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# Improving the representation of roots in terrestrial models

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## ABSTRACT

Root biomass, root production and lifespan, and root-mycorrhizal interactions govern soil carbon fluxes and resource uptake and are critical components of terrestrial models. However, limitations in data and confusions over terminology, together with a strong dependence on a small set of conceptual frameworks, have limited the exploration of root function in terrestrial models. We review the key root processes of interest to both field ecologists and modelers including root classification, production, turnover, biomass, resource uptake, and depth distribution to ask (1) what are contemporary approaches for modeling roots in terrestrial models? and (2) can these approaches be improved via recent advancements in field research methods? We isolate several emerging themes that are ready for collaboration among field scientists and modelers: (1) alternatives to size-class based root classifications based on function and the inclusion of fungal symbioses, (2) dynamic root allocation and phenology as a function of root environment, rather than leaf demand alone, (3) improved understanding of the treatment of root turnover in models, including the role of root tissue chemistry on root lifespan, (4) better estimates of root stocks across sites and species to parameterize or validate models, and (5) dynamic interplay among rooting depth, resource availability and resource uptake. Greater attention to model parameterization and structural representation of roots will lead to greater appreciation for belowground processes in terrestrial models and improve estimates of ecosystem resilience to global change drivers.

## INTRODUCTION

Forecasting the resilience of Earth's ecosystems to perturbation or stress induced by climate change increasingly requires an understanding of the influence of belowground processes on ecosystem function. Roots couple the aboveground vegetation and the soil media, yet they are arguably the least understood portion of the ecosystem. As a result they are represented idealistically in many process-based ecosystem models, and remain the most simplistic component of contemporary Earth System Models (ESMs). Despite this, feedbacks between aboveground and belowground function are expected to influence ecosystem responses to changes in climate and atmospheric [$CO_2$]. For example, models currently predict that rising [$CO_2$] and temperature may increase aboveground productivity (Millar et al., 2007; Mote et al., 2003; Parmesan and Yohe, 2003), but productivity may be limited by soil nutrients and water availability (Albani et al., 2006; Boisvenue and Running, 2010; Jain et al., 2013; Luo et al., 2004; Norby et al., 2010). There is an urgent need for scientists to improve prognostic approaches for understanding how roots govern changes in resource availability and how root responses influence ecosystem productivity.

There are several common assumptions that have historically guided the treatment of root function in terrestrial models. One of the primary assumptions is that net primary productivity is influenced by soil nutrient and water availability, with root investment increasing water and nutrient uptake. These effects are often modeled indirectly through stoichiometric relationships among limiting nutrients that govern productivity in above- and belowground pools and/or demand-supply relationships rather than through direct representation of the physical processes that control root uptake. Second, root biomass is often determined using allometric relationships between above- and belowground pools, rather than determined independently. Third, carbon

(C) flux from roots to soil or the atmosphere is dependent on root turnover and respiration rates, which are dependent on soil conditions.  These turnover and respiration rates are often grouped by plant functional type, rather than species, and root respiration is lumped with microbial respiration to calculate the total loss of C to the atmosphere.

These relatively simple algorithms belie a growing understanding of complex root dynamics emerging from empirical root ecology studies.  Root order (Guo et al., 2008b), fungal-root associations (Smith and Read, 2008), and root-rhizosphere interactions such as priming (Zhu and Cheng, 2011) are viewed as critically important by empiricists, but these are not currently implemented in most models, with notable exceptions (Orwin et al., 2011; Parton et al., 2010). Moreover, root tissue chemistry and soil conditions dramatically affect root lifespan, but are not included in contemporary model approaches (Smithwick et al., 2013).  There is an opportunity, therefore, to draw renewed attention to how roots are incorporated into model frameworks and encourage future collaborative efforts among empirical scientists and modelers.  Heightened representation of root processes and feedbacks in ecosystem models may unravel relationships that heretofore were obfuscated by representation of roots as black boxes, and may elucidate the conditions that lead to ecosystem resilience or sensitivity under global change stressors.

Historically, incorporating root processes into models has been hampered by (1) a lack of consistent and scalable data on root properties that govern root structure (classification and arrangement) and function (processes that govern root production, turnover, and uptake), (2) differences in terminology between root ecologists and modelers, which have led to confusion even over relatively ‘simple’ terms like turnover (McCormack et al., *in press*), and (3) limited consensus on which root functions are ripe for inclusion in contemporary models.  For example, understanding species-specific root function in mixed-species forests is hampered by empirical observations that are recorded at the stand-level and which do not distinguish among tree species. Similarly, where species-specific estimates exist, spatial and temporal heterogeneity among species is often ignored when summarizing processes at the level of Plant Functional Type (PFT). Yet it is known that species-specific differences in root turnover are important at continental scales and can significantly affect estimates of C storage (McCormack et al., 2013).

Here, we review existing outlooks on root structure and function centered on the three challenges described above (scaling root data, issues of terminology, and assessment of modeling opportunities). The review is organized around root concepts common to both empirical ecologists and modelers, including root classification schema, production, turnover, biomass, resource uptake, and depth distribution (**Table 1**). We present the empirical community with opportunities for future field studies by highlighting gaps in data and theory that hinder the incorporation of belowground feedbacks into models. Similarly, we conclude with recommendations for areas of model advancement that may improve forecasts of terrestrial ecosystems to global change drivers based on contemporary understanding of root function.

