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# Ecosystem-level controls on root-rhizosphere respiration

Author for correspondence:
*Miquel A. Gonzalez-Meler*
*Tel: +1 312 355 3928*
*Email: mmeler@uic.edu*

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**Francesca Hopkins[1], Miquel A. Gonzalez-Meler[2], Charles E. Flower[2], Douglas J. Lynch[2], Claudia Czimczik[1], Jianwu Tang[3] and Jens-Arne Subke[4]**

[1]Department of Earth System Science, University of California, Irvine, CA 92697, USA; [2]Ecology and Evolution Group, Department of Biological Sciences, University of Illinois at Chicago, Chicago, IL 60607, USA; [3]The Ecosystems Center, Marine Biological Laboratory, 7 MBL St, Woods Hole, MA 02543, USA; [4]Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling, FK9 4LA, UK

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## Summary

Recent advances in the partitioning of autotrophic from heterotrophic respiration processes in soils in conjunction with new high temporal resolution soil respiration data sets offer insights into biotic and environmental controls of respiration. Besides temperature, many emerging controlling factors have not yet been incorporated into ecosystem-scale models. We synthesize recent research that has partitioned soil respiration into its process components to evaluate effects of nitrogen, temperature and photosynthesis on autotrophic flux from soils at the ecosystem level. Despite the widely used temperature dependence of root respiration, gross primary productivity (GPP) can explain most patterns of ecosystem root respiration (and to some extent heterotrophic respiration) at within-season time-scales. Specifically, heterotrophic respiration is influenced by a seasonally variable supply of recent photosynthetic products in the rhizosphere. The contribution of stored root carbon (C) to root respiratory fluxes also varied seasonally, partially decoupling the proportion of photosynthetic C driving root respiration. In order to reflect recent insights, new hierarchical models, which incorporate root respiration as a primary function of GPP and which respond to environmental variables by modifying C allocation belowground, are needed for better prediction of future ecosystem C sequestration.

## Introduction

The majority of the 140 Pg of carbon (C) fixed annually by terrestrial gross primary productivity (GPP) passes through soil, with 8–52% respired back to the atmosphere by the rhizosphere (Lambers *et al.*, 2008), and 23–83% of GPP ending up in plant tissue C (DeLucia *et al.*, 2007) which is ultimately returned to the atmosphere as $CO_2$ via the activity of decomposer organisms. Soil respiration is a primary process governing net C sequestration in terrestrial ecosystems (Valentini *et al.*, 2000); this soil flux is likely to change as a result of the impacts of global change factors such as nitrogen (N) deposition, warming, and rising $CO_2$ concentrations (Houghton *et al.*, 1998). Because of its importance to the global C cycle, soil respiration has been intensively studied for several decades (Luo & Zhou, 2006), yet the ability to predictively model soil respiration and its components through time and space is still elusive (Chen *et al.*, 2011; Leuzinger & Thomas, 2011).

Spatial and temporal heterogeneity of soil respiration is a major challenge to ecosystem scientists, making it difficult to interpret effects of climate variables on soil $CO_2$ efflux (Davidson & Janssens, 2006). This variability stems from the multitude of different sources and pathways for the production of $CO_2$ throughout the soil profile, each of which is controlled to a varying extent by biotic and abiotic drivers (Janssens *et al.*, 2001; Gonzalez-Meler *et al.*, 2004; Davidson & Janssens, 2006; Fig. 1). A fundamental distinction between soil $CO_2$ sources in terms of C turnover and temporal dynamics is that of $CO_2$ derived from the decomposition of organic matter by soil fauna and microbial organisms (fungi, bacteria and protozoans), from that originating from plant roots and rhizospheric organisms (including symbiotic mycorrhizal fungi). These two generic $CO_2$ sources are commonly referred to as heterotrophic and autotrophic soil $CO_2$ flux (Högberg *et al.*, 2001), with some debate about how heterotrophic organisms associated with autotrophic C supply should be categorized (Högberg *et al.*, 2006).

Autotrophic contributions represent a substantial component of seasonal soil $CO_2$ efflux (Gonzalez-Meler & Taneva, 2005), and may even represent the majority of soil respired $CO_2$ during periods

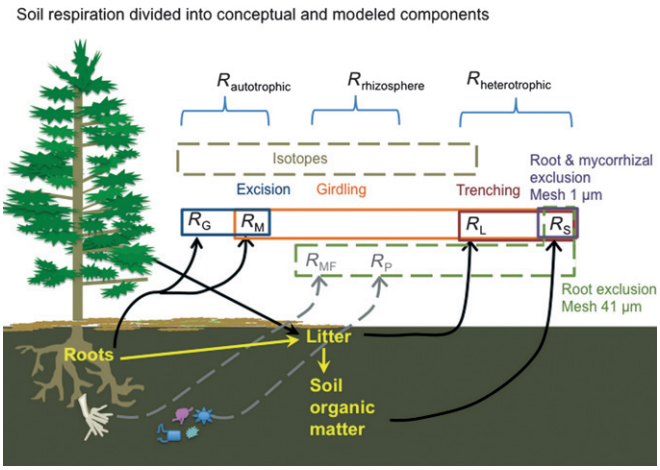


**Fig. 1** Soil respiration divided into conceptual and modeled components. Autotrophic respiration consists of growth respiration ($R_G$) and maintenance respiration ($R_M$), which are derived from new photosynthate and plant carbon (C) storage pools. Heterotrophic respiration consists of respiration from litter decomposition ($R_L$) and soil organic matter decomposition ($R_S$). It is increasingly being recognized by experimentalists that a significant portion of soil respiration is neither strictly autotrophic, as it passes through microorganisms such as mycorrhizal fungi, nor heterotrophic, as substrates are coming directly from roots (they do not pass as tissue through the litter pool to decomposers). This respiration has been termed 'rhizosphere respiration,' and is thought to include respiration of mycorrhizal fungi ($R_{MF}$) and respiration from soil decomposer organisms that is 'primed' by additions of labile substrates in root exudates ($R_P$). Rhizosphere processes are identified in gray as they are not implicitly incorporated into ecosystem-scale models. Colored boxes represent different methods of isolating different conceptual respiration fluxes. Addition of C isotope measurements to measurements of these fluxes can provide information on the source pool and/or turnover time of C and the combination of methods can theoretically resolved any source of soil $CO_2$ efflux.

of high productivity (Subke *et al.*, 2006; Gomez-Casanovas *et al.*, 2012). As the temporal dynamics of this flux component are linked to aboveground C assimilation and C transport to roots via the plants' phloem, it is not exclusively controlled by soil temperature or moisture (Högberg *et al.*, 2001; Trueman & Gonzalez-Meler, 2005). As the peak growing season generally coincides with the warmest time of year (at least in ecosystems not limited by soil moisture), high apparent responses of autotrophic soil $CO_2$ efflux with temperature may have been reported. Indeed, much of the observed variation in soil respiration, and its temperature sensitivity in particular, is probably attributable to variation in substrate availability in space and time (Davidson *et al.*, 2006; Subke & Bahn, 2010). Nevertheless, temperature is still used as the primary driver for descriptive and prognostic models of soil respiration (Davidson *et al.*, 2006 and references therein).

