

## Root Structural and Functional Dynamics in Terrestrial Biosphere Models – Evaluation and Recommendations

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## **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 is closely associated with control of plant water and nutrient uptake from the soil, plant 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.

## 1 I. Introduction

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

10

11 Notwithstanding the many important roles of roots, dynamic root functions are still largely  
12 absent in land surface models (Woodward and Osborne 2000, Ostle et al. 2009, Matamala and  
13 Stover 2013, Iversen 2014), hereafter referred to by the more inclusive term Terrestrial Biosphere  
14 Models (TBMs). Root representation in TBMs is rudimentary, with carbon allocation, root  
15 distribution, water uptake and nutrient (almost solely limited to nitrogen) extraction generally  
16 based on fixed parameters or plant demand, independent of dynamic root functionality. Key root  
17 attributes that are missing include the capacity of roots to shift distribution under changing  
18 environmental conditions, regulate water uptake (e.g., via aquaporins), regulate nutrient uptake  
19 (e.g., via enzyme-mediated Michaelis-Menten kinetics), or associate with mycorrhizal fungi. The  
20 limited representation of roots in TBMs is partially due to a lack of appropriate global root  
21 datasets, but also due to the fact that TBM representation of vegetation processes under current  
22 climatic conditions appears to work fairly well with little or no representation of roots. TBMs use  
23 of implicit parameters of bulk water and nutrient uptake independent of roots can correlate to  
24 total root uptake (Norby and Jackson 2000, Woodward and Osborne 2000, Feddes et al. 2001),  
25 and requires minimal root data or computational resources. Yet while the simplified models may  
26 be roughly adequate, they do not allow dynamic root functionality, and thereby (we believe)  
27 limit application to future environments, and limit mechanistic linkages that establish model  
28 validity. Without inclusion of root dynamics, the current representation of roots in TBMs may

29 not be sufficient to capture their roles in ecosystem function, nor adequate to understand  
30 potential controls that expressed root function may have in response to environmental change.

31  
32 Feddes et al. (2001) argued “that the functioning of roots [...] needs to receive more attention in  
33 land surface and climate modeling.” Model representation of canopy structure and function has  
34 progressed significantly (e.g. Mercado et al., 2007; Bonan et al., 2011; Loew et al., 2013) since  
35 the big-leaf approach cited by Feddes et al. (2001). Alternately, and with some notable  
36 exceptions (e.g., hydraulic redistribution of water, Lee et al. 2005; multi-process nitrogen uptake,  
37 Fisher et al. 2010), the representation of root structure and function in TBMs has seen only  
38 limited progress. Improved representation of root water uptake has stalled despite demonstration  
39 of model sensitivity to roots in climate and vegetation distribution simulations over a decade ago  
40 (Kleidon & Heimann, 1998, 2000; Hallgren & Pitman, 2000, Feddes et al. 2001).

41  
42 In contrast to simplified TBM’s that must represent the dynamics of roots associated with the  
43 entirety of the global land surface, mechanistic models at the scale of single root processes  
44 include the necessary complexity to capture water and nutrient uptake functions in response to  
45 environmental stimuli at quite high resolution in both space and time (Gardner 1960, Barber  
46 1962, Hillel et al. 1975, Raats 2007). Higher-order model development often makes simplifying  
47 assumptions about such processes, potentially missing a fundamental control point for plant  
48 function under varying resource availability.

49  
50 A whole universe of knowledge on root characteristics and functions exists that has not been  
51 exercised within TBMs. Novel nondestructive imaging techniques of roots have provided new  
52 insights in form and function of roots *in situ* (Fig. 2). Confocal laser microscopy has been used to  
53 assess dynamic gene expression of root initiation and cell growth within the root tissues (Busch  
54 et al. 2012, Vermeer et al. 2014). Linked studies of gene regulation, growth regulators,  
55 intercellular communication and tissue development have led to advances in mechanistic  
56 multiscale modeling that can be used to predict root phenotypes (Band et al. 2012). Actively  
57 controlled root membrane aquaporins have been identified as implicit control points for water

58 transfer across roots (Javot and Maurel 2002; Maurel et al. 2008). Next generation  
59 minirhizotrons are yielding unprecedented insight into fine-root and mycorrhizal exploration and  
60 turnover at high temporal resolution (Allen and Kitajima 2013), and have been paired with CO<sub>2</sub>  
61 sensors to allow concurrent measurements of respiration in situ (Vargas and Allen 2008).  
62 Neutron imaging has recently been used to assess in situ soil-root-rhizosphere hydration  
63 (Carminati et al. 2010) and individual root water uptake and transport dynamics (Warren et al.  
64 2013). Soil moisture sensors continue to evolve, and allow for highly precise measurements of  
65 root water extraction dynamics and hydraulic redistribution throughout the soil profile (e.g.,  
66 Warren et al. 2011). Such measurements provide insight into soil, rhizosphere and root  
67 resistances, data that can be used to refine models of physical flow of water through the soil-  
68 plant system (Gardner 1965, Sperry et al. 1998). Other root functional processes including C  
69 flux, water and ion uptake, water potential and rhizosphere nutrient competition have been  
70 elucidated using novel biosensors (Herron et al. 2010), isotope tracers (Bingham et al. 2000), and  
71 *in situ* field observations (Lucash et al. 2007). Despite this extensive knowledge of single root  
72 processes, the scaling of such processes spatially within the soil profile and across the landscape  
73 through time has not been achieved.

74  
75 The knowledge gap that exists in mechanistic model representation of root processes across  
76 scales (i.e., between roots, individual plants, ecosystems or land surfaces) is in part a  
77 consequence of inadequate datasets and the difficulty in linking root function to characteristic  
78 root traits, root distribution and root growth dynamics across landscapes (Fig. 3). For model  
79 veracity, simplified processes modeled in TBMs "...should be based on mechanistic  
80 understanding of the processes at lower scales..." (Schulze 2013) – an understanding that has not  
81 been well-translated for roots or root function. As such, the gap in knowledge transfer across  
82 scales leads to decreases in the expression of detailed root function as the predictive scale of the  
83 model increases (Ostle et al., 2009). To model climate and the Earth System, TBMs must  
84 simulate the land surface energy, water and carbon balances at broad spatial (e.g., km)  
85 resolutions and at timescales ranging from every 15 minutes to potentially several hundred years  
86 (Pitman, 2003). The models must therefore integrate across the microscopic (e.g., sub-mm) and

87 comparably short-term (e.g., seconds to minutes) scales relevant for actual root tissue function.  
88 Thus the *microscopic*, mechanistic approach of single root modeling is not readily scaled to the  
89 landscape, which led to development of *macroscopic*, bulk, sink-based modeling (Skaggs et al.,  
90 2006) at the plant or ecosystem scales.

91

92 This review considers how root function is represented by models across scales, ranging from  
93 single roots to whole land surfaces, and provides recommendations for improved representation  
94 of roots in TBMs. The current state of knowledge regarding root structure and function is  
95 considered, and the inherent and dynamic plasticity in those characteristics is described.

96 Leveraging this mechanistic knowledge, a focus was placed on identifying aspects of root  
97 structure and function that could affect root water and nutrient uptake dynamics in context of  
98 carbon cycling within TBMs. Specific targets for model improvement are noted. Since data are  
99 required for model parameterization and validation, data availability is examined as a limitation  
100 of the application of root function into models across scales. The scope of the review was limited  
101 to living root characteristics that directly affect whole plant function, including growth, and ion  
102 and water uptake. The indirect implications of root exudation, turnover and rhizosphere ecology  
103 (Young 1998, Cheng et al. 2014), while critically important, were not considered in this review.

104

## 105 **II. Current representation of root function in models**

### 106 1. Single root models of water and nutrient uptake

107

108 Single root water uptake occurs across a diversity of spatial scales requiring different approaches  
109 to best model water extraction. The microscopic approach involves physical first-principle  
110 mechanistic descriptions of radial flow to, and uptake by, individual roots (Hillel et al., 1975). In  
111 contrast, the macroscopic approach models uptake with a sink term in the Richards equation that  
112 ignores or implicitly averages uptake over a large number of roots (Skaggs et al., 2006). Early  
113 experimental and modeling work was carried out by Gardner (1960) where a root was modeled  
114 to be an infinitely long cylinder of uniform radius and water uptake characteristics. Although this  
115 formulation of root water uptake stimulated much research (Gardner, 1964 and 1965), it was



116 soon emphasized that it was not practical to develop field-scale models of water transport if flow  
117 to each individual root of a complete root system must be considered (Molz and Remson, 1970;  
118 Molz, 1981). Thus, various extraction term models have been developed where the fundamental  
119 premise is to describe root water uptake for the rooting zone rather than individual roots. In these  
120 models, soil-root processes are generally reduced to a root sink term that is incorporated into a  
121 detailed description of soil water balance (Doussan et al., 2006).

