Tansley review

Root structural and functional dynamics in terrestrial biosphere models – evaluation and recommendations

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Summary

There is wide breadth of root function within ecosystems that should be considered when modeling the terrestrial biosphere. Root structure and function are closely associated with control of plant water and nutrient uptake from the soil, plant carbon (C) assimilation, partitioning and release to the soils, and control of biogeochemical cycles through interactions within the rhizosphere. Root function is extremely dynamic and dependent on internal plant signals, root traits and morphology, and the physical, chemical and biotic soil environment. While plant roots have significant structural and functional plasticity to changing environmental conditions, their dynamics are noticeably absent from the land component of process-based Earth system models used to simulate global biogeochemical cycling. Their dynamic representation in large-scale models should improve model veracity. Here, we describe current root inclusion in models across scales, ranging from mechanistic processes of single roots to parameterized root processes operating at the landscape scale. With this foundation we discuss how existing and future root functional knowledge, new data compilation efforts, and novel modeling platforms can be leveraged to enhance root functionality in large-scale terrestrial biosphere models by improving parameterization within models, and introducing new components such as dynamic root distribution and root functional traits linked to resource extraction.

I. Introduction

Roots are key regulators of plant and ecosystem function through their role in water and nutrient extraction from soils, and through the plasticity of their responses to changing resource availability or environmental conditions (Hodge, 2004; Schenk, 2005). In this capacity, roots act as a key mediator of vegetation evapotranspiration, which dominates the control of land surface energy and water balances. Similarly, through uptake of nitrogen (N) and other nutrients, roots are critical for biogeochemical cycling and the interwoven carbon (C) cycle that regulates C balance (Fig. 1). Our knowledge of root functional processes is extensive and continues to improve with new research initiatives and advanced experimental techniques.

Notwithstanding the many important roles of roots, dynamic root functions are still largely absent in land surface models (Woodward & Osborne, 2000; Ostle *et al.*, 2009; Matamala & Stover, 2013; Iversen, 2014), hereafter referred to by the more inclusive term terrestrial biosphere models (TBMs). Root representation in TBMs is rudimentary, with C allocation, root distribution, water uptake and nutrient (almost solely limited to N) extraction generally based on fixed parameters or plant demand, independent of dynamic root functionality. Key root attributes that are missing include the capacity of roots to shift distribution under changing environmental conditions, regulate water uptake (e.g. via aquaporins), regulate nutrient uptake (e.g. via enzyme-mediated Michaelis–Menten kinetics), or associate with mycorrhizal fungi. The limited representation of roots in TBMs is partially a consequence of a lack of appropriate global root data sets, but also a consequence of the fact that TBM representation of vegetation processes under current climatic conditions appears to work fairly well with little or no representation of roots. Use in TBMs of implicit parameters of bulk water and nutrient uptake independent of roots can correlate to total root uptake (Norby & Jackson, 2000; Woodward & Osborne, 2000; Feddes *et al.*, 2001), and requires minimal root data or computational resources. Yet, while the simplified models may be roughly adequate, they do not allow dynamic root functionality, and thereby (we believe) limit application to future environments, and limit mechanistic linkages that establish model validity. Without inclusion of root dynamics, the current representation of roots in TBMs may not be sufficient to capture their roles in ecosystem function, nor adequate to understand potential controls that expressed root function may have in response to environmental change.

Feddes *et al.* (2001) argued 'that the functioning of roots [. . .] needs to receive more attention in land surface and climate modeling.' Model representation of canopy structure and function has progressed significantly (e.g. Mercado *et al.*, 2007; Bonan *et al.*, 2011; Loew *et al.*, 2013) since the big-leaf approach cited by Feddes *et al.* (2001). Alternately, and with some notable exceptions (e.g. hydraulic redistribution of water; Lee *et al.*, 2005; multi-process N uptake; Fisher *et al.*, 2010), the representation of root structure and function in TBMs has seen only limited progress. Improved representation of root water uptake has stalled despite demonstration of model sensitivity to roots in climate and vegetation distribution simulations over a decade ago (Kleidon & Heimann, 1998, 2000; Hallgren & Pitman, 2000; Feddes *et al.*, 2001).

In contrast to simplified TBMs that must represent the dynamics of roots associated with the entirety of the global land surface, mechanistic models at the scale of single-root processes include the necessary complexity to capture water and nutrient uptake functions in response to environmental stimuli at quite high resolution in both space and time (Gardner, 1960; Barber, 1962; Hillel *et al.*, 1975; Raats, 2007). Higher order model development often makes simplifying assumptions about such processes, potentially missing a fundamental control point for plant function under varying resource availability.

A whole universe of knowledge about root characteristics and functions exists that has not been exercised within TBMs. Novel

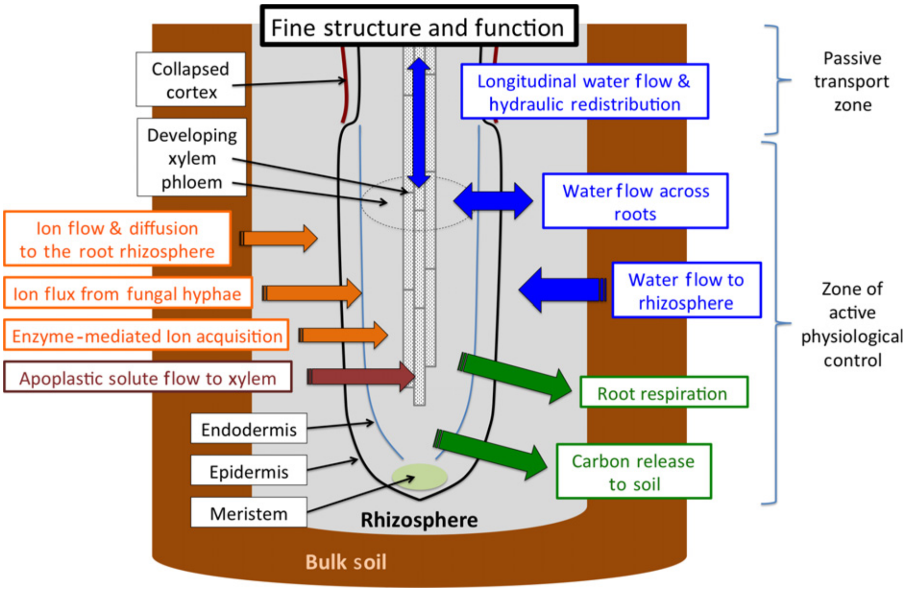

Fig. 1 Diagram of the structural and functional characteristics of fine roots of plant root systems, and their interaction with the soil rhizosphere. Developing fine roots contain zones of active growth and function and zones where changes in anatomical tissue reduce root functions such as water or nutrient uptake. Water and solutes can move passively through the apoplast of the epidermis, cortex and young developing endodermis to the central vascular tissue. As the root tissue matures, endodermal cell walls become suberized, at which point water and nutrient uptake into the symplast is regulated by passive or active transport proteins, such as aquaporins (water) or ion-pumps (mineral nutrients). The functionality of fine roots varies with characteristic morphological traits that are specific to species, and that respond to soil biotic and abiotic signals, such as mycorrhizas or soil drying. In this diagram, functions associated with nutrient uptake are presented in orange text, water transport in blue text, and carbon transport in green text.

nondestructive techniques for the imaging of roots have provided new insights into the form and function of roots *in situ* (Fig. 2). Confocal laser microscopy has been used to assess dynamic gene expression of root initiation and cell growth within the root tissues (Busch *et al.*, 2012; Vermeer *et al.*, 2014). Linked studies of gene regulation, growth regulators, intercellular communication and tissue development have led to advances in mechanistic multiscale modeling that can be used to predict root phenotypes (Band *et al.*, 2012). Actively controlled root membrane aquaporins have been identified as implicit control points for water transfer across roots (Javot & Maurel, 2002; Maurel *et al.*, 2008). Next-generation minirhizotrons are yielding unprecedented insights into fine-root and mycorrhizal exploration and turnover at high temporal resolution (Allen & Kitajima, 2013), and have been paired with CO_2 sensors to allow concurrent measurements of respiration *in situ* (Vargas & Allen, 2008). Neutron imaging has recently been used to assess *in situ* soil–root–rhizosphere hydration (Carminati *et al.*, 2010) and individual root water uptake and transport dynamics (Warren *et al.*, 2013). Soil moisture sensors continue to evolve, and allow for highly precise measurements of root water extraction dynamics and hydraulic redistribution throughout the soil profile (e.g. Warren *et al.*, 2011). Such measurements provide insight into soil, rhizosphere and root resistances, data that can be used to refine models of physical flow of water through the soil–plant system (Gardner, 1965; Sperry *et al.*, 1998). Other root functional processes including C flux, water and ion uptake, water potential and rhizosphere nutrient competition have been elucidated using novel biosensors (Herron *et al.*, 2010), isotope tracers (Bingham *et al.*, 2000), and *in situ* field observations (Lucash *et al.*, 2007). Despite this extensive knowledge of single-root processes, the scaling of such processes spatially within the soil profile and across the landscape through time has not been achieved.