The availability of labile C such as from root exudation or fresh litter input sustains microbial populations capable of decomposing slower-turnover soil organic matter (SOM) (Fontaine *et al.*, 2004; Guenet *et al.*, 2012). This leads to soil C priming (or more specifically a 'rhizosphere priming effect' (RPE); Kuzyakov, 2010), which is a natural process in soils. The dynamics of RPEs are tightly linked to autotrophic C supply, but may affect older soil C pools previously assumed to be stable. Current ecosystem models do not include RPEs, and a better understanding of belowground C dynamics, including roots, rhizosphere and associated organisms, is required.

Most ecosystem-scale C cycle models include the effect of substrate supply on respiration through its relationship to GPP, either indirectly through a fixed ratio of net primary productivity (NPP) to GPP (e.g. the CASA model; Field *et al.*, 1995), or directly through allocation schemes that partition GPP to growth, storage and respiration (e.g. the Biome-BGC model; Thornton & Rosenbloom, 2005). Heterotrophic respiration is determined by litter and SOM pool sizes (which are controlled by GPP at multiple time-scales), and the effect of temperature and soil moisture on decomposition rates. Autotrophic respiration, however, is not always explicitly represented. In models based in units of NPP, autotrophic respiration is an emergent process that represents the remainder of GPP (Gifford, 2003). By contrast, models such as Biome-BGC explicitly represent autotrophic respiration as the sum of growth respiration and maintenance respiration, which in turn depend on plant C pool size and on the magnitude of GPP (Thornton & Rosenbloom, 2005; Fig. 1).

In the hierarchy of biological processes, NPP-based models were designed to represent processes at a higher level than that of physiology (Gifford, 2003); however, physiological processes may be an important part of the response of the C cycle to climate change. In particular, decades-long data sets of ecosystem respiration are increasingly being used to parameterize C cycle sensitivity to climate change (Mahecha *et al.*, 2010). Such data sets will also be an important part of validating the process and climate response in land models (Luo *et al.*, 2012). The incorporation of explicit allocation schemes, storage pools, and substrate supply as drivers of autotrophic respiration in C cycle models will probably help to explain disparities between models and data (Keenan *et al.*, 2012; Richardson *et al.*, 2013). Furthermore, the role of acclimation of soil respiration components to forcing factors is largely ignored in large-scale models (Leuzinger & Thomas, 2011).

Here we review the evidence for effects of N, temperature, and photosynthate supply (including stored C) on root respiration in order to identify their importance as drivers of autotrophic respiration for ecosystem-scale models. We place particular emphasis on photosynthetic controls on root respiration assessed using recent $^{14}C$ and $^{13}C$ data, which show patterns of stored C use in root respiration, and elaborate on a continuous $^{13}C$ whole-ecosystem tracer that gives powerful insights into effects of current photosynthesis on soil autotrophic respiration.

## Techniques to measure root respiration at the ecosystem level

Soil respiration is a combination of root respiration, microbial respiration, and possibly root-associated mycorrhizal respiration. In order to determine effects of environmental change and substrate supply on root-rhizosphere respiration alone, the components of soil respiration must be separated, and their dynamics analyzed independently (Taneva & Gonzalez-Meler, 2011). However, partitioning of soil respiration has been notoriously difficult (Hanson *et al.*, 2000; Kuzyakov & Larionova, 2005; Trumbore, 2006), and there is no ideal method to separate soil respiration into

its functional components. Current methods isolate a different set of respiration processes (Fig. 1), having corresponding strengths and weaknesses.

In root exclusion experiments (Fig. 1), a physical barrier prevents roots from entering excluded soils, and this method is widely used to obtain *in situ* measurements of root respiration by subtracting respiration from the root-free plot from respiration from the control. Trenching, soil coring, root in-growth cores, and gap analysis are common root exclusion methods. Trenching requires digging a narrow trench around an open plot (1–10 $m^2$), inserting plastic sheets to block root in-growth, and then refilling trenched area with soil to replicate original conditions (Tang *et al.*, 2005a). Soil coring consists of placing polyvinyl chloride (PVC) pipes (*c.* 10–30 cm diameter) into soils to block the in-growth of roots (Bond-Lamberty *et al.*, 2011) and can be modified through the use of mesh bags that allow mycorrhizas to grow in but exclude roots (41 μm), or exclude both mycorrhizas and roots (1 μm) (Heinemeyer *et al.*, 2007). The gap analysis method subtracts heterotrophic respiration measured in natural ecosystem gaps (no roots) from respiration measured in vegetated areas (with roots) (e.g. Tang & Baldocchi, 2005).

Drawbacks to the root exclusion method center on the assumption that heterotrophic respiration remains unchanged after elimination of root inputs (Ewel *et al.*,1987; Bowden *et al.*, 1993; Epron *et al.*, 1999; Tang *et al.*, 2005a). This assumption has been challenged (Trueman & Gonzalez-Meler, 2005), as root exclusion methods alter substrate supply to microbes by decreasing labile root inputs to microbial activity and initial increases in substrate supply from dead roots (Subke *et al.*, 2006). Root exclusion zones also block root water uptake, resulting in higher soil water contents compared with 'control' areas, thereby confounding differences in microbial activity between experimental treatments (Heinemeyer *et al.*, 2012).

Root excision measures root respiration directly as excised intact roots are directly picked from soils, and their $CO_2$ efflux measured on a per unit mass basis (Burton *et al.*, 2008; Fig. 1). Flux rates show considerable variation with this method, with significant impacts of $CO_2$ concentration in measuring cuvettes, time elapsed between root excision and $CO_2$ flux measurement, and whether roots were separated under 'wet' or 'dry' conditions (Subke *et al.*, 2006). Cuvettes attached to excavated surface roots without excision may circumvent some of these problems (Chen *et al.*, 2010). Root biomass is needed to calculate autotrophic respiration from soils but the few roots sampled for respiration may not be representative of the entire fine-root community.

Tree girdling can estimate root respiration from soils without disturbance of the physical integrity of roots (Högberg *et al.*, 2001; Fig. 1). Tree girdling terminates the supply of recent photosynthate to roots through the phloem while not disturbing water flow through the xylem (Högberg *et al.*, 2001, 2009; Subke *et al.*, 2011; Levy-Varon *et al.*, 2012; Liu *et al.*, 2012). This technique has problems similar to those of trenching methods; however, root respiration and root-rhizosphere effects could be maintained by carbohydrates stored in roots, and root water uptake is maintained in treatment plots.

