Relationships between stem CO_2 efflux, substrate supply, and growth in young loblolly pine trees

Chris A. Maier[1], Kurt H. Johnsen[1], Barton D. Clinton[2] and Kim H. Ludovici[1]

[1]USDA Forest Service, SRS, Research Triangle Park, NC, USA; [2]USDA Forest Service, SRS, Coweeta Hydrologic Laboratory, Otto, NC, USA

Summary

Author for Correspondence:
Chris A. Maier
Tel: +1 919 5494072
Email: cmaier@fs.fed.us

• We examined the relationships between stem CO_2 efflux (E_s), diameter growth, and nonstructural carbohydrate concentration in loblolly pine trees. Carbohydrate supply was altered via stem girdling during rapid stem growth in the spring and after growth had ceased in the autumn. We hypothesized that substrate type and availability control the seasonal variation and temperature sensitivity of E_s.
• The E_s increased and decreased above and below the girdle, respectively, within 24 h of treatment. Seasonal variation in E_s response to girdling corresponded to changes in stem soluble sugar and starch concentration. Relative to nongirdled trees, E_s increased 94% above the girdle and decreased 50% below in the autumn compared with a 60% and 20% response at similar positions in the spring.
• The sensitivity of E_s to temperature decreased below the girdle in the autumn and spring and increased above the girdle but only in the autumn. Temperature-corrected E_s was linearly related to soluble sugar ($R^2 = 0.57$) and starch ($R^2 = 0.62$) concentration.
• We conclude that carbohydrate supply, primarily recently fixed photosynthate, strongly influences E_s in *Pinus taeda* stems. Carbohydrate availability effects on E_s obviate the utility of applying short-term temperature response functions across seasons.

Introduction

Carbon dioxide efflux the surface of tree stems (E_s) contributes 15–25% of autotrophic respiration in managed forest ecosystems (Ryan *et al.*, 1994; Maier *et al.*, 2004). Stem CO_2 efflux is a complex process comprising CO_2 released from the metabolism of phloem, cambium and xylem ray cells, and varies depending on tissue type and function (i.e. transport, growth, or storage), growth rate, phenology, stand age, and environmental conditions. In addition, exogenous CO_2 transported and stored in the xylem stream can strongly influence E_s (McGuire & Teskey, 2004). The E_s is regulated by both external (temperature) and internal (water stress, sap flow and carbohydrate supply) drivers. These drivers vary simultaneously making it difficult to determine the temporal and spatial importance of individual causal factors (Teskey *et al.*, 2008). Despite this complexity, most

tree and stand-level process models estimate E_s in a rudimentary way as a function of temperature (i.e. Q_{10}) and it is often considered independent of carbohydrate supply (Thornley & Cannell, 2000). Temperature-independent E_s is highly variable spatially and temporally within trees and across stands. For example, temperature-normalized E_s varied 10- to 40-fold between the base of the stem and crown in mature *Abies amablis* (Sprugel, 1990) and *Fagus sylvatica* (Damesin *et al.*, 2002) stands. Seasonal variation in temperature normalized E_s in a young *Pinus taeda* plantation correlated with changes in radial growth and nitrogen concentration (Maier, 2001). In large oak and maple trees, E_s was correlated with sapwood volume during the dormant season but not while trees were growing (Edwards & Hanson, 1996) indicating that cambial activity had a large impact on E_s (Lavigne *et al.*, 2004).

Photosynthetic rates, carbohydrate status and respiration are tightly coupled (Azcon-Bieto & Osmond, 1983; Azcon-Bieto *et al.*, 1983) and carbohydrate availability regulates respiration in growing tissues (Penning de Vries *et al.*, 1979). In trees, carbohydrate concentration and

supply via recent photosynthesis appear to regulate the diel magnitude of leaf respiration (Whitehead *et al.*, 2004), control temperature acclimatization, and the response to elevated $[CO_2]$ (Tjoelker *et al.*, 1999). The dynamics of carbohydrate storage and movement within tree stems (branches, boles, and roots) and its relationship to E_s is not well understood. In *Populus deltoides* saplings, Wertin & Teskey (2008) found that experimentally induced changes in canopy photosynthesis via atmospheric $[CO_2]$ or light caused concomitant changes in E_s within 24 h. This suggests a close coupling between recently fixed carbohydrates and E_s. In large trees, long-distance transport of photosynthates from the canopy to lower stems via symplastic and apoplastic phloem loading and unloading can temporally uncouple E_s from recent canopy photosynthesis. Despite this, some studies indicate that the availability of recently fixed carbon substantially alters the rate of rhizosphere respiration and soil CO_2 efflux (Högberg *et al.*, 2001; Johnsen *et al.*, 2007) even on a diurnal time scale (Tang *et al.*, 2005). Temperature independent diel patterns of root respiration in *Pinus ponderosa* seedlings were correlated with preceding radiation regimes (Lipp & Andersen, 2003) indicating the importance of recently fixed carbohydrates for root metabolism. From this, it is expected that stem phloem, cambium, and xylem tissue metabolism would also be coupled with canopy photosynthesis in large trees. In support, diel patterns of E_s in *Liriodendron tulipfera* trees were correlated with phloem sugar concentration (Edwards & McLaughlin, 1978). Edwards *et al.* (2002) concluded that increased E_s in *Liquidambar styraciflua* under elevated atmospheric $[CO_2]$ was in part driven by increased substrate supply. Experimental reduction in stem carbohydrate supply through canopy pruning (Lavigne *et al.*, 2004), girdling (Ogawa, 2006), fire (B. Clinton, unpublished) or phloem chilling (Johnsen *et al.*, 2007) lowered E_s within several days. By contrast, Martin *et al.* (1994) found that while photosynthesis regulated E_s in stems of *P. taeda* seedlings, concluded the response was too slow to effect diel patterns.

Tree and stand level E_s is often modeled as an exponential function of temperature expressed in terms of Q_{10} (Sprugel *et al.*, 1995). Atkin & Tjoelker (2003) hypothesized that the temperature response of respiration is dependent on carbohydrate availability. In *Pinus banksiana*, seasonal values of temperature-normalized foliar respiration was inversely correlated with air temperature, but positively correlated with foliar carbohydrate concentration (Tjoelker *et al.*, 2008). Little is known about how short-term variation in carbohydrate supply will affect the E_s temperature response. A better understanding of how substrate availability and demand controls woody tissue respiration and E_s is necessary for constructing and modeling plant and ecosystem carbon budgets and for predicting the effects of climate change on these processes.