The knowledge gap that exists in mechanistic model representation of root processes across scales (i.e. between roots, individual plants, ecosystems or land surfaces) is in part a consequence of inadequate data sets and the difficulty in linking root function to characteristic root traits, root distribution and root growth dynamics across landscapes (Fig. 3). For model veracity, simplified processes modeled in TBMs '. . .should be based on mechanistic understanding of the processes at lower scales. . .' (Schulze, 2014) – an understanding that has not been well translated for roots or root function. As such, the gap in knowledge transfer across scales leads to decreases in the expression of detailed root function as the predictive scale of the model increases (Ostle *et al.*, 2009). To model climate and the Earth System, TBMs must simulate the land surface energy, water and C balances at broad spatial (e.g. km) resolutions and at time-scales ranging from every 15 min

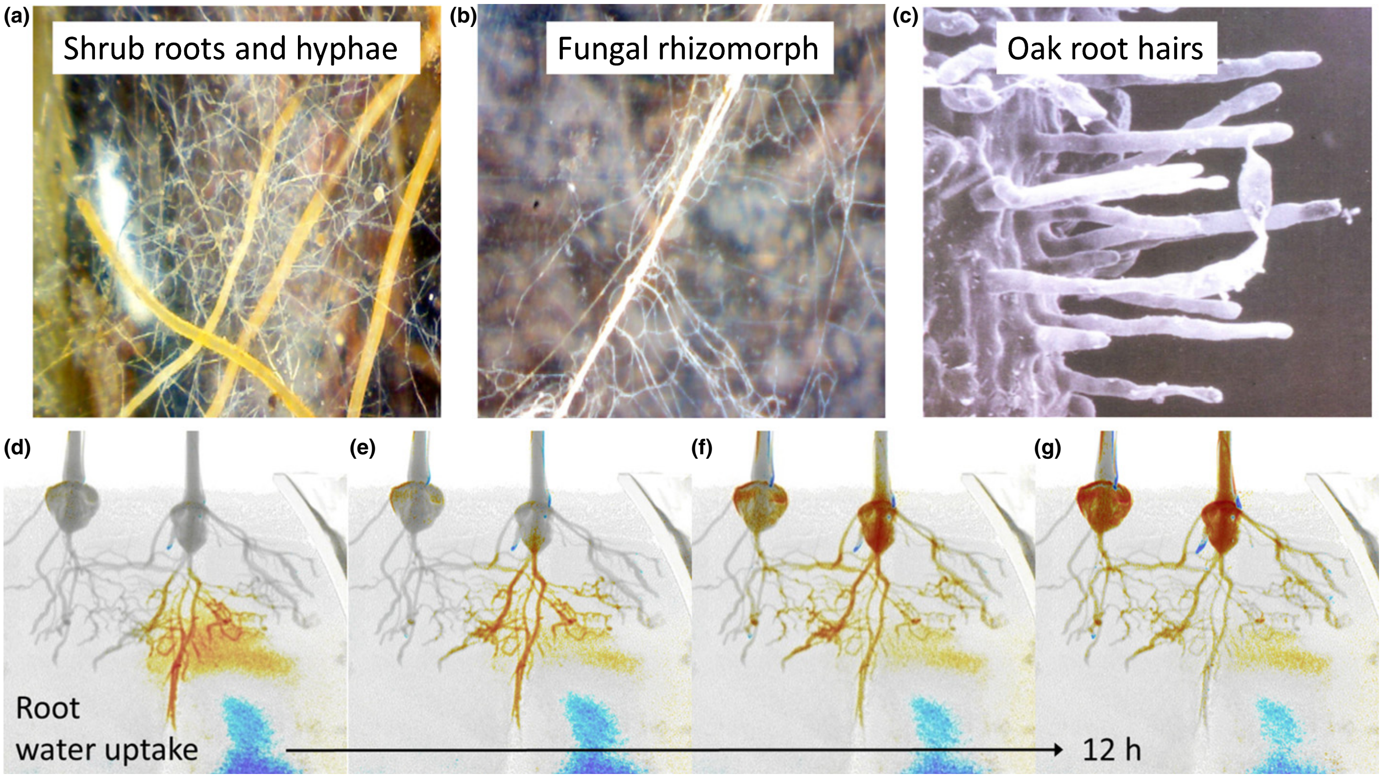

Fig. 2 Advanced techniques provide novel insights into root structure and dynamic root processes. (a) Ericaceous shrub roots and associated mycorrhizal hyphae and (b) a fungal rhizomorph from an automated minirhizotron system deployed in a peatbog (image scale *c.* 2.5 × 3 mm). (c) Scanning electron micrograph of *c.* 30–50-μm-long root hairs of *Quercus rubra*. (d–g) Neutron imaging time-series of water uptake and internal transport (orange colors) through corn (*Zea mays*) seedlings over *c.* 12 h following a pulse of water below the roots (blue). Such data can be used to validate model simulations of root structure, production, turnover and water uptake.

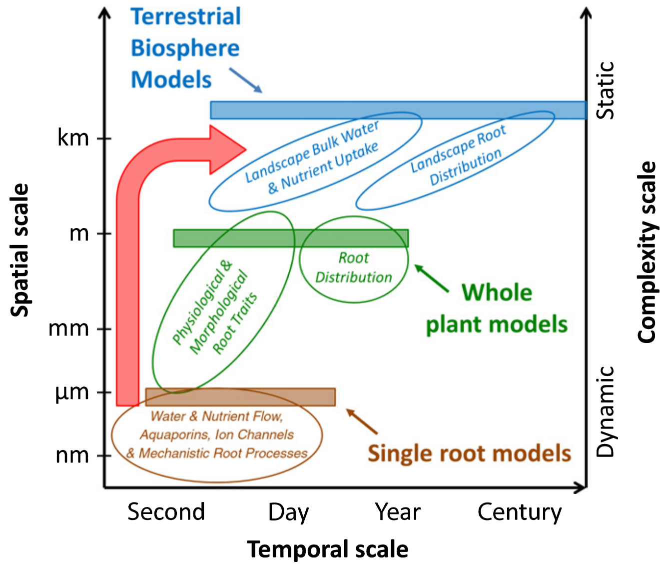

Fig. 3 Root, whole-plant, and terrestrial biosphere models (TBMs) in relation to the spatial and temporal scales at which they operate. Mechanistic root processes are readily modeled for single roots, but process-based knowledge is dramatically lost for higher order models, resulting in more static and less complex representation as spatial scale increases. Landscape-level bulk root distribution and water and nutrient uptake are estimated and not dynamic in most TBMs. Root traits can provide a framework for scaling dynamic root functions (such as fine-root proliferation, loss of root conductivity, or hydraulic redistribution) into TBMs to improve model veracity – a pathway indicated by the large arrow.

to potentially several hundred years (Pitman, 2003). The models must therefore integrate across the microscopic (e.g. submillimeter) and comparably short-term (e.g. seconds to minutes) scales relevant for actual root tissue function. Thus the *microscopic*, mechanistic approach of single-root modeling is not readily scaled to the landscape, which led to development of *macroscopic*, bulk, sink-based modeling (Skaggs *et al.*, 2006) at the plant or ecosystem scale.

This review considers how root function is represented by models across scales, ranging from single roots to whole land surfaces, and provides recommendations for improved representation of roots in TBMs. The current state of knowledge regarding root structure and function is considered, and the inherent and dynamic plasticity in those characteristics is described. Leveraging this mechanistic knowledge, a focus was placed on identifying aspects of root structure and function that could affect root water and nutrient uptake dynamics in the context of C cycling within TBMs. Specific targets for model improvement are noted. As data are required for model parameterization and validation, data availability is examined as a limitation of the application of root function in models across scales. The scope of the review was limited to living root characteristics that directly affect whole-plant function, including growth, and ion and water uptake. The indirect implications of root exudation, turnover and rhizosphere ecology (Young, 1998; Cheng *et al.*, 2014), while critically important, were not considered in this review.

II. Current representation of root function in models

1. Single-root models of water and nutrient uptake

Single-root water uptake occurs across a diversity of spatial scales requiring different approaches to best model water extraction. The microscopic approach involves physical first-principle mechanistic descriptions of radial flow to, and uptake by, individual roots (Hillel *et al.*, 1975). By contrast, the macroscopic approach models uptake with a sink term in the Richards equation that ignores or implicitly averages uptake over a large number of roots (Skaggs *et al.*, 2006). Early experimental and modeling work was carried out by Gardner (1960), where a root was modeled to be an infinitely long cylinder of uniform radius and water uptake characteristics. Although this formulation of root water uptake stimulated much research (Gardner, 1964, 1965), it was soon emphasized that it was not practical to develop field-scale models of water transport if flow to each individual root of a complete root system must be considered (Molz & Remson, 1970; Molz, 1981). Thus, various extraction term models have been developed where the fundamental premise is to describe root water uptake for the rooting zone rather than individual roots. In these models, soil–root processes are generally reduced to a root sink term that is incorporated into a detailed description of soil water balance (Doussan *et al.*, 2006).

Classical models of nutrient acquisition at the scale of a single root have provided many insights into the complex dynamics that occur at the root–soil interface. Early pioneering research by Barber (1962), Nye (1966), and Nye & Marriot (1969) indicated that nutrient uptake could be modeled as a single cylindrical root in an infinite extent of soil, where diffusion and mass flow supply nutrients to the root absorbing surface (Rengel, 1993). In most models that derive from the Nye–Barber framework, the central hypothesis is that the driving force of nutrient acquisition is the absorption of nutrients by the root, which results in a decrease in nutrient concentration at the surface of the root, leading to a diffusion gradient and movement of nutrients in the soil pore water (Hinsinger *et al.*, 2011). Although early models were confirmed by kinetic studies using plants grown in hydroponic culture, the differences in nutrient acquisition between well-stirred solution and heterogeneous soil are large (Rengel, 1993). As a result, uptake can be overestimated by these models because nutrient concentrations calculated at the root surface may be too high.

