Is Temporal Variation of Soil Respiration Linked to the Phenology of Photosynthesis?

Eric A. Davidson and N. Michele Holbrook

Abstract If recent photosynthate is the primary source of carbohydrates for root respiration and possibly for much of soil microbial respiration through root exudates, then temporal variation in soil respiration (SR) may be linked to plant phenological patterns at hourly to seasonal time scales. Here we review the evidence for this linkage and identify the research needs for improving our understanding of the physiological and ecological linkages between photosynthesis and respiration in ecosystems. The linkage is clearest at the season time scale, where the importance of substrate supply to belowground carbon processes follows a seasonal pattern in temperate and boreal ecosystems. Correlations of SR with canopy light, temperature, and vapor pressure deficit also suggest a link between root respiration and canopy photosynthesis on times scales of a few hours to about 3 weeks. Temporal correlations between photosynthetic activity and SR make it tempting to view patterns in SR as the direct outcome of variation in substrate delivery rates, but these analyses provide only inferential evidence of a physiological linkage. Isotopic labeling studies indicate that the lag between fixation by foliage and respiration of the label in the rhizosphere is usually on the order of a day or more in forest ecosystems. More rapid transmission of pressure/concentration waves through the phloem is theoretically possible, and current understanding of phloem physiology and the regulation of growth suggests that the linkage between canopy and root processes is based on more than the mass transport of substrate from sources to sinks. However, improved understanding of assimilate transport and partitioning is needed before variation in SR patterns can be linked mechanistically to the physiology and the phenology of the plants fueling belowground metabolism.

E.A. Davidson (✉)
The Woods Hole Research Center, Woods Hole, MA, USA
e-mail: edavidson@whrc.org

N.M. Holbrook
Department of Organismic and Evolutionary Biology,
Harvard University, Cambridge, MA, USA
e-mail: holbrook@fas.harvard.edu

A. Noormets (ed.), *Phenology of Ecosystem Processes*,

DOI 10.1007/978-1-4419-0026-5_8,

1 Introduction

The efflux of CO_2 from the soil surface, known as soil respiration (SR), is primarily a combination of microbial respiration and root respiration, mediated by gas transport within the soil. Hence, SR is affected by a suite of environmental factors that control the biological metabolism of a variety of soil-dwelling organisms and that control physical processes of gaseous diffusion and convection. Among these environmental factors, temperature is the most obvious and the one most commonly correlated with SR (Davidson and Janssens 2006; Hibbard et al. 2005). However, the role of substrate supply to roots and to soil microbes is gaining increasing recognition as an important determinant of variation in SR (Davidson et al. 2006a; Ryan and Law 2005). Rapid changes in substrate availability that accompany wetting of dry soil (Birch 1958; Borken et al. 2003; Bottner 1985; Kieft et al. 1987), girdling of trees (Högberg et al. 2001), and shading and clipping of grasses (Craine et al. 1999; Wan and Luo 2003) clearly affect soil respiration independently of temperature at time scales from hours to months. The ultimate source of carbohydrates for root and soil microbial respiration is primarily plant photosynthate, which suggests a potentially important link between plant phenology and SR, as mediated by the supply of photosynthate for respiration of roots, mycorrhizae, and heterotrophs utilizing root exudates within the rhizosphere. The objectives of this chapter are to review the evidence for this linkage from diel to seasonal scales and to identify the research needs for improving our understanding of these physiological and ecological linkages between photosynthesis and respiration in ecosystems.

2 The Evidence for Linkages Between Plant Phenology and Soil Respiration

Variation among ecosystems in annual rates of SR is due primarily to differences in site productivity (Hibbard et al. 2005; Janssens et al. 2001; Reichstein et al. 2003; Ryan and Law 2005; Sampson et al. 2007). Leaf area index (LAI), used as a crude surrogate for site productivity, has been correlated with annual respiration among forest and grassland study sites, presumably because the greater the site LAI, the more substrates were produced for respiration (Hibbard et al. 2005; Reichstein et al. 2003).

2.1 Seasonal Variation

Seasonal variation in SR in temperate and boreal ecosystems usually covaries with temperature, but substrate supply also varies seasonally, and its effects may be confounded, in part, by variation attributed to temperature variation. Variation in

SR due to seasonal patterns of plant phenology can, in turn, affect the apparent temperature sensitivities of respiration. Curiel-Yuste et al. (2004) argued that greater apparent Q_{10} values (the factor by which observed respiration increases for each 10-degree increase in temperature) for SR measured across seasons in a Belgian hardwood forest compared to an adjacent conifer forest reflected greater seasonality of belowground C allocation by the hardwoods. When Q_{10}'s were calculated for only 2-month intervals, soil respiration in the hardwood and conifer stands had nearly identical temperature sensitivities, indicating similar responses to diel and synoptic scale variation of temperature. Only when winter and summer observations were combined, did the hardwoods appear to have greater temperature sensitivity for soil respiration, presumably due to the greater seasonality of photosynthesis and subsequent supply of substrate belowground in the hardwood stand. Hence, the greater seasonal Q_{10} in the hardwood site may have been mostly a phenological response rather than different temperature sensitivity, *per se*.

