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2 **Improving the representation of roots in terrestrial models**

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21 **KEYWORDS:** ROOTS, TURNOVER, CARBON, MODELING, ALLOCATION, PARAMETERIZATION

22

23 **ABSTRACT**

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

42

43 **INTRODUCTION**

44 Forecasting the resilience of Earth's ecosystems to perturbation or stress induced by
45 climate change increasingly requires an understanding of the influence of belowground processes
46 on ecosystem function. Roots couple the aboveground vegetation and the soil media, yet they
47 are arguably the least understood portion of the ecosystem. As a result they are represented
48 idealistically in many process-based ecosystem models, and remain the most simplistic
49 component of contemporary Earth System Models (ESMs). Despite this, feedbacks between
50 aboveground and belowground function are expected to influence ecosystem responses to
51 changes in climate and atmospheric [CO₂]. For example, models currently predict that rising
52 [CO₂] and temperature may increase aboveground productivity (Millar et al., 2007; Mote et al.,
53 2003; Parmesan and Yohe, 2003), but productivity may be limited by soil nutrients and water
54 availability (Albani et al., 2006; Boisvenue and Running, 2010; Jain et al., 2013; Luo et al.,
55 2004; Norby et al., 2010). There is an urgent need for scientists to improve prognostic
56 approaches for understanding how roots govern changes in resource availability and how root
57 responses influence ecosystem productivity.

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

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

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

82 Historically, incorporating root processes into models has been hampered by (1) a lack of
83 consistent and scalable data on root properties that govern root structure (classification and
84 arrangement) and function (processes that govern root production, turnover, and uptake), (2)
85 differences in terminology between root ecologists and modelers, which have led to confusion
86 even over relatively ‘simple’ terms like turnover (McCormack et al., *in press*), and (3) limited
87 consensus on which root functions are ripe for inclusion in contemporary models. For example,
88 understanding species-specific root function in mixed-species forests is hampered by empirical

89 observations that are recorded at the stand-level and which do not distinguish among tree
90 species. Similarly, where species-specific estimates exist, spatial and temporal heterogeneity
91 among species is often ignored when summarizing processes at the level of Plant Functional
92 Type (PFT). Yet it is known that species-specific differences in root turnover are important at
93 continental scales and can significantly affect estimates of C storage (McCormack et al., 2013).

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

103

104 **EMERGING OUTLOOKS IN ROOT STRUCTURE AND FUNCTION**

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

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

112 (Pregitzer, 2002). More recently, however, researchers have begun to question the utility of this
113 simple dichotomous separation, increasingly recognizing the complexity of root structure (**Fig.**
114 **1**) and the need to more precisely quantify the root properties associated with these classification
115 schemes. For example, within the fine root size class, distal tips of roots (first- and second-order
116 roots) are often thinner, more active in nutrient uptake, richer in nitrogen (N) and have higher
117 respiration rates than basal roots (Pregitzer, 2002; Pregitzer et al., 1998). The majority of root
118 length and surface area is also concentrated in these first- and second-order roots, which provide
119 the high surface area needed for resource acquisition (Guo et al., 2004; Pregitzer, 2002). In a
120 comprehensive, cross-species study, branching order was a more accurate indication of root
121 function than size, with the traditional two-diameter class approach overestimating absorptive
122 root length by 25% (Guo et al., 2008b). The response to these findings by some has been to
123 classify fine roots into more size classes (e.g., Park et al., 2008). However, another approach
124 may be to identify functional breaks across root orders or size classes. For example, first and
125 second order roots may be classed together as ephemeral root modules with high rates of
126 respiration, uptake and turnover, while higher order roots with secondary development are
127 assumed to have limited uptake capacity and function more for transport and storage (Xia et al.,
128 2010).

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

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

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

156 In sum, despite increasing recognition of alternative root classification strategies
157 regarding species, rooting order, and fungal associations, many models continue to segregate

158 roots by size classes. This size categorization may serve to represent the functional duality of
159 having both shorter-lived, absorptive roots and longer-lived, transport or structural roots,
160 independent of whether they are termed “fine” or “coarse”. However, additional testing of
161 alternative root classification strategies would allow for exploration of functional implications of
162 root structure on terrestrial C, water, and nutrient dynamics (Gaudinski et al., 2010).

