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Root-derived CO_2 efflux via xylem stream rivals soil CO_2 efflux

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Summary

- Respiration consumes a large portion of annual gross primary productivity in forest ecosystems and is dominated by belowground metabolism. Here, we present evidence of a previously unaccounted for internal CO_2 flux of large magnitude from tree roots through stems. If this pattern is shown to persist over time and in other forests, it suggests that belowground respiration has been grossly underestimated.
- Using an experimental *Populus deltoides* plantation as a model system, we tested the hypothesis that a substantial portion of the CO_2 released from belowground autotrophic respiration remains within tree root systems and is transported aboveground through the xylem stream rather than diffusing into the soil atmosphere.
- On a daily basis, the amount of CO_2 that moved upward from the root system into the stem via the xylem stream (0.26 mol CO_2 m^{-2} d^{-1}) rivalled that which diffused from the soil surface to the atmosphere (0.27 mol CO_2 m^{-2} d^{-1}). We estimated that twice the amount of CO_2 derived from belowground autotrophic respiration entered the xylem stream as diffused into the soil environment.
- Our observations indicate that belowground autotrophic respiration consumes substantially more carbohydrates than previously recognized and challenge the paradigm that all root-respired CO_2 diffuses into the soil atmosphere.

Introduction

Forest ecosystems account for the majority of terrestrial net primary productivity and are therefore a major focus of global carbon budgets (Jobbágy & Jackson, 2000; Geider *et al.*, 2001). Ecosystem respiration (R_E) consumes *c.* 77–85% of annual gross primary productivity in forest ecosystems across the globe (Law *et al.*, 2002; Luyssaert *et al.*, 2007; Baldocchi, 2008). Comprised of both autotrophic (leaves, stems and roots) and heterotrophic (fungi, bacteria and animals) components, R_E releases one of the largest annual CO_2 fluxes of the global carbon cycle – a flux nearly 16 times that of the annual fossil fuel combustion from 2000 to 2005 (Prentice *et al.*, 2001; IPCC, 2007). Belowground autotrophic and heterotrophic contributions to R_E are difficult to separate. However, the combined contribution of autotrophic and heterotrophic respiration (i.e. soil CO_2 efflux) represents a substantial portion of forest R_E – accounting for 30–88% of total annual R_E (Goulden *et al.*, 1996; Law *et al.*, 1999; Janssens *et al.*, 2001; Davidson *et al.*, 2006; Baldocchi, 2008; Cavaleri *et al.*, 2008; Tang *et al.*, 2008). The remainder of R_E is contributed by aboveground foliar and woody tissue respiration.

A mechanistic understanding of forest respiratory flux pathways is imperative to understanding forest carbon cycles and forest ecosystem responses to climate change.

A long-standing paradigm in plant physiological ecology is that root-respired CO_2 diffuses from inside the root outward and is released into the soil atmosphere (Hanson *et al.*, 2000; Kuzyakov, 2006; Trumbore, 2006). A corollary is that all CO_2 derived from root respiration can be measured as part of soil CO_2 efflux to the atmosphere. However, CO_2 dissolved in the soil solution can be transported from roots to shoots via the xylem stream (Ford *et al.*, 2007; Moore *et al.*, 2008). Tree stems contain CO_2 concentrations many times greater than those of the atmosphere (Teskey *et al.*, 2008) and high CO_2 concentrations at the base of tree stems indicate that much of the CO_2 in stem xylem originates belowground (Teskey & McGuire, 2007). The estimated contribution of dissolved inorganic carbon absorbed by roots from the soil solution is far less than the quantity found at the base of tree stems and suggests that much of it originates within the root system (Teskey & McGuire, 2007). Thus, it is likely that not all root-respired CO_2 diffuses into the soil atmosphere, indicating that conventional methods for measuring belowground respiration may underestimate actual rates.

Given these observations, it is plausible that a considerable amount of respired CO_2 can remain within tree root systems, where it dissolves in xylem sap and is subsequently transported aboveground via the xylem stream. However, the relative importance of internally transported CO_2 remains unclear as no empirical investigations have quantified the magnitude of this flux or compared it with flux of CO_2 from the soil surface to the atmosphere. Using an experimental *Populus deltoides* plantation as a model system, we tested the hypothesis that a substantial portion of belowground autotrophic respiration remains within tree root systems and is transported aboveground via the xylem stream rather than diffusing outward into the soil atmosphere.