## EMERGING OUTLOOKS IN ROOT STRUCTURE AND FUNCTION

### *Root Classification: Root size, function and mycorrhizal status*

All roots are not created equally in terms of growth and resource acquisition. Physical separation of roots into two size classes, fine (< 2 mm in diameter) and coarse (> 2 mm diameter), has been the classic approach (Jackson et al., 1997) for correlating root function and structure in both experimental and modeling approaches. In this classification, fine roots are considered to be non-woody, ephemeral roots that absorb nutrients and water, whereas coarse roots explore large volumes of soil and function primarily in anchorage, transport, and storage

(Pregitzer, 2002). More recently, however, researchers have begun to question the utility of this simple dichotomous separation, increasingly recognizing the complexity of root structure (**Fig. 1**) and the need to more precisely quantify the root properties associated with these classification schemes. For example, within the fine root size class, distal tips of roots (first- and second-order roots) are often thinner, more active in nutrient uptake, richer in nitrogen (N) and have higher respiration rates than basal roots (Pregitzer, 2002; Pregitzer et al., 1998). The majority of root length and surface area is also concentrated in these first- and second-order roots, which provide the high surface area needed for resource acquisition (Guo et al., 2004; Pregitzer, 2002). In a comprehensive, cross-species study, branching order was a more accurate indication of root function than size, with the traditional two-diameter class approach overestimating absorptive root length by 25% (Guo et al., 2008b). The response to these findings by some has been to classify fine roots into more size classes (e.g., Park et al., 2008). However, another approach may be to identify functional breaks across root orders or size classes. For example, first and second order roots may be classed together as ephemeral root modules with high rates of respiration, uptake and turnover, while higher order roots with secondary development are assumed to have limited uptake capacity and function more for transport and storage (Xia et al., 2010).

Although species differ in their growth and resource acquisition, identifying roots to the species-level in a mixed-species ecosystem is not a simple task and more field method development is critical. Visually distinguishing among roots of some hardwood species requires tracing each distal, fine root to a larger root (> 2 mm diameter) to examine its secondary growth (Yanai et al., 2008), which is time-consuming and not always feasible. Genetic approaches can be used to identify single root fragments to species using polymerase chain reaction techniques

(Bobowski et al., 1999), but their use remains rare. Species can also be identified in bulked root samples (Fisk et al., 2010; Mommer et al., 2008), though there remain concerns about time constraints (Fisk et al., 2010) and biases based on species and root size (Yanai et al., 2008).

Additionally, root systems must be contextualized in terms of their mycorrhizal status, which fundamentally influences root function and ecosystem dynamics. As has been long appreciated, the extramatrical hyphae of mycorrhizae increases surface area for water and nutrient absorption, with the effect varying by fungal species (Agerer, 2001) and ion mobility (Bolan, 1991; Eltrop and Marschner, 1996). Mycorrhizal communities are influenced by disturbances such as fire or elevated nutrient concentrations (Treseder et al., 2007) with potentially significant influences on ecosystem function. However, *in situ* measurements of mycorrhizal influences on whole root system dynamics remain sparse, given that it is difficult to isolate root function between mycorrhizal and non-mycorrhizal roots and because extramatrical fungal hyphae are often severed when the roots are excavated (Bloom and Caldwell, 1988). Thus, developing quantifiable relationships between fungal-root associations and ecosystem function remain elusive; yet, there have been increasing calls for improved representation of microbial communities in ESMs. Treseder et al. (2012) suggested that modeled decomposition rates could benefit from the inclusion of second-order dynamics dependent on microbial biomass. Specific to mycorrhizal associations, the increasing availability of regionally and globally extensive data (e.g., Öpik et al., 2013), together with increased analytical understanding of root-mycorrhizal relationships (e.g., Clemmensen et al., 2013), suggests that incorporation of these dynamics into regional and ESMs is now tractable.

In sum, despite increasing recognition of alternative root classification strategies regarding species, rooting order, and fungal associations, many models continue to segregate roots by size classes. This size categorization may serve to represent the functional duality of having both shorter-lived, absorptive roots and longer-lived, transport or structural roots, independent of whether they are termed “fine” or “coarse”. However, additional testing of alternative root classification strategies would allow for exploration of functional implications of root structure on terrestrial C, water, and nutrient dynamics (Gaudinski et al., 2010).

### ***Root Production***

Field-based estimates are often used to improve parameterization of root production in models. However, measurement of root production *in situ* is time-consuming and fraught with measurement error. For example, ingrowth cores involve the removal of all roots from a soil core, after which the clean, root-free soil is returned; the core is revisited after a given period of time and the amount of new roots that have grown into the core is used to represent root production over that time. However, the process of inserting the initial core into the soil severs roots and may elicit a wounding response from neighboring roots and increase local production above normal levels in the short-term (Hendricks et al., 2006). Minirhizotrons are also used to estimate production but installation of minirhizotron tubes artificially increases root production for one to three years. Minirhizotron measurements of observed root length or root number also must be converted to production estimates on a g $m^{-3}$ basis that, ironically, can only be derived using site-specific information of root biomass from soil cores and information about soil volume or depth. Ultimately, the most reliable approach for estimating root production is through sequential coring campaigns, but the frequency and intensity required to compensate for the high spatial heterogeneity observed in natural systems often prohibits this approach. These methods, together with a few others (e.g. budgeting approaches) provide the basis for most estimates of root production. The strengths and weaknesses of each method is covered more thoroughly in previous reviews (Hendricks et al., 2006; Milchunas, 2009; Ostonen et al., 2005; Smit et al., 2000; Vogt et al., 1998).