163

164 ***Root Production***

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

181 estimates of root production. The strengths and weaknesses of each method is covered more
182 thoroughly in previous reviews (Hendricks et al., 2006; Milchunas, 2009; Ostonen et al., 2005;
183 Smit et al., 2000; Vogt et al., 1998).

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

200 The phenology of root production is also important, describing how plants utilize
201 temporally-variable water and nutrient resources during the growing season. Efforts to record
202 leaf phenology have increased in recent years since climate change affects spring leaf emergence
203 and fall leaf senescence (Diez et al., 2012; Fridley, 2012; Richardson et al., 2012), but few

204 scientists document phenology in roots. Root production may occur at different rates and
205 starting points throughout the growing season and may not be synchronous with aboveground
206 productivity. Field studies suggest that asynchronicity in root and shoot phenology is present in
207 both woody species and grasses, and may be significant, ranging from 2 weeks to 2 months
208 (Steinaker et al., 2010). Recent studies have also shown that new roots may be constructed from
209 C acquired in previous growing seasons and stored within the plant, as opposed to only recently
210 acquired photosynthate (Gaudinski et al., 2009; Vargas, 2009). This allows for the possibility
211 that, at times, root production may be entirely decoupled from active photosynthesis (Oleson et
212 al., 2010; Schaefer et al., 2008; Shevliakova et al., 2009; Zaehle and Friend, 2010), and that
213 models should incorporate lag effects across seasons and years.

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

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

233

234 ***Root turnover***

235 Modelers often treat turnover as, simply, the inverse of lifespan. Technically, fine root
236 turnover rate represents the number of times a population of roots is replaced during a given time
237 period (e.g. annually) and can incorporate information regarding root production, standing
238 biomass, and lifespan. Empirically, turnover is variably calculated, yielding comparable but
239 slightly different estimates of turnover. For example, if root production equals $1000 \text{ g m}^{-2} \text{ yr}^{-1}$,
240 and standing root biomass is measured 5 times over the course of the year at 700, 1000 1300,
241 1100, 900 g m^{-2} , then using either the maximum, minimum, or average standing biomass from
242 that year to calculate turnover rate would result in estimates of 0.77, 1.4, and 1.0 yr^{-1} ,
243 respectively. Additionally, fine root turnover rates have also been calculated as the inverse of
244 observed fine root lifespan, which also may produce similar estimates of turnover as other
245 methods but never the quite the same. Overall, an important first step in modeling fine root
246 turnover is recognizing the differences in methods for calculating turnover and appreciating
247 potential bias among the different methods (McCormack et al., *in press*).

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

250 Jackson, 2000; Iversen et al., 2008; McCormack et al., *in press*; Withington et al., 2006).
251 Globally, there is likely to be close to an order of magnitude of variation in measured turnover
252 rates. Importantly, this level of variation may also exist at the site level due to variation among
253 species or across years. However, because calculations of turnover rate often involve estimates
254 of production, mortality and standing biomass, it is not always clear whether this variation is due
255 to consistent differences in root longevity and replacement or short-term (season to annual)
256 changes in production or mortality. Furthermore, within a single root branch, turnover times of
257 distal roots active in resource absorption typically range from months to a few years while
258 turnover times of more proximal, resource conducting fine roots are frequently in excess of a
259 decade (Gaudinski et al., 2010). Therefore, some of this variation may be due simply to the pool
260 of roots that is most emphasized by different methods. Minirhizotron cameras enable direct
261 observation and measurement of root lifespan of fine roots. Additionally, isotopic tracers have
262 been used to measure residence times of root C to calculate turnover rates (Gaudinski et al.,
263 2010; Matamala et al., 2003), but tracers tell more about when C was fixed and don't directly
264 quantify root age. Each approach (traditional coring, minirhizotrons, isotopes) has strengths and
265 weaknesses that have been discussed extensively elsewhere (Gaudinski et al., 2010; Guo et al.,
266 2008a; Tierney and Fahey, 2002) and much of the reliability of each method to estimate root
267 turnover depends on which root pool is of interest. In general, minirhizotrons are likely better
268 suited for determining lifespan and turnover times of the more ephemeral, absorptive fine roots
269 while isotopes may be more appropriate for higher order, longer-lived fine roots and coarse
270 roots.