Isotopic methods are often noninvasive and require either the use of natural C tracers or the experimental addition of isotopically altered $CO_2$ ($^{13}CO_2$ or $^{14}CO_2$) to separate root respiration from microbial respiration. Isotopic labeling experiments include free air $CO_2$ enrichment (FACE), where $CO_2$ added to the ecosystem is fossil-derived (Pataki *et al.*, 2003; Taneva *et al.*, 2006), and pulse-chase experiments, where a one-time supply of isotopically distinct $CO_2$ is tracked to belowground tissues and soil efflux (Brüggemann *et al.*, 2011). Tracer addition techniques measure the oxidation of labeled C by roots but not necessarily total autotrophic flux because contributions of unlabeled stored C to root respiration are not accounted for (Fig. 1). Low-level $^{14}C$ pulse labeling studies can potentially circumvent this problem on subannual time-scales by comparing $^{14}CO_2$ values before and after the pulse (Carbone & Trumbore, 2007).

In certain conditions, natural differences in both $^{13}C$ (Hanson *et al.*, 2000; Kuzyakov & Larionova, 2005; Gomez-Casanovas *et al.*, 2012) and $^{14}C$ (Borken *et al.*, 2006; Czimczik *et al.*, 2006; Schuur & Trumbore, 2006) can be utilized to partition autotrophic and heterotrophic components. Natural abundance $^{14}C$ measurements allow the determination of the mean age of C pools and fluxes (Trumbore, 2000). This technique takes advantage of a spike in atmospheric $^{14}C$ content resulting from nuclear weapons testing in the early 1960s and subsequent decline following the banning of testing in 1963 (Levin *et al.*, 2010). The current annual change in atmospheric $\Delta^{14}C$ values (5‰; Levin *et al.*, 2010) is similar to or greater than the precision at which $\Delta^{14}C$ measurements can currently be made (2–5‰; Southon & Santos, 2004) and therefore useful to separate current-year C from stored C fueling root respiration.

Some problems are associated with isotope analyses. Analyses of $^{13}C$ are sensitive to post-photosynthetic fractionation of respiratory substrates which may challenge the quantification of C sources and their ages to root respiration (Lynch *et al.*, 2013). In the field, isotopic fractionation during diffusive non-steady-state gas transport may induce errors in quantification of plant respired $CO_2$ from soils (Risk *et al.*, 2012). For $^{14}C$ analyses, cost and sampling size are major drawbacks. Also, the time resolution at natural abundance levels can encompass 1–3 yr (error of $^{14}C$ measurement with accelerator mass spectrometry (AMS)). In addition, isotopic techniques may be unable to distinguish between decomposition originating from the turnover of very short-lived roots (heterotrophic) and maintenance respiration from roots (autotrophic), as these two sources are composed of C of similar ages (Fig. 1).

These methods remain imperfect approximations of the continuum of physiological processes that govern soil respiration and the conceptual components represented in process models (Fig. 1). Nevertheless, their application has begun to disentangle the often opposing effects of global change factors on autotrophic and heterotrophic respiration. Future progress will be made by further studies that combinethese partitioning techniques (which can potentially identify multiple sources of soil respired $CO_2$) in global change manipulation experiments to quantify these fluxes and their biotic and abiotic controls.

## Nitrogen effects on root respiration

At the tissue level, specific respiration rates are often proportional to N content (Ryan, 1991, 1995; Reich *et al.*, 1996; Ryan *et al.*, 1996; Gonzalez-Meler *et al.*, 2004), as N constitutes most of the

maintenance costs of tissues (Bouma *et al.*, 1994). This is the case for fine roots, as increased N content correlates well with increased specific respiration rates (Burton *et al.*, 2002; Chen *et al.*, 2010; Jia *et al.*, 2010; Wang *et al.*, 2010). Therefore, root N content has been used as a proxy to estimate total fine-root respiration (Jia *et al.*, 2011). However, scaling this relationship to ecosystems is problematic, as fine roots have many-fold differences in N content within a diameter class (Iversen, 2010), affecting the function and respiratory activity of individual roots (Lambers *et al.*, 1996; Pregitzer *et al.*, 1998; Scheurwater *et al.*, 1998; Burton *et al.*, 2000; Chapin *et al.*, 2002), and hence preventing the use of root N to estimate total root respiration in some ecosystems (Vose & Ryan, 2002). Despite these problems, the relationship between N content and respiration of fine roots has become important in C-cycling modeling to estimate autotrophic respiration from soils (Thornton & Rosenbloom, 2005).

Despite the clear relationship between N content and specific respiration rates of roots, the direction and magnitude of the response of autotrophic respiration to increased N availability (e.g. N deposition) are less certain (Smithwick *et al.*, 2013). Increased nutrient availability has been shown to both increase (Ryan *et al.*, 1996; Pregitzer *et al.*, 2000; Gough *et al.*, 2004; Jia *et al.*, 2011) and reduce root respiration (Zogg *et al.*, 1996; Maier & Kress, 2000; Janssens *et al.*, 2010; Burton *et al.*, 2012). These contrasting results are probably attributable to changes in standing crop root biomass which have been documented in $CO_2$ and N fertilization experiments (Matamala & Schlesinger, 2000; Iversen, 2010; Burton *et al.*, 2012). Therefore, N-driven changes in root biomass may impact autotrophic respiration from soils to a greater extent than intrinsic variations in N content (Burton *et al.*, 2012).

N deposition changes the way in which roots interact with other soil organisms, by reducing C allocation to mycorrhizas (Högberg *et al.*, 2010; Vallack *et al.*, 2012), although changes in mycorrhizal respiration may depend on the quantity of N applied (Hasselquist *et al.*, 2012). Additionally, N deposition may reduce root exudation rates and associated microbial activity (Phillips *et al.*, 2011), which may be the cause of observed changes in heterotrophic respiration rates with added N (Neff *et al.*, 2002; Nowinski *et al.*, 2009). Future research efforts are needed to examine how N-induced changes in C allocation belowground will affect not just autotrophic respiration, but associated heterotrophic processes, including the RPE. Although changes in root biomass (and thus autotrophic flux from soils) in response to global change factors are beginning to be documented, these effects are seldom included in ecosystem models, which largely predict changes in the autotrophic component of soil respiration to passively respond to changes in soil temperature.

## Temperature effects on the autotrophic and heterotrophic soil C flux

There is considerable concern that an increase in mean air temperatures globally will erode C stored in soils (Davidson & Janssens, 2006; Hartley & Ineson, 2008; Bond-Lamberty & Thomson, 2010; Hopkins *et al.*, 2012) and significant research effort has been directed at distinguishing between temperature responses of labile and stable SOM which have different importance to soil C storage (Taneva *et al.*, 2006; Hartley & Ineson, 2008; Karhu *et al.*, 2010; Taneva & Gonzalez-Meler, 2011). Predicting the rate and amount of soil C vulnerable to loss with warming has posed an important challenge for empirical studies and model predictions (Schlesinger & Andrews, 2000; Fang *et al.*, 2005; Reichstein *et al.*, 2005; Davidson & Janssens, 2006; Friedlingstein *et al.*, 2006; Hartley & Ineson, 2008). Many studies rely on the temperature sensitivity ($Q_{10}$) of bulk soil respiration and its components, yet these estimates are confounded by the temporally and environmentally varying role of the different processes controlling soil flux. Attempts to predict the fate of soil C stocks simply based on changes in temperature alone are clearly unrealistic, as shifts in climate will have profound impacts on vegetation composition and activity. Consequential changes in plant C assimilation, belowground C allocation, root growth, rooting depth, and mycorrhizal associations are all likely to impact soil C inputs and mineralization rates (Fontaine *et al.*, 2007; Milcu *et al.*, 2011), changing soil C stores at long time-scales. To gain a better understanding of the temperature sensitivity of these distinct processes, it is paramount to separately assess the independent temperature responses of the autotrophic and heterotrophic components of soil respiration (Moyano *et al.*, 2008; Gomez-Casanovas *et al.*, 2012; Fig. 1).