Materials and Methods

To determine the magnitude of autotrophically respired and soil-derived CO_2 transported from root systems to stems (F_T), we instrumented *Populus deltoides* Bartr. trees to measure the internal xylem CO_2 concentration ($[CO_2]$) and sap flux and simultaneously measured soil CO_2 efflux near each tree to elucidate the relative importance of F_T for total belowground CO_2 efflux. The difference between F_T and the amount of dissolved CO_2 originating in the soil solution is the internal flux of autotrophically respired CO_2, hereafter referred to as root-respired CO_2. We define root-respired CO_2 as a fusion of CO_2 produced from root and root-associated fungal symbiont sources.

Study site

The experiment was conducted in an intensively managed 9-yr-old *P. deltoides* experimental plantation located within the Department of Energy Savannah River Site in Aiken County, SC, USA. The soil at the site is predominately a Blanton sand with a loamy subsoil at a depth of 120–200 cm (Rogers, 1990). The litter layer within the measurement plots was thin and heterogeneously distributed. Complete competition control was maintained over the entire 9-yr stand history, so all autotrophic contributions to belowground CO_2 efflux resulted from *P. deltoides* trees. We randomly selected four trees that ranged in diameter from 15.7 to 16.5 cm at 1.3 m stem height. We compared the magnitudes of belowground CO_2 flux pathways by scaling both F_T and soil CO_2 efflux to the same unit area. The explicit spacing (2.5×3 m) and consistent stocking of trees allowed for comparisons of F_T and soil CO_2 efflux at the same spatial scale. We assumed that the soil area occupied by the root system of each tree was equivalent to 7.5 m^2. Soil CO_2 efflux was expressed on a m^2 area basis, so F_T was divided by 7.5 m^2 to place both soil and stem fluxes on the same unit area scale. Measurements of F_T and soil CO_2 efflux were collected every 15 min over 7 consecutive days in August 2008. To illustrate the importance of F_T for our understanding of belowground processes, we estimated the total autotrophic and heterotrophic contributions of total belowground CO_2 flux by assuming that 50% of soil CO_2 efflux was contributed by autotrophic respiration. Hanson *et al.* (2000) report a range of 10–90% for the autotrophic component of soil CO_2 efflux for instantaneous measurements and 45–60% for annual budgets in forest ecosystems. Based on this information, we chose 50% as a reasonable assumption of growing season autotrophic contribution at our site. Although the actual proportion on this site is not known, this approximation provides an initial insight into the potential impact of F_T on the primary components of belowground CO_2 efflux.

Soil CO_2 efflux

Soil CO_2 efflux was measured using the $[CO_2]$ gradient method which relies on Fick's first law of diffusion to calculate efflux based on the $[CO_2]$ gradient in the soil and soil diffusivity properties (Tang *et al.*, 2003). The gradient approach allowed high-frequency measurements of soil CO_2 efflux which our study required. Soil $[CO_2]$ was measured in soil profile arrays with nondispersive infrared (NDIR) CO_2 sensors (model GMT220; Vaisala Inc., Helsinki, Finland) housed in PVC sleeves that were inserted to the appropriate depth (2, 22 and 42 cm) 0.75 m northwest of each tree. Sensors were sealed into the housings with rubber O-rings. Thermocouples were placed at each depth to correct soil $[CO_2]$ for temperature. Soil $[CO_2]$ was also corrected for barometric pressure (model PTB110; Vaisala). Soil bulk density was determined before the study. Volumetric water content was measured using dielectric sensors (10HS soil moisture sensor; Decagon Devices, Pullman, WA, USA). We validated the gradient method at our site by regressing gradient measurements with chamber-based measurements (LI-6400; Li-Cor Biosciences, Lincoln, NE, USA)

obtained from soil collars at each profile array ($m = 0.91$, $r^2 = 0.89$, $n = 40$). Measurements for this comparison were collected in August 2008. To determine potential spatial heterogeneity of soil efflux and to ensure that our profile array locations were adequate representations of the larger growing space for each tree, we inserted soil collars at four additional locations around each tree and found that there was no statistical difference between our array location (4.6 ± 0.7 μmol CO_2 m^{-2} s^{-1}; mean ± SE) and the mean of the four additional locations (4.7 ± 0.7 μmol CO_2 m^{-2} s^{-1}; $P = 0.4892$, $n = 9$). Measurements for this comparison were collected in July 2008.