122  
123 Classical models of nutrient acquisition at the scale of a single root have provided many insights  
124 into the complex dynamics that occur at the root-soil interface. Early pioneering research by  
125 Barber (1962), Nye (1966), and Nye and Marriott (1969) indicated that nutrient uptake could be  
126 modeled as a single cylindrical root in an infinite extent of soil, where diffusion and mass flow  
127 supply nutrients to the root absorbing surface (Rengel, 1993). In most models that derive from  
128 the Nye-Barber framework, the central hypothesis is that the driving force of nutrient acquisition  
129 is the absorption of nutrients by the root, which results in a decrease in nutrient concentration at  
130 the surface of the root, leading to a diffusion gradient and movement of nutrients in the soil pore  
131 water (Hinsinger et al., 2011). Although early models were confirmed by kinetic studies using  
132 plants grown in hydroponic culture, the difference between nutrient acquisition between well-  
133 stirred solution and heterogeneous soil are large (Rengel, 1993). As a result, uptake can be  
134 overestimated by these models because nutrient concentrations calculated at the root surface may  
135 be too high.

136  
137 While the pioneering studies of single-root water and nutrient uptake established the modeling  
138 framework for basic root resource acquisition, a wealth of new knowledge from genomic to  
139 cellular to whole root scales has emerged over the last several decades and improved our  
140 understanding of root structure and function (Fig. 1, 2). These insights offer novel understanding  
141 of single root functional plasticity that might be leveraged into better representation in TBMs (as  
142 discussed later).

143

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

145 Whole-plant models require more sophisticated approaches and involve a higher level of  
146 complexity in the description of root structure and function than single root models. These  
147 approaches include an expanded consideration of how photosynthate is allocated to roots given  
148 competing sinks, and how the processes of root tip initiation, branching, and geotropism give rise  
149 to three-dimensional patterns of root distribution in soils (e.g., Thaler and Pagès, 1998, Ge et al.  
150 2000).

151  
152 Various models have been developed over the last 25 years to describe the structure and function  
153 of whole plant root systems (Clausnitzer and Hopmans, 1994; Jourdan and Rey, 1997; Spek,  
154 1997; Dupuy et al., 2007; Dupuy et al. 2009, Schnepf et al., 2012). Five models in particular  
155 stand out as addressing the comprehensive suite of processes that govern photosynthate  
156 allocation to root growth, root system architecture, and acquisition of water and nutrients from  
157 heterogeneous soils (Table 1). These models simulate the production of daily photosynthate and  
158 its allocation to plant organs based on general source-sink concepts (Franklin et al., 2012).  
159 Growth and respiration of leaves, stems, and roots are often represented as competing sinks for  
160 photosynthate. The SPACSYS model (Wu et al., 2007) is an exception in that roots receive  
161 photosynthate with the highest priority, followed by leaves then by stems. Interestingly, several  
162 models include options for allocation of photosynthate (Table 1). Most notable is the scheme  
163 implemented in Root Typ (Thaler and Pagès, 1998), where allocation can be modeled either as a  
164 function of competing sinks (i.e., without priorities) or where photosynthate is totally allocated to  
165 meet the demands of all plant organs. Each of the root growth models described in Table 1 can  
166 provide realistic spatial complexity of root system architectures consisting of distinct root  
167 classes (Wu et al., 2007; Pagès et al., 2004; Postma and Lynch, 2011a), where each root is  
168 represented by a growing number of root segments interacting with the soil. Comparison of  
169 model results with visual images from excavated plants (Clausnitzer and Hopmans, 1994; Pagès  
170 et al., 2004; Wu et al., 2007) and measured root density by depth (Somma et al., 1998) provide  
171 encouraging support for the realism and utility of these simulations.

172

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

186  
187 Two or three-dimensional modeled root architecture frameworks could be further refined to  
188 allow differential plasticity in growth and function that might be incorporated into future models,  
189 especially if dynamic root water and nutrient uptake capacity could be assigned based on root  
190 age, root order, or differential hydraulic conductivity (Valenzuela-Estrada et al. 2008). Indeed,  
191 two-dimensional bulk soil water uptake has been successfully modeled as a series of resistances  
192 through the soil, root, plant and atmosphere continuum, regulated by water potential gradients  
193 and verified with field data (Sperry et al. 1998, Hacke et al. 2000, Wang et al. 2002, Manzoni et  
194 al. 2013). Manoli et al. (2014) introduced a three-dimensional model based on pathway  
195 resistances that includes hydraulic redistribution and that allows root systems of multiple trees to  
196 compete for water extraction from different soil layers. Such models are noteworthy in that they  
197 retain first principle, physics-based *Darcian* water flow at the stand level, while allowing  
198 dynamic root functionality under drying conditions, a feature often lost in ecosystem models.

199

200 3. Ecosystem models

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

215  
216 In order to represent the interaction of roots with aboveground plant parts and the surrounding  
217 soil environment (Fig. 1), ecosystem models must represent the functional balance of carbon  
218 partitioning belowground to root growth, the distribution of roots throughout the soil, active root  
219 functions, and the changes in partitioning and root distribution in response to changing  
220 environmental conditions (Grant, 1998). Accurate model representation of root function and its  
221 importance to land surface fluxes of carbon, water and nutrients is dependent on *how many* roots  
222 there are, *where* roots are in the soil profile, and *which* roots are active. Unfortunately, the  
223 different approaches taken with plant- and ecosystem-scale models appear to have created a gap  
224 through which the representation of roots, and in particular, root function, has fallen. Some  
225 ecosystem-scale process models and TBMs do not explicitly represent fine roots (Hanson et al.  
226 2004), while in others, root representation is cursory, or solely to extract water from the soil.  
227 Figure 4 describes model inclusion of various root processes, including root production and  
228 structure, and if structure is linked to water or nutrient uptake.

229

230 In ecosystem models, plant water and nutrient uptake is usually empirically-derived from  
231 functional or allometric drivers rather than mechanistically propagated based on tissue function  
232 and energy expenditures (Hopmans & Bristow, 2002). N uptake from the soil profile is rarely  
233 modeled in a way that depends on root properties (Table 2), although for some models N uptake  
234 requires respiratory energy (Hopmans & Bristow, 2002, Fisher et al. 2010) that indicates linkages  
235 to C partitioning belowground to fulfill root demand. Mycorrhizae have a large role in nutrient  
236 acquisition by plants but their inclusion in root models is rare, although they are explicitly  
237 represented in the detailed *ecosys* model (Grant, 1998), and implicitly represented in the *Fixation*  
238 *and Uptake of Nitrogen* (FUN) root module as an extension of the root system (e.g., Fisher et al.,  
239 2010), and now explicitly represented in FUN 2.0 (Brzostek et al. in review).

240  
241 There are several distinct types of ecosystem models that vary in their treatment of root function:

242  
243 (1) Simple modules focused on one aspect of the ecosystem that might be incorporated into  
244 TBMs. For example, the Radix model estimates growth and turnover for various root classes in  
245 context of internal C partitioning (Riley et al., 2009; Gaudinski et al. 2010) – such a model might  
246 be leveraged to allow water and nutrient uptake dynamics from roots of different functional ages.  
247 Another module, the FUN model simulates N availability and uptake based on internal C and N  
248 availability, root microbial associations, water use and environmental conditions (Fisher et al.,  
249 2010). This N module includes passive and active ion uptake kinetics, requiring substantial  
250 respiratory energy. The model framework applies detailed ecophysiological processes to simulate  
251 N uptake and internal cycling. FUN can be run as a stand-alone module or applied within TBMs  
252 (e.g., JULES; Fisher et al., 2010), and ongoing work will leverage FUN into additional TBMs  
253 including CLM 4.5, Noah-MP and LPJ.

254  
255 (2) Whole-ecosystem models that vary in the complexity of their representation of ecosystem  
256 processes (e.g., *Ecosys* (Grant 1998), G'DAY (McMurtrie et al. 2000), SPA (Williams et al.  
257 1996) and TEM (Raich et al. 1991)). These four ecosystem models include representation of a  
258 range of root-specific processes, based in large part on the initial ecosystem and questions

259 devised by the developers (detailed in Table 2). The models include the highly complex *ecosys*  
260 model that has detailed root architecture, production and mycorrhizal colonization that can  
261 respond to changing water and nutrient availability (Grant, 1998). Root water uptake in *ecosys* is  
262 a function of water content, and root radial and axial resistances – the latter allows for expression  
263 of dynamic root function (resistance) that can control water uptake (Grant, 1998). The *ecosys*  
264 model can also differentiate nitrogen sources ( $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$ ) and includes phosphorus (P)  
265 cycling, whereas most other models focus solely on nitrogen. At the opposite end of the  
266 spectrum, the TEM model operates at coarse temporal and spatial scales, with focus on C and N  
267 balance in soils and vegetation (Reich et al. 1991) (Table 2). There are no roots or root functions  
268 present in the model. Water use is based on a water balance sub-model that includes broad site  
269 characteristics including vegetation type, soils and climate. N uptake is based primarily on  
270 availability, and C:N uptake costs.

