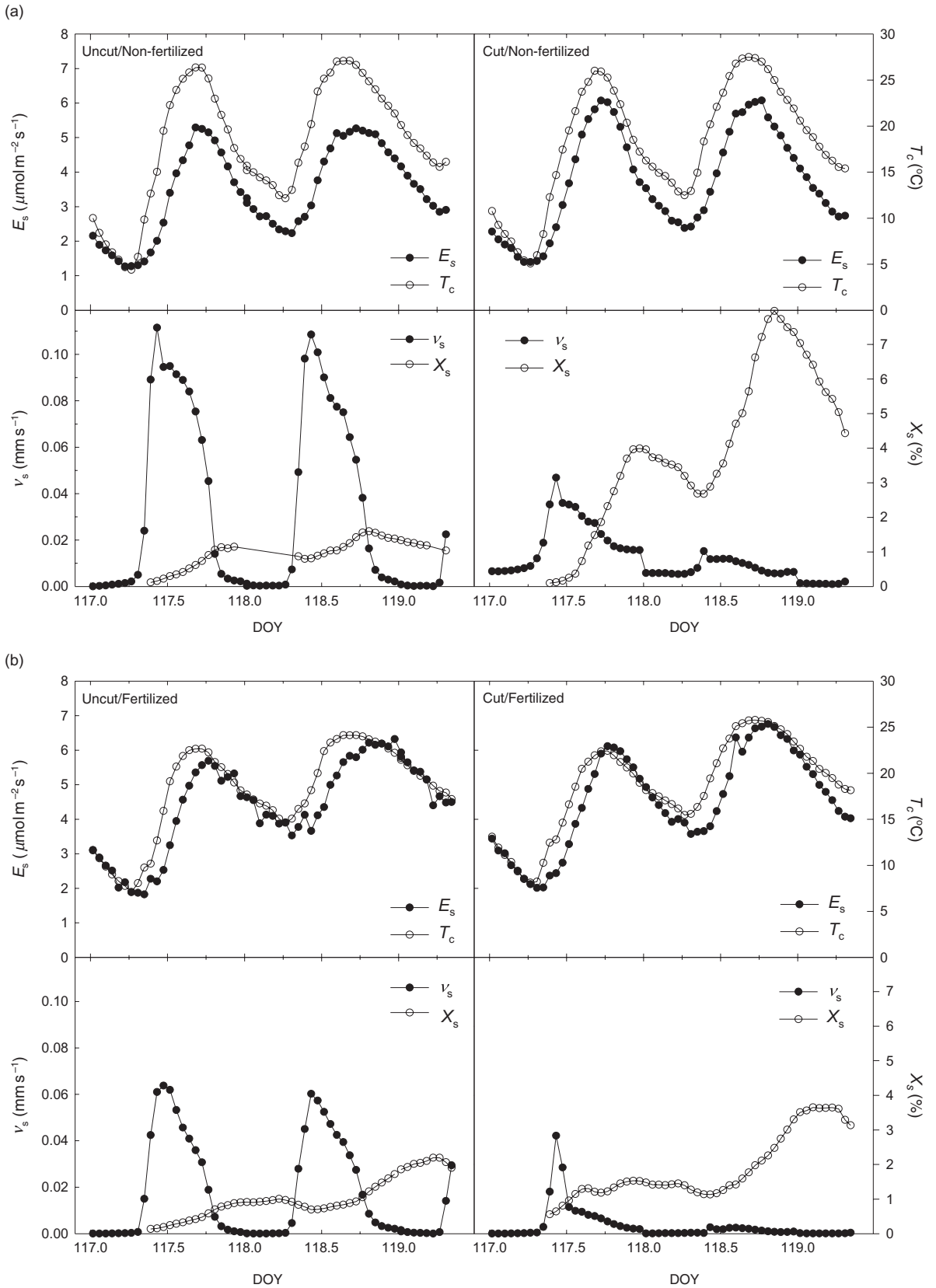

Figure 6. Comparison of stem surface CO_2 efflux (E_s), cambium temperature (T_c), sap velocity (v_s) and xylem CO_2 concentration (X_s) for a tree with an intact canopy (uncut) and one with the canopy removed (cut) in the (a) non-fertilized and (b) fertilized plots. Measurements are for the last 2 d of the study. The final cutting treatment was completed by 1000 h on day of year (DOY) 117.

partial reduction (≈ 33 and 63%) in canopy leaf area maintaining v_s near pre-treatment rates as observed in Pataki *et al*. (1998). Only after removal of most of the canopy (> 90%) was v_s substantially reduced. Even though we were unable to create a progressive reduction in v_s, it was evident that reducing v_s to near zero by removing almost all canopy foliage had little effect on E_s. Diel patterns of E_s and the daily maximum values were similar between cut and uncut trees throughout the experiment indicating that xylem CO_2 transport in the sap had little effect on E_s in these trees. In addition, if v_s strongly affected E_s then the magnitude of the diel hysteresis between E_s and T_c should be smaller or eliminated in cut trees as v_s approached zero. However, in our trees neither the pattern nor magnitude of the diel hysteresis was affected by large changes in v_s (Fig. 1). These data suggest that v_s and E_s are uncoupled in these trees and the *a priori* assumption that the diel hysteresis is a function of xylem CO_2 transport and storage is incorrect. Thus, the correlation between E_r/E_p and v_s (Fig. 3) does not represent a causative response.