Flux of root-derived CO_2 through xylem (F_T)

We calculated F_T as the product of sap flux and dissolved CO_2 concentration in the xylem. Sap flux was measured using constant heat Granier-type thermal dissipation probes with thermocouples at 15 and 70 mm depth with 80 mm vertical separation (TDP-80; Dynamax Inc., Houston, TX, USA). Zero flow was calculated daily as the mean difference between vertical thermocouple pairs between 03:00 and 05:00 h. We developed and applied our own calibration parameters to the sap flux values. Xylem [CO_2] was measured in gaseous phase by inserting an NDIR sensor and thermocouple into xylem tissue at 15 cm above ground level. Gaseous [CO_2] was corrected for temperature and barometric pressure. Concentrations of dissolved CO_2 in xylem were determined by measuring the temperature and pH of xylem sap and applying Henry's Law (McGuire & Teskey, 2002). Xylem sap was obtained from stem increment cores (Suunto Oy, Vantaa, Finland) by inserting cored tissue segments into a vice and applying pressure to express sap which was collected with a Pasteur pipette and immediately transferred to a solid-state pH microsensor connected to a pH meter (Red-Line Standard Sensor, Argus meter; Sentron Europe BV, Roden, the Netherlands). The mean pH for the observation period was 7.2 ± 0.2. We accounted for the amount of dissolved CO_2 originating in the soil solution that was transported via water uptake by assuming that the soil solution [CO_2] was at equilibrium with that of the soil. We determined the soil [CO_2] throughout the rooting zone from [CO_2] measurements used to calculate soil CO_2 efflux as described in soil CO_2 efflux methods. The amount of dissolved CO_2 originating in the soil solution was calculated as the product of mean soil [CO_2] at the three depths and sap flux.

Statistical analyses

We compared daily totals of F_T and soil CO_2 efflux, as well as estimated belowground autotrophic and heterotrophic respiration, using repeated measures ANOVA. The pathway of belowground CO_2 efflux ($n = 2$) and day of measurement ($n = 7$) were treated as fixed factors whereas the individual tree ($n = 4$) was treated as the random subject factor. We used

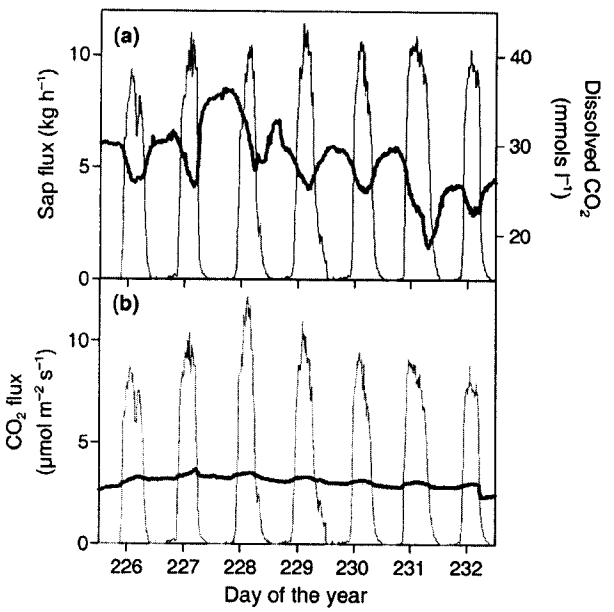

Fig. 1 (a) Diel pattern of mean total tree sap flux (thin line) and mean concentration of dissolved CO_2 in xylem sap (thick line) measured at the base of the trees over the 7-d observation period ($n = 4$). (b) Mean diel pattern of the flux of CO_2 transported from the root system through the xylem into the stem (thin line) and soil CO_2 efflux (thick line) over the 7-d observation period ($n = 4$).

