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Erica A.H. Smithwick
Pennsylvania State University

Melissa S. Lucash
Portland State University, lucash@pdx.edu

M. Luke McCormack
Synthesis Research Center of Chinese Ecosystem Research Network

Gajan Sivandran
Ohio State University - Main Campus

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

3 **Erica A.H. Smithwick¹, Melissa S. Lucash², M. Luke McCormack³, and Gajan Sivandran⁴**

4 ¹Department of Geography and Intercollege Graduate Program in Ecology, The Pennsylvania
5 State University, 302 Walker Building, University Park, Pennsylvania 16802, USA

6 ²Department of Environmental Science and Management, Portland State University, B1-24A
7 Science Research and Teaching Center, Portland, OR 97201, USA

8 ³Key Laboratory of Ecosystem Network Observation and Modeling, Synthesis Research Center
9 of Chinese Ecosystem Research Network, Institute of Geographic Sciences and Natural
10 Resources Research, Chinese Academy of Sciences, Beijing, 100101, China.

11 ⁴ Department of Civil, Environmental and Geodetic Engineering, Ohio State University
12 483B Hitchcock Hall, Columbus, OH 43210

13 Corresponding Author:

14 Erica A. H. Smithwick
15 Department of Geography

16 302 Walker Building
17 University Park, Pennsylvania 16802, USA

18 Tel: 814-865-6693

19 Email: smithwick@psu.edu

20 Fax: 814-863-7943

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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568 **REFERENCES**

- 569 Aber, J., Ollinger, S.V., Driscoll, C.T., 1997. Modeling nitrogen saturation in forest ecosystems
570 in response to land use and atmospheric deposition. *Ecol Model* 101, 61-78.
- 571 Agerer, R., 2001. Exploration types of ectomycorrhizae. *Mycorrhiza* 11, 107-114.
- 572 Albani, M., Medvigy, D., Hurtt, G.C., Moorcroft, P.R., 2006. The contributions of land-use
573 change, CO₂ fertilization, and climate variability to the Eastern US carbon sink. *Global*
574 *Change Biol* 12, 2370-2390.
- 575 Amenu, G.G., Kumar, P., 2008. A model for hydraulic redistribution incorporating coupled soil-
576 root moisture transport. *Hydrology and Earth System Sciences* 12, 55-74.
- 577 Baker, I.T., Prihodko, L., Denning, A.S., Goulden, M., Miller, S., da Rocha, H.R., 2008.
578 Seasonal drought stress in the Amazon: Reconciling models and observations. *J.*
579 *Geophys. Res.* 113, G00B01.
- 580 Bertrand, G., Masini, J., Goldscheider, N., Meeks, J., Lavastre, V., Celle-Jeanton, H., Gobat, J.-
581 M., Hunkeler, D., 2012. Determination of spatiotemporal variability of tree water uptake
582 using stable isotopes ($\delta^{18}\text{O}$, $\delta^2\text{H}$) in an alluvial system supplied by a high-altitude
583 watershed, Pfyn forest, Switzerland. *Ecohydrology*, n/a-n/a.
- 584 Bleby, T.M., McElrone, A.J., Jackson, R.B., 2010. Water uptake and hydraulic redistribution
585 across large woody root systems to 20 m depth. *Plant, Cell & Environment* 33, 2132-
586 2148.
- 587 Bloom, A.J., Caldwell, R.M., 1988. Root Excision Decreases Nutrient Absorption and Gas
588 Fluxes. *Plant Physiology* 87, 794-796.
- 589 Bloom, A.J., Chapin, F.S., Mooney, H.A., 1985. Resource limitation in plants - an economic
590 analogy. *Ann Rev Ecol Syst* 16, 363-392.

591 Bobowski, B.R., Hole, D.J., Wolf, P.G., Bryant, L., 1999. Identification of roots of woody
592 species using polymerase chain reaction and RFLP analysis. . *Molecular Ecology* 8, 485-
593 491.

594 Boisvenue, C., Running, S.W., 2010. Simulations show decreasing carbon stocks and potential
595 for carbon emissions in Rocky Mountain forests over the next century. *Ecol Appl* 20,
596 1302-1319.

597 Bolan, N.S., 1991. A critical review on the role of mycorrhizal fungi in the uptake of phosphorus
598 by plants. *Plant Soil* 134, 189-207.

599 Brassard, B.W., Chen, H.Y.H., Bergeron, Y., 2009. Influence of environmental variability on
600 root dynamics in northern forests. *Critical Reviews in Plant Science* 28, 179-197 % @
601 0735-2689.