In models, root production is commonly estimated either: (1) as a fixed proportion of recent photosynthate or (2) to maintain a fixed ratio between biomass pools, e.g., roots and leaves (Harmon, 2011; Keane et al., 2011) (**Fig. 2**). Many models assume this allocation is optimized to meet plant demands for nutrients, growth, light, or survival (Bloom et al., 1985; Brassard et al., 2009; Ingestad and Agren, 1991; Johnson and Thornley, 1987; Poorter and Nagel, 2000), but adjust the allocation dynamically based on environmental conditions. For example, the CENTURY model adjusts root allocation as a function of annual precipitation, with increasing rainfall resulting in reduced root allocation (Metherell et al., 2010). Similarly, the Community Land Model (CLM) begins with a fixed ratio of C allocation between leaves and fine roots, which is then shifted to favor allocation to fine roots as water stress increases (Levis et al., 2004). CLM-Carbon-Nitrogen (CLM-CN) shifts allocation from roots to woody stems during favorable growth years (Oleson et al., 2010). Interestingly, in a global meta-analysis, Yuan and Chen (2012) showed that relaxation of nutrient limitations has a greater influence on aboveground versus belowground production. However, other factors, such as tree ontogeny, seasonality and differences among individuals, species, and communities, can also mediate dynamic allocation between root, leaf and wood production.

The phenology of root production is also important, describing how plants utilize temporally-variable water and nutrient resources during the growing season. Efforts to record leaf phenology have increased in recent years since climate change affects spring leaf emergence and fall leaf senescence (Diez et al., 2012; Fridley, 2012; Richardson et al., 2012), but few scientists document phenology in roots.  Root production may occur at different rates and starting points throughout the growing season and may not be synchronous with aboveground productivity.  Field studies suggest that asynchronicity in root and shoot phenology is present in both woody species and grasses, and may be significant, ranging from 2 weeks to 2 months (Steinaker et al., 2010).  Recent studies have also shown that new roots may be constructed from C acquired in previous growing seasons and stored within the plant, as opposed to only recently acquired photosynthate (Gaudinski et al., 2009; Vargas, 2009).  This allows for the possibility that, at times, root production may be entirely decoupled from active photosynthesis (Oleson et al., 2010; Schaefer et al., 2008; Shevliakova et al., 2009; Zaehle and Friend, 2010), and that models should incorporate lag effects across seasons and years.

In models, phenology is primarily expressed through the seasonality of aboveground vegetation, i.e. leaf area index (Oleson et al., 2010; Richardson et al., 2012), and roots are influenced indirectly through allocation paradigms described above.  As a result, root production is effectively limited to the active growing season, which likely serves as a reasonable first order approximation. Encouragingly, some models explore more detailed descriptions of whole plant phenology.  The effects of soil temperature on root turnover and respiration (e.g., the Ecosystem Demography model (ED2: Medvigy et al., 2009) and changes to constrain C allocation for woody stem growth to a shorter period that reflects observed phenology of stem growth (e.g., ForCENT; Parton et al. 2010) are recent examples.  It may also be possible to limit root production to earlier or later parts of the growing season to reflect patterns for particular species or PFTs.  For example, observations of root phenology in a common garden experiment found that root production in some species generally peaked around mid-June (e.g. *Liriodendron tulipifera*) while others peaked in mid- to late-July (e.g. *Pinus* spp) (McCormack et al., *in press*).

Another modeling approach allows for a root storage pool, as has been found in experimental studies (Gaudinski et al., 2009; Vargas, 2009), which may allow for lagged responses. More empirical studies that provide data of sufficient temporal resolution to allow for identification of generalizable patterns of root production phenology (Burton et al., 2000; McCormack et al., *in press;* Steinaker et al., 2010) would improve the simulation of seasonal root production in terrestrial models.

### ***Root turnover***

Modelers often treat turnover as, simply, the inverse of lifespan. Technically, fine root turnover rate represents the number of times a population of roots is replaced during a given time period (e.g. annually) and can incorporate information regarding root production, standing biomass, and lifespan. Empirically, turnover is variably calculated, yielding comparable but slightly different estimates of turnover. For example, if root production equals 1000 g $m^{-2}$ $yr^{-1}$, and standing root biomass is measured 5 times over the course of the year at 700, 1000 1300, 1100, 900 g $m^{-2}$, then using either the maximum, minimum, or average standing biomass from that year to calculate turnover rate would result in estimates of 0.77, 1.4, and 1.0 $yr^{-1}$, respectively. Additionally, fine root turnover rates have also been calculated as the inverse of observed fine root lifespan, which also may produce similar estimates of turnover as other methods but never the quite the same. Overall, an important first step in modeling fine root turnover is recognizing the differences in methods for calculating turnover and appreciating potential bias among the different methods (McCormack et al., *in press*).