Akaike's information criterion with a second order correction for small sample sizes to determine the covariance structure that best estimated the correlation among individual trees over time. The analyses were performed using the mixed models procedure of SAS (Version 9.1.3; SAS Inc., Cary, NC, USA) using an alpha of 0.05. All values presented in the text are mean ± SE.

Results

Sap flux showed a typical diel pattern during the measurement period (Fig. 1a). We also observed a diel pattern in the concentration of dissolved CO_2 in xylem sap. The pattern appeared to be partially related to the rate of sap flow. The concentration of dissolved CO_2 reached a maximum before the start of transpiration. As sap flow began, the concentration of dissolved CO_2 declined and reached a minimum when sap flow reached a maximum.

The internal flux of CO_2 from roots through xylem is a function of dissolved CO_2 concentration of xylem sap and quantity of transported water. The diel pattern of F_T mimicked that of sap flow, but the magnitude also depended on dissolved CO_2 concentration (Fig. 1b). F_T ranged from 0 μmol m^{-2} s^{-1} at night to a maximum of 12.0 μmol m^{-2} s^{-1} at peak sap flux. Soil CO_2 efflux was relatively stable during the measurement period, ranging from 2.4 to 3.5 μmol m^{-2} s^{-1} (Fig. 1b). During most daylight hours, F_T exceeded soil CO_2 efflux, but at night the pattern was reversed.

Table 1 Mean (± SE) daily total flux of CO_2 transported from the root system through the xylem into the stem (Xylem) and soil CO_2 efflux (Soil)

Flux pathway	CO_2 flux (mol m^{-2} d^{-1})
Xylem	0.26 ± 0.02
Soil	0.27 ± 0.01

Table 2 Estimated mean daily total of CO_2 derived from belowground autotrophic or heterotrophic respiration

Respiratory source	Respiration (mol CO_2 m^{-2} d^{-1})
Autotrophic	0.38 ± 0.03
Heterotrophic	0.14 ± 0.01

Mean cumulative daily F_T was not statistically different from mean cumulative soil CO_2 efflux (Table 1; $P = 0.6695$). Thus, the quantity of CO_2 moving internally from roots through xylem was equivalent to the total amount of CO_2 diffusing from the soil to the atmosphere from autotrophic and heterotrophic sources combined. Total belowground CO_2 flux (F_T + soil CO_2 efflux) was 0.53 mol CO_2 m^{-2} d^{-1}, with 47% attributed to F_T and 53% to soil CO_2 efflux (Table 1). Based on soil [CO_2] and sap flux, we calculated that 0.017 mol CO_2 m^{-2} d^{-1} entered the tree via water uptake, representing only 7.8% of F_T and 3.2% of total belowground CO_2 flux. Thus, 92% of the dissolved CO_2 in F_T was derived from autotrophic respiration.

We used our measurements of F_T and soil CO_2 efflux to estimate autotrophic and heterotrophic contributions to total belowground CO_2 flux by assuming that 50% of soil CO_2 efflux is derived from autotrophic respiration (Hanson *et al.*, 2000). It follows that the CO_2 dissolved in the soil solution that enters the tree via water uptake would also be derived from equal proportions of autotrophic and heterotrophic respiration. Under these assumptions, the autotrophic component (72%) of total belowground CO_2 flux was more than twice as large as the heterotrophic component (28%) (Table 2; $P = 0.0012$).

Discussion

Our study provides empirical evidence demonstrating an alternative flux pathway for root-respired CO_2 that can be of greater magnitude than the soil pathway. We estimated that twice the amount of root-respired CO_2 entered the xylem stream as diffused into the soil environment. We also observed substantial increases in dissolved xylem CO_2 at night, suggesting that roots, like tree stems (Teskey *et al.*, 2008), may possess substantial barriers to outward diffusion which allow CO_2 to concentrate in xylem sap. Some of the xylem-transported CO_2 can be used as a substrate for corticular (Cernusak & Marshall, 2000; Pfanz & Aschan, 2001; Aschan & Pfanz, 2003) and leaf (Zelawski *et al.*, 1970; Stringer & Kimmerer, 1993) carbon fixation. The large flux of CO_2 from roots through xylem may be part of a recycling mechanism whereby trees retain respired CO_2 for assimilation to compensate for respiratory losses.