271  
272 (3) Optimization models attempt to avoid the pitfalls of extensive parameterization (e.g., May,  
273 2004) by focusing on a few analytic expressions. One example is *MaxNup*, which optimizes the  
274 vertical distribution of root biomass throughout the soil profile to maximize annual N supply to  
275 aboveground plant organs (McMurtrie et al., 2012). This type of annual optimization is apparent  
276 in other ‘demand’ based models, which provides a limited framework for addition of root  
277 functional dynamics.

278

#### 279 4. Terrestrial biosphere models (TBMs)

280

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

287

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

296  
297 **Water uptake in TBMs** As in the ecosystem models, water uptake in TBMs operates at the  
298 macroscopic scale, determined by supply and demand. Uptake is described by a sink term in the  
299 volumetric mass balance (Raats, 2007) rather than explicitly simulating the root-soil interface as  
300 described in the *single root* and *individual plant* scale model sections. Plant water demand is  
301 calculated as a function of atmospheric vapor pressure deficit and a series of water transport  
302 resistances caused by stomata, leaf and atmospheric boundary layers, and in some cases  
303 includes modeled root and stem resistances (Table 3) (e.g., SPA (Williams et al. 2001), CLM4.5  
304 (GB Bonan, unpublished)). When sufficient water is available, water uptake is simulated based  
305 on the plant water demand with rooting distribution or absolute rooting depth used to determine  
306 the location within the soil column of water taken up by the plant. Substantial amounts of data on  
307 global root distributions are available (e.g., Jackson et al. 1996, Schenk and Jackson 2002), and  
308 root distribution is the most widely included root component in TBMs.

309  
310 When insufficient water is available to meet demand, TBMs model uptake as a function of water  
311 supply, rather than allowing for mechanistic reduction in root conductivity. Most often, supply  
312 limited uptake is simulated by multiplying physiological variables with a soil water stress scalar  
313 (0-1, often referred to as  $\beta$ ), which serves to reduce demand (Feddes et al. 1978, Verhoef and  
314 Egea 2014). The ' $\beta$ ' soil water limitation factor can be represented as a piecewise linear function  
315 of soil water matric potential, matric potential at wilting point (e.g.,  $\psi_{wp} = -1.5$  MPa) and matric  
316 potential at a critical point below which supply limitation begins (e.g.,  $\psi_{fc} = -0.033$  MPa). Some

317 TBMs (e.g. CLM, Oleson et al. 2010) simulate  $\beta$  as a function of matric potential in relation to  
318 when stomata are fully open or closed, while others (e.g. JULES (Clark et al. 2011) and CABLE  
319 (Wang et al., 2010)) simulate  $\beta$  as function of soil water content ( $\theta$ ). Due to the strongly non-  
320 linear relationship between  $\psi$  and  $\theta$  (soil water retention curves), the two formulations allow for  
321 very different supply limitation of soil water uptake. In addition, since the retention curves can  
322 vary dramatically within a single profile due to changes in soil physical characteristics, relative  
323 soil water availability for heterogeneous soils is not well expressed by a single relationship  
324 (Warren et al. 2005), indicating a need for model parameterization of multiple soil layers  
325 simultaneously where data exist.

326

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

338

339 **Nitrogen uptake in TBMs** Root nitrogen (N) uptake in TBMs is also simulated at the  
340 macroscopic scale by using available soil N concentrations. N uptake is simulated primarily as a  
341 function of supply and often demand, as in CLM or CABLE (Thornton et al., 2007; Wang et al.,  
342 2010), though the implementation varies across models far more than the implementation of  
343 water uptake. Most TBMs integrate soil carbon and N cycling throughout the entire soil profile,  
344 thus N uptake is from bulk soil regardless of root or N distributions within the profile, although



345 new multi-layer biogeochemical cycling algorithms are becoming available for some models  
346 (e.g. CLM4.5; Koven et al., 2013).

347  
348 Some TBMs use root mass as a proxy for root length density, and formulate N uptake as a linear  
349 function of root mass (e.g., LM3 (Gerber et al., 2010), LPJ-GUESS (Smith et al., 2013) and O-  
350 CN (Zaehle & Friend, 2010)). The linear dependence of N uptake on root mass contrasts with the  
351 optimality formulation of McMurtrie et al. (2012), whereby a saturating relationship of N uptake  
352 to root mass results from over-lapping nutrient depletion zones vertically within the soil profile  
353 as root mass increases. Models use of biomass only, without knowledge of root anatomical or  
354 functional distribution has limited ability to indicate differences between species within a plant  
355 functional type (PFT). Linking biomass to function through structure is thus a key area for  
356 improvement.

357  
358 The LM3 and O-CN models employ a Michaelis-Menten kinetic function of N uptake, but one  
359 that saturates as N supply increases. Thomas et al. (2013) modified the N dynamics of CLM4,  
360 improving model accuracy at simulating N addition experiments. They showed that a key model  
361 development leading to the improvement was the implementation of Michaelis-Menten kinetics  
362 saturating with N supply and linearly dependent on root mass.

363  
364 A number of models, e.g., LPJ-GUESS (Smith et al., 2013), O-CN (Zaehle & Friend, 2010),  
365 CLM4 (Thomas et al. 2013), also simulate N uptake as a function of temperature to account for  
366 the effect of temperature on metabolic rates. However, none of the models surveyed simulate N  
367 uptake as a function of soil water content despite the importance of water for rhizosphere  
368 nutrient cycling, for mass flow and diffusion of N to the root surface (de Willigen and van  
369 Noordwijk, 1994; Cardon et al. 2013), and for oxygen dependence of metabolic rates.

370  
371 **Root production in TBMs** Root growth, production and activity are dependent on carbon  
372 partitioning belowground. There are a variety of different approaches to model C partitioning  
373 within plants (Table 3) (Franklin et al. 2012). One promising approach (functional balance)

374 recently best represented temperate forest carbon partitioning in two Free Air CO<sub>2</sub> Enrichment  
375 (FACE) experiments (DeKauwe et al. 2014). Functional balance approaches partition carbon to  
376 various tissues to balance resource acquisition (Franklin et al., 2012), thus mechanistic model  
377 improvements to allow root functional nutrient or water uptake would be dependent on  
378 partitioning of carbon belowground. Representation of root function will also be necessary to  
379 implement optimization schemes for partitioning in TBMs, similar to that developed by  
380 McMurtrie & Dewar (2013). Flexible partitioning schemes allow vegetation turnover to vary due  
381 to the different turnover times of different tissues.

382  
383 Model inclusion of carbon allocation through roots to mycorrhizae and exudates may be a  
384 parameter that could allow model plasticity of belowground functional dynamics, since these  
385 rhizosphere processes have direct linkages to water and nutrient uptake and carbon cycling. For  
386 example, observed increases in N uptake in response to elevated CO<sub>2</sub> were not explained by 11  
387 ecosystem models (Zaehle et al. 2014) suggesting the need for additional processes by which  
388 plants can stimulate N uptake through expanded effective root surface area, deeper soil mining  
389 (Iversen et al. 2010, McMurtrie et al. 2012) and 'priming' of nutrient cycling (Drake et al. 2011,  
390 Cheng et al. 2014). Focused root 'modules' incorporated into TBMs may allow a pathway for  
391 dynamic root allocation and uptake. Indeed, the FUN nitrogen fixation module indicates  
392 increased root production under elevated CO<sub>2</sub> FACE studies (J. Fisher, personal communication),  
393 in agreement with observations, while balancing the C cost of root N uptake with other  
394 respiratory and growth demands.

### 395 396 **Integration of detailed soil hydrologic and biogeochemical transport models into TBMs**

397 While ecosystem models and TBMs were developed with a strong plant functional component,  
398 there has also been significant model development of sub-surface reactive transport dynamics in  
399 the absence of vegetation (and roots). Modeling unsaturated water flow within the vadose zone is  
400 achieved by mathematical approximations of one- three dimensional Richard's equations (similar  
401 in structure to Darcy's Law describing saturated flow in soils and plant xylem). More recently  
402 root water extraction has been added as a sink term into these detailed, highly computational

403 numerical models (Vrugt et al. 2001; Javaux et. al. 2008), which allows them to be linked into  
404 TBMs. In these sub-surface hydrology models the flow of water from soil to root xylem ‘tubes’  
405 is often modeled as simple one dimensional radial flow (Amenu and Kumar 2008; Schneider et.  
406 al 2010), although since hydraulic conductivity changes at the soil-root interface (e.g., Carminati  
407 et al. 2010) more accurate models have included an interfacial conductivity within the  
408 rhizosphere (e.g., Katul et al. 2012). Modeling efforts that include rhizosphere resistance as a  
409 microscopic soil-root hydraulic conductivity drop function can improve modeled dynamics of  
410 water transport into roots, while actually reducing the computational time (Schroder et. al, 2008,  
411 2009).