We examined the relationships between E_s, stem temperature, diameter growth, and carbohydrate status in a young loblolly pine (*P. taeda*) genotype by fertilization study. Stem girdling was used to stop the basipetal movement of assimilates through the phloem, generally resulting in an accumulation and depletion of soluble sugar and starch, above and below the girdle, respectively (Jordan & Habib, 1996). We conducted girdling experiments at two phenological stages: in the autumn (October–November), after diameter growth ceased when stem carbohydrate concentrations were low, and in the spring (April–May), during rapid diameter growth when carbohydrate concentrations were high (Ludovici *et al.*, 2002). Because fertilized trees have generally higher stem growth rates (Albaugh *et al.*, 2004), growth and maintenance respiration (Maier, 2001), and carbohydrate concentrations (Ludovici *et al.*, 2002) than nonfertilized trees, we expected E_s to respond differently to perturbations in the substrate supply. We predicted that: (1) stem girdling would cause E_s to increase above the girdle and decrease below the girdle; (2) the response in E_s to girdling would vary seasonally with changes in stem growth and availability of stem nonstructural carbohydrates; and (3) stem girdling would alter the response of E_s to diel changes in stem temperature.

Materials and Methods

Site description

The study site was a 12-yr-old loblolly pine (*P. taeda* L.) genotype by fertilization study located in Scotland County, NC, USA (McKeand *et al.*, 2000; Maier & Clinton, 2006). The soil is a Wakulla series characterized as a very infertile, excessively drained sand. Annual precipitation ranges between 1000 mm and 1200 mm evenly distributed throughout the year. Annual temperatures averaged 17°C with summer and winter averages of 26°C and 9°C, respectively. Glasshouse-grown seedlings from five full-sib families of Atlantic coastal plain and Texas origin were planted in 100 tree plots in November 1993. Half of the plots received annual fertilization since planting (McKeand *et al.*, 2000). Our study was confined to a fertilized and unfertilized plot of coastal plain families.

Measurements

Stem CO_2 efflux (E_s, μmol m^{-2} s^{-1}), sap flux density (J_s, g m^{-2} s^{-1}), stem diameter growth (mm) and carbohydrate concentration (mg g^{-1}) were measured on the bole of loblolly pine trees over several weeks in the autumn (October) and in the spring (May). The E_s was measured using an automated, multiport, measurement system (Butnor *et al.*, 2005) designed in an open configuration consisting of stem chambers, an infrared gas analyser (EGM series; PP

Systems, Amesbury, MA, USA) and a series of solenoids that sequentially sampled chambers. Stem chambers surrounded the tree stem and consisted of Teflon film attached to the stem with closed-cell foam tape (Maier & Clinton, 2006). Copper/constantan thermocouples measured chamber air and stem temperature (3 mm depth). Mean daily E_s are the average of 12–13 diel measurements reported on a surface area basis.

Stem sap flux density was measured using custom-made 30-mm long thermal dissipation probes (Granier, 1985, 1987; Maier & Clinton, 2006). Paired probes were inserted radially into the tree such that the probes were c. 5 cm apart, vertically. For each tree, two paired probes were installed on opposite sides (north and south) of the stem just below and above the stem girdle. The J_s was measured every 10 s and averaged every 15 min. In our trees, essentially all of the xylem was hydro-active; however, while we only measured the outer 3 cm, the probes measured the previous 2 yr of growth and captured the majority of stem sap flow in these trees (Ewers & Oren, 2000).

Stem radial growth in the spring was measured using automated point dendrometers (Agricultural Electronics Corporation, Tucson, AZ, USA) (Zweifel *et al.*, 2005). Point dendrometers measure the change in stem radius using a rod and cantilever system that holds a sensor head against the stem surface at a constant force. The dendrometers were 20 cm high, 10 cm wide, and c. 18 cm deep mounted on three 4 mm threaded rods drilled c. 40 mm into the tree. Changes in sensor head displacement were read automatically using a linear variable differential transformer. The dendrometers had 0.002 mm accuracy. Measurements were made every 15 min and averaged hourly. Daily stem growth was estimated as the difference in maximum hourly displacement over consecutive 24-h periods.

The outer ring of wood (phloem, cambium and xylem) was analysed for stem carbohydrate concentration. An increment hammer was used to sample stem tissues. Samples were collected between 09 : 00 h and 11 : 00 h to minimize diurnal variation in carbohydrate concentration (Edwards & McLaughlin, 1978). In the autumn, samples were assayed for starch and soluble sugars (sucrose, glucose, fructose and xylose) using high-pressure liquid chromatography (HPLC) at the Cranberry Experiment Station, University of Massachusetts, Amherst, MA, USA. In the spring, samples were analysed for starch and soluble sugars (sucrose and glucose) at the USDA Forest Service Laboratory (RTP, NC, USA) following the enzymatic assay of Faulkner *et al.* (1993) modified from Jones *et al.* (1977). Data are reported on a mass basis (mg g^{-1}).

Autumn girdling experiment

Stem temperature, E_s, and J_s were measured over a continuous 25-d period (day of year (DOY) 284–308) in the fall