271 Even accepting differences in terminology and accepting a more traditional view of
272 turnover as equal to root mortality requires the understanding that the causes of root mortality are

273 diverse, and include decomposition, herbivory (Hendrick and Pregitzer, 1992), and direct
274 physiological stress. Root herbivory may be important in many systems and differentially affect
275 agricultural systems that are designed to minimize harmful microbial and fungal activity versus
276 natural systems. Other causes of mortality, including cellular toxicity to adverse
277 biogeochemical environments (Cronan and Grigal, 1995) may be important in regions subjected
278 to elevated N deposition (Smithwick et al., 2013). The importance of these mortality factors has
279 not been explored at regional or global scales.

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

290 While turnover remains a fixed parameter in many models, other models allow root
291 turnover rates to vary as functions of environmental factors such as N mineralization rate in
292 PnET-CN, (Aber et al., 1997; Ollinger et al., 2002) or soil water content and temperature in ED2
293 and ForCENT. In LANDIS-II, FORCS Extension, fine root turnover may temporarily increase
294 to reflect a loss of aboveground biomass due to branch mortality or disturbance (Dymond et al.,
295 2012). These and other similar approaches may enable more complete descriptions of root

296 dynamics into models, though the accuracy of these efforts will depend on the ability to
297 accurately link variation in root turnover rates to changes in environmental factors and
298 ecosystem dynamics.

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

308

309 ***Root biomass***

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

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

329 Estimation of root standing crop can be used to initialize model pool sizes but these direct
330 estimates are rare and fraught with error. Thus, in the absence of direct estimates at global
331 scales, modelers rely on surrogates for estimating root biomass, such as fixed relationships
332 between foliar, woody or total aboveground biomass (Wolf et al., 2011). The specific approach
333 used differs among models, highlighting differences in understanding of the factors that govern
334 root biomass. For example, one approach has been to simulate fine roots as a function of leaf
335 biomass; and, using similar logic, coarse roots as analogous to, and a fixed fraction of, woody
336 biomass, as is implemented in the current version of LANDIS-II, Century extension (Scheller et
337 al., 2011). This assumes that fine roots are functionally similar to leaves, acting as belowground
338 scavengers of resources. However, these relationships are often held constant across species,
339 PFT, and site conditions, with unknown implications on model outcomes. Furthermore, as leaves
340 and fine roots are frequently exposed and respond to vastly different environmental pressures, it
341 is unclear how consistent these relationships are in nature and how flexible they should be in

342 models. Wolf et al. (2011) showed that land surface models which incorporated stand-thinning
343 processes or shorter wood turnover times performed better related to observed allometries.
344 Ultimately, root biomass is the net result of root production (gain) and turnover (loss) that each
345 change over time. In practice, root biomass or its associated rates (production,
346 turnover/mortality) are often used to ‘tune’ model responses, given that it’s ‘true’ value is not
347 known. Thus, constraints on pool sizes (minimum, maximum) are sorely needed to bound model
348 estimates of root biomass.

349

350 ***Resource Uptake & Rooting Depth***

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

361 Estimating uptake from the difference of other measured fluxes has been measured at
362 annual scales (Nadezhdina et al., 2008). However, at finer temporal scales, total uptake may
363 differ in response to daily and seasonal patterns in climate and/or resource availability (Gessler et
364 al., 1998). An additional constraint to budgeting approaches is that they are often calculated at

365 the stand-level, precluding any ability to quantify uptake at the species-level, except in
366 monocultures. However, root uptake may be spatially heterogeneous within the soil profile even
367 if total uptake remains unchanged due to localized patterns in water and nutrients (Garrigues et
368 al., 2006; Sharp and Davies, 1985; Wan et al., 2002), which would be difficult to quantify
369 through annual budgeting approaches at the stand level. The degree to which spatial and
370 temporal patterns in root uptake are due to shifts in allocation, active plant regulation of the soil
371 environment, and/or a response to abiotic gradients in water potentials and nutrient gradients that
372 govern mass flow, is an active area of research.