We speculate that CO_2 recycling capabilities in trees may be a vestigial carbon-concentrating mechanism, perhaps with evolutionary origins in aquatic plants. A portion of root-respired, and sediment-derived, CO_2 accumulates in roots of many aquatic and wetland plant species (Brix, 1990; Constable *et al.*, 1992; Li & Jones, 1995; Colmer, 2003). Stems of such plants generally contain arenchyma and CO_2 is transported from root to shoot via diffusion where it becomes a substantial component of carbon balance (Wetzel & Grace, 1983). In fact, some plants entirely lacking stomata acquire all of their photosynthetic substrate from root-respired and sediment-derived CO_2 (Keeley *et al.*, 1984).

The magnitude of belowground autotrophic respiration in forest ecosystems may considerably exceed that of heterotrophic respiration when the amount of CO_2 transported via the xylem stream is considered in addition to autotrophic contributions to soil CO_2 efflux. Our assumption that autotrophic activity accounted for 50% of soil CO_2 efflux suggests that total belowground autotrophic respiration may have been nearly three times larger than heterotrophic respiration when F_T is considered. If only 10% of soil CO_2 efflux resulted from autotrophic activity, the addition of F_T suggests nearly equivalent autotrophic and heterotrophic contributions. If the autotrophic contribution to soil CO_2 efflux was 90%, the addition of F_T would not substantially change the relative autotrophic and heterotrophic contributions. Regardless of the relative contributions, the absolute magnitude of autotrophic respiration was twice as large when F_T is considered. Consequently, belowground autotrophic respiration may consume substantially more carbohydrates in mitochondrial respiration than previously recognized. Because a portion of CO_2 transported from the root system via xylem sap diffuses through the stem into the atmosphere, it also indicates that the carbohydrate cost of stem respiration has been substantially overestimated. These results further suggest that belowground autotrophic respiration may exceed aboveground (leaf and woody tissue) respiration.

Terrestrial ecosystem models estimate how forests will respond to climate change and influence the global carbon cycle, but their utility is ultimately limited by our understanding of processes regulating carbon allocation in forest ecosystems. Belowground carbon allocation represents a sizeable portion of forest gross primary production, yet our understanding of controlling processes remains poor (Giardina *et al.*, 2005; Litton *et al.*, 2007). Our results indicate that belowground carbon allocation may be much larger than previously estimated. For example, belowground carbon allocation has been estimated with mass balance equations under the fundamental assumption that annual changes in soil carbon storage are small relative

to annual soil carbon inputs and losses (Raich & Nadelhoffer, 1989; Giardina & Ryan, 2002). Soil CO_2 efflux comprises the largest flux within the mass balance equation and thus strongly controls the resulting estimates of belowground carbon allocation (Raich & Nadelhoffer, 1989; Giardina & Ryan, 2002). In our study, soil CO_2 efflux only represented about half of the total belowground CO_2 flux. Recent evidence of increased root allocation in forest tree species grown under elevated CO_2 (Norby *et al.*, 2004; Huang *et al.*, 2007) suggests that F_T may increase in importance as atmospheric CO_2 increases toward predicted concentrations over the next century.