2005 after diameter growth had ceased. Seven trees were selected from a fertilized and nonfertilized treatment plot (14 trees total). In each plot, three trees were used as controls (nongirdled, NG), and four were girdled (G). Two stem CO_2 efflux chambers were placed on each tree c. 1.3 m above ground and separated by c. 30 cm in the vertical direction (Fig. 1). Measurements began c. 1 wk before girdling to establish pregirdling conditions. On the girdled trees, c. 5 cm of bark and cambium tissue were removed from the stem at a point halfway between the two chambers (first girdle) using a rasp, being careful not to damage the outer xylem. The girdled area was inspected daily to remove callous tissue. Measurements continued for 18 d after girdling. Stem carbohydrates were measured four times during the experiment on five surrounding nongirdled and girdled the trees. Because of the destructive nature
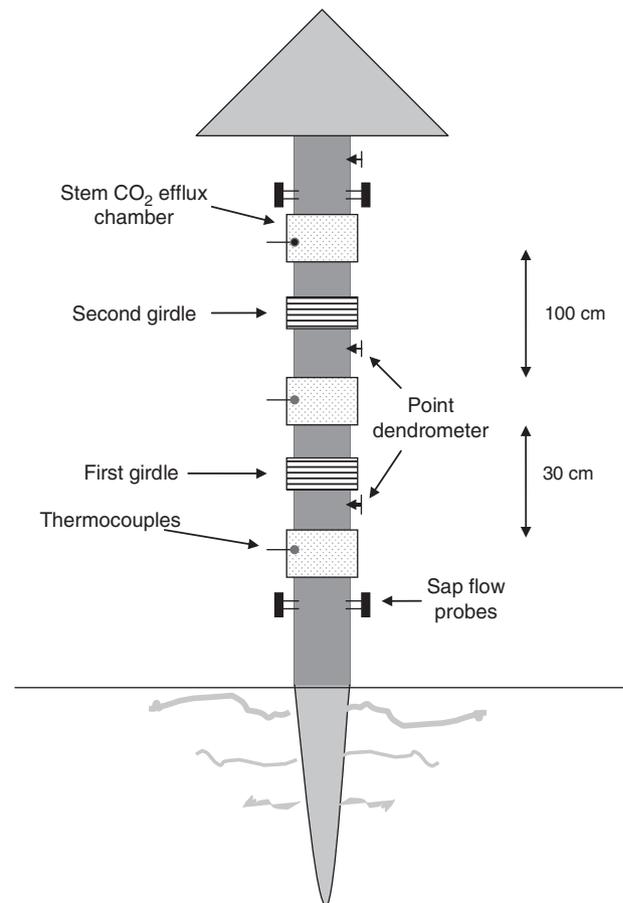
Fig. 1 A schematic showing the relative placement of stem CO_2 efflux chambers, sap flow probes, automated point dendrometers, thermocouples and girdling treatment on 12 yr-old *Pinus taeda* trees. The first and second stem girdles were at c. 1.3 m and 2.3 m aboveground, respectively. During the autumn, stem CO_2 efflux (E_s) and sap flow (J_s) measurements were made at two positions located above and below the first girdle. During the spring, E_s, J_s and continuous diameter growth were measured at three positions: below, between and above the first and second girdles.

of carbohydrate sampling, these measurements were not made on the tree measured for E_s.

Spring girdling experiment

Stem temperature, E_s, J_s and diameter growth were measured continuously over a 65-d period (DOY 116–180) in the spring 2006. Because girdling killed the trees the previous autumn, the spring experiment was confined to the nonfertilized plot to limit the number of damaged trees. Eight trees, three nongirdled and five girdled, were monitored. The E_s in nongirdled trees measured in the autumn experiment indicated no significant difference between below- and above-girdle positions; therefore, only one chamber was used on nongirdled trees in the spring. On girdled trees, E_s and J_s were measured as in the autumn experiment. Stem diameter growth was measured using automated dendrometer bands. On girdled trees, dendrometers were positioned *c.* 60 cm from the girdle to ensure that any callous or scar formation did not interfere with diameter measurement (Fig. 1). Stem carbohydrates were measured six times on surrounding trees at 1.3 m on five nongirdled trees and above and below the girdle on 10 girdled trees.

Fourteen days after the first girdling, two of the five girdled trees used for E_s measurements were girdled a second time *c.* 1 m above the first girdle. The E_s and diameter growth were measured above the second girdle (Fig. 1). The objective of this second girdling treatment was to isolate a stem segment from carbohydrate supply from the canopy and stored starch in the roots. The E_s measurements were continued for another 30 d. In addition, four of the 10 girdled trees used for carbohydrate sampling were girdled a second time. Stem carbohydrate status was measured five times after the second girdling at points below the first girdle, between the first and second girdle, and above the second girdle.

Temperature modeling

Stem CO_2 efflux in pines generally follows an exponential increase with temperature (Ryan *et al.*, 1995; Lavigne *et al.*, 1996; Maier, 2001). In our study trees, the E_s-temperature response exhibits a large diel hysteresis where E_s measured at similar temperatures are higher at night than during the day (Maier & Clinton, 2006). The lower rates during the day are possibly caused by the removal of respired CO_2 in the xylem stream during periods of high sap flow (Teskey & McGuire, 2002; Gansert & Burgdorf, 2005, Saveyn *et al.*, 2008). To eliminate the effects of sap flow on E_s, temperature response functions were constrained to periods when $J_s < 1.2$ g m^{-2} s^{-1} (generally at night between 20 : 00 and 06 : 00 h). Under these conditions, E_s was modeled as a linear function of stem temperature:

$$E_s^* = \beta_{15} + [k(T_s - 15)], \qquad \text{Eqn 1}$$

(E_s^* is measured E_s when $J_s < 1.2$ g m^{-2} s^{-1}; β_{15} is E_s^* at 15°C; k is the temperature coefficient; T_s is stem temperature). Parameter estimates for Eqn 1 were obtained for each tree and girdling position using linear regression. Model performance was examined by plotting residual and normality curves for all regressions to confirm that the data met assumptions of equal variance and normality.

Statistical analyses

To facilitate comparisons of the relative effects of girdling between nongirdled and girdled trees, E_s for each tree was normalized (nE_s) to E_s measured the day before girdling. Normalizing E_s corrects for inherent differences in E_s between trees and allows for an assessment of treatment effects between nongirdled and girdled trees over time. Changes in E_s, nE_s, J_s, carbohydrate status and diameter growth resulting from girdling and fertilization (autumn experiment only) were assessed using repeated measures analysis of variance with DOY as the repeated measure (PROC MIXED; SAS Institute, Cary, NC, USA) using an autoregressive covariance structure. To account for nonindependence of E_s measurements between lower (below girdle, BG) and upper (above girdle, AG) positions on girdled trees, separate comparisons were made for: nongirdled (NG) vs BG, NG vs AG, and BG vs AG. *Post-hoc* comparisons of adjusted least-square means were made using Tukey's paired comparison procedure and were considered significant at α ≤ 0.05. Transformed variables were used when data did not meet assumptions of normality (Shapiro–Wilkes test). All values were expressed as untransformed means and standard errors. Effects of girdling and time-of-year on the parameter estimates of Eqn 1 were assessed using analysis of variance (PROC MIXED).