412  
413 There are encouraging efforts to pair these detailed numerical reactive transport models with  
414 vegetation models at the landscape level. The models have primary focus on improving surface  
415 and subsurface hydrological components and often include detailed soil characteristics,  
416 topography and differential water table depths (e.g., Rihani et al. 2010, Shi et al. 2013).  
417 Sivandran and Bras (2013) implemented multi-layered dynamic root distribution within a  
418 vegetation model (VEGGIE) coupled with a hydrologic model (tRIBS). The model dynamically  
419 allocates carbon to roots at different soil layers to maximize transpiration. Simulations agreed  
420 with catchment data at hourly timescales, indicating the utility for inclusion of detailed numerical  
421 models in TBMs. PIHM (Qu and Duffy 2007) is a fully coupled 2-D hydrological model that has  
422 been validated with extensive data at the Shale Hills Critical Zone Observatory and paired with a  
423 land surface model based on the Noah LSM (Shi et al. 2013). These models include root  
424 biomass-weighted water extraction by layer, and successfully simulate soil hydraulic parameters  
425 and watershed discharge. Another reactive transport model, PFLOTRAN (Mills et al. 2007) has  
426 been specifically designed to scale 3-D numerical hydrological modeling using parallel  
427 supercomputing. PFLOTRAN is currently being linked to the CLM TBM to achieve fully-  
428 coupled detailed hydrological dynamics at the land surface scale. Despite a similar lack of root  
429 functional attributes in these hydrological models, they greatly improve mechanistic modeling of  
430 the subsurface environment, which allows for expanded knowledge of spatial dynamics of water  
431 availability. In turn, roots overlaid across the heterogeneous two-dimensional grids or three-

432 dimensional voxels in these models could be allowed step-wise increases in dynamic  
433 functionality, which would greatly expand their role as a critical control point in subsurface and  
434 surface ecosystem functions. The coupling of detailed subsurface models with TBMs is expected  
435 continue to evolve as computational limitations diminish.

436

### 437 **III. Recommendations for leveraging root knowledge into models**

438

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

457         Unfortunately, there is not a good understanding of TBM model sensitivity to root  
458 function; i.e., if inclusion of mechanistic root functions in models could improve model  
459 performance within the current model framework, although studies that have included more root

460 parameters have yielded better results (e.g., inclusion of dynamic root area (Schymanski et al.,  
461 2008) or hydraulic redistribution (Lee et al. 2005)).

462  
463 In the following section we assess how our current mechanistic knowledge of root function  
464 interacts with and determines ecosystem function, and suggest what should be taken into  
465 consideration when modeling roots in TBMs. Areas of discussion include root distribution and its  
466 utility for scaling, linking root traits to root functions, key regulatory factors such as water  
467 uptake kinetics (including hydraulic redistribution) and nutrient uptake kinetics, data availability,  
468 and strategies for model improvement. Figure 5 provides a framework for root data and model  
469 assessment, and how we might proceed towards improved models or novel stand-alone root  
470 modules that could be embedded within TBMs.

471

#### 472 1. Scaling root function using root architecture

473

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

487

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

500

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

512

## 513 2. Linking root function to traits

514

515 Plant species responses to resource availability vary due to differences in competitive strategies  
516 (Hodge et al. 2004). In context of drought, some species have adapted growth of deep roots to

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

540

541 Key root functional traits to consider for models are root morphology, chemistry and microbial  
542 associations, since they control dynamics of water and nutrient ion flux through the soil into  
543 roots under varying environmental conditions (Figs 1, 5). The white, ephemeral first and second  
544 order roots are the predominant pathway for water and nutrient uptake (Steudle 2000, Guo et al.  
545 2008, Rewald et al. 2011), although coarser suberized woody roots also provide a persistent, yet

546 lower uptake pathway that may be important for seedlings (Hawkins et al. 2014), or seasonally  
547 during periods of low fine root growth or activity (Van Rees and Comerford 1990, Lindenmair et  
548 al. 2004), and which may be associated with sustained root rhizosphere hydration through  
549 hydraulic redistribution (Rewald et al. 2011). Root hairs and mycorrhizal associations can  
550 enhance the effective surface area of the root system and increase the potential for resource  
551 extraction in many species (Read & Boyd 1986; Augé, 2001, Segal et al. 2008).

552  
553 Refinement of the ‘fine:coarse’ root ratios used in some models should reflect root function, not  
554 just root size, which varies by species. Root orders, and their function can be characterized  
555 indirectly by relative degree of mycorrhizal colonization, root density or root C:N ratio  
556 (Valenzuela-Estrada et al. 2008). Root lifespan is another key root attribute that might be  
557 correlated with these and other root traits such as diameter, depth (Pritchard and Strand 2008),  
558 specific root length (McCormack et al. 2012) or root and aboveground traits together (root  
559 diameter and plant growth) as found in twelve temperate tree species (McCormack et al. 2012).  
560 Knowledge of root traits can be used to improve models of water or nutrient uptake kinetics  
561 (e.g., refining active root absorbing area, or classifying root function in the FUN N uptake  
562 module), add functionality to existing modules of root turnover (e.g., Radix ), and to provide  
563 scalable trait data for novel root functional representation in TBMs (Fig. 3).

564  
565 3. Water uptake

566  
567 The process of root water uptake includes some regulatory steps that could be included in TBMs.  
568 Under moist soil conditions, radial resistance limits root water uptake and is actively controlled  
569 by membrane bound transport proteins (aquaporins) that respond to osmotic gradients  
570 (Chrispeels et al. 1999, Steudle 2000, Aroca et al. 2012). Under drying conditions water uptake is  
571 regulated by varying soil and plant resistances to water movement (Blizzard and Boyer 1980,  
572 Sperry et al. 1998, Hacke et al. 2000). Radial hydraulic conductivity through aquaporin  
573 regulation can be rapidly increased or decreased based on perceived environmental stimuli  
574 including mycorrhizal colonization (Lehto and Zwiazek 2011) or suboptimal environmental



575 conditions (e.g., drought, temperature, anoxia; Siemens and Zwiazek 2004). Indeed, deep roots  
576 in wet soils upregulated aquaporins during drought, increasing hydraulic conductivity  
577 substantially as shallow root conductivity declined (Johnson et al. 2014). Root stress responses  
578 are often reflected in production and accumulation of abscisic acid (ABA) or other plant growth  
579 regulators (Davies and Zhang 1991; Wilkinson and Davies 2002; Aroca et al. 2012). Root  
580 derived plant regulators or mycorrhizal-derived inorganic ions can be transported through the  
581 xylem to elicit a response in the leaves, particularly stomatal closure (Davies et al. 1994).  
582 Similarly, two-way hydraulic signaling also connects root and shoot functions allowing  
583 coordinated whole plant response to changing soil or atmospheric conditions (e.g., Blackman and  
584 Davies 1985, Comstock 2002, Meinzer 2002, Vandeleur et al. 2014). Pathway resistances are  
585 included in some TBMs, however, none to our knowledge have active regulation based on  
586 aquaporin expression, which could provide a mechanistic control on water use and improve  
587 model performance, similar to application of a dynamic ABA parameter on the water stress  
588 scalar,  $\beta$ , as described earlier.  $\beta$  is an obvious target for providing dynamic, albeit indirect,  
589 functionality to water uptake since it already exists in many models, and would be particularly  
590 useful if weighted by root *functional* class (e.g., age, order, morphology) within each soil layer.