In addition to variation due to methodology, many studies have also highlighted real and substantial variation in root turnover rate both across and within sites and species (Gill and

Jackson, 2000; Iversen et al., 2008; McCormack et al., *in press;* Withington et al., 2006). Globally, there is likely to be close to an order of magnitude of variation in measured turnover rates. Importantly, this level of variation may also exist at the site level due to variation among species or across years. However, because calculations of turnover rate often involve estimates of production, mortality and standing biomass, it is not always clear whether this variation is due to consistent differences in root longevity and replacement or short-term (season to annual) changes in production or mortality. Furthermore, within a single root branch, turnover times of distal roots active in resource absorption typically range from months to a few years while turnover times of more proximal, resource conducting fine roots are frequently in excess of a decade (Gaudinski et al., 2010). Therefore, some of this variation may be due simply to the pool of roots that is most emphasized by different methods. Minirhizotron cameras enable direct observation and measurement of root lifespan of fine roots. Additionally, isotopic tracers have been used to measure residence times of root C to calculate turnover rates (Gaudinski et al., 2010; Matamala et al., 2003), but tracers tell more about when C was fixed and don't directly quantify root age. Each approach (traditional coring, minirhizotrons, isotopes) has strengths and weaknesses that have been discussed extensively elsewhere (Gaudinski et al., 2010; Guo et al., 2008a; Tierney and Fahey, 2002) and much of the reliability of each method to estimate root turnover depends on which root pool is of interest. In general, minirhizotrons are likely better suited for determining lifespan and turnover times of the more ephemeral, absorptive fine roots while isotopes may be more appropriate for higher order, longer-lived fine roots and coarse roots.

Even accepting differences in terminology and accepting a more traditional view of turnover as equal to root mortality requires the understanding that the causes of root mortality are diverse, and include decomposition, herbivory (Hendrick and Pregitzer, 1992), and direct physiological stress. Root herbivory may be important in many systems and differentially affect agricultural systems that are designed to minimize harmful microbial and fungal activity versus natural systems. Other causes of mortality, including cellular toxicity to adverse biogeochemical environments (Cronan and Grigal, 1995) may be important in regions subjected to elevated N deposition (Smithwick et al., 2013). The importance of these mortality factors has not been explored at regional or global scales.

Though often included in models, root turnover is poorly constrained and contributes significantly to model uncertainty (Ciais et al., 2008; Malhi et al., 2011). Understanding these uncertainties is likely to remain a critical task for unraveling the often complex and contradictory implications of turnover on total ecosystem C (**Fig. 3**). For example, increased root turnover rates could lead to greater root litter inputs, increases in soil organic matter, and therefore higher total ecosystem C stocks. Alternatively, higher turnover may modify resource availability (e.g., through priming) that could shift C–nutrient stoichiometry, increase microbial activity, and potentially increase total soil respiration, leading to total C loss. The relative balance of these processes remains critical in contemporary model frameworks and reinforces the importance of uncertainty analyses focused on turnover dynamics.

While turnover remains a fixed parameter in many models, other models allow root turnover rates to vary as functions of environmental factors such as N mineralization rate in PnET-CN, (Aber et al., 1997; Ollinger et al., 2002) or soil water content and temperature in ED2 and ForCENT. In LANDIS-II, FORCS Extension, fine root turnover may temporarily increase to reflect a loss of aboveground biomass due to branch mortality or disturbance (Dymond et al., 2012). These and other similar approaches may enable more complete descriptions of root dynamics into models, though the accuracy of these efforts will depend on the ability to accurately link variation in root turnover rates to changes in environmental factors and ecosystem dynamics.

Directed field efforts will certainly improve estimates of root turnover rates available for models and may identify useful relationships between root turnover and environmental conditions. Information based on fine root lifespan, rather than more sophisticated definitions of turnover described above, are more widely available via expanded use of minirhizotrons and C isotopes. Applied at broad scales, root turnover may prove to be useful as an output variable and diagnostic tool for modelers to determine whether belowground C fluxes are within a reasonable range or how modeled systems respond given different environmental conditions or perturbations. However, a key consideration is careful attention to turnover parameters derived from field data that may differ across methods and employ different terminology.

### ***Root biomass***

Data that adequately capture spatial and temporal variation in root biomass are rare. As with production, seasonal and interannual variation in root standing crop is large, attributed to changes in resource availability (Hendricks et al., 1993; Nadelhoffer, 2000), tree size (Yuan and Chen 2012a), climate (Lee et al., 2007), and species (McCormack et al., *in press*). As described above, soil cores or pits can be used to measure root biomass and are technically simple, but are notoriously labor intensive. Other approaches are available, including ground-penetrating radar (Butnor et al., 2003), but radar primarily measures coarse root biomass with little seasonal variation, is technically challenging, and still necessitates validation using soil cores (Stover et al., 2007).

In the absence of direct measurements, root biomass can be estimated using allometry. However, surprisingly few studies collect both above- and belowground biomass of vegetation *in situ* across landscape gradients in stand ages and vegetation composition (Kashian et al., 2013; Santantonio et al., 1977). Vadeboncoer et al. (2007) estimated that, across 12 northern hardwood stands in New Hampshire (USA), allometric equations provided accurate estimates of lateral roots (coarsely defined as < 10 cm diameter) when stands were greater than 20 years old (mean error 24 to 32%), but underestimated root biomass by greater than 60% among young stands. This result is consistent with the assertion that allometry underestimates root biomass by ca. 60% (Robinson, 2004). In sum, although conceptually straight-forward, estimating the standing crop of roots is surprisingly difficult and rarely validated at the site or landscape level.