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

388 Land Exchange model) to simulate how water uptake and hydraulic redistribution affected net
389 ecosystem exchange. Including these root dynamics significantly improved agreement between
390 eddy flux tower observations and modeled fluxes of CO₂, latent heat flux, and soil moisture
391 dynamics. Optimization theory has also been used to simulate N uptake; for example, McMurtrie
392 *et al.* (2012) proposed that rooting mass be distributed dynamically in response to the spatial
393 variability of soil N so as to maximize N uptake.

394 Even as indirect methods of modeling resource uptake are being challenged, there
395 remains much room for model improvement. Changes in the soil environment are likely to affect
396 nutrient uptake rates and efficiencies via changes in root tissue physiology. Smithwick *et al.*
397 (2013) reviewed this effect for N deposition, highlighting root physiological studies that have
398 indicated tissue level stress as a function of elevated chemical environments. Understanding
399 mechanisms of root physiology, e.g., concentration thresholds of toxic elements that influence
400 lifespan, remains a frontier in modeling that would benefit from increased interdisciplinary
401 dialogue. Similarly, inclusion of how mycorrhizal fungi affect root uptake is also important
402 (Orwin *et al.*, 2011) particularly for immobile nutrients like phosphate (Smith and Read, 2008).
403 Mathematical modeling of individual roots indicates that phosphate uptake is dominated by
404 hyphal and not root uptake (Schnepf *et al.*, 2008b). Also, recent efforts to simulate the
405 development and extent of the fungal mycelium will be helpful for interpreting species
406 differences in foraging strategies and how this might affect nutrient acquisition (Schnepf *et al.*,
407 2008a). Finally, most models ignore the fact that nutrient and water uptake take place only at
408 the surface of roots, potentially independent of total root biomass. Empirical studies indicate that
409 specific root length (length per unit mass, m g⁻¹) and surface area can vary by an order of

410 magnitude between species (Comas and Eissenstat, 2009; Tjoelker et al., 2005), which may
411 dramatically affect resource uptake.

412 Given that rooting depth affects nutrient and water uptake (Dawson, 1995; Göransson et
413 al., 2006; Kulmatiski and Beard, 2012), it is important to understand how rooting depth varies
414 across species and sites (Göransson et al., 2006; Kulmatiski et al., 2010). Most experimentalists
415 confine their measurements of root processes to the upper 10 or 20 cm of soil because *most* fine
416 roots are located in surface layers. For example, (Soethe et al., 2006) found that 32 to 43 % of
417 the total N taken up by trees, shrubs and herbs was obtained from the organic layer, while only 2
418 to 19 % was derived from a soil depth of 40 cm. However, several studies, e.g., free-air-CO₂-
419 enrichment (FACE) experiments, have shown the greatest increases in root mass occurred at soil
420 depths below 30 cm (Iversen, 2010), leading to greater N extraction from depth, either due to
421 increased N availability or deeper rooting (Iversen et al., 2008). In some arid systems, pools of
422 P, Ca and Mg at 2-3 m depth appear to be utilized by deep roots (McCulley et al., 2004); other
423 studies have shown maximum rooting depths from 5 m to 25 m (Jackson et al., 1999). Deep
424 roots may be particularly important in arid systems where trees utilize groundwater as their
425 primary water sources (Dawson, 1996) but may also be important in wet, tropical environments
426 during periods of low rainfall (Davidson et al., 2011). Plants can also modify their resource
427 environment by depth through hydraulic redistribution (Amenu and Kumar, 2008; Bleby et al.,
428 2010; Jarvis, 2011; Simunek and Hopmans, 2009), the effects of which vary dramatically across
429 ecosystems (Neumann and Cardon, 2012). Rooting depth may also be responsive to preferred
430 flow paths in soils. As a result of these and other processes, the source of water utilized by plants
431 can vary seasonally, with soil conditions, and with depth (Bertrand et al., 2012; Yang et al.,
432 2011).