591

#### 592 4. Hydraulic redistribution

593

594 Hydraulic redistribution (HR) can maintain fine root function (Domec et al. 2004), extend root  
595 life (Bauerle et al. 2008), rehydrate the rhizosphere (Emerman and Dawson 1996), enhance  
596 nutrient availability (Cardon et al. 2013) and acquisition (Matimati et al. 2014), and should  
597 prolong soil-root contact under dry conditions. HR's contribution to total site water use is known  
598 to vary widely depending on the ecosystem (Neumann and Cardon 2012); yet even minor HR  
599 can provide significant benefits for continued root and mycorrhizal function during drying  
600 conditions. HR has been represented by variation in water transport between soil layers, dynamic  
601 soil-plant-atmosphere resistances, radial/axial conductivity *big root* models, and root optimality  
602 models (Neumann and Cardon 2012). Results indicate that the inclusion of HR can help explain  
603 patterns of soil and plant water flux for individual trees (e.g., David et al. 2013), resulting in

604 significant implications for stand- (Domec et al. 2010) and landscape-scale (Lee et al. 2005,  
605 Wang et al. 2011) carbon uptake and water release. Application to the large-scale models  
606 included HR as an additional water flux term in the NCAR Community Atmospheric Model  
607 Version 2 (CAM2) coupled with the Community Land Model (CLM) (Lee et al. 2005) and in  
608 CLM3 coupled with a dynamic global vegetation model (CLM3-DGVM) (Wang et al. 2011).  
609 Results suggest inclusion of HR can increase dry season water use in the Amazon forests by 40%  
610 (Lee et al. 2005), but may exacerbate plant water stress under extended drought if soil water is  
611 exhausted (Wang et al. 2011) – both efforts illustrate how a small change in root function can  
612 result in substantial implication for global scale. HR is a process that should be included in large-  
613 scale models, but it will require consideration of depth specific soil-plant water dynamics,  
614 internal competition for water within the plant vascular system (Sperry et al. 1998), plant water  
615 capacitance (Scholtz et al. 2007) and nocturnal transpiration (Caird et al. 2007, Dawson et al.  
616 2007, Fisher et al. 2007, Zeppel et al. 2012) to account for concurrent uptake and release  
617 dynamics (Neumann and Cardon 2012).

618

#### 619 5. Ion uptake kinetics

620

621 Mineral ions are transported into the root cortex via mass flow, diffusion, or through mycorrhizal  
622 absorption, which is particularly important for uptake of immobile nutrients such as phosphorus.  
623 Movement through the plasma membrane of root endodermal cells is facilitated by a variety of  
624 passive or active transport proteins, including ATP-fueled ion pumps (Chrispeels et al. 1999). Ion  
625 absorption kinetics vary by species depending upon the nutrient concentration, with multiple low  
626 and high affinity mechanisms controlled by environmental conditions (Epstein 1966, Chapin  
627 1980, Chrispeels et al. 1999, BassiriRad 2000). Root nutrient uptake kinetics are often measured  
628 on intact or excised roots under well hydrated conditions, i.e., not under water stress. In drought  
629 tolerant woody sagebrush, nitrogen and phosphorus uptake rates were maintained or even  
630 increased under laboratory water potential stress, illustrating the uncoupling of water and  
631 nutrient flux into the root (Matzner and Richards 1996). Under drying conditions, *in situ* nutrient  
632 absorption does not appear to be limited by uptake kinetics, but rather by diffusion of ions

633 through the soil to the root surface (Chapin 1980). Mycorrhizae can span soil-root gaps and help  
634 to maintain a viable transport pathway from soil to root under drying conditions.

635

636 Absolute uptake kinetics for specific ions are thus a function of a variety of control points.  
637 Improved mechanistic representation of ion uptake in models will require inclusion and  
638 expanded consideration of Michaelis–Menten kinetics used in some TBMs (Fig. 4). One key  
639 improvement would be to allow the kinetics to vary by depth in response to environmental  
640 conditions such as temperature or soil water content (i.e., through the  $\beta$  stress scalar), weighted  
641 by specific root traits and root functional classes. Root hydraulic conductivity (i.e., aquaporin  
642 function) is often upregulated by soil ion concentrations such as nitrate, resulting in whole plant  
643 hydraulic signaling (Gorska et al. 2008, Cramer et al. 2009), increased root uptake kinetics  
644 (Jackson et al. 1990) and proliferation of roots in resource rich areas (reviewed in Hodge et al.  
645 2004). Such plasticity in function might require a multicomponent ion uptake kinetic model that  
646 includes the appropriate regulatory and substrate parameters. One modeling framework to  
647 consider involves a modification of the HYDRUS reactive transport model. The model was  
648 modified to allow a ‘root adaptability factor’ which compensates for reduced water and nutrient  
649 uptake by stressed roots in resource poor areas by increasing uptake of roots in unstressed soil  
650 (Šimůnek and Hopmans 2009). Such efforts to refine existing models through use of dynamic  
651 scalars allows improved approximation of the processes inherent in more complex models,  
652 without the necessity of novel modeling frameworks and collection of additional data.

653

## 654 6. Available Root data – a Serious Limitation

655

656 A fine balance exists between accurately representing ecological processes, and the added  
657 uncertainty that comes with model complexity in terms of appropriate and accurate  
658 parameterization, which may require regional or global data sets (Fisher et al., 2010). A  
659 concentrated effort needs to be made to fill the gaps in the trait database to obtain accurate  
660 representation of the trait space of terrestrial plants and ecosystems. There is a need for  
661 development of databases across PFTs of both root distribution, root structure and root functional

662 traits that are linked to specific plant responses to environmental conditions. Recent investigation  
663 of root traits of 96 subtropical angiosperm trees illustrates the broad variation and plasticity in  
664 traits within a single PFT (Kong et al. 2014), as well as the necessity to identify trait covariance  
665 and linkages to function (Iversen 2014). Key root traits to compile into databases include length,  
666 diameter, order, display, age, C:N and mycorrhizal associations.

667  
668 A wealth of belowground datasets exist globally – including detailed soil and physical  
669 characteristics (described in Feddes 2001), and estimates of minimum, mean and maximum  
670 rooting depths (e.g., Canadell 1996; Schenk and Jackson 2002) and root biomass, length and  
671 nutrient content (Jackson et al. 1997) for different biomes. Characteristics of the root system  
672 most amenable to use in TBM's include root biomass, depth distribution, production and  
673 turnover, fine:coarse root ratios and nutrient content (Feddes 2001). Information on dynamic root  
674 functioning under varied environmental conditions, however, remains disparate, non-  
675 standardized and dispersed. Certainly, there is an immense amount of data regarding root  
676 phenotypic plasticity to water, nutrient and temperature treatments for different species, different  
677 root anatomies and at various ontogenetic stages. For future application to TBMs, root functional  
678 data should be linked with scalable root traits whenever possible (Iversen 2014), including  
679 covariate plant traits (e.g., height, leaf area)(McCormack et al. 2012, Wullschleger et al. 2014),  
680 and correlated to concurrent data collection of environmental conditions that regulate root  
681 function (e.g., root depth, soil temperature, texture, water content and nutrient availability,  
682 atmospheric vapor pressure deficit, etc.)

683  
684 Scaling root traits to the landscape level can be facilitated by leveraging the expansive research  
685 and data derived from existing (e.g., Fluxnet, LTER, Critical Zone Observatories) and new (e.g.,  
686 NEON, AnaEE) long term ecological research sites (described by Peters et al. 2014).

687 Observational studies can be nested in plots within an ecosystem (Bradford et al. 2010), within a  
688 watershed (Anderson et al. 2010), or within the footprint of eddy covariance towers (Law et al.  
689 2006) to provide scaling across the landscape. Such nested studies provide a valuable framework

690 to allow scaling of discrete mechanistic knowledge of root function to realized fluxes at the land  
691 surface.

692

## 693 7. Novel modeling platforms

694

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

709

710 An essential component to improve model representation of root functional processes is to  
711 partition function throughout the soil profile, similar to how some models treat the leaf canopy.  
712 Some TBMs are being improved to include more than energy or water dynamics in each soil  
713 layer by addition of C and N dynamics through the soil profile (e.g., CLM4.5; Koven et al.,  
714 2013). Root dynamics should be progressively integrated into those multilayered soil  
715 formulations by moving beyond just a parameterized value of root distribution.

716

717 Specific model improvements might include the addition of spatial and temporal dynamics of  
718 root production and turnover, and water/nutrient uptake kinetics linked to refined functional

719 classes of roots (i.e., based on traits such as length, diameter, order, display, age, C:N and  
720 mycorrhizal associations ) that vary in their functional response to environmental conditions or  
721 internal signals. The distribution of roots might be seasonally and annually dynamic to  
722 proliferate (or upregulate function) into resource rich areas, and diminish in stressful, resource  
723 poor areas (e.g., Schymanski et al. 2008). The differential root activity and turnover reflected by  
724 such a model could further be linked to rhizosphere microbial carbon and nutrient cycling  
725 processes.