Estimation of root standing crop can be used to initialize model pool sizes but these direct estimates are rare and fraught with error. Thus, in the absence of direct estimates at global scales, modelers rely on surrogates for estimating root biomass, such as fixed relationships between foliar, woody or total aboveground biomass (Wolf et al., 2011). The specific approach used differs among models, highlighting differences in understanding of the factors that govern root biomass. For example, one approach has been to simulate fine roots as a function of leaf biomass; and, using similar logic, coarse roots as analogous to, and a fixed fraction of, woody biomass, as is implemented in the current version of LANDIS-II, Century extension (Scheller et al., 2011). This assumes that fine roots are functionally similar to leaves, acting as belowground scavengers of resources. However, these relationships are often held constant across species, PFT, and site conditions, with unknown implications on model outcomes. Furthermore, as leaves and fine roots are frequently exposed and respond to vastly different environmental pressures, it is unclear how consistent these relationships are in nature and how flexible they should be in models. Wolf et al. (2011) showed that land surface models which incorporated stand-thinning processes or shorter wood turnover times performed better related to observed allometries. Ultimately, root biomass is the net result of root production (gain) and turnover (loss) that each change over time. In practice, root biomass or its associated rates (production, turnover/mortality) are often used to 'tune' model responses, given that it's 'true' value is not known. Thus, constraints on pool sizes (minimum, maximum) are sorely needed to bound model estimates of root biomass.

### *Resource Uptake & Rooting Depth*

Resource uptake by roots can be measured using a combination of direct or proxy estimates. Water uptake can be measured directly using sapflow gauges (Brooks et al., 2002), but involves excavation of individual roots and/or sometimes the use of caves to access deep roots (Bleby et al., 2010). Directly measuring nutrient uptake in intact root systems in the field is equally difficult (for a review see Lucash et al., 2007). A few recent studies have measured nutrient uptake in sand with intact mycorrhizal roots (Lucash et al., 2008) using labeled isotopes (Proe et al., 2000) and intact soil with isotopic pulse-chase experiments in large plants and trees (e.g., Soethe et al., 2006). These studies assume that soil nutrients are not limiting and uptake rates are constant across concentration (but see Lucash *et al.*, 2007), and are seldom linked with measurements of resource availability or plant demand.

Estimating uptake from the difference of other measured fluxes has been measured at annual scales (Nadezhdina et al., 2008). However, at finer temporal scales, total uptake may differ in response to daily and seasonal patterns in climate and/or resource availability (Gessler et al., 1998). An additional constraint to budgeting approaches is that they are often calculated at the stand-level, precluding any ability to quantify uptake at the species-level, except in monocultures. However, root uptake may be spatially heterogeneous within the soil profile even if total uptake remains unchanged due to localized patterns in water and nutrients (Garrigues et al., 2006; Sharp and Davies, 1985; Wan et al., 2002), which would be difficult to quantify through annual budgeting approaches at the stand level. The degree to which spatial and temporal patterns in root uptake are due to shifts in allocation, active plant regulation of the soil environment, and/or a response to abiotic gradients in water potentials and nutrient gradients that govern mass flow, is an active area of research.

Recent modeling efforts have highlighted the need to understand resource (nutrients, water) availability to capture observed behaviors and lend credibility to predicted responses of terrestrial vegetation to climate change (Thornton et al., 2007). Given that roots determine nutrient uptake, it is surprising that uptake is commonly modeled indirectly. For example, many models simulate water or nutrient uptake as a function of soil resource availability, weighted by the relative root fraction or relative root length density within a soil layer, relative to leaf demand, which is a function of either canopy biomass or productivity (Dybzinski et al., 2011; Hopmans and Bristow, 2002; Keane et al., 2011; Li et al., 2012; Medvigy et al., 2009; Metherell et al., 2010). The influence of roots is indirect in that rates of root turnover affect the soil N cycle and N availability, while leaf C to N ratios determine actual uptake. However, recent efforts coupling C and N dynamics using second generation dynamic global vegetation models (Tian et al., 2011; Zaehle and Friend, 2010) and modular approaches such as the Fixation and Uptake of Nitrogen module (FUN) by Fisher et al. (2010) incorporate root-level physiology to model N uptake and transport and allow for dynamic patterns of allocation. Li et al. (2012) recently tested alternate root functions in a land surface model (CABLE – Community Atmosphere Biosphere

Land Exchange model) to simulate how water uptake and hydraulic redistribution affected net ecosystem exchange.  Including these root dynamics significantly improved agreement between eddy flux tower observations and modeled fluxes of $CO_2$, latent heat flux, and soil moisture dynamics. Optimization theory has also been used to simulate N uptake; for example, McMurtrie *et al.* (2012) proposed that rooting mass be distributed dynamically in response to the spatial variability of soil N so as to maximize N uptake.

Even as indirect methods of modeling resource uptake are being challenged, there remains much room for model improvement.  Changes in the soil environment are likely to affect nutrient uptake rates and efficiencies via changes in root tissue physiology.  Smithwick *et al.* (2013) reviewed this effect for N deposition, highlighting root physiological studies that have indicated tissue level stress as a function of elevated chemical environments.  Understanding mechanisms of root physiology, e.g., concentration thresholds of toxic elements that influence lifespan, remains a frontier in modeling that would benefit from increased interdisciplinary dialogue.  Similarly, inclusion of how mycorrhizal fungi affect root uptake is also important (Orwin et al., 2011) particularly for  immobile nutrients like phosphate (Smith and Read, 2008). Mathematical modeling of individual roots indicates that phosphate uptake is dominated by hyphal and not root uptake (Schnepf et al., 2008b).  Also, recent efforts to simulate the development and extent of the fungal mycelium will be helpful for interpreting species differences in foraging strategies and how this might affect nutrient acquisition (Schnepf et al., 2008a).   Finally, most models ignore the fact that nutrient and water uptake take place only at the surface of roots, potentially independent of total root biomass.  Empirical studies indicate that specific root length (length per unit mass, m $g^{-1}$) and surface area can vary by an order of magnitude between species (Comas and Eissenstat, 2009; Tjoelker et al., 2005), which may dramatically affect resource uptake.