433 Modeling water extraction by depth has been undertaken at various levels of
434 sophistication (**Fig. 4**). In the simplest ‘bucket model’ approach (Budyko, 1974; Manabe, 1696),
435 the subsurface is represented as a single layer, with transpiration evenly extracted throughout the
436 soil column. In models that represent the subsurface with multiple soil layers, the rooting
437 architecture of vegetation is described with temporally and spatially invariant macroscopic
438 parameters such as root depth and/or root shape that are dictated by the type of vegetation being
439 modeled (Feddes et al., 2001; Pitman, 2003; Schenk and Jackson, 2002). Typically, these models
440 distribute the transpiration based on upon the fraction of roots that reside in each soil layer.
441 Parameterization of the root profile is often only determined by empirical data organized by PFT
442 which may not directly match the vegetation classifications found in many ESMs (Zeng, 2001).
443 Moreover, these parameters do not consider local abiotic and biotic interactions. Jackson et al.
444 (2000) details the various model treatments of root distribution, highlighting that rooting
445 parameters are frequently determined independently of local soil texture and climatic region. As
446 a consequence, these models do not take into account the strong influence that soils and climatic
447 variability have on the partitioning of precipitation at the surface and the flow of moisture
448 through the root zone. This simplification also ignores the long history of observational data
449 (Weaver 1926) that recognized that under myriad soil textures or precipitation regimes the same
450 plant species can exhibit alternative rooting strategies to cope with different belowground
451 moisture distribution (Caylor et al., 2006; Gentine et al., 2012). Through a series of synthetic
452 simulations, Sivandran and Bras (2012) illustrated the influence of local abiotic conditions on
453 determining the optimal rooting depth and extended this work to include a dynamic root C
454 allocation algorithm driven by the vertical distribution of soil moisture (Sivandran and Bras,

455 2013). By allowing the belowground rooting structure to adapt and evolve with local soil,
456 topography and climatic conditions, improvement of water, energy and C fluxes was achieved.

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

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

470 Recently, authors have explored the role of rooting depth and distribution on a wide
471 variety of ecological responses (Collins and Bras, 2007; Guswa, 2008; Hildebrandt, 2005;
472 Hwang et al., 2009; Lai and Katul, 2000; Schenk, 2008; Schymanski et al., 2008; Schymanski et
473 al., 2009). For example, using the model MC1 (MAPPS-Century 1), Daly et al. (2000) explored
474 the influence of rooting depth of trees and grasses on C and nutrient fluxes in Wind Cave
475 National Park, South Dakota, USA. Results showed significant influence of rooting depth on
476 model outcomes. In particular, rooting depth had a larger effect than climate on biogeochemical
477 pools under both historical and future climate scenarios. Deeper roots increased vegetation

478 productivity and modified fire regimes through competitive interactions with grasses. At the
479 global scale, the lack of representation of deep water access may explain why ESMs cannot
480 simulate adequately the response of tropical forests to seasonal drought (Baker et al., 2008).
481 Even if root profiles can be identified empirically for given plant types, these results suggest that
482 dynamic profiles are necessary to emulate vegetation resilience under increasingly common
483 global change factors such as drought. In conclusion, although model structural and functional
484 flexibility to rooting depth profiles is currently being implemented in models (e.g., Li et al.,
485 2012; McMurtrie et al., 2012; Sivandran and Bras, 2013), implications of these changes on total
486 model responses must be explored across broader gradients of environmental conditions.

487

488 *SYNTHESIS & RECOMMENDATIONS*

489 In the traditional view of root dynamics in regional ecosystem models and ESMs (**Fig.**
490 **5a**), allocation governs root production, influencing the root C stock available for turnover,
491 which in turn governs soil C and nutrient dynamics. In these black box approaches, roots
492 indirectly respond to altered conditions but do not themselves influence their environment or
493 whole-plant function directly, which is known to be an overly simplistic assumption. Notably,
494 these dynamics are persistently guided by only a few key principles, e.g., dynamic and/or
495 optimum allocation or the evolutionary principle. While these principles are reasonable at global
496 scales, they obviate the need to model root uptake directly through physiological mechanisms,
497 precluding prognostic understanding of root responses to global change drivers. In addition,
498 through experimentation and observation, several shortcomings are additionally evident in model
499 approaches to root dynamics, such as the general lack of representation of mycorrhizal-root
500 associations, limited attention to root phenology or stored C pools, and the simulation of uptake

501 rates conditioned on biomass or demand rather than active surface area. Perhaps most strikingly,
502 the factors that govern root lifespan and influence root mortality directly are not included, such
503 as herbivory or physiological tissue stress.