Results

Autumn girdling experiment

Stem temperatures ranged between 0 and 31°C and were not affected by fertilization ($P = 0.82$) or girdling ($P = 0.68$) (Fig. 2a,d). The E_s was not significantly different between upper and lower chambers on NG trees (nonfertilized, $P = 0.34$; fertilized, $P = 0.45$); therefore the average of the two chambers were used for analysis. Following girdling treatment, E_s simultaneously decreased below the girdle and increased above the girdle (Fig. 2b,e). Significant differences between girdling positions occurred within 24 h of girdling (data not shown). Because of equipment malfunction, we were unable to measure the E_s in nonfertilized trees before girdling and for 2 d post girdling. Therefore, to examine fertilization by girdling effects on E_s, the
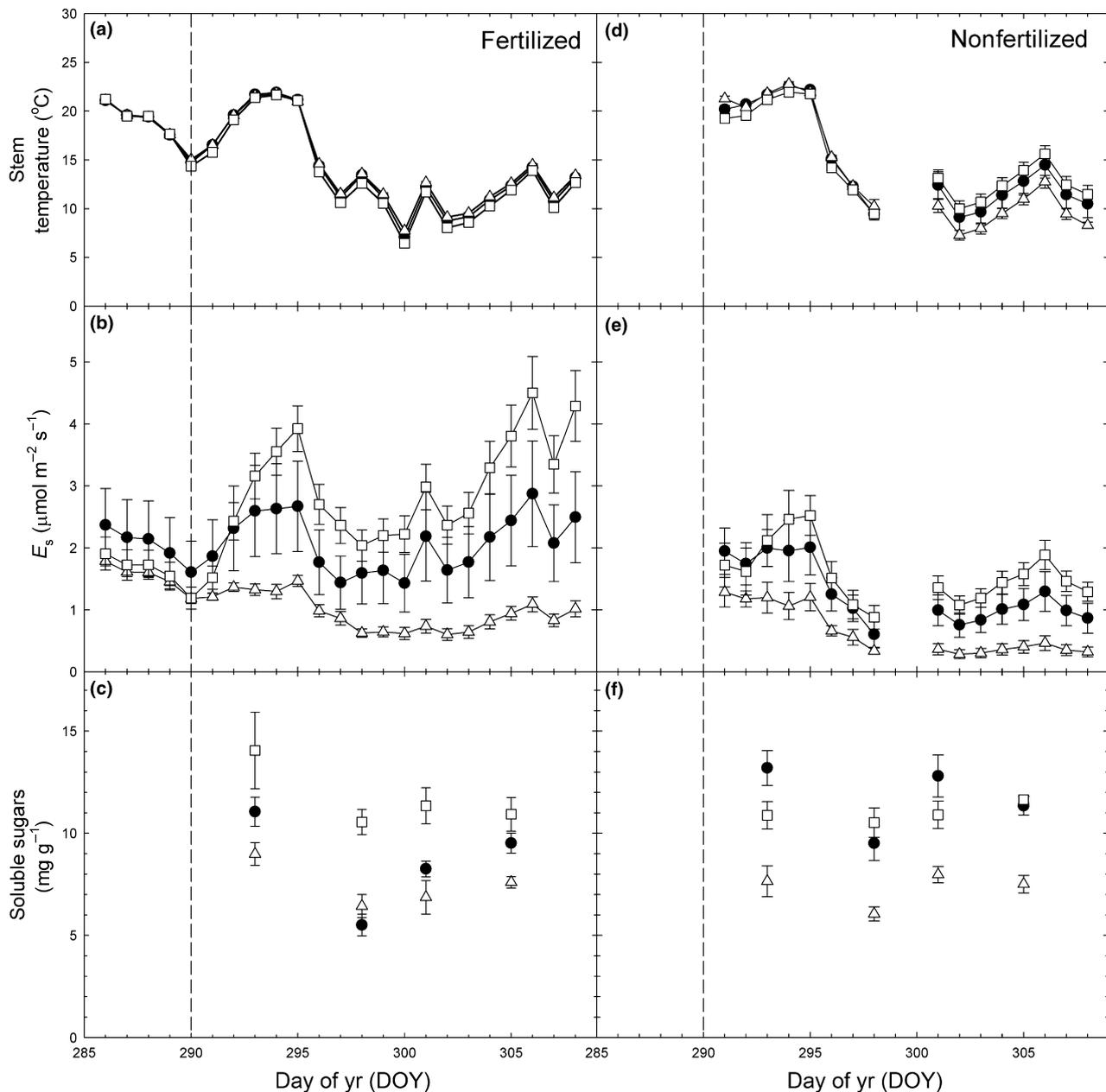
Fig. 2 Autumn measurements of mean daily stem temperature in the fertilized and nonfertilized trees (a,d), mean daily stem CO_2 efflux (E_s) (b,e) and soluble sugar concentration (c,f) of nongirdled (NG) and girdled trees below (BG) and above (AG) the first girdle. The dotted vertical line represents time of girdling. In (a), (b), (d) and (e) each point is the mean ($\pm$ SE) of three nongirdled or four girdled trees. In (c) and (f) each point is the mean ($\pm$ SE) of five trees surrounding the trees used for measuring E_s. Closed circles, nongirdled; open triangles, below girdle; open squares, above girdle.

data were constrained to two post-girdling periods (DOY 291–298 and 301–308) and analysed separately. Stem CO_2 efflux in NG trees was significantly greater in fertilized than nonfertilized trees (e.g. DOY 291–298; fertilized: E_s = 2.10 µmol m^{-2} s^{-1}, nonfertilized: E_s = 1.56 µmol m^{-2} s^{-1}; P = 0.04). The difference in E_s between girdling positions (BG vs AG) was greater in fertilized trees (fertilization × girdling position: DOY 291–298, P < 0.0001; DOY

301–308, P < 0.0001). However, the relative difference in E_s below and above the girdle was similar between plots. For example 5 d after girdling (DOY 295), E_s was 2.1 × and 2.6 × greater above the girdle than below in nonfertilized and fertilized trees, respectively. After 15 d (DOY 305), E_s was 3.9 times greater above the girdle than below in nonfertilized trees and 4.0 times greater in fertilized trees.
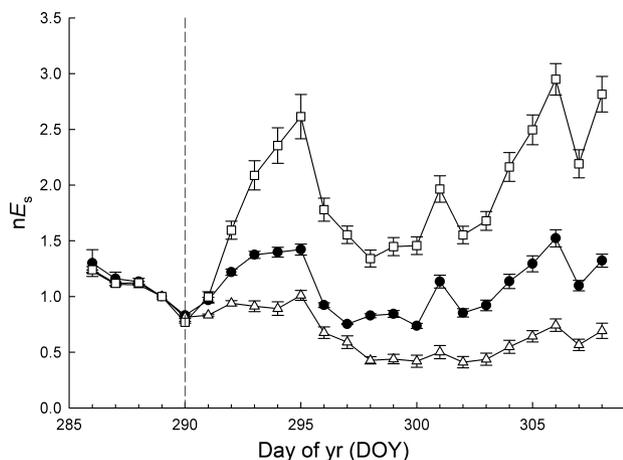
Fig. 3 Autumn measurements of mean daily stem CO_2 efflux normalized to rates measured on DOY 289 (nE_s) for fertilized trees. Treatments are nongirdled (NG) and girdled below (BG) and above (AG) the first girdle. The dotted vertical line represents time of girdling. Each point is the mean (± SE) of three nongirdled or four girdled trees. Closed circles, nongirdled; open triangles, below girdle; open squares, above girdle.