While the pioneering studies of single-root water and nutrient uptake established the modeling framework for basic root resource acquisition, a wealth of new knowledge from genomic to cellular to whole-root scales has emerged over the last several decades and improved our understanding of root structure and function (Figs 1,2). These insights offer novel understanding of single-root functional plasticity that might be leveraged into better representation in TBMs (as discussed in section II.4).

2. Individual plant models of carbon allocation, architecture and resource acquisition

Whole-plant models require more sophisticated approaches and involve a higher level of complexity in the description of root structure and function than single-root models. These approaches include an expanded consideration of how photosynthate is allocated to roots given competing sinks, and how the processes of root tip initiation, branching, and geotropism give rise to three-dimensional patterns of root distribution in soils (e.g. Thaler & Pagès, 1998; Ge *et al.*, 2000).

Various models have been developed over the last 25 yr to describe the structure and function of whole plant root systems (Clausnitzer & Hopmans, 1994; Jourdan & Rey, 1997; Spek, 1997; Dupuy *et al.*, 2007, 2009; Schnepf *et al.*, 2012). Five models in particular stand out as addressing the comprehensive suite of processes that govern photosynthate allocation to root growth, root system architecture, and acquisition of water and nutrients from heterogeneous soils (Table 1). These models simulate the production of daily photosynthate and its allocation to plant organs based on general source–sink concepts (Franklin *et al.*, 2012). Growth and respiration of leaves, stems, and roots are often represented as competing sinks for photosynthate. The SPACSYS model (Wu *et al.*, 2007) is an exception in that roots receive photosynthate with the highest priority, followed by leaves then by stems. Interestingly, several models include options for allocation of photosynthate (Table 1). Most notable is the scheme implemented in Root Typ (Thaler & Pagès, 1998), where either allocation can be modeled as a function of competing sinks (i.e. without priorities) or photosynthate is totally allocated to meet the demands of all plant organs. Each of the root growth models described in Table 1 can provide realistic spatial complexity of root system architectures consisting of distinct root classes (Wu *et al.*,

Table 1 Five individual plant models that represent carbon allocation, root architecture and uptake of water and nutrients

Model	Allocation	Architecture	Acquisition	Reference
ROOTMAP	Calculates balance between plant demand and the capacity of individual roots to supply soil resources, which drives allocation of assimilates and resultant growth of root tips and branching	Basic attributes affecting growth are elongation rate, branching density, direction, initiation times, and duration of apical nonbranching with sensitivities to temperature and soil density	Water uptake is based on a sink term; nitrate uptake is an approximate solution to the convection–dispersion equation using Michaelis–Menten kinetics	Diggle (1988); Dunbabin *et al.* (2002, 2003)
Root Typ	Allocation to growth occurs at a potential rate for all sinks when sufficient carbohydrate is available; else, reduced growth is determined *with* or *without* competing source–sink priorities	Root tips interact with soil temperature, mechanical impedance, and oxygen status to determine root elongation, direction, branching, radial growth, decay, and abscission	Water transfer into and along the root is represented by a set of connected hydraulic axial conductances and radial conductivities distributed within the root system	Pagès *et al.* (1989, 2004); Thaler & Pagès (1998); Doussan *et al.* (2006)
R-SWMS	Root growth is described in three ways; most complex application root growth is a function of dynamic allocation of assimilate to shoot and root (Level 3)	Root axes are generated at defined times; branching and spacing are a function of root age; sensitive to temperature, soil strength, and solute concentration	Water transfer represented by axial and radial conductances as a function of root age and root type; nutrient transport described by convection-diffusion equation	Somma *et al.* (1998); Javaux *et al.* (2008); de Willigen *et al.* (2012)
*Sim*Root	Carbon allocation rules based on a hierarchical binary partitioning method where sink strength, priority, and limits determine the carbon allocated to competing sinks	Spatial patterns determined by types of root branches, branch angles, growth velocities, and sensitivities to temperature, nutrient stress, and carbon availability	Nutrient (N, P, K) uptake is a function of root class, root development, root hair development, and intra-root competition; water uptake not represented in current model	Nielsen *et al.* (1994); Lynch *et al.* (1997); Postma & Lynch (2011a,b)
SPACSYS	Roots receive photosynthate with the highest priority; allocation is dependent on plant developmental stage; elongation and volume expansion depend on carbohydrate supply	Root system develops based on elongation rates of various root types, growth direction, branching, and mortality; processes are sensitive to soil temperature, soil strength, and solute concentration	N uptake depends on the concentration of nutrient at the root surface and the kinetics of uptake; water uptake is determined by a localized extraction function modified by soil water potential	Wu & McGechan (1998); Wu *et al.* (2007)

2007; Pagès *et al.*, 2004; Postma & Lynch, 2011a), where each root is represented by a growing number of root segments interacting with the soil. Comparison of model results with visual images from excavated plants (Clausnitzer & Hopmans, 1994; Pagès *et al.*, 2004; Wu *et al.*, 2007) and measured root density by depth (Somma *et al.*, 1998) provides encouraging support for the realism and utility of these simulations.

The ability to model root architecture allows coupling of root distribution with mechanistic descriptions of water and nutrient uptake (Table 1) (Dunbabin *et al.*, 2004; Ho *et al.*, 2004; Janott *et al.*, 2011). For example, the R-SWMS model has been used to simulate the dynamic and spatial patterns of root water extraction (Draye *et al.*, 2010). Results indicated that it was the interplay between root architecture, root axial and radial hydraulic properties, and water distribution in spatially heterogeneous soils that controlled patterns of water extraction. The *Sim*Root model has been coupled to a phosphorus acquisition and inter-root competition model (Ge *et al.*, 2000). Results indicated that phosphorus acquisition differed across different root system geometries, with greater phosphorus uptake per unit C cost for shallow root systems compared with deeper root systems. In similar fashion, using ROOTMAP, Dunbabin *et al.* (2003) found that the optimal root architecture for nitrate capture in sandy soils was one that quickly produces a high density of roots in upper soils to facilitate nitrate uptake during the early season, but also has vigorous taproot growth for nitrate acquisition later in the season.

Two- or three-dimensional modeled root architecture frameworks could be further refined to allow differential plasticity in growth and function that might be incorporated into future models, especially if dynamic root water and nutrient uptake capacity could be assigned based on root age, root order, or differential hydraulic conductivity (Valenzuela-Estrada *et al.*, 2008). Indeed, two-dimensional bulk soil water uptake has been successfully modeled as a series of resistances through the soil, root, plant and atmosphere continuum, regulated by water potential gradients and verified with field data (Sperry *et al.*, 1998; Hacke *et al.*, 2000; Wang *et al.*, 2002; Manzoni *et al.*, 2013). Manoli *et al.* (2014) introduced a three-dimensional model based on pathway resistances that includes hydraulic redistribution and that allows root systems of multiple trees to compete for water extraction from different soil layers. Such models are noteworthy in that they retain first-principle, physics-based *Darcian* water flow at the stand level, while allowing dynamic root functionality under drying conditions, a feature often lost in ecosystem models.

3. Ecosystem models

While root and individual plant models are highly detailed, they usually do not have the appropriate temporal and spatial resolution to simulate plant interactions with the surrounding soil at the ecosystem level (Agren *et al.*, 1991). Ecosystem process models were developed to simulate feedbacks and linkages among ecosystem components (plants, microbes, and resource pools) to assess whole-ecosystem C, water, and nutrient cycling across biomes such as forest stands (Running & Coughlan, 1988) or grasslands (Parton *et al.*, 1988). While ecosystem process models encompass spatial scales and processes ranging from the plot level (Running & Coughlan, 1988) to the global land surface (Hopmans & Bristow, 2002), they are distinct from TBMs in that they are not generally intended to be scaled to the global land surface or informed with products of remote sensing (Running & Coughlan, 1988). However, many ecosystem process models were developed to interface with TBMs (Parton *et al.*, 1988; Riley *et al.*, 2009; Fisher *et al.*, 2010), often at a specific spatial, temporal, or process-level scale, depending on the question of interest (Ostle *et al.*, 2009). Some ecosystem models were later linked with TBMs in order to understand vegetation patterns under current and future conditions (Pan *et al.*, 2002).

In order to represent the interaction of roots with aboveground plant parts and the surrounding soil environment (Fig. 1), ecosystem models must represent the functional balance of C partitioning belowground to root growth, the distribution of roots throughout the soil, active root functions, and the changes in partitioning and root distribution in response to changing environmental conditions (Grant, 1998). Accurate model representation of root function and its importance to land surface fluxes of C, water and nutrients is dependent on *how many* roots there are, *where* roots are in the soil profile, and *which* roots are active. Unfortunately, the different approaches taken with plant- and ecosystem-scale models appear to have created a gap through which the representation of roots and, in particular, root function has fallen. Some ecosystem-scale process models and TBMs do not explicitly represent fine roots (Hanson *et al.*, 2004), while in others, root representation is cursory, or solely to extract water from the soil. Fig. 4 describes model inclusion of various root processes, including root production and structure, and if structure is linked to water or nutrient uptake.