726

#### 727 **IV. Conclusions**

728

729 Interactions between plant roots and the surrounding soil environment (especially gradients,  
730 distributions, and functions with depth) are required to accurately represent root uptake of  
731 nutrients and water under changing environmental conditions, as well as plant C release to soils  
732 (Grant, 1998). Current model distribution of roots is usually static and discrete and thus is not  
733 representative of actual dynamic root exploration, function or turnover, nor linked to mechanistic  
734 biotic and biogeochemical cycling within the rhizosphere. Despite substantial mechanistic  
735 knowledge of root function, data assimilation, oversimplification and scaling issues continue to  
736 limit detailed representation of roots in TBMs. Development of well-documented, error-checked  
737 databases of root, soil and environmental dynamics are a priority that will be critical to porting  
738 mechanistic function into TBMs – key examples include the successful plant trait-based *TRY*  
739 (Kattage et al. 2011) and photosynthetic *LeafWeb* (Gu et al. 2010) databases. Emphasis should be  
740 placed on assessing model sensitivity to root processes, then development and refining the root  
741 modules and functional testing platforms that can lead to improved mechanistic representing of  
742 root processes in TBMs (Fig. 5). Promising root processes that might be included in future  
743 modeling activities include addition of dynamic root distribution, production and turnover,  
744 proportions of highly active, ephemeral roots, mycorrhizal associations, dynamic water and ion  
745 extraction, and hydraulic redistribution. Paired with new data compilation efforts, new model  
746 tools, and new model development, the representation of roots in TBMs is expected to continue

747 to evolve and lead to advances in predictive capacity of carbon, water and energy fluxes at the  
748 land surface.

749

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- 1280

1281 **Figure Titles**

1282

1283 **Figure 1.** Diagram of the structural and functional characteristics of fine roots of plant root  
1284 systems, and their interaction with the soil rhizosphere. Developing fine roots contain zones of  
1285 active growth and function and zones where changes in anatomical tissue reduces root functions  
1286 such as water or nutrient uptake. Water and solutes can move passively through the apoplast of  
1287 the epidermis, cortex and young developing endodermis to the central vascular tissue. As the root  
1288 tissue matures endodermal cell walls become suberized, at which point water and nutrients  
1289 uptake into the symplast is regulated by passive or active transport proteins, such as aquaporins  
1290 (water) or ion-pumps (mineral nutrients). Functionality of fine roots varies with characteristic  
1291 morphological traits that are specific to species, and that respond to soil biotic and abiotic  
1292 signals, such as mycorrhizae or soil drying.. In this diagram functions associated with nutrient  
1293 uptake are presented in orange text, water transport in blue text, and carbon transport in green  
1294 text.

1295

1296 **Figure 2.** Advanced techniques illustrate novel insight into root structure and dynamic root  
1297 processes, such as (a) Ericaceous shrub roots and associated mycorrhizal hyphae and (b) a fungal  
1298 rhizomorph from an automated minirhizotron system deployed in a peatbog (scale  $\sim 2.5 \times 3$  mm);  
1299 (c) scanning electron micrograph of  $\sim 30$ - $50$   $\mu\text{m}$ -long root hairs of *Quercus rubra*; (d-g) neutron  
1300 imaging time-series of water uptake and internal transport (orange colors) through corn seedlings  
1301 over  $\sim 12$  hours following a pulse of water below the roots (blue). Such data can be used to  
1302 validate model simulations of root structure, production, turnover and water uptake.

1303

1304 **Figure 3.** Root, whole plant, and terrestrial biosphere models (TBMs) in relation to spatial and  
1305 temporal scales at which they operate. Mechanistic root processes are readily modeled for single  
1306 roots, but process-based knowledge is dramatically lost for higher-order models, resulting in  
1307 more static and less complex representation as spatial scale increases. Landscape-level bulk root  
1308 distribution, water and nutrient uptake are estimated and not dynamic in most TBMs. Root traits  
1309 can provide a framework for scaling dynamic root functions (such as fine root proliferation, loss

1310 of root conductivity, or hydraulic redistribution) into TBMs to improve model veracity – a  
1311 pathway indicated by the large arrow.

1312

1313 **Figure 4.** Key root structural and functional attributes and their inclusion in several well-known  
1314 ecosystem and terrestrial biosphere models (TBMs) – filled circles represent model inclusion.  
1315 Dynamic root functions such as Michaelis-Menten (M-M) nutrient uptake kinetics, hydraulic  
1316 redistribution of water (HR) and downregulation due to low oxygen (Anoxia) are rarely included  
1317 in the models. Other functions such as water uptake are widely represented when linked  
1318 specifically to root depth, but rarely consider actual root biomass. Model references as in Tables  
1319 2, 3.

1320

1321 **Figure 5.** Framework for assessment of root data, and its importance in scaling ecosystem  
1322 function through root traits for modeling the terrestrial biosphere. (left) Root distribution is the  
1323 most common dataset available, and is used in many TBMs to regulate water use (Fig 4).  
1324 Improved modeling will include root structural traits (e.g., size, age, order, display, C:N,  
1325 mycorrhizal associations), and their associated functions (e.g., water and nutrient uptake, and  
1326 carbon release through respiration, exudation and turnover). (right) Model evaluation should first  
1327 assess the presence of roots or root functions, including both direct (e.g., water uptake based on  
1328 root distribution) and indirect (e.g., nitrogen uptake based on plant demand) functions. Efforts  
1329 must be made to understand the role of roots for specific processes at the appropriate spatial and  
1330 temporal scales (Fig 3). Key root functions should be prioritized based on current mechanistic  
1331 knowledge of root processes and dynamic biotic/abiotic regulation of those processes, as well as  
1332 by their relative importance to the model. Addition of new root functionality to a model will  
1333 require development of trait databases that can be scaled across landscapes based on species and  
1334 plant functional type (PFT) characteristics, soil and environmental conditions.

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

<b>Model</b>	<b>Allocation</b>	<b>Architecture</b>	<b>Acquisition</b>	<b>Reference</b>
ROOTMAP	Calculates balance between plant demand and the capacity of individual roots to supply soil resources, to drive 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 non-branching 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; Dunbabin et al., 2003
Root Typ	Allocation to growth occurs at a potential rate for all sinks when sufficient carbohydrate is available; else, reduced growth is determined <i>with</i> or <i>without</i> 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; Thaler and Pagès, 1998; Pagès et al., 2004; 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
<i>SimRoot</i>	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 and 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 and McGechan, 1998; Wu et al., 2007

**Table 2.** The representation of carbon allocation, root architecture and uptake of water and nutrients in a subset of ecosystem models.

Model	Time step	Allocation		Architecture/ Distribution	Acquisition /Ecosystem Function		
		Carbon	Phenology	By depth	Water uptake	N uptake	Root Turnover & C loss
<b>ECOSYS</b> <sup>1</sup>	Hourly	Functional balance of N, P Demand adjusted so that allocation increases when root storage C:N/C:P > than that required to support new growth	Remaining C from R – MR is available for GR subject to water and N&P status; resistance from soil and root and myco turgor. Allocated to each root by comparative conductance	Controlled by primary root growth, distribution by primary root length and secondary root lengths	$f(\text{root radial and axial resistances, soil water content})$ Uptake (Q) = $(\psi_{\text{shoot}} - \psi_{\text{soil}}) / (\text{sum of radial and axial resistances})$	$f(\text{root N, P})$  diffusion, mass transport, adsorption, microbial immobilization so that uptake = solution concentration at root surface. Demand adjusted so that uptake is inhibited when root storage C:N/C:P > than that required to support new growth	<b>Maintenance respiration</b> (MR, priority): $f(\text{soil temperature, O}_2)$ <b>Growth respiration (GR):</b> $f(\text{water, N, P})$ <b>Nutrient uptake respiration (N<sub>u</sub>R):</b> Exudation Turnover: if(MR < M + GR) M&GR = $f(T, O_2)$ status, comparative C conductance, turgor)
<b>G'DAY</b> <sup>2</sup>	Daily / Weekly	Fixed fraction of NPP	None	None	Assumed non-limiting; 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	<b>Respiration:</b> Fixed fraction of GPP; not root-specific <b>Exudation:</b> Fixed fraction of NPP <b>Turnover:</b> Equal to 1.0
<b>SPA</b> <sup>3</sup>	30 minutes	Prescribed	None	Maximum root biomass per unit soil volume prescribed; exponential decline in biomass with depth to a prescribed maximum rooting depth. Dmax input parameter as is max root mass in soil volume	$f(\text{root and soil hydraulic resistance, root biomass and distribution, soil water content})$ $E_{\text{max}} = (\psi_{\text{shoot}} - \psi_{\text{soil}}) / (\text{sum of plant resistances})$  capacitance accounted for $\psi_{\text{soil}}$ is weighted by root distribution and soil resistance	None	None

Model	Time step	Allocation		Architecture/ Distribution	Acquisition /Ecosystem Function		
TEM <sup>4</sup>	1 month	none	none	Max rooting depth used to estimate water availability	$f$ (ET demand, soil properties, SWC)	$f$ (soil available N, SWC, C:N energy balance)	$f$ (NPP), above and belowground C loss is single term

<sup>1</sup>Grant 1998, <sup>2</sup>McMurtrie et al. 2000, <sup>3</sup>Williams et al. 1996, <sup>4</sup>Raich et al. 1991

