

Editorial

Hidden Challenges in Ecosystem Responses to Climate Change

Miquel A Gonzalez-Meler*, Douglas J Lynch, and Elena Blanc-Betes

Ecology and Evolution, University of Illinois at Chicago, USA

Terrestrial ecosystems exchange vast amounts of C with the atmosphere between the processes of gross primary photosynthesis (GPP) and ecosystem respiration. As such, land surface processes that affect the balance between photosynthesis and respiration should affect the atmospheric concentration of CO₂. Because atmospheric CO₂ concentrations have been stable over millennia during the Holocene, it can be hypothesized that any process that has affected one biospheric C flux component has been compensated by changes in the other component. However, human activities are causing a net release of CO₂ into the atmosphere, which is altering the C flux balance between global GPP and terrestrial ecosystem respiration. Reliable predictions of direct effects of CO₂ and related climate forcing factors on vegetation and their feedbacks on the climate system depend deeply on our understanding of this global photosynthesis-ecosystem respiration balance. Tremendous progress has been made on understanding the photosynthetic flux of the terrestrial biosphere, but our understanding of the respiration flux and its components has advanced at a much slower pace [1]. As the majority of the ecosystem respiration flux originates from soils, understanding plant and soil biota interactions in terrestrial ecosystems represent a major challenge for climate predictions. Belowground processes are complex and govern major feedbacks between the terrestrial biosphere and climate. Here, we identified two major belowground biogeochemical processes that have been elusive to ecosystem scientists.

BELOWGROUND PLANT CARBON ALLOCATION AND IMPACTS ON SOIL RESPIRATION

Increases in respiratory demand by belowground tissues influence total belowground carbon allocation in vegetation. Because plants allocate C to maximize photosynthesis and growth [2], plants will partition GPP into tissues that would minimize negative impacts of limiting resources on growth [1,3,4]. Increased allocation of C to belowground tissues could be to meet nutrient and water demands [5], potentially increasing respiration costs and reducing the proportion of GPP invested in growth [1]. Although climate and phenological factors may lead to proportional changes in aboveground and belowground C allocation, factors such as water, temperature, atmospheric CO₂ or nutrient availability have been documented to affect

***Corresponding author**

Miquel A Gonzalez-Meler, Ecology and Evolution, University of Illinois at Chicago, 845 West Taylor St, Chicago IL-60527, USA, Tel: 312-3553928; Email: mmeler@uic.edu

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total belowground carbon allocation and autotrophic and heterotrophic respiration from soil [6,7,8]. In addition to root biomass, the fraction of GPP shunted belowground support maintenance and nutrient uptake costs, exudates, and nutrient-carbon trade with symbiotic organisms. A significant portion of the GPP allocated belowground to sustain processes other than biomass appears to modulate soil heterotrophic activity [9], suggesting that plants exert some control on soil heterotrophic respiration from ecosystems.

An increasing body of recent literature shows a direct influence of GPP on the autotrophic component of soil respiration [10,8]. This contrasts with simple temperature response functions often seen in model representations of root respiration from soils [9] and the empirical evidence showing acclimation and adaptation of respiration to climate change factors [11-13]. In fact, GPP has also been shown to influence soil heterotrophic respiration to a similar or greater extent than soil temperature or moisture [14-16]. The mechanisms of these connections are not fully understood [9], but may include stimulation of soil microbial activity via the rhizosphere priming effect [17]. The connection between GPP and heterotrophic respiration may reflect a complex network of hierarchical effects of environmental change on belowground factors. Therefore, soil microorganisms not only respond to changes in soil moisture, temperature or disturbance regimes but also to how plants respond to the very same environmental factors. Changes in root biomass, root depth distribution or plant nutrient demand in response to biotic and abiotic factors need to be characterized in the context of C allocation patterns [18] and its effects on soil heterotrophic activity.