In ecosystem models, plant water and nutrient uptake is usually empirically derived from functional or allometric drivers rather than mechanistically propagated based on tissue function and energy expenditures (Hopmans & Bristow, 2002). N uptake from the soil profile is rarely modeled in a way that depends on root properties (Table 2), although for some models N uptake requires respiratory energy (Hopmans & Bristow, 2002; Fisher *et al.*, 2010) that indicates linkages to C partitioning belowground to fulfill root demand. Mycorrhizas have a large role in nutrient acquisition by plants but their inclusion in root models is rare, although they are explicitly represented in the detailed *ecosys* model (Grant, 1998), and implicitly represented in the Fixation and Uptake of Nitrogen (FUN) root module as an extension of the root system (e.g. Fisher *et al.*, 2010), and now explicitly represented in FUN 2.0 (Brzostek *et al.*, 2014).

There are several distinct types of ecosystem model that vary in their treatment of root function.

(1) Simple modules focused on one aspect of the ecosystem that might be incorporated into TBMs. For example, the Radix model estimates growth and turnover for various root classes in the context of internal C partitioning (Riley *et al.*, 2009; Gaudinski *et al.*, 2010) – such a model might be leveraged to allow water and nutrient uptake dynamics from roots of different functional ages. Another module, the FUN model, simulates N availability and uptake based on internal C and N availability, root microbial associations, water use and environmental conditions (Fisher *et al.*,

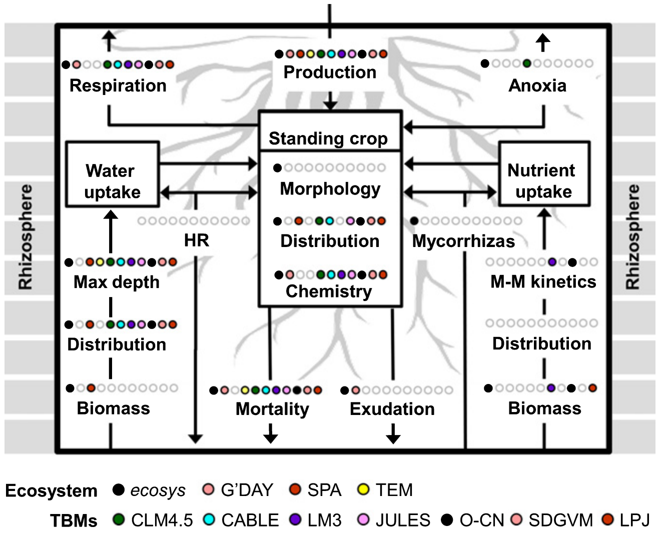

Fig. 4 Key root structural and functional attributes and their inclusion in several well-known ecosystem and terrestrial biosphere models (TBMs) – filled circles represent model inclusion. Dynamic root functions such as Michaelis–Menten (M-M) nutrient uptake kinetics, hydraulic redistribution of water (HR) and down-regulation as a result of low oxygen (anoxia) are rarely included in the models. Other functions such as water uptake are widely represented when linked specifically to root depth, but rarely consider actual root biomass. Model references are as in Tables 2 and 3.

2010). This N module includes passive and active ion uptake kinetics, requiring substantial respiratory energy. The model framework applies detailed ecophysiological processes to simulate N uptake and internal cycling. FUN can be run as a stand-alone module or applied within TBMs (e.g. JULES; Fisher *et al*., 2010), and ongoing work will leverage FUN into additional TBMs including CLM4.5 (Oleson *et al*., 2013), Noah-MP (Niu *et al*., 2011) and LPJ (Sitch *et al*., 2003).

(2) Whole-ecosystem models that vary in the complexity of their representation of ecosystem processes; for example, *ecosys* (Grant, 1998), G'DAY (McMurtrie *et al*., 2000), SPA (Williams *et al*., 1996) and TEM (Raich *et al*., 1991). These four ecosystem models include representation of a range of root-specific processes, based in large part on the initial ecosystem and questions devised by the developers (detailed in Table 2). The models include the highly complex *ecosys* model that has detailed root architecture, production and mycorrhizal colonization that can respond to changing water and nutrient availability (Grant, 1998). Root water uptake in *ecosys* is a function of water content, and root radial and axial resistances – the latter allows for expression of dynamic root function (resistance) that can control water uptake (Grant, 1998). The *ecosys* model can also differentiate N sources (NH_4-N and NO_3-N) and includes phosphorus cycling, whereas most other models focus solely on N. At the opposite end of the spectrum, the TEM model operates at coarse temporal and spatial scales, with focus on C and N balance in soils and vegetation (Raich *et al*., 1991) (Table 2). There are no roots or root functions present in the model. Water use is based on a water balance submodel that includes broad site characteristics including vegetation type, soils and climate. N uptake is based primarily on availability, and C : N uptake costs.

(3) Optimization models attempt to avoid the pitfalls of extensive parameterization (e.g. May, 2004) by focusing on a few analytic expressions. One example is *MaxNup*, which optimizes the vertical distribution of root biomass throughout the soil profile to maximize annual N supply to aboveground plant organs (McMurtrie *et al*., 2012). This type of annual optimization is apparent in other 'demand'-based models, which provides a limited framework for addition of root functional dynamics.

4. Terrestrial biosphere models (TBMs)

TBMs were designed to be linked into Earth system models to provide broad predictive capabilities of C cycling, energy balance and climate in the context of shifting natural and anthropogenic forcing of the system. As with ecosystem models, TBMs must align select mechanistic processes into a framework that is conducive for scaling, relying on bulk, landscape-level ecosystem components and fluxes (Fig. 3). Roots, when present in a model, must be scaled up from empirical data collected for specific species, or the relevant plant functional types (PFTs).

Constrained by the structure of TBMs, root distribution must be represented in a single vertical dimension, generally as the proportion of root mass in each of a number of soil layers, or simply as a maximum rooting depth. These tend to be fixed parameters which do not exhibit dynamic functionality. Root function is not usually linked with root biomass. There are some exceptions, such as O-CN (Zaehle & Friend, 2010) and LPJ-GUESS (Smith *et al*., 2013), that allow root biomass to be dynamic, although even in those models, the fraction of *functional*:*nonfunctional* root biomass is not dynamic. Table 3 describes how 10 commonly used TBMs represent root distribution, water and nutrient uptake.

Water uptake in TBMs As in the ecosystem models, water uptake in TBMs operates at the macroscopic scale, determined by supply and demand. Uptake is described by a sink term in the volumetric mass balance (Raats, 2007) rather than explicitly simulating the root–soil interface as described in the *single-root* and *individual-plant* scale model sections. Plant water demand is calculated as a function of atmospheric vapor pressure deficit and a series of water transport resistances caused by stomata, leaf and atmospheric boundary layers, and in some cases includes modeled root and stem resistances (Table 3) (e.g. SPA; Williams *et al.,* 2001; CLM4.5; G. B. Bonan, unpublished). When sufficient water is available, water uptake is simulated based on the plant water demand with rooting distribution or absolute rooting depth used to determine the location within the soil column of water taken up by the plant. Substantial amounts of data on global root distributions are available (e.g. Jackson *et al*., 1996; Schenk & Jackson, 2002), and root distribution is the most widely included root component in TBMs.

When insufficient water is available to meet demand, TBMs model uptake as a function of water supply, rather than allowing for mechanistic reduction in root conductivity. Most often, supply-limited uptake is simulated by multiplying physiological variables by a soil water stress scalar (0–1, often referred to as β), which serves

Table 2 The representation of carbon (C) allocation, root architecture and uptake of water and nutrients in a subset of ecosystem models

		Allocation		Architecture/ distribution	Acquisition/ecosystem function		
Model	Time step	Carbon	Phenology	By depth	Water uptake	N uptake	Root turnover and C loss
ECOSYS[1]	Hourly	Functional balance of nitrogen (N) and phosphorus (P). Demand adjusted so that allocation increases when root labile (C, N, P) > than that required to support new growth	Remaining C from respiration (R) – MR is available for GR subject to water and N and P status; resistance from soil and root and mycorrhizal turgor. Allocated to each root by comparative conductance	Root or mycorrhizal hyphae: f (allocation, primary root extension rate, secondary root initiation and extension rates, and cumulative soil temperatures > 0)	*f* (root radial and axial resistances and soil water content) Uptake (Q) = $(\psi_{\mathrm{shoot}} - \psi_{\mathrm{soil}})$/(sum of radial and axial resistances), where ψ is water potential	Root or hyphae: f(soil solution concentration at root/hyphal surface, mass flow, diffusion, root/hyphal length) Demand adjusted so that uptake is inhibited when root labile (C, N, P) > than that required to support new growth	MR is priority: *f* (soil temperature and O_2) GR: *f* (water, N and P) Nutrient uptake respiration (N_uR): f(N, P uptake rates) Exudation: f (root or hyphal soluble C, N, P pools : soil soluble C, N, P pools) Turnover: if (R < MR) MR&GR = *f* (T,O_2 status, comparative C conductance, turgor)
G′DAY[2]	Daily/weekly	Fixed fraction of NPP	None	None	Assumed nonlimiting; no specific uptake function. Updated model version will have two layers with root proportion linked to uptake	Not root-specific: fixed fraction of net soil N mineralization	Respiration: fixed fraction of GPP (not root-specific) Exudation: Fixed fraction of NPP Turnover rate fixed = 1.0 yr^{-1}
SPA[3]	30 min	Prescribed	None	Maximum root biomass per unit soil volume prescribed; exponential decline in biomass with depth to a prescribed maximum rooting depth.	*f* (root and soil hydraulic resistance, root biomass and distribution, and SWC). Maximum water use limited by root to leaf hydraulic resistance and stomatal closure at threshold leaf water potential prior to cavitation.	None	None
TEM[4]	1 month	None	None	Max rooting depth used to estimate water availability	*f* (ET, demand, soil properties, and SWC)	*f* (soil available N, SWC, and C : N energy balance)	*f* (NPP); above and below ground C loss is single term

[1] Grant (1998).
[2] McMurtrie *et al.* (2000).
[3] Williams *et al.* (1996).
[4] Raich *et al.* (1991).
ET, evapotranspiration; GPP, gross primary production; GR, growth respiration; MR, maintenance respiration; NPP, net primary productivity; Q, uptake; R, respiration; SWC, soil water content; ψ, water potential.