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

Model	Time Step	Allocation		Architecture/ Distribution	Acquisition /Ecosystem Function		
		Carbon	Phenology	By depth	Water uptake	N uptake	Root Turnover & C loss
<b>CLM4.0<sup>1</sup></b> <b>CLM4.5<sup>2</sup></b>	30 minutes	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, soil matric potential)	If supply > demand, N uptake = demand to meet growth requirements  If supply < demand, N uptake = $f$ (soil mineral N, plant demand, microbial demand)  (no root dependence)	Linked 1:1 to leaf turnover
<b>CABLE<sup>3</sup></b>	30 minutes	Fixed fraction (varied by phenological phase)	Phased, opposite to leaf phenology	Decreasing proportion with depth	$f$ (plant demand, root proportion, SWC)	$f$ (soil mineral N, plant demand)	Fixed fraction
<b>LM3<sup>4</sup></b>	30 minutes	Functional balance: to maintain root:shoot ratio, root:shoot ratio $f$ (water stress)	Same as leaf			Michaelis-Menten kinetics $f$ (soil mineral N, root mass)	
<b>JULES<sup>5</sup></b>	30 minutes	Fixed fraction (1:1 leaf allocation)	Growth: same as leaf Turnover: fixed fraction	Exponential	$f$ (plant demand, root proportion, SWC)	na	Fixed fraction 0.15-0.25 yr <sup>-1</sup>
<b>O-CN<sup>6</sup></b>	30 minutes to 1 day	Functional balance: to maintain root:shoot ratio, root:shoot ratio $f$ (water or N stress)	balance between allocation and turnover	Decreasing with depth (2 soil layers)	$f$ (plant demand, root proportion, SWC)	Michaelis-Menten kinetics $f$ (soil mineral N, root mass, plant demand, temperature)	$f$ (age) mean turnover rate of 0.7 yr <sup>-1</sup>
<b>SDGVM<sup>7</sup></b>	1 day	Fixed fraction: 0.0015	If GPP > 0	Fixed proportions	$f$ (plant demand,	$f$ (soil C)	$f$ (age) and self-

Model	Time Step	Allocation		Architecture/ Distribution	Acquisition /Ecosystem Function		
		of labile C pool			root proportion, SWC)		thinning mortality
<b>LPJ-GUESS</b> <sup>8</sup>	1 day	Functional balance: to maintain root:shoot ratio, root:shoot ratio $f$ (water or N stress)	None	Decreasing with depth (2 soil layers)	$f$ (plant demand, root proportion, SWC)	$f$ (soil mineral N, root mass, plant demand, soil T)	Fixed fraction 0.5–0.7 yr <sup>-1</sup>
<b>MBL-GEM III</b> <sup>9</sup>	1 month	Functional balance	Result of allocation	None	na	$f$ (root N content, air T)	Fixed fraction 0.164 yr <sup>-1</sup>
<b>DVM-DOSTEM</b> <sup>10</sup>	1 month	Fixed fraction	Same as leaf	Exponential to max rooting depth	$f$ (plant demand, root proportion, SWC)	$f$ (plant demand, root proportion and mass, root respiration, air T, SWC, available soil N)	$f$ (standing crop, production) 0.25–1 yr <sup>-1</sup>

<sup>1</sup>Thornton et al. 2007, Oleson et al. 2010, <sup>2</sup>Koven et al. 2013, Oleson et al. 2013, <sup>3</sup>Wang et al. 2010, <sup>4</sup>Gerber et al. 2010, <sup>5</sup>Clark et al. 2011, <sup>6</sup>Zaehle and Friend 2010, <sup>7</sup>Woodward and Lomas 2004, <sup>8</sup>Smith et al. 2013, <sup>9</sup>Rastetter et al. 1991, <sup>10</sup>Euskirchen et al. 2009



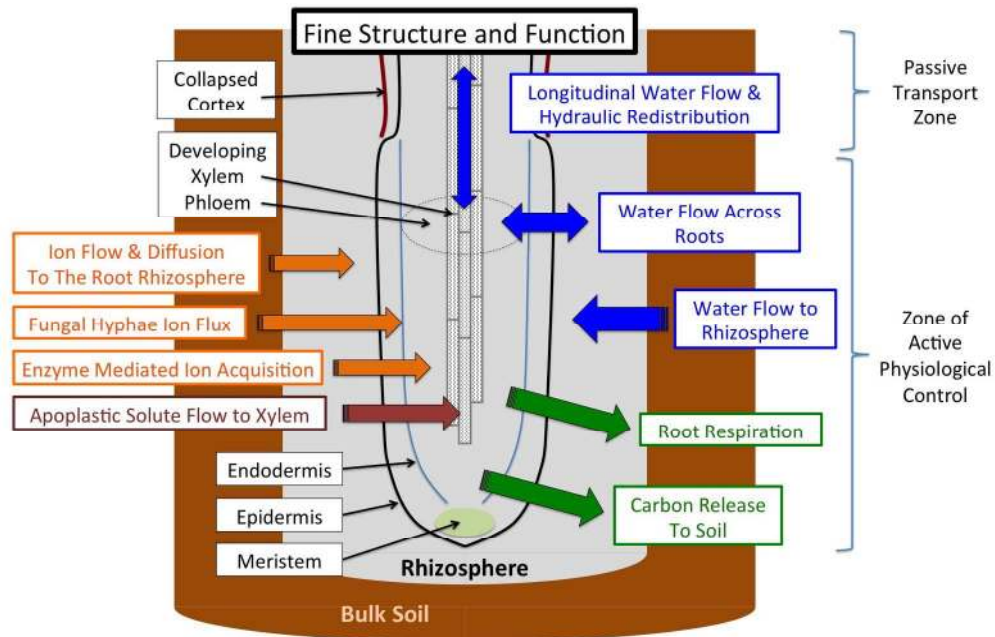


Figure 1. Diagram of the structural and functional characteristics of fine roots of plant root systems, and their interaction with the soil rhizosphere. Developing fine roots contain zones of active growth and function and zones where changes in anatomical tissue reduces root functions such as water 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 nutrients uptake into the symplast is regulated by passive or active transport proteins, such as aquaporins (water) or ion-pumps (mineral nutrients). 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 mycorrhizae 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.

746x477mm (72 x 72 DPI)

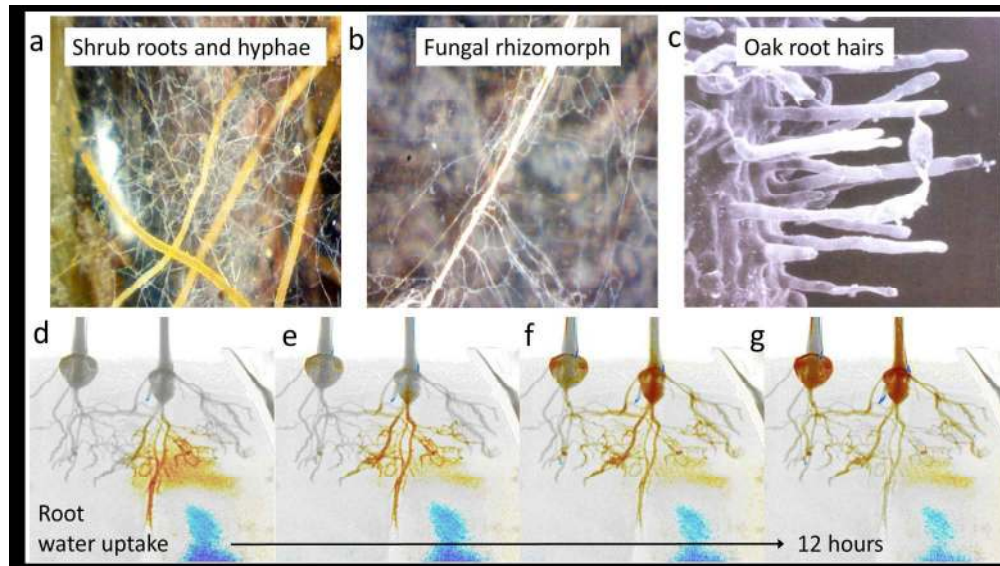


Figure 2. Advanced techniques illustrate novel insight into root structure and dynamic root processes, such as (a) Ericaceous shrub roots and associated mycorrhizal hyphae and (b) a fungal rhizomorph from an automated minirhizotron system deployed in a peatbog (scale  $\sim 2.5 \times 3$  mm); (c) scanning electron micrograph of  $\sim 30$ - $50$   $\mu\text{m}$ -long root hairs of *Quercus rubra*; (d-g) neutron imaging time-series of water uptake and internal transport (orange colors) through corn seedlings over  $\sim 12$  hours 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.