Seasonal variation in C allocation can affect both maintenance respiration and growth of roots, mycorrhizae, and rhizosphere microorganisms. When a pulse of root growth occurs in the spring, then the amount of respiring tissue increases simultaneously with temperature-dependent increases in specific root respiration (i.e., CO_2 production per gram of tissue or per unit of enzyme capacity). In this case, the apparent Q_{10} of soil respiration (i.e., observed CO_2 efflux as a function of temperature) across seasons reflects a combination of seasonal variation in root growth and the temperature responses of specific root respiration rates, both of which correlate positively with temperature. Hanson et al. (2003) reported a lower Q_{10} for soil respiration in an oak forest in Tennessee, USA, when dates associated with root growth (observed in minirhizotrons) were excluded. Similarly, in trenched plots without roots and control plots with roots in temperate forests, Boone et al. (1998) reported Q_{10}'s of 2.5 and 3.5, respectively, and Epron et al. (1999) reported 2.3 and 3.9, respectively. Boone et al. (1998) calculated a Q_{10} of 4.6 for the root respiration inferred from the difference between the control and trenched plots. However, as Boone et al. (1998) also pointed out, this root respiration Q_{10} includes the effects of both seasonal changes in root biomass (i.e., root growth) and direct responses of existing root biomass to changing temperature.

Root elongation has been shown to peak several weeks after foliar expansion in the hardwood forest of Oak Ridge and at several other northern mixed forests (Joslin et al. 2001), thus suggesting that the autotrophic component of soil respiration probably lags aboveground autotrophic respiration in the spring. Cardon et al. (2002) found that SR was inversely correlated with shoot flush in potted oaks, which is consistent with allocation to roots after leaves have expanded and become mature, reflecting a higher prioritization within the plant for springtime shoot growth compared to root growth (Marcelis 1996; Wardlaw 1990). Contrary to earlier studies that related root elongation only to temperature, Joslin et al. (2001) found that a phenology index and soil water content were the most important correlates with root elongation, and that temperature was not significant. There is good evidence that at least some of the root elongation in these tree species is fueled by recently fixed photosynthate (Gaudinski et al. 2001; Joslin et al. 2001).

The carbon source for root respiration in a boreal forest has been shown to come from stored carbohydrates in early spring and from more recent photosynthate in late spring (Cisneros-Dozal et al. 2006). Thus, in addition to the temperature responses of extant enzymes, it is also important to understand phenological changes in the abundance of reactive enzymes present in temporally varying stocks of roots, fungi, leaves, and non-structural carbohydrate.

The components of total ecosystem respiration do not respond to temperature and phenology in complete synchrony. At both Howland (Maine) and Harvard (Massachusetts) forests, aboveground respiration accelerates first in the early spring, coincident with bud break and foliar expansion, which results in soil respiration being only 30–40% of total ecosystem respiration in the early spring Fig. 1. Soil respiration then gradually increases to about 60–70% of total ecosystem respiration during the summer and 90–100% in the autumn and winter.

This asynchrony of aboveground and belowground phenological patterns may contribute to seasonal hysteresis of apparent temperature sensitivities. Seasonal hysteresis of apparent Q_{10}'s for total ecosystem respiration and soil respiration at a spruce-dominated study site in Howland, Maine, USA, provides an example of multiple processes interacting to produce highly variable apparent temperature sensitivities. Soil respiration always exhibited a higher Q_{10} in the spring than in the

