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Review

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.

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1. 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 accurate root activity 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 (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., 2014), 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

Table 1
Issues and approaches (empirical and modeling) for the five key root processes described here.

	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), Õpik et al. (2010), Xia et al. (2010), Guo et al. (2008b), Pregitzer (2002), Treseder et al. (2012)[a] and Parton et al. (2010)[a]
(2) Production and 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	Yuan and Chen (2012), Brassard et al. (2011), Burton et al. (2000), Steinaker et al. (2010), Oleson et al. (2010)[a] and Parton et al. (2010)[a]
(3) Turnover and lifespan	Turnover can be defined differently, leading to confusion; root physiology may directly influence lifespan	Smithwick et al. (2013), McCormack et al. (2012), Guo et al. (2011), Iversen et al. (2008), Withington et al. (2006), Gill and Jackson (2000) and 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, and species	McCormack et al. (2012), Jackson et al. (2009), Iversen et al. (2008), Park et al. (2008), Pregitzer et al. (2008), Butnor et al. (2003), Nadelhoffer (2000) and Jackson et al. (1997)
(5) Resource uptake and rooting depth	Increasing evidence that roots influence the soil resource environment (i.e., priming, hydraulic lift), but field measurements remain limited; models show large sensitivities to rooting depth and 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 (2000), Gessler et al. (1998), Sivandran and Bras (2012)[a], Sivandran and Bras (2013)[a], Li et al. (2012)[a], McMurtrie et al. (2012)[a], Tian et al. (2011)[a], Fisher et al. (2010)[a], Zaehle and Friend (2010)[a], Collins and Bras (2007)[a], Zeng (2001)[a], Kleidon and Heimann (1998)[a]

[a] Model or analytical study.