Table 3 The representation of carbon (C) allocation, root architecture and uptake of water and nutrients in a subset of terrestrial biosphere models (TBMs) and dynamic global vegetation models

		Allocation		Architecture/distribution	Acquisition/ecosystem function		
Model	Time step	Carbon	Phenology	By depth	Water uptake	N uptake	Root turnover and C loss
CLM4.0[1] CLM4.5[2]	30 min	Fixed fraction (1 : 1 leaf allocation)	Same as leaf	CLM4.0 Double-exponential for water (PFT-specific) CLM4.5 Double-exponential for water; exponential for C inputs (PFT-specific)	*f* (plant demand, root distribution, and soil matric potential)	If supply > demand, N uptake = demand to meet growth requirements. If supply < demand, N uptake = *f* (soil mineral N, plant demand, and microbial demand) (no root dependence)	Linked 1 : 1 to leaf turnover
CABLE[3]	30 min	Fixed fraction (varied by phenological phase)	Phased, opposite to leaf phenology	Decreasing proportion with depth	*f* (plant demand, root proportion, and SWC)	*f* (soil mineral N and plant demand)	Fixed fraction
LM3[4]	30 min	Functional balance: to maintain root : shoot ratio, root : shoot ratio *f* (water stress)	Same as leaf			Michaelis–Menten kinetics *f* (soil mineral N and root mass)	
JULES[5]	30 min	Fixed fraction (1 : 1 leaf allocation)	Growth: same as leaf. Turnover: fixed fraction	Exponential	*f* (plant demand, root proportion and SWC)	Not applicable	Fixed fraction 0.15–0.25 yr^{-1}
O-CN[6]	30 min to 1 d	Functional balance: to maintain root : shoot ratio, root : shoot ratio *f* (water or N stress)	Balance between allocation and turnover	Decreasing with depth (two soil layers)	*f* (plant demand, root proportion and SWC)	Michaelis–Menten kinetics *f* (soil mineral N, root mass, plant demand and temperature)	*f* (age). Mean turnover rate of 0.7 yr^{-1}
SDGVM[7]	1 d	Fixed fraction: 0.0015 of labile C pool	If GPP > 0	Fixed proportions through four soil layers. 0.5, 0.3, 0.15, and 0.05	*f* (plant demand, root proportion and SWC)	*f* (soil C)	*f* (age) and self-thinning mortality
LPJ-GUESS[8]	1 d	Functional balance: to maintain root : shoot ratio, root : shoot ratio *f* (water or N stress)	None	Decreasing with depth (two soil layers)	*f* (plant demand, root proportion and SWC)	*f* (soil mineral N, root mass, plant demand and soil *T*)	Fixed fraction 0.5–0.7 yr^{-1}
MBL-GEM III[9]	1 month	Functional balance	Result of allocation	None	None	*f* (root N content and air *T*)	Fixed fraction 0.164 yr^{-1}
DVM-DOS-TEM[10]	1 month	Fixed fraction	Same as leaf	Exponential to max rooting depth	*f* (plant demand, root proportion and SWC)	*f* (plant demand, root proportion and mass, root respiration, air *T*, SWC and available soil N)	f (root production : biomass) 0.25–1 yr^{-1}

[1] Thornton *et al.* (2007), Oleson *et al.* (2010).
[2] Koven *et al.* (2013), Oleson *et al.* (2013).
[3] Wang *et al.* (2010).
[4] Gerber *et al.* (2010).
[5] Clark *et al.* (2011).
[6] Zaehle & Friend (2010).
[7] Woodward & Lomas (2004).
[8] Smith *et al.* (2013).
[9] Rastetter *et al.* (1991).
[10] Euskirchen *et al.* (2009).
GPP, gross primary production; PFT, plant functional type; SWC, soil water content; *T*, temperature.

to reduce demand (Feddes *et al.*, 1978; Verhoef & Egea, 2014). The 'β' soil water limitation factor can be represented as a piecewise linear function of soil water matric potential, matric potential at wilting point (e.g. $\psi_{wp} = -1.5$ MPa) and matric potential at a critical point below which supply limitation begins (e.g. at field capacity (fc), where $\psi_{fc} = -0.033$ MPa). Some TBMs (e.g. CLM; Oleson *et al.*, 2010) simulate β as a function of matric potential in relation to when stomata are fully open or closed, while others (e.g. JULES (Clark *et al.*, 2011) and CABLE (Wang *et al.*, 2010)) simulate β as a function of soil water content (θ). As a consequence of the strongly nonlinear relationship between ψ and θ (soil water retention curves), the two formulations allow for very different supply limitation of soil water uptake. In addition, as the retention curves can vary dramatically within a single profile as a result of changes in soil physical characteristics, relative soil water availability for heterogeneous soils is not well expressed by a single relationship (Warren *et al.*, 2005), indicating a need for model parameterization of multiple soil layers simultaneously where data exist.

The β term has a direct link to water uptake, and thus is an obvious avenue for novel introduction of dynamic root function in future TBMs. Various alternate formulations of β exist (reviewed by Verhoef & Egea, 2014). One of the most interesting is the inclusion of root : shoot chemical (especially abscisic acid (ABA)) and hydraulic signaling to control stomatal aperture and thereby regulate root water uptake (Dewar, 2002; Verhoef & Egea, 2014). Inclusion of this ABA-based water stress function provided the best fit to experimental data, although it requires additional and accurate soil and plant parameter data sets – data not readily obtained at the landscape scale, which limits the application and refinement of this function in TBMs. Another expression of β allows for a decrease in root function under saturated, hypoxic conditions as a result of oxygen limitation in the rhizosphere (Feddes *et al.*, 1978), although most TBMs only consider a reduction in root function in response to drying soils.

Nitrogen uptake in TBMs Root N uptake in TBMs is also simulated at the macroscopic scale by using available soil N concentrations. N uptake is simulated primarily as a function of supply and often demand, as in CLM or CABLE (Thornton *et al.*, 2007; Wang *et al.*, 2010), although the implementation varies across models far more than the implementation of water uptake. Most TBMs integrate soil C and N cycling throughout the entire soil profile, and thus N uptake is from bulk soil regardless of root or N distributions within the profile, although new multi-layer biogeochemical cycling algorithms are becoming available for some models (e.g. CLM4.5; Koven *et al.*, 2013).

Some TBMs use root mass as a proxy for root length density, and formulate N uptake as a linear function of root mass (e.g. LM3 (Gerber *et al.*, 2010), LPJ-GUESS (Smith *et al.*, 2013) and O-CN (Zaehle & Friend, 2010)). The linear dependence of N uptake on root mass contrasts with the optimality formulation of McMurtrie *et al.* (2012), whereby a saturating relationship of N uptake to root mass results from overlapping nutrient depletion zones vertically within the soil profile as root mass increases. Models' use of biomass only, without knowledge of root anatomical or functional distribution, has limited ability to indicate differences between species within a PFT. Linking biomass to function through structure is thus a key area for improvement.

The LM3 and O-CN models employ a Michaelis–Menten kinetic function of N uptake, but one that saturates as N supply increases. Thomas *et al.* (2013) modified the N dynamics of CLM4, improving model accuracy at simulating N addition experiments. They showed that a key model development leading to the improvement was the implementation of Michaelis–Menten kinetics saturating with N supply and linearly dependent on root mass.

A number of models, for example, LPJ-GUESS (Smith *et al.*, 2013), O-CN (Zaehle & Friend, 2010) and CLM4 (Thomas *et al.*, 2013), also simulate N uptake as a function of temperature to account for the effect of temperature on metabolic rates. However, none of the models surveyed simulate N uptake as a function of soil water content despite the importance of water for rhizosphere nutrient cycling, for mass flow and diffusion of N to the root surface (de Willigen & van Noordwijk, 1994; Cardon *et al.*, 2013), and for oxygen dependence of metabolic rates.