These findings have important implications for how we currently understand physiological functioning of trees, carbon cycling in forests and global carbon budgets. We suggest that F_T should be measured concurrently with soil CO_2 efflux to understand the metabolism of root systems and the carbon economy of trees and forests. We acknowledge that our findings are limited to four individual trees of the same species during a single week. To more fully understand this process, it must be examined under changing environmental conditions in a wide variety of tree functional groups and ecosystems at annual time-scales. For example, F_T will be negligible when deciduous species enter dormancy. Therefore, there is a need to understand the relative importance of F_T in deciduous and evergreen species. The magnitude of F_T may decline with reduced rates of transpiration, so it will also be important to understand how factors affecting transpiration such as drought, vapor pressure deficit and soil water holding capacity influence F_T. Factors affecting the rate of diffusion of CO_2 through the soil, including soil texture, water content and $[CO_2]$, may also play a part in determining the relative importance of F_T. The influence of F_T on annual budgets of total belowground CO_2 efflux may also be related to growing season length. Equatorial systems represent an obvious hotspot for further research into F_T as the annual importance may diminish as seasonality becomes more pronounced at increasing latitudes. Still, annual magnitudes of F_T may be quite large in temperate systems because growing season respiration rates greatly exceed those of the dormant season. Clearly, further research is required to improve our understanding of the importance of F_T for terrestrial carbon cycling and the controlling environmental factors.

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References

Aschan G, Pfanz H. 2003. Nonfoliar photosynthesis – a strategy of additional carbon acquisition. *Flora* 198: 81–97.

Baldocchi D. 2008. Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany* 56: 1–26.

Brix H. 1990. Uptake and photosynthetic utilization of sediment-derived carbon by *Phragmites-australis* (Cav.) Trin. ex Steudel. *Aquatic Botany* 38: 377–389.

Cavaleri MA, Oberbauer SF, Ryan MG. 2008. Foliar and ecosystem respiration in an old-growth tropical rain forest. *Plant, Cell & Environment* 31: 473–483.

Cernusak LA, Marshall JD. 2000. Photosynthetic refixation in branches of western white pine. *Functional Ecology* 14: 300–311.

Colmer TD. 2003. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant, Cell & Environment* 26: 17–36.

Constable JVH, Grace JB, Longstreth DJ. 1992. High-carbon dioxide concentrations in aerenchyma of *Typha latifolia*. *American Journal of Botany* 79: 415–418.

Davidson EA, Richardson AD, Savage KE, Hollinger DY. 2006. A distinct seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest. *Global Change Biology* 12: 230–239.

Ford CR, Wurzburger N, Hendrick RL, Teskey RO. 2007. Soil DIC uptake and fixation in *Pinus taeda* seedlings and its C contribution to plant tissues and ectomycorrhizal fungi. *Tree Physiology* 27: 375–383.

Geider RJ, Delucia EH, Falkowski PG, Finzi AC, Grime JP, Grace J, Kana TM, La Roche J, Long SP, Osborne BA *et al.* 2001. Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. *Global Change Biology* 7: 849–882.

Giardina CP, Coleman MD, Binkley D, Hancock JE, King JS, Lilleskov EA, Loya WM, Pregitzer KS, Ryan MG, Trettin CC. 2005. The response of belowground carbon allocation in forests to global change. In: Binkley D, Menyailo O, eds. *Tree species effects on soils: implications for global change*. Dordrecht, the Netherlands: Springer, 119–154.

Giardina CP, Ryan MG. 2002. Total belowground carbon allocation in a fast-growing eucalyptus plantation estimated using a carbon balance approach. *Ecosystems* 5: 487–499.

Goulden ML, Munger JW, Fan SM, Daube BC, Wofsy SC. 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biology* 2: 169–182.

Hanson PJ, Edwards NT, Garten CT, Andrews JA. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48: 115–146.

Huang JG, Bergeron Y, Denneler B, Berninger F, Tardif J. 2007. Response of forest trees to increased atmospheric CO_2. *Critical Reviews in Plant Sciences* 26: 265–283.

IPCC. 2007. *IPCC WGI Fourth Assessment Report. Climate Change 2007: the physical science basis*. Geneva, Switzerland: Intergovernmental Panel on Climate Change.

Janssens IA, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grunwald T *et al.* 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology* 7: 269–278.

Jobbágy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* **10**: 423–436.

Keeley JE, Osmond CB, Raven JA. 1984. *Stylites*, a vascular land plant without stomata absorbs CO_2 via its roots. *Nature* **310**: 694–695.

Kuzyakov Y. 2006. Sources of CO_2 efflux from soil and review of partitioning methods. *Soil Biology & Biochemistry* **38**: 425–448.

Law BE, Falge E, Gu L, Baldocchi DD, Bakwin P, Berbigier P, Davis K, Dolman AJ, Falk M, Fuentes JD *et al.* 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology* **97**: 97–120.