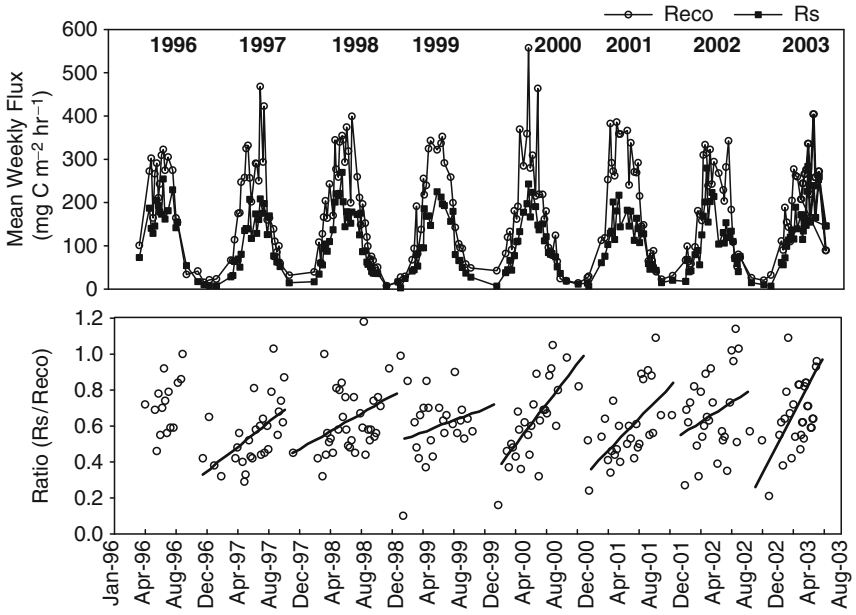

Fig. 1 Total ecosystem respiration (Reco), soil respiration (Rs) at the Howland Forest, Maine, USA (*upper panel*); and the ratio of soil respiration:ecosystem respiration (*lower panel*). Note that the ratio falls below 0.4 every spring and increases to near 1.0 by the autumn. From Davidson et al. (2006b).

Table 1 Ratio of ecosystem respiration (ER) and soil respiration (SR) at 15°C to respiration at 5°C (Q_{10}) at the Howland forest, Maine, USA (from Davidson et al. 2006b)

Season	Flux	1997	1998	1999	2000	2001	2002	All years
Spring	ER	2.8	2.7	3.2	3.9	3.5	2.9	3.1
	SR	4.5	3.0	3.3	5.0	3.9	3.2	3.5
Fall	ER	4.1	3.5	3.2	4.1	3.1	3.1	3.4
	SR	2.8	2.6	3.2	3.0	2.3	1.9	2.5

autumn Table 1, perhaps because of springtime root growth, as discussed above. Soils warm from the top downward in the spring, and they cool from the top downward in the autumn, so hysteresis based on temperature measured at a fixed depth could also be influenced by varying soil depths of CO_2 production (Reichstein et al. 2005). During the spring, soil respiration Q_{10} was always higher than total ecosystem respiration Q_{10}, but the reverse was observed in the autumn (Table 1). In the autumn, both nighttime respiration and daytime net ecosystem exchange of CO_2 dropped sharply immediately after the first frost and remained low for the rest of the autumn and winter (Hollinger et al. 1999). If both photosynthesis and respiration drop sharply in response to the first autumn frost, the apparent temperature sensitivity of ecosystem respiration may be elevated in the autumn because of this physiological threshold effect that induces relatively abrupt dormancy.

2.2 Synoptic Scale Variation

Synoptic scale variation in weather patterns are known to affect canopy processes, but the link to belowground processes is only beginning to be recognized. Variation in rates of soil respiration have been correlated with air temperature and vapor pressure deficit (VPD) that occurred 1–4 days earlier in a Norway spruce stand (Ekblad et al. 2005) and in a mixed coniferous boreal forest stand (Ekblad and Högberg 2001), inferring a lag time of several days between the effect of weather on photosynthesis and the subsequent effect on root respiration and exudation. Analysis of $^{13}CO_2$ in soil respiration in the Norway spruce sites also revealed a 3–7 day lag between drought-induced fractionation of photosynthate and the isotopic signal of the soil CO_2 efflux (Ekblad et al. 2005). *In situ* radiocarbon labeling in a black spruce forest of Manitoba, Canada, revealed that the peak of the ^{14}C appearance in roots and in rhizosphere respiration occurred 4 days after labeling (Carbone et al. 2007), which is consistent with previously inferred lags from ^{13}C analyses in boreal forests (Eklad et al. 2005), but longer than the 2-day lag measured with ^{14}C in young poplar trees (Horwath et al. 1994). A lag of 5–10 days was observed between variation in VPD and the ^{13}C signature of total ecosystem respiration in several temperate forests of Oregon, USA (Bowling et al. 2002). A 4–5 day lag was observed between ^{13}C in total ecosystem respiration and the ratio of VPD to photosynthetically active radiation in a deciduous forest in Germany (Knohl et al. 2005).

Using automated soil CO_2 profile measurements and a diffusivity model to estimate SR, Baldocchi et al. (2006) found significant correlations between SR and eddy-covariance-based measurements of canopy photosynthesis in an oak savanna, with lags of zero and 14 days. They interpreted the zero lag to demonstrate diel effects and the 14-day lag to be the impact of a similar 14-day lag observed between canopy photosynthesis and VPD. Gaumont-Guay et al. (2008) found a 2–3 week lag between mean daytime photosynthesis measured by eddy covariance and mean nighttime root respiration calculated from root exclusion plots in a boreal black spruce forest. Hence the evidence from treed ecosystems indicates a lag of several days to 3 weeks between canopy processes and SR.