Table 1 Soluble sugar concentration for 12 yr-old loblolly pine trees in nongirdled (NG) and girdled trees at positions below (BG) and above (AG) the girdle

	Girdling position	Soluble sugars (mg g^{-1})
Nonfertilized	NG	11.71 a
	BG	7.30 b
Fertilized	NG	8.58 c
	BG	7.47 b
Nonfertilized	NG	11.71 a
	AG	10.99 a
Fertilized	NG	8.58 b
	AG	11.72 a
Nonfertilized	BG	7.30 a
	AG	10.99 b
Fertilized	BG	7.47 a
	AG	11.72 b

Measurements were made in fertilized and nonfertilized trees during the autumn. Values are least square means over the study period (n = 4). To account for nonindependence of observations within girdled trees, significant differences between NG, BG, AG positions were identified using separate pairwise comparisons for each measurement position. Values within a fertilization by girdling position comparison followed by a different letter are significantly different at α = 0.05.

The response to girdling was much greater above the girdle than below. This is illustrated by comparing normalized E_s (nE_s) in nongirdled and girdled trees (Fig. 3). Relative to the nongirdled trees, significant differences in nE_s were observed 2 d after girdling (NG vs BG: P = 0.01; NG vs AG: P = 0.0002). Girdling resulted in a 94% increase in nE_s above the girdle and a 50% reduction below the girdle. We were unable to assess nE_s in the nonfertilized trees.

Nonfertilized trees had higher concentrations of soluble sugars than fertilized trees in the nongirdled treatment (fertilized: 8.57 mg g^{-1}, nonfertilized: 11.71 mg g^{-1}; P < 0.0001). There were significant fertilization × girdling treatment interactions (NG vs BG: P < 0.0001; NG vs AG: P < 0.0001) (Fig. 2c,f; Table 1). Compared with nongirdled trees, soluble sugars declined below the girdle in fertilized and nonfertilized trees and accumulated above the girdle, but only in fertilized trees. Within girdled trees, soluble sugar concentration was significantly greater above the girdle than below (P < 0.0001) and there was no fertilization × girdling position interaction (P = 0.47). Stem starch concentration at this time of year was low (< 2 mg g^{-1}). Girdling had no effect on J_s and there was no girdling treatment by position interaction on maximum daily J_s before girdling (P = 0.37), 5 d (P = 0.78) or 15 d (P = 0.46) after girdling.

Spring girdling

Stem temperatures in spring ranged between 10°C and 30°C with no response to girdling (P = 0.12, Fig. 4a). Girdled trees exhibited similar patterns of E_s to those observed in the autumn except the response was muted. Stem CO_2 efflux above the girdle was 1.4 times greater than below the girdle 5 d (DOY 127) after girdling and 1.8 times greater 13 d (DOY 135) after girdling (Fig. 4b). Relative to nongirdled trees, nE_s above the girdle increased c. 60% and significant differences were observed 2 d after girdling (NG vs AG: P = 0.001) (Fig. 5). By contrast, the response of E_s below the girdle was much slower. Significant reductions in the E_s below the girdle occurred after 9 d (NG vs BG: P = 0.002) and nE_s stabilized between 15–19% below rates in non-girdled trees (DOY 130–135).
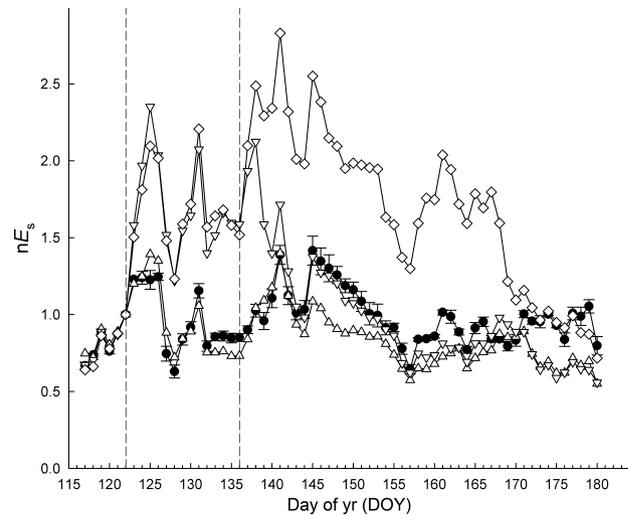
Mean soluble sugar concentration (DOY 121–136) was significantly greater above the girdle than below (AG = 11.99 mg g^{-1}; BG = 6.87 mg g^{-1}; P < 0.0001) and compared with nongirdled trees (9.68 mg g^{-1}), girdling caused a depletion below the girdle (P < 0.001) and a slight accumulation above the girdle (P = 0.08) (Fig. 4c). Starch concentrations also increased above the girdle and decreased below the girdle, although these were not as distinct (Fig. 4d). Mean starch concentration was significantly greater above the girdle than below (AG = 4.58 mg g^{-1}, BG = 3.18 mg g^{-1}, P = 0.004). Compared with nongirdled trees (4.14 mg g^{-1}), starch was significantly different below the girdle (P = 0.026), but not above (P = 0.50). Starch concentration below the first girdle was depleted (< 2 mg g^{-1}) within 24 d of treatment. Girdling had no effect on J_s at any position (data not shown).