In the absence of acclimation, kinetic theory predicts that the metabolic processes governing root and microbial respiration respond positively to warming. However, if we further partition root respiration into growth respiration and maintenance respiration (Ryan, 1990) and add respiratory acclimation, the temperature sensitivity of autotrophic respiration from soils becomes more likely to vary with season. Because root growth may vary across species and seasons, growth respiration is probably driven by phenology and fuelled by the availability of C transported from recent photosynthate or from stored C pools. Maintenance respiration of roots (which includes nutrient uptake costs) is primarily driven by tissue N concentration and influenced by temperature. Therefore, nutrient and energy demands largely determine rates of growth and maintenance respiration, suggesting that root respiration will rapidly acclimate to temperature (Atkin *et al.*, 2008). However, root respiration may appear correlated with temperature in model assessments because peak GPP and plant phenology are often correlated with temperature in most ecosystems (Subke & Bahn, 2010).

Indeed, increasing evidence that photosynthesis influences soil respiration rates (Craine *et al.*, 1999; Högberg *et al.*, 2001; Janssens *et al.*, 2001; Irvine *et al.*, 2005; Tang *et al.*, 2005b; Gomez-Casanovas *et al.*, 2012; Savage *et al.*, 2013) confirms the importance of current photosynthetic substrate for soil respiration. In addition, diel and seasonal effects on substrate supply belowground are a major confounding factor for assessments of the temperature sensitivity of soil respiration, explaining the existence of hysteresis patterns common in soil respiration data (Davidson *et al.*, 2006) and the wide range of belowground autotrophic $Q_{10}$ values reported in the literature (Boone *et al.*, 1998; Lavigne *et al.*, 2003; Tang *et al.*, 2005a; Hartley *et al.*, 2007; Burton *et al.*, 2008). Ecosystem-scale studies are lacking, but a grassland study showed

that GPP and soil moisture interactions were the major drivers for the soil autotrophic flux at multiple time-scales, whereas GPP and temperature interactions explained variations in the heterotrophic component of soil respiration (Gomez-Casanovas *et al.*, 2012). In fact, a recent meta-analysis (using 84 manipulation studies) suggests that soil respiration may be more sensitive to changes in precipitation than to changes in temperature (Wu *et al.*, 2011). Consequently, the apparent empirical relationship between temperature and soil respiration data sets may simply be the result of temperature fluctuations co-occurring with variations in GPP on diel and seasonal time-scales influencing at least the root-rhizosphere component of soil respiration.

Recent results indicate that the RPE leads to an apparent increase in the temperature sensitivity of heterotrophic respiration (Zhu & Cheng, 2011), and the stability of supposedly recalcitrant organic matter depends strongly on how accessible it is to decomposing organisms (Dungait *et al.*, 2012), rather than on changes in temperature *per se.* The confounding phenomena of the RPE implicitly recognize the connection of plant root activity with the activity of soil heterotrophs which may affect SOM mineralization. In fact, photosynthate supply may exert a strong control on both autotrophic and heterotrophic respiration (Bahn *et al.*, 2009; Taneva & Gonzalez-Meler, 2011; Gomez-Casanovas *et al.*, 2012), highlighting the intermediate area between strictly autotrophic and heterotrophic processes, such as photosynthate-derived, substrate-supply-driven respiration by mycorrhizal associates (Drigo *et al.*, 2010). The emerging paradigm for heterotrophic respiration is that substrate supply (GPP) influences not only the component of respiration most closely associated with the rhizosphere (Phillips *et al.*, 2011) but also the overall heterotrophic component of soil respiration after some time lag (Gomez-Casanovas *et al.*, 2012).

For the purpose of prognostic modeling, therefore, $Q_{10}$ and temperature dependences of soil respiration and its flux components are not meaningful proxies, as the magnitude of autotroph-derived soil $CO_2$ efflux is determined by the amount of C assimilated by plants and subsequent allocation to roots (Subke & Bahn, 2010). In order to model this particular flux component, it would be necessary to provide estimates of the assimilation and allocation patterns of vegetation under globally changed conditions, including overall warmer temperatures, changes in precipitation, higher $CO_2$ concentrations, and (regionally) altered light conditions. A better process understanding of the availability of photosynthetic products (including reserves) at diurnal and seasonal time-scales (Lloyd & Taylor, 1994; Högberg *et al.*, 2001; Tang *et al.*, 2005b; Davidson *et al.*, 2006; Taneva & Gonzalez-Meler, 2011) as a predictor of autotrophic respiration rates (and accounting for acclimation and adaptation of root respiration to soil thermal changes; Rachmilevitch *et al.*, 2007; Atkin *et al.*, 2008) provides a more meaningful basis for a realistic projection of ecosystem responses to environmental change. Combinations of soil warming and air warming experiments provide an opportunity to tease apart the confounding influence of temperature on photosynthesis and autotrophic respiration from soils. Soil warming would initially (before soil nutrient availability is significantly changed by warming) illustrate the effects of temperature on soil processes without the similar temperature effect on GPP (other than natural variation), and therefore direct effects of temperature on root respiration could be untangled from natural variation in air temperature influencing GPP. Recent advances have been made using time-scale analysis of high-frequency soil respiration data sets to relate temporal patterns of soil respiration to biophysical drivers (Vargas *et al.*, 2011); however, the most progress will be made by combining multiple measurement techniques (including partitioning techniques reviewed here) and manipulations (soil and air warming combinations) with process-based models (including photosynthesis, C allocation, and plant functional type) to link to the ecosystem scale.

## $^{14}C$ and $^{13}C$ measurements of root respiration to infer contributions of stored C

Forest trees appear to use stored carbohydrates that are several years old and would buffer changes in GPP or belowground C allocation over days or seasons. Combined with manipulative experiments, $^{14}C$ approaches have the potential to inform studies about the use of stored C in ecosystem metabolism and its role in the resistance of forests to stress, disturbance or responses to climate change. Here, we review $^{14}C$ and some $^{13}C$ evidence highlighting the use of stored carbohydrates in forests during the growing season, among growing seasons and over successional stages.