Given that rooting depth affects nutrient and water uptake (Dawson, 1995; Göransson et al., 2006; Kulmatiski and Beard, 2012), it is important to understand how rooting depth varies across species and sites (Göransson et al., 2006; Kulmatiski et al., 2010). Most experimentalists confine their measurements of root processes to the upper 10 or 20 cm of soil because *most* fine roots are located in surface layers. For example, (Soethe et al., 2006) found that 32 to 43 % of the total N taken up by trees, shrubs and herbs was obtained from the organic layer, while only 2 to 19 % was derived from a soil depth of 40 cm. However, several studies, e.g., free-air-$CO_2$-enrichment (FACE) experiments, have shown the greatest increases in root mass occurred at soil depths below 30 cm (Iversen, 2010), leading to greater N extraction from depth, either due to increased N availability or deeper rooting (Iversen et al., 2008). In some arid systems, pools of P, Ca and Mg at 2-3 m depth appear to be utilized by deep roots (McCulley et al., 2004); other studies have shown maximum rooting depths from 5 m to 25 m (Jackson et al., 1999). Deep roots may be particularly important in arid systems where trees utilize groundwater as their primary water sources (Dawson, 1996) but may also be important in wet, tropical environments during periods of low rainfall (Davidson et al., 2011). Plants can also modify their resource environment by depth through hydraulic redistribution (Amenu and Kumar, 2008; Bleby et al., 2010; Jarvis, 2011; Simunek and Hopmans, 2009), the effects of which vary dramatically across ecosystems (Neumann and Cardon, 2012). Rooting depth may also be responsive to preferred flow paths in soils. As a result of these and other processes, the source of water utilized by plants can vary seasonally, with soil conditions, and with depth (Bertrand et al., 2012; Yang et al., 2011).

Modeling water extraction by depth has been undertaken at various levels of sophistication (**Fig. 4**). In the simplest ‘bucket model’ approach (Budyko, 1974; Manabe, 1696), the subsurface is represented as a single layer, with transpiration evenly extracted throughout the soil column. In models that represent the subsurface with multiple soil layers, the rooting architecture of vegetation is described with temporally and spatially invariant macroscopic parameters such as root depth and/or root shape that are dictated by the type of vegetation being modeled (Feddes et al., 2001; Pitman, 2003; Schenk and Jackson, 2002). Typically, these models distribute the transpiration based on upon the fraction of roots that reside in each soil layer. Parameterization of the root profile is often only determined by empirical data organized by PFT which may not directly match the vegetation classifications found in many ESMs (Zeng, 2001). Moreover, these parameters do not consider local abiotic and biotic interactions. Jackson et al. (2000) details the various model treatments of root distribution, highlighting that rooting parameters are frequently determined independently of local soil texture and climatic region. As a consequence, these models do not take into account the strong influence that soils and climatic variability have on the partitioning of precipitation at the surface and the flow of moisture through the root zone. This simplification also ignores the long history of observational data (Weaver 1926) that recognized that under myriad soil textures or precipitation regimes the same plant species can exhibit alternative rooting strategies to cope with different belowground moisture distribution (Caylor et al., 2006; Gentine et al., 2012).  Through a series of synthetic simulations, Sivandran and Bras (2012)  illustrated the influence of local abiotic conditions on determining the optimal rooting depth and extended this work  to include a dynamic root C allocation algorithm driven by the vertical distribution of soil moisture (Sivandran and Bras, 2013). By allowing the belowground rooting structure to adapt and evolve with local soil, topography and climatic conditions, improvement of water, energy and C fluxes was achieved.

Several studies have applied the evolutionary principle which states that environmental (abiotic) and competitive (biotic) pressures have resulted in a set of species that have adapted to the local conditions by expressing traits that maximize the benefit to the plant and improve the probability of success of the individual. Kleidon and Heimann (1998) applied this philosophy to optimize the depth of a bucket model for different vegetation classes forced with climate data and soil texture information. They observed increases in ANPP as a result of using an optimized root depth parameter rather than the model default values.

Physically-based modelling approaches that resolve the soil water flow, plant water uptake and the impact of soil characteristics within a three-dimensional representation of the root system have begun to produce the required functional relationships needed by larger scale models (Couvreur et al., 2012; Javaux et al., 2013). In fact, Javaux et al. (2012) outlined a methodology by which physically-based models can inform the parameterization of large-scale models that, due to their scale, necessitate the use of macroscopic parameters.

Recently, authors have explored the role of rooting depth and distribution on a wide variety of ecological responses (Collins and Bras, 2007; Guswa, 2008; Hildebrandt, 2005; Hwang et al., 2009; Lai and Katul, 2000; Schenk, 2008; Schymanski et al., 2008; Schymanski et al., 2009). For example, using the model MC1 (MAPPS-Century 1), Daly et al. (2000) explored the influence of rooting depth of trees and grasses on C and nutrient fluxes in Wind Cave National Park, South Dakota, USA. Results showed significant influence of rooting depth on model outcomes. In particular, rooting depth had a larger effect than climate on biogeochemical pools under both historical and future climate scenarios. Deeper roots increased vegetation productivity and modified fire regimes through competitive interactions with grasses. At the global scale, the lack of representation of deep water access may explain why ESMs cannot simulate adequately the response of tropical forests to seasonal drought (Baker et al., 2008). Even if root profiles can be identified empirically for given plant types, these results suggest that dynamic profiles are necessary to emulate vegetation resilience under increasingly common global change factors such as drought.  In conclusion, although model structural and functional flexibility to rooting depth profiles is currently being implemented in models (e.g., Li et al., 2012; McMurtrie et al., 2012; Sivandran and Bras, 2013), implications of these changes on total model responses must be explored across broader gradients of environmental conditions.