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

511 To enable a community of modelers to test these and other changes in root function on
512 ecosystem function, we have identified the following research opportunities that cut across the
513 specific tests described above (**Table 2**). First, models must include roots in data assimilation,
514 variance partitioning, and optimization. These approaches should explore the effect of parameter
515 and structural uncertainty and identify conditions that lead to threshold responses. Models that
516 do not have significant feedbacks between belowground pools to aboveground function are likely
517 to have little internal sensitivity to root parameters or algorithms, whereas models that couple
518 roots to nutrient or water availability with feedbacks to aboveground function are likely to be
519 influenced heavily by belowground dynamics. Using this approach with ED2, it has been shown
520 that allocation, turnover, and water conductance (which moderates root water uptake), have high
521 parameter variance and can contribute significantly to overall model sensitivity (LeBauer et al.,
522 2013; Wang et al., 2012).

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

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

543 While model improvements of root function may seem daunting, it is equally true that
544 significant empirical understanding of root function has emerged in recent years. Significant
545 interdisciplinary work and collaboration between empiricists and modelers is still needed to

546 guide data collection and model improvement. Yet, the new framework shown here highlights
547 an opportunity to incorporate new functionality into models with the goal of developing field-
548 testable hypotheses. Modelers must increasingly strive to quantify root activity, request data
549 where needed, and use models to develop testable hypotheses about root function. While staying
550 honest to available data, modelers have an opportunity to challenge widely held paradigms and
551 to explore tradeoffs – both mechanistic and computational – in improving root function in
552 models. The goal of this effort ought to be increasing the coupling between leaves, roots and
553 soil, and further constraining model predictions of terrestrial ecosystem responses to global
554 change drivers. The degree to which these additional changes, e.g., splitting roots into explicit
555 functional versus size classes, or including fungal-root associations, may be required to
556 accurately forecast ecosystem resilience to global change must be weighed against costs in
557 model complexity and increased model variance.

558

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

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

(5) Resource uptake & Rooting depth Increasing evidence that roots influence the soil resource environment (i.e., priming, hydraulic lift), but field measurements remain limited; Models show large sensitivities to rooting depth & resource supply; analytical model approaches, based on dynamic allocation with resource supply by depth and root-level physiology, are emerging

Gentine *et al.* 2012; Lucash *et al.* 2007; Caylor *et al.* 2006; Soethe *et al.* 2006; Comas and Eissenstat 2004; Schenk and Jackson 2002; Jackson *et al.* 2000; Proe *et al.* 2000; BassiriRad *et al.* 1999; Gessler *et al.* 1998; Sivandran and Bras 2012*, 2013*; Li *et al.* 2012*; McMurtrie *et al.* 2012*; Tian *et al.* 2011*; Fisher *et al.* 2010*; Zaehle and Friend 2010*; Collins and Bras 2007*; Zeng 2001*; Kleidon and Heimann 1998*

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

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

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982 **Figure Legends**

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

991
992 **Fig. 2.** Depiction of current model algorithms of allocation of C to roots showing three dominant
993 pathways (fixed allocation, proportional allocation, or carbon cascade).

994
995 **Fig 3.** Alternate pathways by which root allocation can alter total ecosystem carbon. In (a)
996 increases in root allocation can either increase or decrease total ecosystem carbon, depending on
997 whether models consider tradeoffs in ANPP among plant pools, respiratory losses, and resource
998 feedbacks. In (b), constant root allocation can impact total ecosystem C fluxes if root biomass is
999 independently altered.

1000
1001 **Fig. 4.** Primary questions that determine model treatment of root function at different soil
1002 depths. Upper left panel describes multiple approaches used to model water uptake in many
1003 terrestrial biosphere models where soil water uptake is modeled with canopy resistance (r_c) as a
1004 function of soil water potential (ψ), or water supply (S) is modeled as a function of volumetric
1005 soil water content (W).

1006 **Fig. 5.** Traditional and emerging frameworks for incorporation of root processes into ecosystem
1007 models and dynamic vegetation models.