### Seasonal variability

Data from temperate deciduous and coniferous forest in the northeastern USA (Borken *et al.*, 2006; S. Trumbore, unpublished) suggest a decline in the mean C age of root respiration ($\Delta\Delta^{14}C$, the difference in $\Delta^{14}C$ between a sample and the atmosphere; Trumbore, 2006) between June and September (Fig. 2). In a *Quercus* spp. dominated woodland, Cisneros-Dozal (2005) observed a decline in the $\Delta^{14}C$-$CO_2$ emitted by excised roots ($\Delta^{14}C_{root\ respiration}$) throughout the growing season (May to July, and March to May). Analysis of the $^{14}C$ isotopic composition of starch pools extracted from live roots at this oak site suggested that stored C contributed 70% (before leaf-out) to < 10% (August)

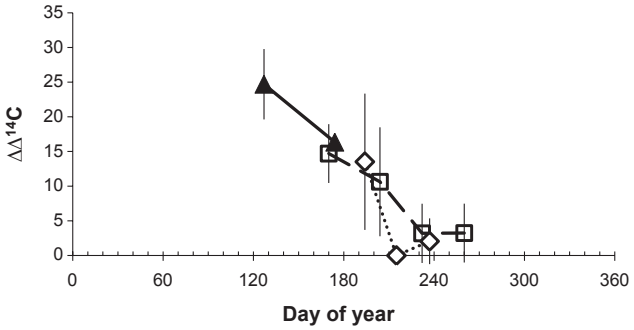


**Fig. 2** The $\Delta\Delta^{14}C$ of root respiration over the growing season for Howland forest (91% conifer, 8% hardwood (solid triangles)) and Harvard forest (mixed site 86% hardwood, 14% conifer (open squares); hemlock (*Tsuga canadensis*) roots only (open diamonds)). $\Delta\Delta^{14}C$, which gives an estimate of C age, is calculated as the difference between $\Delta^{14}C$ of root respiration and the $\Delta^{14}C$ of the atmosphere in the year of sampling. The error bars are the standard deviation of the mean of replicate samples, or the propagated error of the $\Delta\Delta^{14}C$ calculation, taking the larger value.

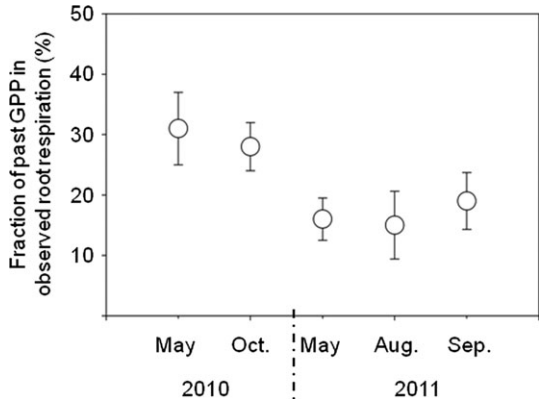


**Fig. 3** Fraction of stored carbon (C) from past gross primary productivity (GPP) contributing to root respiration at a free air $CO_2$ enrichment (FACE) site in a *Liquidambar styraciflua* plantation at Oak Ridge, TN, USA. Storage C was determined using an isotope mixing model taking advantage of the cessation of a long-term ecosystem $^{13}C$ isotopic tracer (1998–2009) that was incorporated during $CO_2$ fumigation. Results demonstrate that C stored during fumigation was utilized for root respiration in 2010 (storage C that is at least 1 yr old) and in 2011 (storage C that is at least 2 yr old). Data were extracted and redrawn from Lynch *et al.* (2013) with the authors' permission.

of the total root-respired $CO_2$ (Cisneros-Dozal, 2005). In a temperate *Liquidambar styraciflua* plantation, Lynch *et al.* (2013) found that carbohydrates stored from GPP in a given year can substantially fuel root respiration for at least two subsequent years (Fig. 3). These results indicate that stored carbohydrates can be mobilized under different scenarios, particularly under conditions of low GPP.

### Interannual variability

Stored carbohydrates are used by roots to balance energy demands during periods of low GPP (e.g. prior to leaf expansion), in response to stressful conditions (e.g. drought, high vapor deficit and/or high temperature), or when C allocation belowground is limited. Czimczik *et al.* (2006) found a greater use of stored C in a dry and warm year, compared with the following normal year, where root respired C had a $\Delta^{14}C$ value consistent with the current atmosphere. Schuur & Trumbore (2006) also found a small difference in $\Delta^{14}C$ (*c.* 2 yr) in respiration of *Picea mariana* roots between two consecutive sampling years. The age of stored C can be multiple years old (Figs 2–4), so increasing storage reserves during years of high productivity can ameliorate current photosynthetic supply shortages during years when conditions are not favorable.

**Stand age** Forest productivity declines with stand age, possibly as a result of increases in respiration costs over constant GPP (DeLucia *et al.*, 2007; Goulden *et al.*, 2011), suggesting that the respiratory demand for stored carbohydrates may be higher as forest stands age. There is some evidence that stand age may affect the $\Delta^{14}C$ value of root respired $CO_2$. For instance, *P. mariana* (black spruce) trees at least 40 yr old were respiring stored C up to 6 yr old, but young *P. mariana* trees from adjacent sites involved almost no stored carbohydrates during the normal respiration of roots (Czimczik *et al.*, 2006).

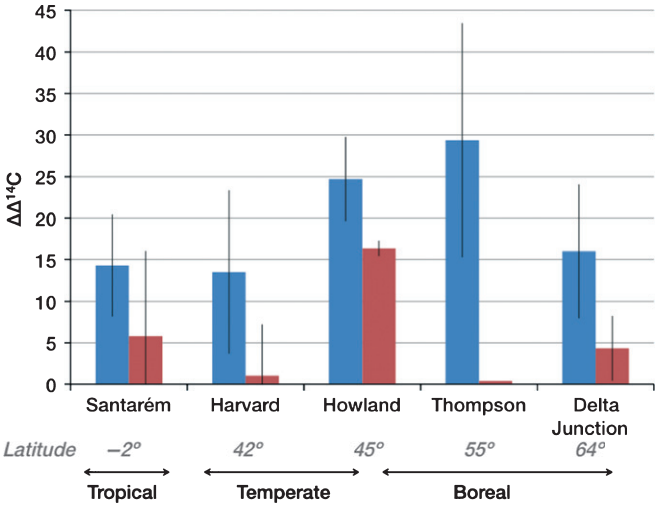


**Fig. 4** Minimum and maximum $\Delta\Delta^{14}C$ for available measurements at one tropical, two temperate, and two boreal forest sites. Sites are: Harvard Forest (Borken *et al.*, 2006); Thompson (Czimczik *et al.*, 2006); Delta Junction (Schuur & Trumbore, 2006); and Santarém (Trumbore *et al.*, 2006). Mean C age is quantified by $\Delta\Delta^{14}C$ (the difference between $\Delta^{14}C$ of root respiration and the $\Delta^{14}C$ of the atmosphere in the year of sampling). The error bars are the standard deviation of the mean of replicate samples.