Two trees were girdled a second time (second girdle) 14 d after the first girdling (DOY136) at a point 1 m above the first girdle (Fig. 1). Two days following the second girdling, nE_s below the second girdle declined relative
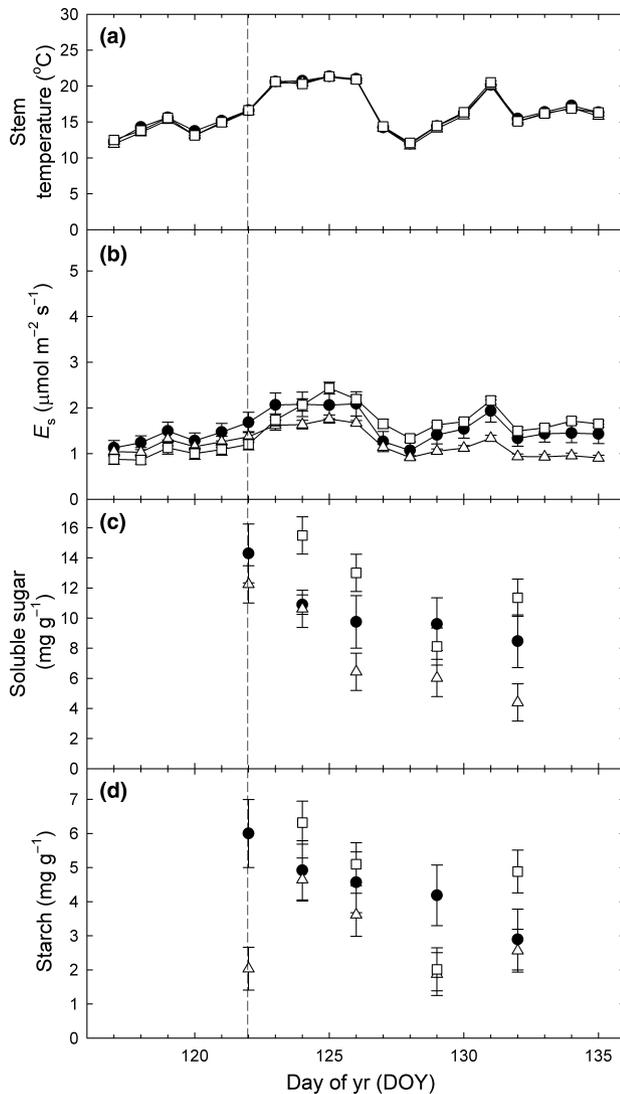
Fig. 4 Spring measurements of daily stem temperature in the non-fertilized trees (a), mean daily stem CO_2 efflux (E_s) (b), soluble sugar concentration (c), starch (d) of nongirdled (NG) and girdled trees below (BG) and above (AG) the first girdle. The dotted vertical line represents time of girdling. In (a) and (b) each point is the mean (± SE) of three nongirdled or five girdled trees. In (c) and (d), each point is the mean (± SE) of five nongirdled or 10 girdled trees surrounding the trees used for measuring E_s. Closed circles, nongirdled; open triangles, below girdle; open squares, above girdle.

Fig. 5 Spring measurements of mean daily stem CO_2 efflux normalized to DOY 121 (nE_s) in nonfertilized trees. The dotted vertical lines represent times of girdling for the first (DOY 122) and second (DOY 136) girdle. Each point is the mean (± SE) of three nongirdled or two girdled trees. Closed circles, nongirdled; open triangles, below the first girdle; open upside down triangles, between first and second girdle; open diamonds, above the second girdle.

Cumulative stem growth in nongirdled trees was 2.6 mm over the experiment (Fig. 6). In girdled trees, girdling caused an almost complete cessation of diameter growth (0.8 mm) below the girdle, whereas growth above the girdle was accelerated (3.4 mm). The growth response following the second girdle was unclear (data not shown). One tree had increased growth above the second girdle whereas the other tree did not respond.
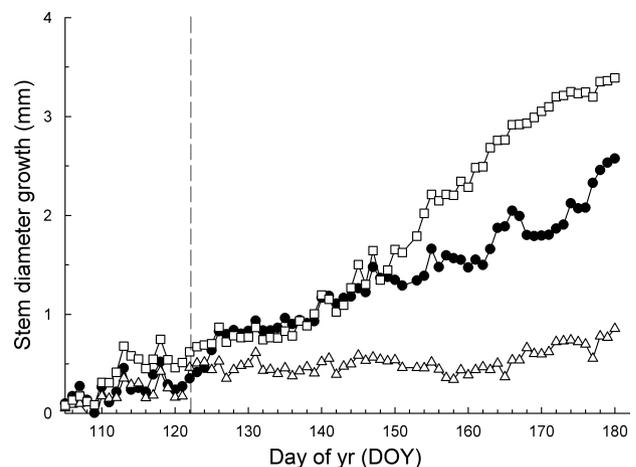
Fig. 6 Stem diameter growth (mm) measured with automated point dendrometers. Each point is the maximum daily valued measured in nongirdled (NG) and girdled trees below (BG) and above (AG) the first girdle. The dotted vertical lines represent times of girdling. Each point is the mean of three trees. Closed circles, nongirdled; open triangles, below girdle; open squares, above girdle.

to above the girdle and rates were similar to nongirdled trees after 7 d (Fig. 5). Reduced E_s below the second girdle corresponded with a decline in soluble sugar and starch concentrations (data not shown). Stem CO_2 efflux E_s above the second girdle initially increased after the second girdling but then began to slowly decline followed by a rapid decline after 32 d (DOY 168). Normalized at all three girdling positions were equal to or below nE_s in nongirdled trees 40 d after the initial girdling treatment. All girdled trees died within 6 months.

Temperature modeling

Data from the autumn and spring experiments in the non-fertilized plot were pooled to examine girdling and seasonal effects on Eqn 1 parameters. A continuous 5-d period postgirdling after E_s had stabilized was selected from each experiment (autumn: DOY 301–305; spring: DOY 128–132). The E_s^* (E_s when $J_s < 1.2$ g m^{-2} s^{-1}) was strongly correlated with stem temperature (R^2 ranged from 0.77 to 0.95). In nongirdled trees, β_{15} was significantly higher ($P < 0.001$) in the spring than in the autumn, but there was no significant difference in temperature sensitivity (k, $P = 0.42$) (Table 2). Compared with nongirdled trees, girdling resulted in a decline in β_{15} below the girdle ($P = 0.002$), but had no effect on β_{15} above the girdle ($P = 0.12$). Girdling resulted in a decrease in k below the girdle in the autumn ($P = 0.0004$) and spring ($P = 0.003$) and an increase in k above the girdle in the autumn ($P = 0.02$), but not in the spring ($P = 0.12$). There was no season × girdling treatment interaction on either parameter. There was a strong relationship between E_s^* and carbohydrate concentration for days when both variables were measured. Combining data across all treatments, E_s^* was linearly correlated with the soluble sugar ($P < 0.0001$, $R^2 = 0.57$) (Fig. 7a) and starch ($P < 0.0001$, $R^2 = 0.61$) (Fig. 7b) concentration.