Using radiocarbon labeling in California grasses and shrubs, Carbone and Trumbore (2007) reported that about half of the label transported belowground was respired within 24 h of labeling, about another quarter during the next 5 days, and the remainder during the subsequent month. Wan and Luo (2003) demonstrated that clipping of a tallgrass prairie significantly reduced soil respiration within 2 days. Although the number of studies remains small, it is tempting to draw the conclusion that, as might be expected, the lag time between canopy processes and SR is shorter for grasses and shrubs than for trees. This response presumably reflects the time required for substrate to travel from the canopy to the roots. In any case, evidence is accumulating that meteorological conditions affecting photosynthesis in a variety of ecosystems may also affect SR with lag times of 1 day to 2 weeks.

2.3 Diel Variation

Diel variation in SR has been correlated to diel variation in soil temperature (Janssens and Pilegaard 2003; Xu and Ye 2001), but the diel pattern of SR sometimes lags that of soil temperature. Hence, several studies have been designed to decompose the diel variation of SR into two components – one that is sensitive to soil temperature and one that is not. Tang et al. (2005) showed that SR under oak canopies appears to be decoupled from soil temperature, whereas SR in grassy areas showed the expected correlation with soil temperature. The SR under oak canopies was, instead, correlated with photosynthesis, but with a lag of 7–12 h. The authors inferred that the lack of correlation with soil temperature under the tree canopy and the lagged correlation with photosynthesis was the result of oak rhizosphere respiration that was linked to lagged diel patterns of substrate availability. Gaumont-Guay et al. (2008) showed a similar 12-h lag between photosynthesis and root respiration in a boreal black spruce forest. Liu et al. (2006) also demonstrated that part of the diel cycle of SR in a mixed deciduous forest of Tennessee, USA, was independent of soil temperature and was correlated with photosynthetically active radiation (PAR) with a 1-h lag. No correlation with PAR was observed during the dormant season, so this diel response appears to interact with the phenology of photosynthesis.

Several oral presentations at a workshop on automated measurements of soil respiration, held in Durham, New Hampshire, USA, in September 2007, presented similar

observations of diel variation in SR being out of phase with soil temperature and related in some way to light, temperature, or VPD of the aboveground environment (Carbone and Vargas 2007). Although this body of work is not yet available in the literature, it appears that the evidence for an effect of supply of recent photosynthate on diel patterns of SR is rapidly growing. However, the published data are too few to begin investigation of what controls variation in the observed lag times among sites or the relative importance of temperature-dependent and substrate-dependent processes. Moreover, correlations between components of SR diel patterns with canopy light, temperature, and VPD provide only inferential evidence of a physiological linkage. Care must be taken to rule out confounding factors, such as diel variation in wind speed, which could change soil CO_2 concentration profiles and fluxes. At present, we cannot explain the physiological mechanism of how canopy processes can affect rhizosphere respiration within hours.

3 Physiological Links of Phloem Transport

Although isotopic labeling studies indicate that the lag between fixation by foliage and respiration of the label in the rhizosphere is usually on the order of a day or more (Carbone and Trumbore 2007; Carbone et al. 2007; Ekblad et al. 2005; Horwath et al. 1994; Högberg et al. 2008), more rapid transmission of pressure/concentration waves through the phloem, which could provide roots with information on shoot level processes, is theoretically possible (Thompson and Holbrook, 2004). Because root respiration and microbial respiration of root exudates comprise a large fraction of total SR, substrate supply to roots is increasingly recognized as an important controlling factor (Davidson et al. 2006a; Ryan and Law 2005), but we know little about controls on phloem transport to roots and communication between canopy and root processes. In this section, we explore the physiological basis for transport of substrate and signals between the canopy and roots, nearly all of which comes from the study of relatively small, non-woody plants.

What is the nature of the linkage between shoot activity and root growth? Temporal correlations between photosynthetic activity and SR make it tempting to view patterns in SR as the direct outcome of variation in substrate delivery rates. Indeed, the lag times are in approximate agreement with our best understanding of phloem transport rates (Fisher 2002), and because much of the organic substrates for SR are carried there via the phloem, it is hard to imagine how phloem transport could not, at some level, provide some degree of control. Nevertheless, the literature examining what is often referred to as "sink strength," which describes the ability of growing regions to acquire or compete for phloem-transported materials, makes it clear that treating the phloem as nothing more than a conveyor belt is overly simplistic, with the opportunities for physiological control over the distribution of photoassimilates occurring at multiple levels (Fisher 2002). In addition to failing to take into account the active role played by sink tissues, this perspective ignores the buffering capacity of the phloem itself resulting from the leakage and retrieval of solutes along the transport pathway (Thorpe et al. 2005).