Seasonal, ontogenic or environmental conditions affect the amount of stored carbohydrates used to support autotrophic respiration from soils. Therefore, the demand for stored carbohydrates will increase as growing season length shortens with latitude. A synthesis of current $^{14}C$ data provides some indication of a latitudinal trend in minimum and maximum $\Delta\Delta^{14}C$ (Fig. 4). Specifically, at the tropical site, where there is very little seasonality, there is a small difference between the minimum and maximum $\Delta\Delta^{14}C$ in root respiration values. Maximum $\Delta\Delta^{14}C$ appears to increase with latitude, suggesting a larger role for stored C pools at higher latitudes, which experience greater seasonality and more temperature variations affecting GPP. By contrast, there is no regular trend in minimum $\Delta\Delta^{14}C$, suggesting a period when surplus photosynthate is available, and is used exclusively in root respiration and allocated to storage for use in subsequent years.

Radiocarbon evidence indicates the ability of plants to draw on carbohydrate reserves to support root respiration when energy demand by the root system surpasses the substrate availability supplied by current photosynthesis. An important emerging outcome from these isotope approaches is that stored carbohydrates buffer the variability of current photosynthate supply to roots during ontogeny, phenology or environmental conditions that lead to low GPP, suggesting that root respiration may be limited by substrate availability. Therefore, current photosynthesis may play a more important role in regulating autotrophic respiration from soils than temperature (Street *et al.*, 2011; Gomez-Casanovas *et al.*, 2012; Subke *et al.*, 2012).

## Current photosynthate supply effects on root respiration: the Duke FACE case study

Carbon isotope tracers and pulse-chase experiments have been used across a wide range of vegetation types to investigate the way in

which C assimilated by plants is exchanged with the atmosphere and the soil biota (Taneva *et al.*, 2006; Bowling *et al.*, 2008; Subke *et al.*, 2012; Figs 2, 3). The speed of transfer between photosynthesis and soil efflux differs between vegetation types, with belowground transfer reported in the range of hours to days (Högberg *et al.*, 2001; Trueman & Gonzalez-Meler, 2005; Carbone & Trumbore, 2007; Bahn *et al.*, 2009; Mencuccini & Holtta, 2010) to months and years for more stable soil pools (Taneva *et al.*, 2006). There are further reported differences between species, probably linked to phloem anatomy, assimilation rates or life history (Dannoura *et al.*, 2011). In addition, whole-plant or ecosystem-level isotopic experiments can help unravel the transfer of assimilated C to heterotrophic microbes in the soil. These experiments have shown that root-associated mycorrhizal fungal species have high uptake rates of plant assimilated C and contribute greatly to soil respiration (Subke *et al.*, 2012). Pulse labeling experiments have enabled isotope-specific model descriptions (Ohlsson, 2011) to estimate patterns of C allocation, C use efficiency (CUE) or mobilization of stored C for root respiration (Bahn *et al.*, 2009; Street *et al.*, 2011; Subke *et al.*, 2012). These experiments indicate that photosynthesis has a substantial effect on root respiration, with stored carbohydrates buffering respiratory demand for photosynthate when assimilation rates are not sufficient (Figs 2–4).

At the Duke FACE experiment, a *Pinus taeda* plantation was exposed to elevated $CO_2$ starting in 1996 using a constant isotopically depleted source of $^{13}CO_2$ (see Supporting Information Notes S1; Figs S1–S4). The C turnover rates of leaves and soil pools at the site are relatively slow and in the range of 3–20+ yr (Schlesinger & Lichter, 2001; Matamala *et al.*, 2003; Taneva *et al.*, 2006; Feng *et al.*, 2010). In addition, the continuous isotope label has been used to separate the autotrophic from the heterotrophic components of soil respiration (Andrews *et al.*, 1999; Luo *et al.*, 2001a; Moore *et al.*, 2008; Taneva & Gonzalez-Meler, 2011; see Table S1). This plethora of data along with the extensive ecosystem fluxes and biomass pools measured at the site (DeLucia *et al.*, 1999; Matamala & Schlesinger, 2000; Luo *et al.*, 2001b; Hui & Luo, 2004; Taneva *et al.*, 2006; Table S2; Fig. S5) offer a unique opportunity to investigate the effects of GPP on root respiration. This is particularly true during the first year of the experiment, when the newly labeled treatment C was marginally incorporated into litter and soil pools (Table 1, Fig. 5).

In the first year of fumigation, GPP increased by 27% in forests grown at elevated $CO_2$ (Table 1). Although trees exposed to elevated $CO_2$ conditions allocated more C belowground in absolute terms than those exposed to ambient $CO_2$, trees in both treatments invested roughly 40% of GPP to belowground tissues and root-rhizosphere respiration and maintained similar values for CUE (i.e. NPP-to-GPP ratio; Table 1). As a result, increases in belowground autotrophic respiration in plants grown at elevated $CO_2$ appeared to be proportional to both increases in GPP and increases in root biomass. These results are consistent with successive observations made at the site, where root respiration had a clear diel and seasonal pattern not solely driven by temperature and moisture variations (Taneva & Gonzalez-Meler, 2011). Further evidence that photosynthesis may exert a larger leverage on root respiration than soil moisture or temperature has recently been obtained in grasslands (Gomez-Casanovas *et al.*, 2012) and this has also been suggested in other ecosystems (Street *et al.*, 2011; Subke *et al.*, 2012).

The isotope mixing models used here identify the amount of recently assimilated C respired from roots during the first year of

**Table 1** Carbon partitioning to above- and belowground components during the first year of fumigation (1997) in a pine forest plantation exposed to ambient and elevated $CO_2$ at the Duke free air $CO_2$ enrichment (FACE) study

| | Ambient | Elevated | Elevated/ ambient |
|---|---|---|---|
| Gross primary production | 1277 | 1624 | 1.27 |
| Total aboveground allocation (including coarse roots) | 768 | 941 | 1.22 |
| Aboveground respiration | 335 | 391 | 1.17 |
| Aboveground biomass | 433 | 549 | 1.27 |
| Total belowground allocation | 509 | 683 | 1.34 |
| Belowground biomass | 105 | 150 | 1.42 |
| Belowground respiration | 403 | 533 | 1.32 |
| Carbon use efficiency | 0.42 | 0.43 | 1.02 |

Units are in g C $m^{-2}$ and are the average of three replicated rings. Data were extracted from Andrews *et al.* (1999), DeLucia *et al.* (1999), Matamala & Schlesinger (2000), Luo *et al.* (2001a,b), Hamilton *et al.* (2002), Matamala *et al.* (2003) and Taneva *et al.* (2006).