Many models apply carbon allocation patterns to predict growth and C balance of ecosystems under climate change scenarios [19,20,4]. These models operate at temporal and spatial scales that often differ from field observations which are much longer and larger [3]. This is in part due to the difficulty of measuring total belowground C allocation at multiple scales [21,3]. 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 [22]. The transport of soil and root-respired CO₂

to aboveground tissues via xylem and its potential re-fixation in leaves has recently been quantified [23,24] and it is often ignored in ecosystem C budgets. At the very least, the addition of the active responses of GPP and C allocation patterns to environmental change (rather than implying first-order kinetics of passive responses of C flux to temperature and moisture) has been shown to improve models [17,9]. Therefore, the amount and proportion of GPP allocated belowground in response to climate forcing factors can impact soil C and nutrient cycling, which, in turn, affect ecosystem productivity, resilience and adaptation.

THE ROOT-SOIL ORGANIC MATTER CONTINUUM

A substantial proportion of the C allocated belowground is invested in fine root biomass. Fine roots (usually defined as roots less than 2 mm diameter) are active in uptake of water and nutrients from the soil. Individual fine roots turnover and decompose, serving as a major source of carbon (C) for soils [25]. Production of new fine roots could be a significant component of net primary production (NPP) in terrestrial ecosystems, though current estimates of the magnitude of fine-root contribution to NPP vary widely [26,27]. Similar to belowground C allocation, most of the range in root productivity arises from the different methodologies employed.

No current technology allows real-time monitoring of root production and senescence in a natural setting. Comparisons between root sampling methods reveal large differences in turnover times and productivity for fine roots, with estimates between minirhizotrons or isotopic tracer methods at the same site varying more than 5-fold [28]. Each method fundamentally measures a different parameter; minirhizotrons measure longevity of individual roots while isotope tracers measure residence time of carbon in the root system. A major barrier to improved understanding of fine roots is a lack of a paradigm for the fundamental unit of turnover. In contrast to an arbitrary diameter size classification for fine roots, the branching structure of roots has been utilized to categorize root traits from each branching order [29], providing evidence that clusters of lower order roots are produced and senesce together in 'ephemeral root modules' [30].

The last decade of research has shown that heterogeneity exists for many root properties, including function, turnover, and longevity. With increased branching order, nitrogen content and respiration rate decreases [31], and diameter and non-structural carbohydrate content increases [32]. Importantly, turnover within fine roots is best fit by models incorporating a small C pool replaced rapidly (months) and a larger C pool replaced more slowly (years to decades) [33,27]. Therefore, modeling fine roots with a single turnover time insufficiently captures root dynamics. The amount of carbon within each root pool can have significant impact on C and nutrient cycling in terrestrial ecosystems. Consequently, improved quantification of the size and turnover rate for multiple root C pools is a high research priority. Longevity of roots is likely impacted by resource availability, similar to allocation patterns [3]. Currently, little is known about the impact of global change on root longevity, or how changes in allocation itself will influence root longevity.

Compared to leaves, the number of studies analyzing traits

of individual roots is miniscule. In fact, global leaf trait data-sets allowed the determination of specific traits common to either short-lived or long-lived leaves, or a leaf economics spectrum [34]. Unfortunately, similar data for root traits are only available from a very limited number of sites and species. Increasing the number of studies that examine root traits could eventually lead to the creation of a root economics spectrum that would go a long way towards understanding of fine-root longevity. Another important unresolved question regarding fine roots is the rate at which fine root carbon is transferred to soils. Root chemistry seems to play an important role in soil organic matter stabilization [35]. Currently, models (e.g. CENTURY) assume 50% of root litter accumulates as soil organic matter. Little empirical evidence exists to support this rate [27], and further studies validating it should be a high research priority.

In summary, the long-term terrestrial ecosystem C balance is likely controlled by below-ground processes. Belowground modeling paradigms, including simple abiotic controls on soil respiration rates and a single homogenous C pool for fine roots are being challenged by the last decade of research. Important parameters, such as temperature dependencies of respiration [36] or the 50% transfer rate of decomposing root C to soil organic matter [27,37] remain largely invalidated. Carbon allocation is a dynamic process, and roots respond actively to environmental change, the dynamics of which are not currently captured in ecosystem models. This emphasis is even more important in climate sensitive ecosystems in tropical and Arctic regions. Improved understanding of below-ground carbon dynamics controlled by plants is a necessary step to create prognostic terrestrial carbon cycle models.

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