A major paradox in understanding the coordination of above and belowground processes is that although increased shoot activity appears to lead to increased root activity (e.g., Muller et al. 1998), there is little evidence that the growth of roots or other sinks is dictated by substrate availability (Farrar 1996; Pritchard et al. 2005). Manipulating substrate availability in barley by removing part of the root system or exogenous sugar application had no effect on growth or respiration within an hour (Bingham and Farrar 1988; Farrar and Minchin 1991). However, excised roots responded immediately (Williams and Farrar 1990), suggesting that if root growth was substrate limited, then increasing substrate availability should have elicited a response. Manipulations of pH to increase elongation rates in maize roots had no effect on either turgor or osmotic pressure (Winch and Pritchard 1999), indicating that solute delivery must have also increased to maintain turgor and demonstrating a close relationship between solute import and extension growth. Of course, it is possible to create a situation in which growth is substrate limited. Extension growth in *Arabidopsis* roots grown on agar at low light responded to exogenous sugars (Freixes et al. 2002). However, when the leaves were provided with adequate light levels, root extension rates were insensitive to the presence of sugars in the media. The take-home message from these studies is that the unloading of solutes from the phloem and the growth that they support are highly coordinated. Treatments that speed up or retard elongation do so without significantly perturbing turgor or osmotic pressures, indicating substantial homeostasis of water relations within the growing zone (Pritchard et al. 2005).

The fact that root growth is not necessarily the passive outcome of mass transport through the phloem does not mean that belowground activity is uncoupled from aboveground metabolism. Indeed, the ability of sinks to control over their own activity may allow them to respond more effectively to changes in resource availability at the whole plant level. Sieve tubes experience substantial turgor pressures as a consequence of their high solute concentrations (van Bel and Hafke 2005). Although pressure drops must accompany the movement of phloem sap from source to sink regions, these are likely to be small relative to the pressure drops that exist between the phloem and surrounding tissues. Thus, the phloem can be thought of as forming a "high pressure manifold system" (Fisher 2002) in which the positional effects on phloem delivery are small relative to the control exerted by the sink tissues. In the case of developing roots, phloem unloading into the apical region of increasing relative elemental growth rate occurs via plasmodesmata (symplasmic unloading) (Oparka et al. 1994). More recent work (Pritchard et al. 2005) suggests that unloading across the plasma membrane into the cell wall (apoplasmic unloading) may dominate in more proximal regions of the root zone. Both provide opportunities for regulating solute delivery. Symplasmic unloading takes place through plasmodesmata and thus is sensitive to changes in plasmodesmatal resistance (Baluska et al. 2001; Fisher and Oparka 1996; Schulz 1995), while apoplasmic unloading rates can be modified by changes in the expression of enzymes that influence both diffusion gradients within the cell wall and the uptake of solutes into living cells (including resorption back into the phloem). The point here is that there are substantial opportunities for physiological control of unloading rates and that this may dictate rates

of solute delivery, resulting in transport that is at least as much sink-controlled as source-controlled. Because it takes time for sinks to alter their ability to utilize more photosynthate (Minchin and Lacointe 2005; Minchin et al. 1997), linkages between activities above and belowground will reflect the physiology of both sources and sinks.

There is no doubt that coordination between belowground growth and metabolism and the output and activity of aboveground meristems is critical for all plants (Bloom 2005). Coordination between shoot and root activity requires some means of communicating changes in the fortunes of one sphere to the other. The existence of many sucrose sensitive genes (e.g., Koch et al. 1996) demonstrates that, in addition to being both a product and a substrate, sucrose can have a regulatory role (Farrar 1996). From the point of view of linking above and belowground phenology, however, this distinction could be viewed as moot as both depend on mass transfer of sucrose. Vascular tissues can transport information faster than they convey materials via mass transport, both by electrical signals, thought to be important in communicating herbivore damage, and by pressure pulses that propagate at much higher speeds. Mathematical analysis of phloem transport indicates that changes in loading rates results in pressure-concentration waves that have the potential to transmit information rapidly to distant sinks (Thompson and Holbrook 2004). Although research on whether such pressure-concentration waves actually elicit changes in sink physiology is lacking, it raises the possibility of a more rapid and potentially nuanced form of communication between sources and sinks. This mathematical analysis of the potential for pressure-concentration waves within the phloem has been cited as support for a physiological basis for rapid (≤ 12 h) linkage between photosynthesis and root respiration (Gaumont-Guay et al. 2008; Tang et al. 2005), but the empirical evidence from studies of phloem physiology can neither confirm nor refute the importance of this mechanism for trees at the ecosystem scale.