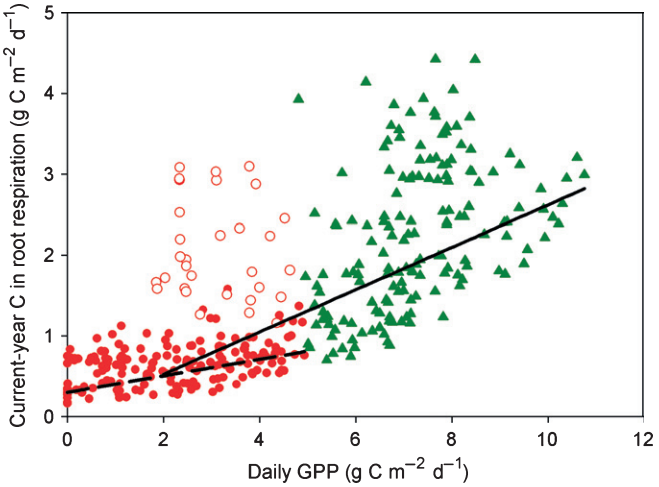


**Fig. 5** The relationship between daily gross primary productivity (GPP) and daily respiration of labeled new photosynthetic carbon (C) by root-rhizosphere respiration during the first year of fumigation (1997) in a *Pinus taeda* forest plantation exposed to elevated $CO_2$ at the Duke free air $CO_2$ enrichment (FACE) study. Each point represents a 24-h mean of respiration and GPP. A k-means clustering analysis was performed and data were separated into clusters, which segregated by seasonal changes in GPP (Supporting Information Table S4). Nongrowing season, closed circles; growing season with low GPP, open circles; growing season, triangles. A third cluster (open squares), imposed ad hoc, revealed anomalies that occurred during the growing season under conditions with high autotrophic respiration from soils and comparatively low GPP, probably because of overcast days during the growing season, and where C storage could have buffered low GPP. The fit of the piece-wise linear model is $R^2 = 0.51$. Soil respiration and isotope data were obtained from Andrews *et al.* (1999), Hui & Luo (2004) and Taneva *et al.* (2006) and GPP from Luo *et al.* (2001b), and calculations were performed as described in Notes S1.

$CO_2$ fumigation (1997) at Duke FACE (Fig. 5, following Andrews *et al.*, 1999 and Taneva *et al.*, 2006; Table S1). As a result of the contribution of stored C (e.g. Bahn *et al.*, 2009; Gaudinski *et al.*, 2009; Lynch *et al.*, 2013; Figs 2–4), total root respiration is probably underestimated, as storage C would have the pretreatment isotopic signal. Nevertheless, we used these data to further investigate the relationships between photosynthesis and the use of current-year fixed C in root-rhizosphere respiration at the ecosystem level (Fig. 5). A nonhierarchical k-means cluster analysis (Sugar & James, 2003) identified two distinct clusters of respiration rate which was determined by seasonal GPP (Figs 5, S6–S8; Table S4). Thus, during periods of high GPP, root respiration is also high, correlating with high demands for whole-plant water and nutrients (Janssens *et al.*, 2001; Notes S1; Tables S2, S3). These results also suggest that root respiration can respond to shifts in GPP at daily time-scales, indicating a rapid response of root activity to environmental variables, changes in plant demands and/or C availability. Furthermore, a piece-wise linear model indicates that GPP can explain ~51% of the variance in use of current-year C for root respiration (Fig. 5). While GPP approaches zero for several days during the year, an apparent basal maintenance rate of respiration of $0.3\,g\,C\,m^{-2}$ represents a minimum substrate contribution to root respiration. Total root respiration was probably supported by storage C during the low GPP periods, as suggested above (Fig. 2; Lynch *et al.*, 2013; Gough *et al.*, 2009). These results suggest that models should consider a hierarchical approach to parameterize root respiration, which responds directly to environmental drivers such as soil temperature and moisture but also responds rapidly to changes in photosynthesis.

## Synthesis and goals for future research

Methods to separate *in situ* the autotrophic from the heterotrophic components of soil respiration have biases that have weakened the formulation of clear biotic and abiotic controls on soil fluxes (Fig. 1). Among all the methods currently used, pulse-chase isotope methods and natural abundance $^{13}C$ and $^{14}C$ methods show the most promise in unraveling ecosystem controls on soil respiration and its components, particularly when used in combination with other approaches (Table 2). These methods are revealing the importance of GPP and stored C as factors that drive root respiration at the ecosystem level. However, there is still much to be done to fully document patterns of photosynthate use by roots and their variation in time and space through phenology, ontogeny, succession, and climate regimes (Table 2). Comparisons made across successional stages within an ecosystem and between ecosystems or biomes are desperately needed (e.g. comparisons oftropical versus temperate versus boreal forests, grassland types, and managed ecosystems). Separating autotrophic from heterotrophic soil flux in combination with long-term monitoring or manipulation experiments (e.g. flux sites and National Ecological Observatory Network) would be highly beneficial to identifying the role of biotic and abiotic influences on each of the soil components over time under a variety of ecosystems and environmental conditions. A summary of these challenges and potential approaches is given in Table 2.

Current models can simulate GPP relationships with autotrophic soil flux, yet the parameterization of models to capture the apparent physiological temperature response of ecosystems is an emerging challenge for both the modeling and flux communities. Both communities need to adopt a hierarchical approach to advance our process understanding at small scales (Table 2) to increasingly larger temporal and spatial scales and ultimately earth system models (ESMs; Table 2). The predictive ability of ESMs will be improved by explicit representations of root respiration that are primarily driven by GPP and plant C allocation which are currently absent.

Future progress will be made by using the continuous ecosystem $CO_2$ flux data that exist for a wide range of natural, semi-natural and agricultural ecosystems, across most biomes (Luyssaert *et al.*, 2007), to ask questions that either challenge or improve model representations of the temporal controls on photosynthesis and C storage (Table 2). A recent example of this approach identified the importance of endogenous circadian rhythms as a control on GPP (Resco de Dios *et al.*, 2012). Incorporating this process into ESMs could help drive diel photosynthesis patterns without invoking a simple temperature response function. Similarly, the importance of photosynthesis-driven priming processes to heterotrophic SOM turnover should be tested using model–data fusion approaches. Key challenges for future research are the detection of RPE in more heterogeneous ecosystems than those used in manipulative experiments or tightly controlled field and laboratory studies. This will provide boundaries to the temperature sensitivity of belowground C fluxes and hierarchical responses of GPP to air temperature, as well as root respiratory responses to GPP acclimation and soil temperature change (Table 2). Soil versus air warming experiments may offer an opportunity to disentangle the effects of temperature–GPP interactions on soil fluxes (Table 2), but most current warming experiments have been focused on total soil respiration instead of, more importantly, the autotrophic and heterotrophic components.