## ***SYNTHESIS & RECOMMENDATIONS***

In the traditional view of root dynamics in regional ecosystem models and ESMs (**Fig. 5a**), allocation governs root production, influencing the root C stock available for turnover, which in turn governs soil C and nutrient dynamics.  In these black box approaches, roots indirectly respond to altered conditions but do not themselves influence their environment or whole-plant function directly, which is known to be an overly simplistic assumption. Notably, these dynamics are persistently guided by only a few key principles, e.g., dynamic and/or optimum allocation or the evolutionary principle. While these principles are reasonable at global scales, they obviate the need to model root uptake directly through physiological mechanisms, precluding prognostic understanding of root responses to global change drivers.  In addition, through experimentation and observation, several shortcomings are additionally evident in model approaches to root dynamics, such as the general lack of representation of mycorrhizal-root associations, limited attention to root phenology or stored C pools, and the simulation of uptake rates conditioned on biomass or demand rather than active surface area. Perhaps most strikingly, the factors that govern root lifespan and influence root mortality directly are not included, such as herbivory or physiological tissue stress.

Given the literature reviewed here, we propose a new framework that illuminates a more nuanced understanding of root dynamics (**Fig. 5b**). In this new understanding, feedbacks from roots to aboveground pools and fluxes may result in behavior that is not captured by treating roots as 'passive portals' or 'black boxes'. In this new framework, we propose that earth system modelers could incorporate changes into their existing frameworks (**Table 1**), while encouraging empirical scientists to collect data at the temporal and spatial resolution necessary for modeling at a large spatial scale.

To enable a community of modelers to test these and other changes in root function on ecosystem function, we have identified the following research opportunities that cut across the specific tests described above (**Table 2**). First, models must include roots in data assimilation, variance partitioning, and optimization. These approaches should explore the effect of parameter and structural uncertainty and identify conditions that lead to threshold responses. Models that do not have significant feedbacks between belowground pools to aboveground function are likely to have little internal sensitivity to root parameters or algorithms, whereas models that couple roots to nutrient or water availability with feedbacks to aboveground function are likely to be influenced heavily by belowground dynamics. Using this approach with ED2, it has been shown that allocation, turnover, and water conductance (which moderates root water uptake), have high parameter variance and can contribute significantly to overall model sensitivity (LeBauer et al., 2013; Wang et al., 2012).

Second, it is critical that global datasets become increasingly available, taking the 'guesswork' out of root parameterization. This is dependent on several factors, including the coalescence of existing data sets to archives that modelers are able to access readily (e.g., Gordon and Jackson, 2003), as well as methodologies that encourage new field data to be obtained in regions that are currently data-sparse. Particularly important is the identification of target ecosystems in which small investments in data retrieval will aid global upscaling efforts. In the development of globally available datasets, database management must include the prioritization of key parameters, and identification of protocols and criteria for empirical data collection. Given the confusion over even common terms such as 'turnover', and differences among methodologies, careful attention here is critical. Widespread use of global root datasets in models is emerging for some key variables, e.g., rooting profiles (Schenk and Jackson, 2002) but is not widely available for other parameters such as root lifespan. Additional studies are needed to link the distribution of mycorrhizal species or functional types with root function in a manner that facilitates incorporation of mycorrhizas into simulation models.

Third, contemporary root physiological studies, some of which are highlighted in this review, foretell of a substantial opportunity to develop improved mechanistic feedbacks between aboveground and belowground pools. If tissue-level root functions can be related physiologically to key ecosystem processes, as has been widely accepted for photosynthesis in leaves (Farquhar et al., 1980), it will be possible to explore how roots directly influence and are influenced by the soil environment and aboveground systems.

While model improvements of root function may seem daunting, it is equally true that significant empirical understanding of root function has emerged in recent years. Significant interdisciplinary work and collaboration between empiricists and modelers is still needed to guide data collection and model improvement.  Yet, the new framework shown here highlights an opportunity to incorporate new functionality into models with the goal of developing field-testable hypotheses.  Modelers must increasingly strive to quantify root activity, request data where needed, and use models to develop testable hypotheses about root function.  While staying honest to available data, modelers have an opportunity to challenge widely held paradigms and to explore tradeoffs – both mechanistic and computational – in improving root function in models.   The goal of this effort ought to be increasing the coupling between leaves, roots and soil, and further constraining model predictions of terrestrial ecosystem responses to global change drivers. The degree to which these additional changes, e.g., splitting roots into explicit functional versus size classes, or including fungal-root associations, may be required to accurately forecast ecosystem resilience to global change must be weighed against costs in model complexity and increased model variance.