4 Conclusions

At the seasonal time scale, ample evidence regarding the importance of substrate supply to belowground carbon processes suggests that the answer to the question posted in the title of the chapter must be yes, that seasonal variation of soil respiration is linked to the phenology of photosynthesis. The evidence at shorter time scales is also compelling, but less complete, and confounding factors still need to be disentangled. Studies that combine automated SR and eddy covariance measurements are producing growing evidence for a link between root respiration and canopy photosynthesis on times scales of hours to weeks, but we lack sufficient knowledge of the processes of phloem transport to explain this linkage through physiological mechanisms. It is important to underscore the tremendous knowledge gaps regarding control of assimilate partitioning and growth. Not only are the tools available for studying phloem transport limited, but most studies have been conducted on relatively small, typically agronomic, plants. Whether insights derived from such studies

apply equally well to trees and other woody species remains to be seen. Nevertheless, coordination between belowground growth and metabolism and the output and activity of aboveground meristems is critical for all plants. Current understanding of phloem physiology and the regulation of growth suggests that this linkage is based on more than the mass transport of substrates from sources to sinks. Thus, the often-observed pattern of root growth occurring only after spring shoot growth has ceased reflects a lower prioritization within the plant, rather than their distant location from the leaves. Similarly, while increases in photosynthesis typically result in increased growth rates (but not altered partitioning), these should not be interpreted as indicating a causal role for mass action. Instead, we are forced to accept a more physiological perspective on the linkage between the phenology of photosynthesis and the temporal patterns of soil respiration. While this does not provide an easy (or a single) answer to the question of the time scale at which such linkages may exist, it does offer the promise that as we understand better the nature of assimilate transport and partitioning we will be able to connect variation in SR patterns with the biology of the plants fueling belowground metabolism.

Acknowledgements This research was supported by the U.S. Department of Energy's Office of Science (BER) through Grant Nos. DE-FG02–00ER63002 and 07-DG-11242300–091 and through the Northeastern Regional Center of the National Institute for Climatic Change Research, Grant No. DE-FC02–06ER64157.

References

Baldocchi, D., Tang, J. and Xu, L. (2006) How switches and lags in biophysical regulators affect spatial-temporal variation of soil respiration in an oak-grass savanna. J. Geophys. Res. 111, 1–13.

Baluska, F., Cvrckova, F., Kendrick-Jones, J. and Volkmann, D. (2001) Sink plasmodesmata as gateways for phloem unloading. Myosin VIII and calreticulin as molecular determinants of sink strength? Plant Physiol. 126, 39–46.

Bingham, I.J. and Farrar, J.F. (1988) Regulation of respiration in roots of barley. Physiol. Plantarum 70, 491–498.

Birch, H.F. (1958) The effect of soil drying on humus decomposition and nitrogen availability. Plant Soil 10, 9–32.

Bloom, A. (2005) Coordination between roots and shoots. In: N.M. Holbrook and M.A. Zwieniecki (Eds.), Vascular Transport in Plants. Academic, New York, pp. 241–256.

Boone, R.D., Nadelhoffer, K.J., Canary, J.D. and Kaye, J.P. (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396, 570–572.

Borken, W., Davidson, E.A., Savage, K., Gaudinski, J. and Trumbore, S.E. (2003) Drying and wetting effects on carbon dioxide release from organic horizons. Soil Sci. Soc. Am. J. 67, 1888–1896.

Bottner, P. (1985) Response of microbial biomass to alternate moist and dry conditions in a soil incubated with ^{14}C- and ^{15}N-labelled plant material. Soil Biol. Biochem. 17, 329–337.

Bowling, D.R., McDowell, N.G. and Bond, B. (2002) ^{13}C content of ecosystem respiration is linded to precipitation and vapor pressure deficit. Oecologia 131, 113–124.

Carbone, M.S. and Vargas, R. (2007) Automated soil respiration measurements: new information, opportunities and challenges. New Phytol. 177, 295–297.

Carbone, M.S. and Trumbore, S.E. (2007) Contribution of new photosynthetic assimilates to respiration by perennial grasses and shrubs: residence times and allocation patterns. New Phytol. 176, 1–12.

Carbone, M.S., Czimczik, C.I., McDuffee, K.E. and Trumbore, S.E. (2007) Allocation and residence time of photosynthetic products in a boreal forest using a low-level ^{14}C pulse-chase labeling technique. Global Change Biol. 13, 466–477.

Cardon, Z.G., Czaja, A.D., Funk, J.L. and Vitt, P.L. (2002) Periodic carbon flushing to roots of *Quercus rubra* saplings affects soil respiration and rhizosphere microbial biomass. Oecologia 133, 215–223.