Discussion

We observed a strong effect of girdling on E_s concurrent with an accumulation of soluble sugars and starch above the

Table 2 Parameter estimates for the relationship between stem CO_2 efflux when $J_s < 1.2$ g m^{-2} s^{-1} (E_s^*) and stem temperature (Eqn 1) in 12-yr-old loblolly pine trees

		β_{15} (SE)	k (SE)
NG vs BG			
Autumn	NG	0.74 a (0.09)	0.077 a (0.002)
	G	0.33 b (0.11)	0.024 b (0.006)
Spring	NG	1.51 c (0.13)	0.091 a (0.003)
	G	1.09 d (0.10)	0.044 b (0.001)
NG vs AG			
Autumn	NG	0.74 a (0.11)	0.077 a (0.008)
	G	0.90 a (0.14)	0.133 b (0.010)
Spring	NG	1.51 b (0.16)	0.091 ab (0.012)
	G	1.81 b (0.12)	0.066 bc (0.009)

Comparisons are for nongirdled (NG) vs below the girdle (BG) and NG vs above the girdle (AG). Values within a column by girdling position comparison followed by a different letter are significantly different at α = 0.05.

girdle and depletion below it (prediction 1). Significant differences in E_s occurred across the girdle within 24 h of treatment and the response was much larger above the girdle. The quick response of E_s to girdling indicates that the availability of recently formed photosynthates, primarily soluble sugars, is an important factor controlling rates of E_s and may explain much of the temporal and spatial variation of E_s in forest ecosystems. The large and rapid decline of E_s following the second girdling in the spring and the linear relationship between E_s^* and carbohydrate concentration are further evidence for this linkage. Girdling had no immediate effect on J_s, so rapid changes in E_s were directly
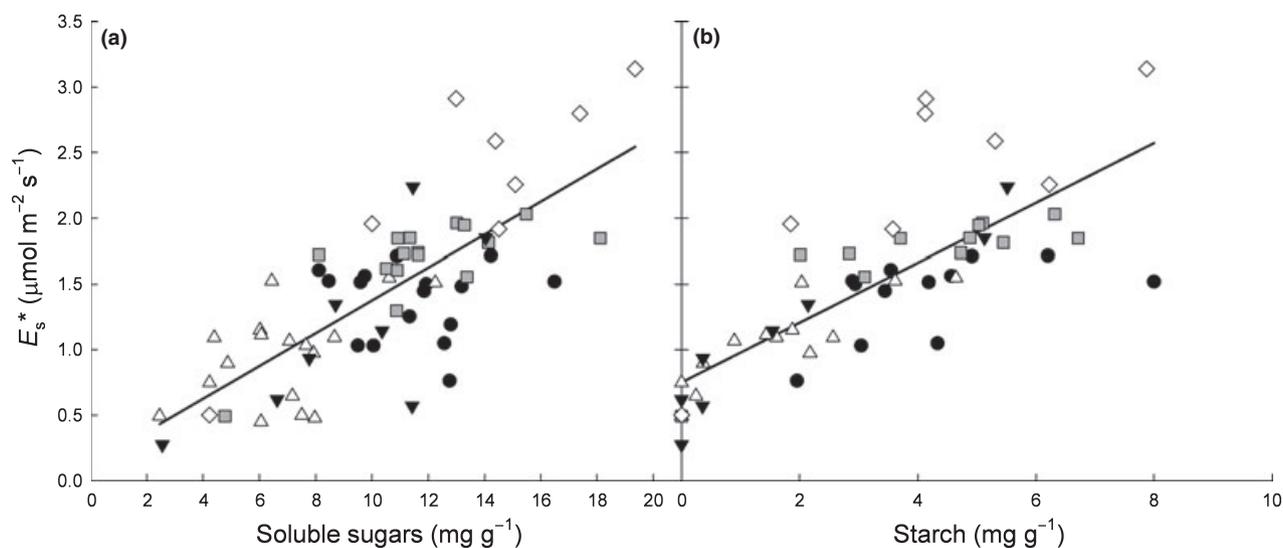
Fig. 7 Scatter plot showing the relationship between mean daily stem CO_2 efflux (E_s) corrected to 15°C (E_s^*) and the concentration of stem (a) soluble sugars in the autumn and spring and (b) starch in the spring. The E_s^* is stem CO_2 efflux when $J_s < 1.2$ g m^{-2} s^{-1} on days when carbohydrates were measured. Regression equations for (a) $y = 0.127 + 0.125x$, $R^2 = 0.57$, $P < 0.0001 = 0.043$; and (b) $y = 0.751 + 0.227x$, $R^2 = 0.61$, $P < 0.0001$. Closed circles, nongirdled; open triangles, below first girdle; shaded squares, above first girdle; closed upside down triangles, below second girdle; open diamonds, above second girdle.

induced by girdling mediated changes in soluble carbohydrates, rather than by transport, storage, and out-gassing of exogenous CO_2 in the xylem (Teskey *et al.*, 2008). In agreement, Wang *et al.* (2006) measured E_s in girdled stems of mature *Pinus koraiensis* and found that the difference in E_s across the girdle was correlated with cumulative photosynthetic photon flux density of the previous day indicating that canopy carbohydrate took *c.* 1 d to be translocated to lower stem sections. In addition, Tang *et al.* (2005) showed that soil CO_2 efflux near trees in an oak–grass savanna was correlated with tree photosynthesis with a 7- to 12-h time-lag.

The response of E_s to girdling varied in degree and timing with season (prediction 2). Seasonal comparisons are only for trees in the nonfertilized plot as fertilized trees were measured only in the autumn. Because of equipment failure in the autumn there was no pregirdling E_s data in the nonfertilized trees, making direct seasonal comparisons of relative effects of girdling (i.e. nE_s) impossible. However, the relative effects of girdling on E_s were similar between fertilized and nonfertilized trees (Fig. 2b,e), thus we can use nE_s in fertilized trees as proxy for nonfertilized trees for seasonal comparisons. Girdling clearly affected E_s to a greater extent in the fall than in the spring. Compared with non-girdled trees, E_s in girdled trees increased 94% above the girdle and decreased 50% below the girdle in the autumn, whereas in the spring, E_s increased only 60% above the girdle and decreased by < 20% below the girdle. In addition, the decrease in E_s below the girdle took longer to develop in the spring. Seasonal differences in starch availability may explain the response in E_s below the girdle. Starch concentrations were low in the autumn, thus, when soluble carbohydrate supply was interrupted, the decline in E_s below the girdle was rapid and large indicating that maintenance processes at this time of year are dependent primarily on current photosynthate. During the spring, the availability of starch below the girdle sustained E_s and the reduction in E_s following girdling was muted. Johnsen *et al.* (2007) observed a similar seasonal response to girdling in soil CO_2 efflux in adjacent stands. In addition, the immediate cessation of growth below the girdle in the spring suggests that stem cambium activation and growth of loblolly pine is derived primarily from current photosynthate (Hansen & Beck, 1994; Oribe *et al.*, 2003). Concomitantly, starch reserves below the girdle did not appear to sustain radial growth, at least in the short-term, indicating that starch is reserved primarily for maintenance processes (Marshall & Waring, 1985).