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**Table 1.** Issues and approaches (empirical and modeling) for the five key root processes described here. * represents model or analytical study.

|  | Issue or Challenge | Relevant empirical or modeling studies |
|---|---|---|
| (1) Classification | Roots currently modeled based on size class, but empirical studies show functional classifications, including fungal symbioses, are important | Gaudinski *et al.* 2010; Opik *et al.* 2010; Xia *et al.* 2010; Clemmensen *et al.* 2010; Guo *et al.* 2008b; Pregitzer 2002; Treseder *et al.* 2012*; Parton *et al.* 2010* |
| (2) Production & Phenology | Root production classically modeled based on optimization to meet aboveground plant demand, making it difficult to predict seasonal mismatches in root vs. aboveground production | McCormack *et al.* in prep.;Yuan and Chen 2012; Brassard *et al.* 2011<br>Burton *et al.* 2000; Steinaker *et al.* 2010; Oleson *et al.* 2010*; Parton *et al.* 2010* |
| (3) Turnover & Lifespan | Turnover can be defined differently, leading to confusion;<br>root physiology may directly influence lifespan | Smithwick *et al.* 2013; McCormack *et al.* 2012; Guo *et al.* 2011; Iverson *et al.* 2008; Withington *et al.* 2006; Gill and Jackson 2000; Cronan and Grigal 1995 |
| (4) Biomass | Estimating root biomass via radar, allometry, or soil cores is difficult; results show variation with resources, tree size, climate, & species | McCormack *et al.* 2012; Jackson 2009; Iversen *et al.* 2008; Park *et al.* 2008; Pregitzer *et al.* 2008; Butnor *et al.* 2003; Nadelhoffer 2000; Jackson *et al.* 1997 |

| | | |
|---|---|---|
| (5) Resource uptake & Rooting depth | Increasing evidence that roots influence the soil resource environment (i.e., priming, hydraulic lift), but field measurements remain limited;<br>Models show large sensitivities to rooting depth & resource supply; analytical model approaches, based on dynamic allocation with resource supply by depth and root-level physiology, are emerging | Gentine *et al.* 2012; Lucash *et al.* 2007; Caylor *et al.* 2006; Soethe *et al.* 2006; Comas and Eissenstat 2004; Schenk and Jackson 2002; Jackson *et al.* 2000; Proe *et al.* 2000; BassiriRad *et al.* 1999; Gessler *et al.* 1998;<br>Sivandran and Bras 2012*, 2013*; Li et al. 2012*; McMurtrie et al. 2012*; Tian *et al.* 2011*; Fisher *et al.* 2010*; Zaehle and Friend 2010*; Collins and Bras 2007*; Zeng 2001*; Kleidon and Heimann 1998* |

Table 2: Recommendations for improving the representation of roots in models and examples of how to implement them.

| Insight | Recommendation | Example(s) |
|---|---|---|
| Classification | Explore alternatives to size-class based root classifications based on function, including fungal symbioses. | Define and re-parameterize root pools by function or mycorrhizal status- not size or root order. |
| Production and phenology | De-couple above- and belowground allocation and phenology. | Re-define root phenology for PFT, species or mycorrhizal status (see McCormack et al. in press) and test for emergent behaviors at broader spatial and temporal scales. |
| Root dynamics | Simulate root dynamics as a function of root environment, rather than leaf demand alone. Re-examine the treatment of root turnover in models, including the role of root morphology and tissue chemistry on root lifespan. | Define root stress indicators that affect production and turnover and examine ecosystem responses. Test the effect of alternate root turnover definitions on whole-tree or whole-ecosystem productivity. |
| Biomass | Incorporate better estimates of root stocks across sites and species to parameterize or validate models. | Use data-assimilation methods (LeBauer et al., 2013) to take advantage of growing empirical datasets to test parameter influence on model uncertainty metrics. |
| Resource uptake and rooting depth | Explore (dynamic) rooting depth patterns on resource availability and uptake. | Develop dynamic approaches to discretize root uptake by matching root mass (or uptake rate) by resource availability in each horizon. |

## Figure Legends

**Fig. 1**. Intact root branch of *Acer saccharum* (a) followed by depictions of historical (b) and emerging views of root classification (c and d). The historical view (b) divides roots into coarse (in black) and fine (in white) roots based on rigid diameter classes. Panel (c) shows a root branch classified by branching order following Pregitzer *et al.* 2002 while panel (d) classifies roots based on function with ephemeral fine roots (white) being responsible for resource uptake and persistent fine roots (gray) provide framework for fine roots and transport water and nutrients to coarse roots (black). Photo in panel (a) taken by Sarah Kulpa care of Ruth Yanai. Panels b-d courtesy of Dali Guo.

**Fig, 2.** Depiction of current model algorithms of allocation of C to roots showing three dominant pathways (fixed allocation, proportional allocation, or carbon cascade).

**Fig 3.** Alternate pathways by which root allocation can alter total ecosystem carbon. In (a) increases in root allocation can either increase or decrease total ecosystem carbon, depending on whether models consider tradeoffs in ANPP among plant pools, respiratory losses, and resource feedbacks. In (b), constant root allocation can impact total ecosystem C fluxes if root biomass is independently altered.

**Fig. 4.** Primary questions that determine model treatment of root function at different soil depths. Upper left panel describes multiple approaches used to model water uptake in many terrestrial biosphere models where soil water uptake is modeled with canopy resistance ($r_c$) as a function of soil water potential ($\psi$), or water supply (S) is modeled as a function of volumetric soil water content (W).

**Fig. 5.** Traditional and emerging frameworks for incorporation of root processes into ecosystem models and dynamic vegetation models.