Cisneros-Dozal, L.M., Trumbore, S.E. and Hanson, P.J. (2006) Partitioning sources of soil-repired CO_2 and their seasonal variation using a uniqe radiocarbon tracer. Global Change Biol. 12, 194–204.

Craine, J.M., Wedin, D.A. and Chapin, F.S. (1999) Predominance of ecophysiological controls on soil CO_2 flux in a Minnesota grassland. Plant Soil 207, 77–86.

Curiel Yuste, J., Janssens, I.A., Carrara, A. and Ceulemans, R. (2004) Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. Global Change Biol. 10, 161–169.

Davidson, E.A. and Janssens, I. (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

Davidson, E.A., Janssens, I.A. and Luo, Y. (2006a) On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}. Global Change Biol. 12, 154–164.

Davidson, E.A., Richardson, A.D., Savage, K.E. and Hollinger, D.Y. (2006b) A distinct seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest. Global Change Biol. 12, 230–239.

Ekblad, A. and Hogberg, P. (2001) Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. Oecologia 127, 305–308.

Ekblad, A., Bostro, B., Holm, A. and Comstedt, D. (2005) Forest soil respiration rate and $d^{13}C$ is regulated by recent above ground weather conditions. Oecologia 143, 136–142.

Epron, D., Farque, L., Lucot, E. and Badot, P.M. (1999) Soil CO_2 efflux in a beech forest: the contribution of root respiration. Ann. Forest Sci. 56, 289–295.

Farrar, J.F. (1996) Sinks - integral parts of a whole plant. J. Exp. Bot. 47, 1273–1280.

Farrar, J.F. and Minchin, P.E.H. (1991) Carbon partitioning in split root systems of barley: relation to metabolism. J. Exp. Bot. 42, 1261–1269.

Fisher, D.B. (2002). Long-distance transport. In: B. Buchanan, W. Gruissem and R.L. Jones (Eds.), Biochemistry and Molecular Biology of Plants. Wiley, New York, pp. 730–785.

Fisher, D.B. and Oparka, K.J. (1996) Post-phloem transport: principles and problems J. Exp. Bot. 47, 1141–1154.

Freixes, S., Thibaud, M., Tardieu, F. and Muller, B. (2002) Root elongation and branching is related to local hexose concentration in Arabidopsis thaliana seedlings. Plant Cell Environ. 25, 1357–1366.

Gaudinski, J.B., Trumbore, S.E., Davidson, E.A., Cook, A.C., Markewitz, D. and Richter, D.D. (2001) The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. Oecologia 129, 420–429.

Gaumont-Guay, D., Black, T.A., Barr, A.G., Jassal, R.S. and Nesic, Z. (2008) Biophysical controls on rhizospheric and heterotrophic components of soil respiration in a boreal black spruce stand. Tree Physiol. 28, 161–171.

Hanson, P.J., O'Neill, E.G., Chambers, M.L.S., Riggs, J.S., Joslin, J.D. and Wolfe, M.H. (2003). Soil respiration and litter decomposition. In: H. P.J. and W. S.D. (Eds.), North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes Springer, New York, pp. 163–189.

Hibbard, K.A., Law, B.E., Reichstein, M. and Sulzman, J. (2005) An analysis of soil respiration across northern hemisphere temperate ecosystems. Biogeochemistry 73, 29–70.

Högberg, P., Högberg, M.N., Göttlicher, S.G., Betson, N.R., Keel, S.G., Metcalfe, D.B., Campbell, C., Schindlbacher, A., Hurry, V., Lundmark, T., Linder, S. and Näsholm, T. (2008) High

temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. New Phytol. 177, 220–228.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Lafvenius, M. and Read, D.J. (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789–792.

Hollinger, D.Y., Goltz, S.M., Davidson, E.A., Lee, J.T., Tu, K. and Valentine, H.T. (1999) Seasonal patterns and environmental control of carbon dioxide and water vapor exchange in an ecotonal boreal forest. Global Change Biol. 5, 891–902.

Horwath, W.R., Pregitzer, K.S. and Paul, E.A. (1994) ^{14}C Allocation in tree-soil systems. Tree Physiol. 14, 1163–1176.

Janssens, I.A. and Pilegaard, K. (2003) Large seasonal changes in Q_{10} of soil respiration in a beech forest. Global Change Biol. 9, 911–918.

Janssens, I.A., Lankreijer, H. and Matteucci, G. (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biol. 7, 269–278.

Joslin, J.D., Wolfe, M.H. and Hanson, P.J. (2001) Factors controlling the timing of root elongation intensity in a mature upland oak forest. Plant Soil 228, 201–212.

Kieft, T.L., Soroker, E. and Firestone, M.K. (1987) Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biol. Biochem. 19, 119–126.