The large increase in E_s above the girdle may be associated with increased substrate-mediated respiration and enzymatic activity (Martin *et al.*, 1994) or growth. The accumulation of soluble sugars above the girdle has three potential fates: the sugar can be rapidly respired, transferred to storage or incorporated into growth. The increase in E_s may help prevent endproduct inhibition of photosynthesis (Myers *et al.*, 1999) by respiring excess substrate. In addition, increased E_s could result from activation of the alternative respiration pathway (Amthor, 2000) that consumes carbohydrates with no net production of ATP (Lambers & Ribas-Carbo, 2005). Transfer of excess sugars into storage was unlikely, as we observed no formation of starch above the girdle in the autumn. Strong carbohydrate sinks such as stem and canopy growth could consume excess carbohydrates. The reduced response of E_s above the girdle in the spring was likely caused by increased stem growth (Fig. 6) (Daudet *et al.*, 2005; Wang *et al.*, 2006). Di Vaio *et al.* (2001) found that girdling peach shoots reduced photosynthesis, presumably because of carbohydrate accumulation; however, the reduction in photosynthetic rates was not as great when developing fruits were present, most likely because they acted as carbon sinks and so decreased feedback inhibition.

The amount, form, and demand for carbohydrate regulates the sensitivity of respiration to changes in temperature (Thornley, 1977; Azcon-Bieto & Osmond, 1983). We found that girdling altered the E_s–temperature response (Prediction 3). The temperature coefficient (*k*) decreased below the girdle concurrent with carbohydrate concentration in the autumn and spring and increased above the girdle but only in the autumn (Table 2). The lack of a response above the girdle in the spring may indicate a seasonal shift in the relative importance of maintenance (temperature sensitive) and growth (temperature insensitive) processes (Sprugel *et al.*, 1995) in the cambium/phloem region. The large girdling effect on *k* in the autumn indicates that maintenance processes dominated E_s at this time of year. In the spring, girdling halted growth and probably growth-related respiration below the girdle (Fig. 6), thus the significant decrease in *k* suggests that maintenance processes dominated E_s. By contrast, growth increased above the girdle and there was no girdling effect on *k* indicating that the majority of increased E_s was related to growth. Ogawa (2006) found that girdling stems during the growing season had no effect on the temperature response in *P. sylvestris*. Our results indicate that carbohydrate availability effects may obviate the utility of applying short-term temperature response functions across seasons (Tjoelker *et al.*, 2008). Furthermore, because canopy carbon assimilation is less sensitive to temperature than is respiration, linking the E_s–temperature response to carbohydrate availability will likely decrease annual estimates of E_s (Dewar *et al.*, 1999; Whitehead *et al.*, 2004). Thus, it is critical to incorporate carbohydrate effects on the E_s–temperature response when developing substrate-based models of respiration (Dewar *et al.*, 1999).

Factors other than carbohydrate supply could have caused the observed E_s and growth responses to girdling. Girdling inhibits the production and transport of root- or shoot-derived growth substances necessary for cambium

development (Allen, 1964; Noel, 1970; Loescher *et al.*, 1990). A continuous supply of auxin is needed for cambial activity, and so reduced stem growth below the girdle may be caused by a lack of shoot-derived auxin (Larson, 1994). Phloem sugar concentrations have important functions in tree water relations. A depletion or accumulation of carbohydrates with girdling can alter stem cell turgor (Daudet *et al.*, 2005) and hydraulic conductance, increasing xylem vulnerability to embolism (Domec & Pruyn, 2008) and decreasing stem hydraulic conductivity (Zwieniecki *et al.*, 2004). Changes in water status control stem growth directly by inhibiting cell division and enlargement and indirectly through stomatal closure reducing net assimilation (Cheng *et al.*, 2008).

The transport and storage of exogenous CO_2 in the xylem can have a large effect on E_s (Teskey *et al.*, 2008). Recent studies have shown that E_s is linearly related to xylem $[CO_2]$ and inversely related to sap flow (Teskey & McGuire, 2002, 2005). We did not measure xylem $[CO_2]$, but a large effect of girdling on xylem-derived exogenous CO_2 could potentially confound our results. Maier & Clinton (2006), using the same stands as in this experiment, showed that manipulating J_s through stepwise removal of canopy leaf area increased xylem $[CO_2]$, but had little effect on measured E_s. They concluded that E_s was largely derived from the metabolism of cambium and phloem tissue and that CO_2 transported in the xylem stream had little influence on E_s for the range of J_s measured under field conditions (< 0.5 cm min^{-1}, Teskey *et al.*, 2008). In the current study, girdling had no immediate effect on J_s, at least in the short-term, and exogenous or locally produced xylem CO_2 likely had only a small effect on E_s. However, we stress that the E_s measured in our trees probably reflects primarily growth and maintenance respiration of the cambium and inner bark and underestimated total stem respiration (McGuire & Teskey, 2004; Teskey *et al.*, 2008).

In conclusion, the quick response of E_s to the girdling treatment suggests that carbohydrate availability is an important factor controlling diel rates of E_s and growth in mid-rotation *P. taeda* stems. The large girdling response in the autumn indicates that maintenance processes at this time of year are carbon limited and rely on recently formed photosynthates, primarily soluble sugars. In the spring, the presence of starch below the girdle and increased growth above both muted the E_s response to girdling. Short-term changes in E_s temperature sensitivity were correlated with carbohydrate supply suggesting that the temperature response is regulated by carbohydrate supply. Furthermore, E_s^* was linearly correlated with carbohydrate concentration (even in nongirdled trees) indicating that E_s may vary daily as a function of canopy photosynthesis. A dynamic mechanistic carbon model that links stem CO_2 efflux with carbon availability (newly fixed and stored), growth and temperature will provide robust estimates of forest carbon budgets and sequestration and help evaluate the extent and timing of carbon limiting stress on stem growth and metabolism.

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