Root production in TBMs Root growth, production and activity are dependent on C partitioning belowground. There are a variety of different approaches to model C partitioning within plants (Table 3) (Franklin *et al.*, 2012). One promising approach (functional balance) recently best represented temperate forest C partitioning in two free air CO_2 enrichment (FACE) experiments (DeKauwe *et al.*, 2014). Functional balance approaches partition C to various tissues to balance resource acquisition (Franklin *et al.*, 2012), and thus mechanistic model improvements to allow root functional nutrient or water uptake would be dependent on partitioning of C belowground. Representation of root function will also be necessary to implement optimization schemes for partitioning in TBMs, similar to that developed by McMurtrie & Dewar (2013). Flexible partitioning schemes allow vegetation turnover to vary as a result of the different turnover times of different tissues.

Model inclusion of C allocation through roots to mycorrhizas and exudates may be a parameter that could allow model plasticity of belowground functional dynamics, as these rhizosphere processes have direct linkages to water and nutrient uptake and C cycling. For example, observed increases in N uptake in response to elevated CO_2 were not explained by 11 ecosystem models (Zaehle *et al.*, 2014), suggesting the need for additional processes by which plants can stimulate N uptake through expanded effective root surface area, deeper soil mining (Iversen, 2010; McMurtrie *et al.*, 2012) and 'priming' of nutrient cycling (Drake *et al.*, 2011; Cheng *et al.*, 2014). Focused root 'modules' incorporated into TBMs may allow a pathway for dynamic root allocation and uptake. Indeed, the FUN nitrogen fixation module indicates increased root production in elevated CO_2 FACE studies (J. Fisher, pers. comm.), in agreement with observations, while balancing the C cost of root N uptake with other respiratory and growth demands.

Integration of detailed soil hydrologic and biogeochemical transport models into TBMs While ecosystem models and

TBMs were developed with a strong plant functional component, there has also been significant model development of subsurface reactive transport dynamics in the absence of vegetation (and roots). Modeling unsaturated water flow within the vadose zone is achieved by mathematical approximations of one- to three-dimensional Richard's equations (similar in structure to Darcy's law describing saturated flow in soils and plant xylem). More recently, root water extraction has been added as a sink term into these detailed, highly computational numerical models (Vrugt *et al.*, 2001; Javaux *et al.*, 2008), which allows them to be linked into TBMs. In these subsurface hydrology models, the flow of water from soil to root xylem 'tubes' is often modeled as simple one-dimensional radial flow (Amenu & Kumar, 2008; Schneider *et al.*, 2010), although, because hydraulic conductivity changes at the soil–root interface (e.g. Carminati *et al.*, 2010), more accurate models have included an interfacial conductivity within the rhizosphere (e.g. Katul *et al.*, 2012). Modeling efforts that include rhizosphere resistance as a microscopic soil–root hydraulic conductivity drop function can improve modeled dynamics of water transport into roots, while actually reducing the computational time (Schroder *et al.*, 2008, 2009).

There are encouraging efforts to pair these detailed numerical reactive transport models with vegetation models at the landscape level. The models have primary focus on improving surface and subsurface hydrological components and often include detailed soil characteristics, topography and differential water table depths (e.g. Rihani *et al.*, 2010; Shi *et al.*, 2013). Sivandran & Bras (2013) implemented multi-layered dynamic root distribution within a vegetation model (VEGGIE) coupled with a hydrologic model (tRIBS). The model dynamically allocates C to roots at different soil layers to maximize transpiration. Simulations agreed with catchment data at hourly time-scales, indicating the utility for inclusion of detailed numerical models in TBMs. PIHM (Qu & Duffy, 2007) is a fully coupled two-dimensional hydrological model that has been validated with extensive data at the Shale Hills Critical Zone Observatory and paired with a land surface model based on the Noah LSM (Shi *et al.*, 2013). These models include root biomass-weighted water extraction by layer, and successfully simulate soil hydraulic parameters and watershed discharge. Another reactive transport model, PFLOTRAN (Mills *et al.*, 2007), has been specifically designed to scale three-dimensional numerical hydrological modeling using parallel supercomputing. PFLOTRAN is currently being linked to the CLM TBM to achieve fully coupled detailed hydrological dynamics at the land surface scale. Despite a similar lack of root functional attributes in these hydrological models, they greatly improve mechanistic modeling of the subsurface environment, which allows for expanded knowledge of spatial dynamics of water availability. In turn, roots overlaid across the heterogeneous two-dimensional grids or three-dimensional voxels in these models could be allowed step-wise increases in dynamic functionality, which would greatly expand their role as a critical control point in subsurface and surface ecosystem functions. The coupling of detailed subsurface models with TBMs is expected to continue to evolve as computational limitations diminish.

III. Recommendations for leveraging root knowledge into models

We have shown that there are a number of existing root models and many known root functions that could be used to better represent the role of roots within TBMs. While high-resolution spatial and temporal dynamics of individual roots may not be amenable for application to TBMs, inclusion of specific mechanistic processes is critical to establishing a processed-based representation of root functionality that can be used to improve predictive capacity. Key root functions that should be included in future model development include root water and nutrient uptake, and C partitioning belowground to production, respiration, exudates and turnover. Knowledge of root traits related to these functions (e.g. morphology, chemistry, and mycorrhizal associations) will allow those functions to be scaled into TBMs (Fig. 3). Specifically, knowledge of root architectural display and distribution, the proportion of highly active ephemeral or less active woody roots (i.e. based on diameter, length, order, and age), mycorrhizal associations, and root production and turnover should be included. While some of these parameters are already included in TBMs, most are not well represented (e.g. Fig. 4), indicating that dynamic functionality could be improved or added. Dynamics to consider include plasticity of roots to environmental conditions – especially increased root water and nutrient uptake kinetics and root proliferation in resource-rich areas, and reduction in root activity in resource-poor areas. These dynamics should be linked to spatial and temporal changes in environmental conditions through both theoretical and empirical studies that intersect process- and trait-based parameterization.

Unfortunately, there is not a good understanding of TBM model sensitivity to root function; that is, if inclusion of mechanistic root functions in models could improve model performance within the current model framework, although studies that have included more root parameters have yielded better results (e.g. inclusion of dynamic root area (Schymanski *et al.*, 2008) or hydraulic redistribution (Lee *et al.*, 2005)).

In the following section, we assess how our current mechanistic knowledge of root function interacts with and determines ecosystem function, and suggest what should be taken into consideration when modeling roots in TBMs. Areas of discussion include root distribution and its utility for scaling, linking root traits to root functions, key regulatory factors such as water uptake kinetics (including hydraulic redistribution) and nutrient uptake kinetics, data availability, and strategies for model improvement. Fig. 5 provides a framework for root data and model assessment, and how we might proceed towards improved models or novel stand-alone root modules that could be embedded within TBMs.

1. Scaling root function using root architecture

Root distribution within the soil profile provides the basic foundation for root function, and is the characteristic most

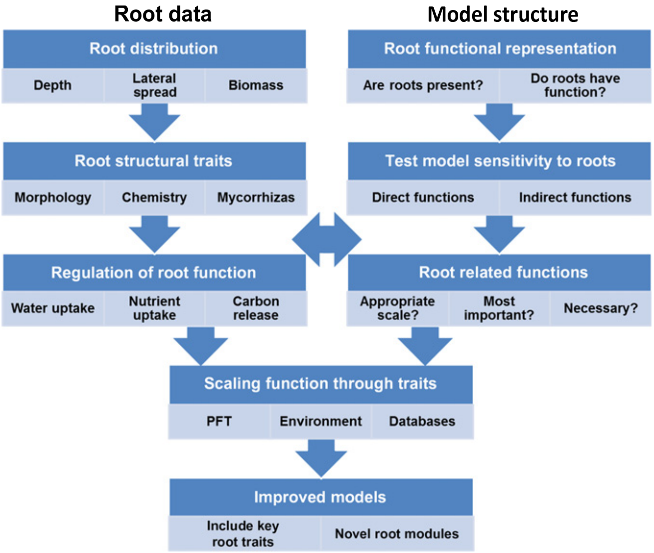

Fig. 5 Framework for assessment of root data, and its importance in scaling ecosystem function through root traits for modeling the terrestrial biosphere. (Left) Root distribution is the most common data set available, and is used in many terrestrial biosphere models (TBMs) to regulate water use (Fig. 4). Improved modeling will include root structural traits (e.g. size, age, order, display, carbon : nitrogen (C : N), and mycorrhizal associations), and their associated functions (e.g. water and nutrient uptake, and C release through respiration, exudation and turnover). (Right) Model evaluation should first assess the presence of roots or root functions, including both direct (e.g. water uptake based on root distribution) and indirect (e.g. N uptake based on plant demand) functions. Efforts must be made to understand the role of roots for specific processes at the appropriate spatial and temporal scales (Fig. 3). Key root functions should be prioritized based on current mechanistic knowledge of root processes and dynamic biotic/abiotic regulation of those processes, as well as their relative importance to the model. Addition of new root functionality to a model will require development of trait databases that can be scaled across landscapes based on species and plant functional type (PFT) characteristics, soil and environmental conditions.

frequently included in large-scale TBMs as a regulator of water uptake (Figs 4,5). Data are widespread and readily obtained destructively through soil coring and excavation (e.g. Nadezhdina & Cermak, 2003), or through *in situ* observations (using rhizotrons or minirhizotrons) (Pierret *et al.*, 2005; Iversen *et al.*, 2012). Specific root structural traits can then be overlaid on this distribution, with allowance for environmental gradients and biotic signals to shift trait functions within that distribution (Fig. 5). For example, during a period when upper soils dry, the upper roots become less functional, only to rapidly increase in function following precipitation inputs (e.g. Warren *et al.*, 2005). Root proliferation can decrease total root system hydraulic resistance under environmental stress, increasing capacity for water uptake and increasing the root : shoot ratio (Steudle, 2001). Inclusion of a dynamic root : shoot ratio in TBMs could bound C and water flux at the landscape level for a specific set of resources, as demonstrated with a plant-scale model by Sperry *et al.* (1998).