The apparent uncoupling of v_s (or X_s) and E_s suggest that that the radial diffusion of CO_2 from the xylem to the stem surface is restricted in these trees. Conifers have few intercellular spaces and radial gas diffusion must occur in the liquid phase which is several magnitudes lower than gas phase diffusion (Hari *et al*. 1991). The large difference between X_s and the ambient air in our trees indicates a high resistance to CO_2 diffusion from the xylem through the bark (Eklund 1990, 1993; Hari *et al*. 1991). Eklund (1990) and Eklund & Lavigne (1996) found little diffusion of O_2 or argon gas from the atmosphere to the xylem or from the xylem to the atmosphere in conifer stems. However, despite a high resistance to gas diffusion through the bark, several studies have shown that artificially manipulating of sap flow (Negisi 1979) and/or X_s (Teskey & McGuire 2002, 2004) clearly influences E_s. So, why did large changes in v_s and X_s in our cut trees have no effect on E_s? We conducted the experiment in the spring when stem respiration and growth were at a maximum for these stands (Maier 2001). At this time of year, the thin cambium and phloem meristems likely respire at a much higher rate than the xylem parenchyma and thus would be a major source of respiratory CO_2 in the stem. Goodwin & Goddard (1940) measured oxygen consumption in black ash stems and found that O_2 uptake was several magnitudes higher in the cambium and phloem compared to the xylem. Similarly, Pruyn, Gartner & Harmon (2002, 2003) showed that the respiratory potential of the inner bark of ponderosa and white pine trees was 3–15 times greater than that of the sapwood. The surface CO_2 efflux we measured was likely a result of growth related respiration associated with differentiating cells in the cambium and from energy expended in phloem transport. Thus, during periods of rapid stem growth, the CO_2 concentration in the stems would be much higher in the cambium and phloem regions than in the xylem. Under these conditions, the CO_2 concentration gradient (i.e. diffusion gradient) would likely decrease from the cambium layer to the xylem effectively isolating the xylem tissue as a source of CO_2 evolved from the stem surface. Although our data is limited, measurements of X_s appear to support this hypothesis. We found in our cut trees that while X_s increased after defoliation ($v_s < 0.01$ mm s^{-1}), it was not followed by increases in E_s which would be expected if the CO_2 concentration gradient decreased radially from the xylem to the stem surface. In addition, the rate and magnitude of E_s was similar on consecutive days with large differences in X_s (Fig. 6) suggesting that X_s had no effect on E_s. It is interesting to note that atmospheric O_2 in the xylem of conifer stems decreases from near ambient to less than 5% of ambient during the growing season (Eklund 1993, 2000); apparently, the active cambial tissue consumes most of the O_2 that diffuses into the stem (Hook *et al*. 1972).

Our measurements of E_s probably reflect respiration associated with diameter growth and phloem transport; however, it underestimates this component of stem respiration as some of the respired CO_2 is expended into the xylem (Eklund & Lavigne 1996; McGuire & Teskey 2004). This is illustrated by the increase in X_s at night when $v_s \approx 0$ and is a result of the metabolism of local xylem parenchyma and from cambial tissue internal to the xylem. This CO_2 is stored in the stem segment and is later transported up the stem as part of the internal CO_2 flux. McGuire & Teskey (2004) used a mass balance approach to estimate total stem respiration from stem segments of several hardwood species. They found that CO_2 respired within the stems either diffused radially through the bark to the atmosphere, is transported upward in the xylem stream, or is temporarily stored in the xylem. For example, surface flux, xylem transport flux and storage account for 85, 15 and 8%, respectively, of stem respiration over a 24 h period in a beech tree. The relative proportion of each component varied during the day depending on sap flow rates. In their analysis, dissolved CO_2 in the xylem served as a sink or a source for CO_2 diffusion to the atmosphere. Our data suggests that internal stem CO_2 dynamics are more complex. It appears that there may be conditions, perhaps during periods of high cambial activity, when E_s is uncoupled from internal xylem CO_2 fluxes. The relationship between v_s, E_s and X_s may be different at other times of the year. For example when growth ceases, X_s may exceed that in the cambium and phloem regions and be a source of CO_2 to E_s. Root absorption of dissolved CO_2 in the soil can potentially contribute large amounts of CO_2 to the xylem (Levy *et al*. 1999). However, because of the porous nature of the sandy soils at our site, soil pCO_2 rarely exceeds 5000 μmol m^{-1} (0.5%) in the top 50 cm and generally is much lower during the spring (≈ 1000–1100 μmol m^{-1}, Maier, unpublished results) hence, soil CO_2 would not likely contribute much CO_2 to the xylem stream in our trees.