Knohl, A., Werner, R.A., Brand, W.A. and Buchmann, N. (2005) Short-term variations in $\delta^{13}C$ of ecosystem respiration reveals link between assimilation and respiration in a deciduous forest. Oecologia 142, 70–82.

Koch, K., Wu, Y. and Xu, J. (1996) Sugar and metabolic regulation of genes for sucrose metabolism: potential influence of maize sucrose synthase and soluble invertase responses on carbon partitioning and sugar sensing. J. Exp. Bot. 47, 1179–1186.

Liu, Q., Edwards, N.T., Post, W.M., Gu, L., Ledford, J. and Lenhart, S. (2006) Temperature-independent diel variation in soil repiration observed from a temperate deciduous forest. Global Change Biol. 12, 2136–2145.

Marcelis, L.F.M. (1996) Sink strength as a determinant of dry matter partitioning in the whole plant. J. Exp. Bot. 47, 1281–1292.

Minchin, P.E.H. and Lacointe, A. (2005) New understanding on phloem physiology and possible consequences for modeling long-distance carbon transport. New Phytol. 166, 771–779.

Minchin, P.E.H., Thorpe, M.R., Wunsche, J., Palmer, J. and Picton, R.F. (1997) Carbon partitioning in apple trees: short and long term adaptation of fruits to change in available photosynthate. J. Exp. Bot. 48, 1401–1406.

Muller, B., Stosser, M. and Tardieu, F. (1998) Spatial distributions of tissue expansion and cell division rates are related to irradiance and to sugar content in the growing zone of maize roots. Plant Cell Environ. 21, 149–158.

Oparka, K.J., Duckett, C.M., Prior, D.A.M. and Fisher, D.B. (1994) Real-time imaging of phloem unloading in the root tip of Arabidopsis. Plant J. 6, 756–766.

Pritchard, J., Ford-Lloyd, B. and Newbury, H.J. (2005). Roots as an integrated part of the translocation pathway. In: N.M. Holbrook and M.A. Zwieniecki (Eds.), Vascular Transport in Plants. Academic, New York, pp. 157–179.

Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y., Grunzweig, J.M., Irvine, J., Joffre, R., Law, B.E., Loustau, D., Migietta, F., Oechel, W., Ourcival, J.M., Pereira, J.S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rosi, F., Tedeschi, V., Tirone, G., Xu, M. and Yakir, D. (2003) Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. Global Biogeochem. Cycles 17, 1–15.

Reichstein, M., Subke, J.-A., Angeli, A.C. and Tenhunen, J.D. (2005) Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? Global Change Biol. 11, 1754–1767.

Ryan, M.G. and Law, B.E. (2005) Interpreting, measuring, and modeling soil respiration. Biogeochemistry 73, 3–27.

Sampson, D.A., Janssens, I.A., Curiel Yuste, J. and Ceulemans, R. (2007) Basal rates of soil respiration are correlated with photosynthesis in a mixed temperater forest. Global Change Biol. 13, 2008–2017.

Schulz, A. (1995) Plasmodesmatal widening accompanies the short term increase in symplastic unloading in pea root tips under osmotic stress. Protoplasma 188, 22–37.

Tang, J., Baldocchi, D. and Xu, L. (2005) Tree photosynthesis modulates soil respiration on a diurnal time scale. Global Change Biol. 11, 1298–1304.

Thompson, M. and Holbrook, N. (2004) Scaling phloem transport: information transmission. Plant Cell Environ. 27, 509–519.

Thorpe, M., Minchin, P., Gould, N. and McQueen, J. (2005). The stem apoplast: a potential communication channel in plant growth regulation. In: N.M. Holbrook and M.A. Zwienieck (Eds.), Vascular Transport in Plants. Academic, New York, pp. 203–221.

van Bel, A.J.E. and Hafke, J.B. (2005). Physiochemical determinants of phloem transport. In: N.M. Holbrook and M.A. Zwienieck (Eds.), Vascular Transport in Plants. Academic, New York, pp. 19–44.

Wan, S. and Luo, Y. (2003) Substrate regulation of soil respiration in a tallgrass prairie: Results of a clipping and shading experiment. Global Biogeochem. Cycles 17, 1054.

Wardlaw, I.F. (1990) The control of carbon partitioning in plants. New Phytol. 116, 341–381.

Williams, J.H.H. and Farrar, J.F. (1990) Control of barley root respiration. Physiol. Plantarum 79, 259–266.

Winch, S.K. and Pritchard, J. (1999) Acid-induced wall loosening is confined to the accelerating region of the root growing zone. J. Exp. Bot. 50, 1481–1487.

Xu, M. and Ye, Q. (2001) Spatial and seasonal variations of Q_{10} determined by soil respiration measurements at a Sierra Nevadan forest. Global Biogeochem. Cycles 15, 687–696.