Shifts in actual or *functional* root distributions within the soil profile represent a dynamic functionality of the root system that is difficult to include in TBMs, although several research directions linked to root function are quite promising, including linking function to root class and characteristic root traits, and consideration of water stress and hydraulic redistribution through the soil profile (e.g. Valenzuela-Estrada *et al.*, 2008). For example, Schymanski *et al.* (2008) used an optimality function to meet canopy demands for water uptake by allowing root surface area to be dynamic and thereby able to shift into moister soil as necessary. The model ran on a 1-d time-step, and, while this may not accurately represent new root growth, it does represent shifts in root functionality within an existing root system. Results including this dynamic functionality improved estimates of water flux from a tropical savanna as compared with a static root system. Inclusion of such plasticity of root function provides a significant step toward better mechanistic representation of roots in models that could improve model performance.

Different PFTs vary in root display (presence of taproot, lateral spread, and dimorphism), maximum depth, and morphological traits that affect their interaction with the soil (Canadell *et al.*, 1996; Schenk, 2005; Pohl *et al.*, 2011). Root distribution varies across biomes and does not necessarily depend on soil depth. A global synthesis indicates that mean maximum rooting depths range from 2.6 m for herbs to 7.0 m for trees (Canadell *et al.*, 1996); although root distributions across biomes tend to be only as deep as necessary to supply evapotranspirational demand, allowing prediction of community root distribution based primarily on precipitation and potential evapotranspiration (Schenk, 2008). While simplified distributions of roots are readily incorporated into models, Feddes *et al.* (2001) suggested the need to continue modeling efforts from a bottom-up mechanistic approach, as well as a top-down approach, in order to provide process-level understanding to these simplified models.

2. Linking root function to traits

The responses of plant species to resource availability vary as a result of differences in competitive strategies (Hodge, 2004). In the context of drought, some species have adapted growth of deep roots to tap groundwater (Meinzer, 1927), in some cases at depths up to 50 m (Canadell *et al.*, 1996), while others with shallower root systems close stomata to limit water use and tolerate arid conditions. Such variation reiterates the necessity to include root traits within PFT classifications in order to adequately scale functionality of root architecture into the models. At the landscape scale, the distribution of root traits, specialized root structures (cluster roots and root hairs) and mycorrhizal associations reflects resource availability (Lambers *et al.*, 2008). Root function can be linked to characteristic root traits that vary across species (e.g. Comas & Eissenstat,2009; Kong *et al.*, 2014) and PFTs (especially annual versus perennial), although, other than root distribution, few if any root traits are included in PFT classifications (Wullschleger *et al.*, 2014), or TBMs. Currently, TBMs use static plant parameters for each PFT, even though phenotypic expression of traits is strongly affected by variations in environmental conditions; inclusion of photosynthetic traits that were allowed to vary linearly with climate within PFTs shifted simulated biomass estimates and PFT cover-type by 10–20% for forests compared with the default simulations (Verheijen *et al.*, 2013). Root turnover rates are a key root trait linked to ecosystem function that can have substantial variation across species within PFT; modeled inter-species shifts in root turnover within PFT under climate change had substantial implications at the landscape level (McCormack *et al.*, 2013). Efforts to understanding gene linkages to turnover and other root traits provide a pathway for screening of individual species' root characteristics, an effort particularly advanced for crop systems where traits are being linked to gross primary production and drought resistance (Comas *et al.*, 2013). Further phenotyping research is required in natural ecosystems to create the database necessary for inclusion of variable, dynamic root traits in TBMs. A trait-based, mechanistic representation of roots in TBMs will have significant impacts on model outputs.

Key root functional traits to consider for models are root morphology, chemistry and microbial associations, as they control dynamics of water and nutrient ion flux through the soil into roots under varying environmental conditions (Figs 1,5). The white, ephemeral first- and second-order roots are the predominant pathway for water and nutrient uptake (Steudle, 2000; Guo *et al.*, 2008; Rewald *et al.*, 2011), although coarser suberized woody roots also provide a persistent, yet lower uptake pathway that may be important for seedlings (Hawkins *et al.*, 2014), or seasonally during periods of low fine-root growth or activity (Van Rees & Comerford, 1990; Lindenmair *et al.*, 2004), and which may be associated with sustained root rhizosphere hydration through hydraulic redistribution (Rewald *et al.*, 2011). Root hairs and mycorrhizal associations can enhance the effective surface area of the root system and increase the potential for resource extraction in many species (Read & Boyd, 1986; Augé, 2001; Segal *et al.*, 2008).

Refinement of the 'fine : coarse' root ratios used in some models should reflect root function, not just root size, which varies by species. Root orders and their function can be characterized indirectly by the relative degree of mycorrhizal colonization, root density or root C : N ratio (Valenzuela-Estrada *et al.*, 2008). Root lifespan is another key root attribute that might be correlated with these and other root traits, such as diameter, root depth (Pritchard & Strand, 2008), and specific root length (McCormack *et al.*, 2012), or root and aboveground traits together, for example root diameter and plant growth, as found in 12 temperate tree species (McCormack *et al.*, 2012). Knowledge of root traits can be used to improve models of water or nutrient uptake kinetics (e.g. refining active root absorbing area, or classifying root function in the FUN N uptake module), add functionality to existing modules of root turnover (e.g. Radix), and provide scalable trait data for novel root functional representation in TBMs (Fig. 3).

3. Water uptake

The process of root water uptake includes some regulatory steps that could be included in TBMs. Under moist soil conditions, radial resistance limits root water uptake and is actively controlled by membrane-bound transport proteins (aquaporins) that respond to osmotic gradients (Chrispeels *et al.*, 1999; Steudle, 2000; Aroca *et al.*, 2012). Under drying conditions, water uptake is regulated by varying soil and plant resistances to water movement (Blizzard & Boyer, 1980; Sperry *et al.*, 1998; Hacke *et al.*, 2000). Radial hydraulic conductivity through aquaporin regulation can be rapidly increased or decreased based on perceived environmental stimuli including mycorrhizal colonization (Lehto & Zwiazek, 2011) or suboptimal environmental conditions (e.g. drought, extreme temperatures, or anoxia; Siemens & Zwiazek, 2004). Indeed, deep roots in wet soils up-regulated aquaporins during drought, increasing hydraulic conductivity substantially as shallow root conductivity declined (Johnson *et al.*, 2014). Root stress responses are often reflected in production and accumulation of ABA or other plant growth regulators (Davies & Zhang, 1991; Wilkinson & Davies, 2002; Aroca *et al.*, 2012). Root-derived plant regulators or mycorrhizal-derived inorganic ions can be transported through the xylem to elicit a response in the leaves, particularly stomatal closure (Davies *et al.*, 1994). Similarly, two-way hydraulic signaling also connects root and shoot functions, allowing coordinated whole-plant response to changing soil or atmospheric conditions (e.g. Blackman & Davies, 1985; Comstock, 2002; Meinzer, 2002; Vandeleur *et al.*, 2014). Pathway resistances are included in some TBMs; however, none to our knowledge has active regulation based on aquaporin expression, which could provide a mechanistic control on water use and improve model performance, similar to application of a dynamic ABA parameter on the water stress scalar, β, as described in Section II.4 'Water uptake in TBMs'. β is an obvious target for providing dynamic, albeit indirect, functionality to water uptake as it already exists in many models, and would be particularly useful if weighted by root *functional* class (e.g. age, order, and morphology) within each soil layer.

4. Hydraulic redistribution

Hydraulic redistribution (HR) can maintain fine-root function (Domec *et al.*, 2004), extend root life (Bauerle *et al.*, 2008), rehydrate the rhizosphere (Emerman & Dawson, 1996) and enhance nutrient availability (Cardon *et al.*, 2013) and acquisition (Matimati *et al.*, 2014), and should prolong soil–root contact under dry conditions. The contribution of HR to total site water use is known to vary widely depending on the ecosystem (Neumann & Cardon, 2012); yet even minor HR can provide significant benefits for continued root and mycorrhizal function during drying conditions. HR has been represented by variation in water transport between soil layers, dynamic soil–plant–atmosphere resistances, radial/axial conductivity *big root* models, and root optimality models (Neumann & Cardon, 2012). Results indicate that the inclusion of HR can help explain patterns of soil and plant water flux for individual trees (e.g. David *et al.*, 2013), resulting in significant implications for stand- (Domec *et al.*, 2010) and landscape-scale (Lee *et al.*, 2005; Wang *et al.*, 2011) C uptake and water release. In several large-scale models, HR has been included as an additional water flux term, as in the NCAR Community Atmospheric Model Version 2 (CAM2) coupled with the Community Land Model (CLM) (Lee *et al.*, 2005) and in CLM3 coupled with a dynamic global vegetation model (CLM3-DGVM) (Wang *et al.*, 2011). Results suggest that inclusion of HR can increase dry season water use in the Amazon forests by 40% (Lee *et al.*, 2005), but may exacerbate plant water stress under extended drought if soil water is exhausted (Wang *et al.*, 2011) – both works illustrate how a small change in root function can have substantial implications at the global scale. HR is a process that should be included in large-scale models, but it will require consideration of depth-specific soil–plant water dynamics, internal competition for water within the plant vascular system (Sperry *et al.*, 1998), plant water capacitance (Scholz *et al.*, 2007) and nocturnal transpiration (Caird *et al.*, 2007; Dawson *et al.*, 2007; Fisher *et al.*, 2007; Zeppel *et al.*, 2012) to account for concurrent uptake and release dynamics (Neumann & Cardon, 2012).