There are other possible explanations for the hysteresis between E_s and T_c: (1) a lag between temperature and surface CO_2 efflux because of high resistance to diffusion (Hari *et al*. 1991; Eklund & Lavigne 1996; Stockfors 2000); (2) refixation of respired CO_2 during corticular photosynthesis (Sprugel & Benecke 1991; Cernusak & Marshall 2000); (3) diel differences in substrate supply (Edwards &

McLaughlin 1978; Martin *et al*. 1994); and (4) diel patterns of stem growth. Because of the high resistance to CO_2 diffusion, T_c measured at the time of flux measurements may not reflect surface CO_2 evolution. Modelling E_s using lagged temperatures, measured sometime earlier, can account for a substantial portion of the hysteresis (Ryan *et al*. 1995; Lavigne 1996; Stockfors 2000; Maier 2001; Bosc *et al*. 2003). We modelled E_s (Eqn 1) for our trees using all of the data (day and night) and found that, E_s was best correlated ($R^2 = 0.91$–0.95) with T_c measured between 42 and 168 min earlier. We note, that residuals from these regressions were not correlated with v_s ($R^2 = 0.23$, $P = 0.45$). If a lag in CO_2 production were a major factor responsible for the hysteresis, then the magnitude of the hysteresis should be a function of tree size (Bosc *et al*. 2003) or bark thickness (Ryan *et al*. 1995). Although the range in tree size was small in our study, we found no relationship between lag times and tree diameter or bark thickness.

Bark photosynthesis can refix a substantial amount of respired CO_2 in woody tissue (Sprugel & Benecke 1991) thus lowering the apparent stem respiration rate during the day. Cernusak & Marshall (2000) estimated that bark refixation rates were 70% of night-time respiration rates in western white pine. However, refixation is not an issue in our study because we used the main stem that had little or no chlorophyll present and we used opaque chambers so there would be no bark photosynthesis at least for the tissue inside the chamber.

Substrate supply can affect respiration rates (Amthor 1989). Edwards & McLaughlin (1978) found that the diel pattern of E_s in yellow poplar trees was correlated with the concentration of reducing sugars in the phloem, indicating that the diel pattern of E_s may in part be driven by transported photosynthate. This response may occur quickly once carbohydrate supply is compromised. Edwards, Tschaplinski & Norby (2002) showed that E_s in sweetgum trees increased in response to elevated CO_2 but decreased to rates measured at ambient CO_2 within several days after the elevated CO_2 treatment was turned off. Removal of photosynthetic surface area would likely affect canopy assimilation and reduce substrate supply to the stem. We could not assess the impact of the cutting treatment on stem carbohydrate supply; however, the cutting treatment slightly reduced E_s in the fertilized trees. Effects of reduced carbohydrate supply on E_s could potentially mask effects of reduced v_s. Martin *et al*. (1994) found in loblolly pine seedlings that E_s declined after girdling the phloem above the respiration chamber; although, they concluded that the response was too slow to account for diel hysteresis.

The hysteresis between E_s and T_c may reflect diel patterns of growth. Daudet *et al*. (2005) measured diel E_s and stem diameter in potted hybrid walnut (*Juglans nigra* × *Juglans regia*) saplings under constant temperature conditions. Diel patterns of E_s were highly correlated with changes in stem diameter. Maximum E_s occurred at night, suggesting that more energy was being expended in growth and maintenance processes at this time.

SUMMARY

Our trees showed a strong diel hysteresis between E_s and stem temperature. The diel variation in temperature-independent E_s was correlated with v_s, such that at high v_s, E_s could be reduced by up to 40%. However, this correlation may not represent a cause-and-effect relationship. Artificially reducing v_s through a progressive defoliation of the canopy had little effect on E_s and had no effect on the magnitude of the diel hysteresis. These data indicate that E_s is uncoupled from v_s in these trees. We suggest that high metabolic activity in the cambium during this time of year (spring) is likely a source of CO_2 to the xylem and thus, CO_2 transported in the xylem stream would not contribute to E_s. This hypothesis is supported by the observation that diel changes in X_s correspond with E_s but the large increase in X_s measured in the cut trees, when $v_s \approx 0$, had no affect on E_s. Increased resolution of measurements of stem $[CO_2]$ in cambium and xylem regions is needed to confirm this. Understanding diel and seasonal variation in surface CO_2 efflux and the relationship to v_s (or sap flow) and X_s will provide a more complete characterization of stem respiration and whole-plant carbon cycles.

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