Law BE, Ryan MG, Anthoni PM. 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biology* **5**: 169–182.

Li MR, Jones MB. 1995. CO_2 and O_2 transport in the aerenchyma of *Cyperus papyrus* L. *Aquatic Botany* **52**: 93–106.

Litton CM, Raich JW, Ryan MG. 2007. Carbon allocation in forest ecosystems. *Global Change Biology* **13**: 2089–2109.

Luyssaert S, Inglima I, Jung M, Richardson AD, Reichsteins M, Papale D, Piao SL, Schulzes ED, Wingate L, Matteucci G *et al.* 2007. CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology* **13**: 2509–2537.

McGuire MA, Teskey RO. 2002. Microelectrode technique for *in situ* measurement of carbon dioxide concentrations in xylem sap of trees. *Tree Physiology* **22**: 807–811.

Moore DJP, Gonzalez-Meler MA, Taneva L, Pippen JS, Kim HS, DeLucia EH. 2008. The effect of carbon dioxide enrichment on apparent stem respiration from *Pinus taeda* L. is confounded by high levels of soil carbon dioxide. *Oecologia* **158**: 1–10.

Norby RJ, Ledford J, Reilly CD, Miller NE, O'Neill EG. 2004. Fine-root production dominates response of a deciduous forest to atmospheric CO_2 enrichment. *Proceedings of the National Academy of Sciences, USA* **101**: 9689–9693.

Pfanz H, Aschan G. 2001. The existence of bark and stem photosynthesis in woody plants and its significance for the overall carbon gain. An eco-physiological and ecological approach. *Progress in Botany* **62**: 477–510.

Prentice IC, Farquhar GD, Fasham MJR, Goulden ML, Heimann M, Jaramillo VJ, Kheshgi HS, Le Quereе C, Scholes RJ, Wallace DWR. 2001. The carbon cycle and atmospheric carbon dioxide. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA, eds. *Climate Change 2001: the scientific basis: contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press, 183–239.

Raich JW, Nadelhoffer KJ. 1989. Belowground carbon allocation in forest ecosystems – global trends. *Ecology* **70**: 1346–1354.

Rogers VA. 1990. *Soil survey of savannah river plant area, parts of Aiken, Barnwell, and Allendale Counties, South Carolina*. Washington, DC, USA: USDA Soil Conservation Service.

Stringer JW, Kimmerer TW. 1993. Refixation of xylem sap CO_2 in *Populus deltoids*. *Physiologia Plantarum* **89**: 243–251.

Tang JW, Baldocchi DD, Qi Y, Xu LK. 2003. Assessing soil CO_2 efflux using continuous measurements of CO_2 profiles in soils with small solid-state sensors. *Agricultural and Forest Meteorology* **118**: 207–220.

Tang JW, Bolstad PV, Desai AR, Martin JG, Cook BD, Davis KJ, Carey EV. 2008. Ecosystem respiration and its components in an old-growth forest in the great lakes region of the United States. *Agricultural and Forest Meteorology* **148**: 171–185.

Teskey RO, McGuire MA. 2007. Measurement of stem respiration of sycamore (*Platanus occidentalis* L.) trees involves internal and external fluxes of CO_2 and possible transport of CO_2 from roots. *Plant, Cell & Environment* **30**: 570–579.

Teskey RO, Saveyn A, Steppe K, McGuire MA. 2008. Origin, fate and significance of CO_2 in tree stems. *New Phytologist* **177**: 17–32.

Trumbore S. 2006. Carbon respired by terrestrial ecosystems – recent progress and challenges. *Global Change Biology* **12**: 141–153.

Wetzel RG, Grace JB. 1983. Aquatic plant communities. In: Lemon ER, ed. *CO_2 and plants – the response of plants to rising levels of atmospheric carbon dioxide*. Boulder, CO, USA: Westview Press, 223–280.

Zelawski W, Riech FP, Stanley RG. 1970. Assimilation and release of internal carbon dioxide by woody plant shoots. *Canadian Journal of Botany* **48**: 1351–1354.