It is important to note that increases in respiratory demand by belowground tissues can also influence total belowground C allocation. Because plants allocate C to maximize photosynthesis and growth (Thornley, 1969; Thornley & Cannell, 2000), plants will partition GPP into tissues that would minimize negative impacts of limiting resources on growth (DeLucia *et al.*, 2007; Litton *et al.*, 2007; Franklin *et al.*, 2012). Increased allocation of C to belowground tissues in response to nutrient and water demands (Gower *et al.*, 1996; Giardina *et al.*, 2003) potentially increases respiration costs (Odum, 1969) and reduces the proportion of GPP invested in growth (DeLucia *et al.*, 2007). Climate and phenological factors may lead to proportional changes in aboveground and belowground C allocation (and potentially maintenance of root-to-shoot ratios of species; Litton *et al.*, 2007; Gough *et al.*, 2010), and factors such as water availability, temperature, atmospheric $CO_2$ or nutrient availability have been documented to affect total belowground C allocation and autotrophic and heterotrophic respiration from soils (Haynes & Gower, 1995; King *et al.*, 2002; Norby *et al.*, 2004; Giardina *et al.*, 2005; Ryan & Law, 2005; Trueman & Gonzalez-Meler, 2005; Bryla *et al.*, 2008). C allocation patterns are used in models to predict the growth and C balance of ecosystems under climate change scenarios (Friedlingstein *et al.*, 2006; Fisher

**Table 2** Suggested future research needs and potential experimental and modeling approaches for understanding the combined effects of abiotic and biotic drivers of root respiration from soils

| Environmental control | Research needs | Experimental and modeling approaches for future research |
|---|---|---|
| Nitrogen (N) | Resolve whether changes in N availability result in changes in root respiration mediated by biomass and/or N content.<br>Impact of N availability on carbon (C) allocation to heterotrophic soil organisms (e.g. mycorrhizas), and ultimately on direction of the plant response to N. | Experiments:<br>Combine N fertilization and isotope tracers with biomass collection, and soil respiration fluxes and flux partitioning approaches.<br>Quantify C allocation to mycorrhizas and the magnitude of the rhizosphere priming effect (RPE).<br>Models:<br>Use this quantitative understanding of how N availability affects belowground C allocation/respiration, and root distribution (size, order and depth).<br>Include RPE effects on N mineralization in models. |
| Temperature | Test root acclimation to temperature in field experiments.<br>Disentangle the relative significance of GPP from temperature in determining root respiration from soils.<br>Understand the effects of temperature on belowground C allocation and nutrient demand that affects root mass and its respi ratory flux.<br>Understand the effects of temperature on nutrient availability mediated by decomposi tion because it will have indirect effects on root mass, plant growth and nutrient demand (seen N). | Experiments:<br>Use multiple temperature treatments to obtain a temperature response function.<br>Combine air and soil warming experiments that will allow for characterization of GPP versus direct temperature effects on root respiration.<br>Document and understand temperature-driven changes in C allocation.<br>Use a hierarchical approach to root respiration where primary (GPP and temperature), secondary (allocation), and tertiary (nutrient availability and heterotrophic responses) effects are identified.<br>Models:<br>Use process-based models to represent hierachical temperature effects (e.g. temperature effect on autotrophic and heterotrophic metabolic rates, allocation patterns, and GPP) rather than simple empirical relationships (e.g. rely less on $Q_{10}$).<br>Incorporate process understanding of the availability of photosynthetic products on root respiration, including stored C, on diurnal and seasonal time-scales. |
| C supply and seasonality | Disentangle phenology and diel patterns from temperature-driven changes in respiration.<br>Document the role of stored C in buffering interannual, seasonal, and diel changes in substrate availability.<br>Quantify C demand and respiratory cost for root turnover.<br>Temporal changes in autotrophic substrate supply in the rhizosphere may be apparent in heterotrophic respiration after a time lag. | Experiments:<br>Use radiocarbon, pulse-chase experiments, biometric approaches and/or phloem sap flux to determine patterns of belowground C allocation and instantaneous C use efficiency.<br>Document the role of stored C in buffering interannual, seasonal, and diel changes in substrate availability.<br>Identify the fraction of fine roots that turns over seasonally using minirhizotrons or isotopes.<br>Determine temporal patterns for C allocation to heterotrophs in the rhizosphere.<br>Models:<br>Include root respiration as a function of current photosynthate or that buffered by stored C when GPP is insufficient.<br>Reconcile the time steps of models with the temporal resolution of empirical data.<br>Incorporate GPP controls on heterotrophic respiration. |

*et al.*, 2010; Franklin *et al.*, 2012). However, these models often operate at longer temporal and larger spatial scales than empirical data at which belowground C allocation are gathered (Gower *et al.*, 1996; Norby *et al.*, 2004; Litton *et al.*, 2007; Table 2). Additionally, poor constraints on C turnover in fine roots increase uncertainties in quantifying C allocation belowground and movement of C from plants to soils (Lynch *et al.*, 2013). New promising methods based on diurnal stem diameter change that correlate phloem sap flow with total sugar flux may provide new insights at tree and stand levels at various temporal scales (Hölttä *et al.*, 2006; Mencuccini *et al.*, 2013).

In summary, the typical representation of the temperature sensitivity of root respiration in models contrasts with empirical evidence gathered at the tissue to ecosystem levels that suggests otherwise. For instance, although tissue N content is a good predictor of specific rates of fine-root respiration, ecosystem-level autotrophic soil respiration may better scale with changes in fine-root biomass than root N content (Table 2). In addition to changes in root biomass, autotrophic soil respiration is further modulated by the respiratory acclimation to changes in temperature (seasonal or resulting from warming). Our findings suggest that while all of these processes act in combination, substrate availability (a product of GPP and storage) is the ultimate driver of the autotrophic soil flux (Table 2). Identifying these factors in a hierarchical way is paramount to advance our predictive understanding of the responses of ecosystems to climate change.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Increasing $CO_2$ by 200 μl $l^{-1}$ lowers the $\delta^{13}C$ of the $CO_2$ in the elevated FACE plots to –20‰.

**Fig. S2** Isotopic composition of fumigation $CO_2$ at the Duke FACE site.

**Fig. S3** Pool size isotope correction for estimating fluxes from pool residence times that was applied to live and dead roots of different diameter classes and soil $CO_2$.

**Fig. S4** Model for correcting incorporation of post-treatment C in root decomposition.

**Fig. S5** Soil respiration for the elevated plots as simulated by Hui and Luo (2004).

**Fig. S6** Cluster profile plots from the k-means analysis demonstrate that GPP is primarily responsible for the clustering, and root respiration rate is not.

**Fig. S7** Daily GPP versus the day of year partitioned into two clusters using k-means cluster analysis.

**Fig. S8** Daily current-year C utilized for root respiration versus the day of year.

**Table S1** Isotope end-members for calculations of pretreatment C (A, ambient) and post- treatment C (E, elevated) at the Duke FACE site

**Table S2** Averaged monthly values of the proportion of current photosynthate (% new C) respired by soils that was not originated in decomposition of leaf and root litter pools

**Table S3** Partitioning of GPP into ecosystem components and fluxes at the Duke FACE site

**Table S4** Summary statistics for k-means clustering analysis

**Notes S1** Contribution of current photosynthate to root-rhizosphere respiration.

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