344x195mm (150 x 150 DPI)

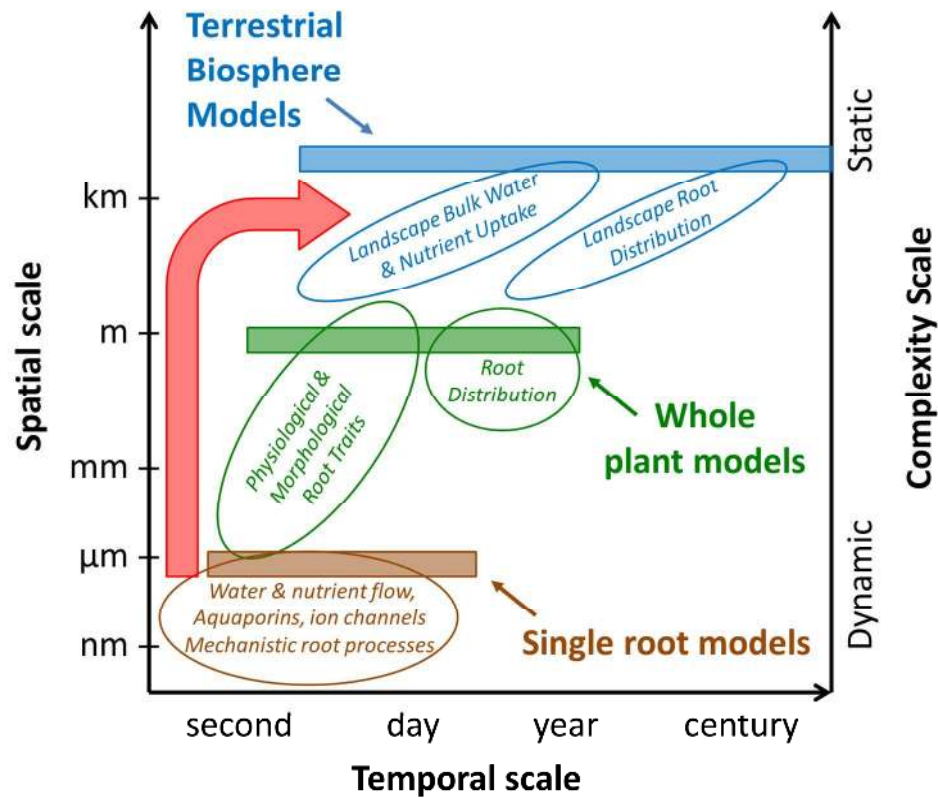


Figure 3. Root, whole plant, and terrestrial biosphere models (TBMs) in relation to spatial and temporal scales at which they operate. Mechanistic root processes are readily modeled for single roots, but process-based knowledge is dramatically lost for higher-order models, resulting in more static and less complex representation as spatial scale increases. Landscape-level bulk root distribution, 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.

340x290mm (150 x 150 DPI)

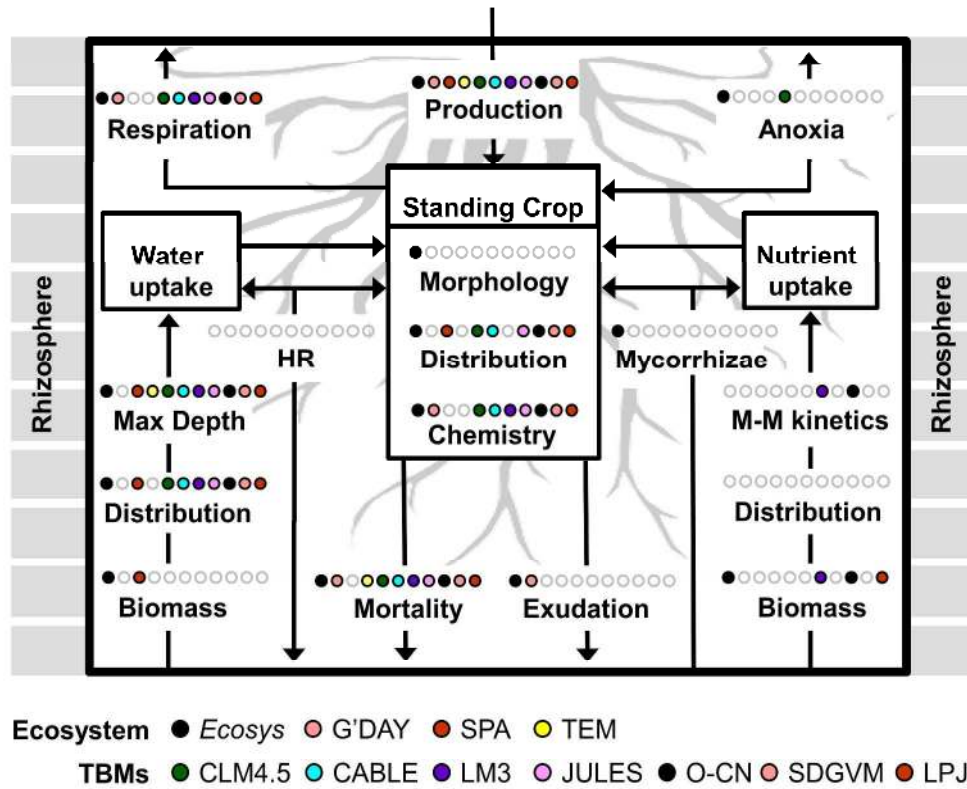


Figure 4. Key root structural and functional attributes and their inclusion in several well-known ecosystem and terrestrial biosphere models (TBMs) – filled circles represent model inclusion. Dynamic root functions such as Michaelis-Menten (M-M) nutrient uptake kinetics, hydraulic redistribution of water (HR) and downregulation due to 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 as in Tables 2, 3.

963x861mm (81 x 81 DPI)

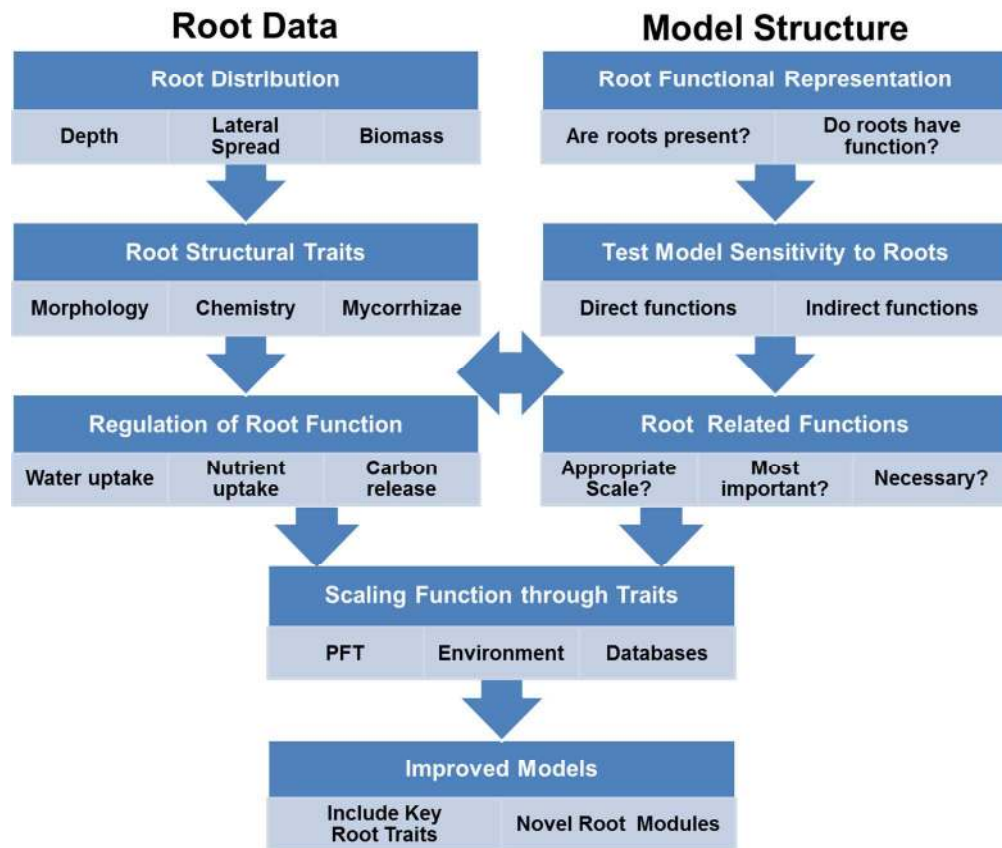


Figure 5. Framework for assessment of root data, and its importance in scaling ecosystem function through root traits for modeling the terrestrial biosphere. (left) Root distribution is the most common dataset available, and is used in many TBMs to regulate water use (Fig 4). Improved modeling will include root structural traits (e.g., size, age, order, display, C:N, mycorrhizal associations), and their associated functions (e.g., water and nutrient uptake, and carbon 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., nitrogen 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 by 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.

239x210mm (150 x 150 DPI)