5. Ion uptake kinetics

Mineral ions are transported into the root cortex via mass flow or diffusion, or through mycorrhizal absorption, which is particularly important for uptake of immobile nutrients such as phosphorus. Movement through the plasma membrane of root endodermal cells is facilitated by a variety of passive or active transport proteins, including ATP-fueled ion pumps (Chrispeels *et al.*, 1999). Ion absorption kinetics vary by species depending upon the nutrient concentration, with multiple low- and high-affinity mechanisms controlled by environmental conditions (Epstein, 1966; Chapin, 1980; Chrispeels *et al.*, 1999; BassiriRad, 2000). Root nutrient uptake kinetics are often measured on intact or excised roots under well-hydrated conditions, that is, not under water stress. In drought-tolerant woody sagebrush (*Artemisia tridentata*), nitrogen and phosphorus uptake rates were maintained or even increased under laboratory water potential stress, illustrating the uncoupling of water and nutrient flux into the root (Matzner & Richards, 1996). Under drying conditions, *in situ* nutrient absorption does not appear to be limited by uptake kinetics, but rather by diffusion of ions through the soil to the root surface (Chapin, 1980). Mycorrhizas can span soil–root gaps and help to maintain a viable transport pathway from soil to root under drying conditions.

Absolute uptake kinetics for specific ions are thus a function of a variety of control points. Improved mechanistic representation of ion uptake in models will require inclusion and expanded consideration of Michaelis–Menten kinetics used in some TBMs (Fig. 4). One key improvement would be to allow the kinetics to vary by depth in response to environmental conditions such as temperature or soil water content (i.e. through the β stress scalar), weighted by specific root traits and root functional classes. Root hydraulic conductivity (i.e. aquaporin function) is often up-regulated by soil ion concentrations such as nitrate, resulting in whole-plant hydraulic signaling (Gorska *et al.*, 2008; Cramer *et al.*, 2009), increased root uptake kinetics (Jackson *et al.*, 1990) and proliferation of roots in resource-rich areas (reviewed in Hodge, 2004). Such plasticity in function might require a multicomponent ion uptake kinetic model that includes the appropriate regulatory and substrate parameters. One modeling framework to consider involves a modification of the HYDRUS reactive transport model. The model was modified to allow a 'root adaptability factor' which compensates for reduced water and nutrient uptake by stressed roots in resource-poor areas by increasing uptake of roots in unstressed soil (Šimůnek & Hopmans, 2009). Such efforts to refine existing models through use of dynamic scalars allow improved approximation of the processes inherent in more complex models, without the necessity for novel modeling frameworks and collection of additional data.

6. Available root data – a serious limitation

A fine balance exists between accurately representing ecological processes and the added uncertainty that comes with model complexity in terms of appropriate and accurate parameterization, which may require regional or global data sets (Fisher *et al.*, 2010). A concentrated effort needs to be made to fill the gaps in the trait database to obtain accurate representation of the trait space of terrestrial plants and ecosystems. There is a need for development of databases across PFTs of root distribution, root structure and root functional traits that are linked to specific plant responses to environmental conditions. Recent investigation of root traits of 96 subtropical angiosperm trees illustrates the broad variation and plasticity in traits within a single PFT (Kong *et al.*, 2014), as well as the necessity to identify trait covariance and linkages to function (Iversen, 2014). Key root traits to compile into databases include length, diameter, order, display, age, C : N and mycorrhizal associations.

A wealth of belowground data sets exist globally – including detailed soil and physical characteristics (described in Feddes *et al.*, 2001), and estimates of minimum, mean and maximum rooting depths (e.g. Canadell *et al.*, 1996; Schenk & Jackson, 2002) and root biomass, length and nutrient content (Jackson *et al.*, 1997) for different biomes. Characteristics of the root system most amenable to use in TBMs include root biomass, depth distribution, production and turnover, fine : coarse root ratios and nutrient content (Feddes *et al.*, 2001). Information on dynamic root functioning under varied environmental conditions, however, remains disparate, nonstandardized and dispersed. Certainly, there is an immense amount of data regarding root phenotypic plasticity to water, nutrient and temperature treatments for different species and different root anatomies and at various ontogenetic stages. For future application to TBMs, root functional data should be linked with scalable root traits whenever possible (Iversen, 2014), including covariate plant traits (e.g. height and leaf area) (McCormack *et al.*, 2012; Wullschleger *et al.*, 2014), and correlated to concurrent data collection of environmental conditions that regulate root function (e.g. root depth, soil temperature, texture, water content and nutrient availability, and atmospheric vapor pressure deficit).

Scaling root traits to the landscape level can be facilitated by leveraging the expansive research and data derived from existing (e.g. Fluxnet, LTER, and Critical Zone Observatories) and new (e.g. NEON and AnaEE) long-term ecological research sites (described by Peters *et al.*, 2014). Observational studies can be nested in plots within an ecosystem (Bradford *et al.*, 2010), within a watershed (Anderson *et al.*, 2010), or within the footprint of eddy covariance towers (Law *et al.*, 2006) to provide scaling across the landscape. Such nested studies provide a valuable framework to allow scaling of discrete mechanistic knowledge of root function to realized fluxes at the land surface.

7. Novel modeling platforms

Many TBMs have quite complex interlinked source files and algorithms that, when paired with earth system models, make testing of specific mechanistic process simulations slow and difficult (Wang *et al.*, 2014). In addition, the structure is not easy to assess or comprehend by nonmodelers, thereby excluding experimentalists from model development and improvement efforts. However, new initiatives to pull out specific functional parameters from TBMs are promising. For example, a new functional testing platform has been developed for CLM (the land component of the Community Earth System Model), which has successfully extracted the photosynthetic subunit from CLM for testing and modification, and includes a user-friendly graphical user interface (GUI) (Wang *et al.*, 2014). Both the extraction of belowground functional modules in current TBMs and the addition of new modules (e.g. FUN and RADIX) provide a pathway for inclusion of novel or refined root components that can lead to model improvements. In addition, TBMs can be run at the 'point' scale, using site-specific parameters to inform model PFTs, to understand processes operating in a plot or experimental manipulation (e.g. Ostle *et al.*, 2009; De Kauwe *et al.*, 2013; Zaehle *et al.*, 2014; Walker *et al.*, 2014).

An essential component to improve model representation of root functional processes is to partition function throughout the soil profile, similar to how some models treat the leaf canopy. Some TBMs are being improved to include more than energy or water dynamics in each soil layer by addition of C and N dynamics through the soil profile (e.g. CLM4.5; Koven *et al.*, 2013). Root dynamics should be progressively integrated into those multilayered soil formulations by moving beyond just a parameterized value of root distribution.

Specific model improvements might include the addition of spatial and temporal dynamics of root production and turnover, and water/nutrient uptake kinetics linked to refined functional classes of roots (i.e. based on traits such as length, diameter, order, display, age, C : N and mycorrhizal associations) that vary in their functional response to environmental conditions or internal signals. The distribution of roots might be seasonally and annually dynamic to proliferate into (or up-regulate function in) resource-rich areas, and diminish in stressful, resource-poor areas (e.g. Schymanski *et al.*, 2008). The differential root activity and turnover reflected by such a model could further be linked to rhizosphere microbial C and nutrient cycling processes.

IV. Conclusions

Interactions between plant roots and the surrounding soil environment (especially resource, environmental and biotic gradients with depth) are required to accurately represent root uptake of nutrients and water under changing environmental conditions, as well as plant C release to soils (Grant, 1998). Current model distribution of roots is usually static and discrete and thus is not representative of actual dynamic root exploration, function or turnover, nor linked to mechanistic biotic and biogeochemical cycling within the rhizosphere. Despite substantial mechanistic knowledge of root function, data assimilation, oversimplification and scaling issues continue to limit detailed representation of roots in TBMs. Development of well-documented, error-checked databases of root, soil and environmental dynamics are a priority that will be critical to porting mechanistic function into TBMs – key examples include the successful plant trait-based *TRY* (Kattge *et al.*, 2011) and photosynthetic *LeafWeb* (Gu *et al.*, 2010) databases. Emphasis should be placed on assessing model sensitivity to root processes, and then developing and refining the root modules and functional testing platforms to provide an improved mechanistic represention of root processes in TBMs (Fig. 5). Promising root processes that might be included in future modeling activities include dynamic root distribution, production and turnover, proportions of highly active, ephemeral roots, mycorrhizal associations, dynamic water and ion extraction, and hydraulic redistribution. In combination with new data compilation efforts, new model tools, and new model development, the representation of roots in TBMs is expected to continue to evolve and lead to advances in the predictive capacity of C, water and energy fluxes at the land surface.

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