602 Brooks, J.R., Meinzer, F.C., Coulombe, R., Gregg, J., 2002. Hydraulic redistribution of soil
603 water during summer drought in two contrasting Pacific Northwest coniferous forests.
604 *Tree Physiology* 22, 1107-1117.

605 Budyko, M.I., 1974. *Climate and Life*. Academic Press, New York 508 pp.

606 Burton, A.J., Pregitzer, K.S., Hendrick, R.L., 2000. Relationships between fine root dynamics
607 and nitrogen availability in Michigan northern hardwood forests. *Oecologia* 125, 389-
608 399.

609 Butnor, J.R., Doolittle, J.A., Johnsen, K.H., Samuelson, L., Stokes, T., Kress, L., 2003. Utility of
610 Ground-Penetrating Radar as a Root Biomass Survey Tool in Forest Systems. *Soil Sci.*
611 *Soc. Am. J.* 67, 1607-1615.

612 Caylor, K.K., D'odorico, P., Rodríguez-Iturbe, I., 2006. On the ecohydrology of structurally
613 heterogeneous semiarid landscapes. *Water Resources Research* 42, WO7424.

614 Ciais, P., Schelhaas, M.J., Zaehle, S., Piao, S.L., Cescatti, A., Liski, J., Luysaert, S., Le-Maire,
615 G., Schulze, E.D., Bouriaud, O., Freibauer, A., Valentini, R., Nabuurs, G.J., 2008.
616 Carbon accumulation in European forests. *Nature Geoscience* 1, 425-429.

617 Clemmensen, K.E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid,
618 J., Finlay, R.D., Wardle, D.A., Lindahl, B.D., 2013. Roots and Associated Fungi Drive
619 Long-Term Carbon Sequestration in Boreal Forest. *Science* 339, 1615-1618.

620 Collins, D.B.G., Bras, R.L., 2007. Plant rooting strategies in water-limited ecosystems. *Water*
621 *Resources Research* 43.

622 Comas, L.H., Eissenstat, D.M., 2009. Patterns in root trait variation among 25 co-existing North
623 American forest species. *New Phytol* 182, 919-928.

624 Couvreur, V., Vanderborght, J., Javaux, M., 2012. A simple three-dimensional macroscopic root
625 water uptake model based on the hydraulic architecture approach. *Hydrology and Earth*
626 *System Sciences* 16, 2957-2971.

627 Cronan, C.S., Grigal, D.F., 1995. Use of calcium aluminum ratios as indicators of stress in forest
628 ecosystems. *Journal of Environmental Quality* 24, 209-226.

629 Daly, C., Bachelet, D., Lenihan, J.M., Neilson, R.P., Parton, W., Ojima, D., 2000. Dynamic
630 simulation of tree-grass interactions for global change studies. *Ecol Appl* 10, 449-469.

631 Davidson, E., Lefebvre, P.A., Brando, P.M., Ray, D.M., Trumbore, S.E., Solorzano, L.A.,
632 Ferrera, J.N., da C. Bustamante, M.M., Nepstad, D.C., 2011. Carbon Inputs and Water
633 Uptake in Deep Soils of an Eastern Amazon Forest. *Forest Science* 57, 51-58.

634 Dawson, T.E., 1995. Determining water use by trees and forests from isotopic, energy balance
635 and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology* 16,
636 263-272.

637 Dawson, T.E., 1996. Determining water use by trees and forests from isotopic, energy balance
638 and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology* 16,
639 263-272.

640 Diez, J.M., Ibáñez, I., Miller-Rushing, A.J., Mazer, S.J., Crimmins, T.M., Crimmins, M.A.,
641 Bertelsen, C.D., Inouye, D.W., 2012. Forecasting phenology: from species variability to
642 community patterns. *Ecology letters* 15, 545-553.

643 Dybzinski, R., Farrior, C., Wolf, A., Reich, P.B., Pacala, S.W., 2011. Evolutionarily stable
644 strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and
645 nitrogen: an analytically tractable, individual-based model and quantitative comparisons
646 to data. *The American naturalist* 177, 153-166.

647 Dymond, C.C., Scheller, R.M., Beukema, S., 2012. A New Model For Simulating Climate
648 Change and Carbon Dynamics in Forested Landscapes. *Journal of Ecosystems and*
649 *Management* 13, 1-2.

650 Eltrop, L., Marschner, H., 1996. Growth and mineral nutrition of non-mycorrhizal and
651 mycorrhizal Norway spruce (*Picea abies*) seedlings grown in semi-hydroponic sand
652 culture. *New Phytologist* 133, 469-478.

653 Farquhar, G.D., Caemmerer, S.V., Berry, J.A., 1980. A biochemical model of photosynthetic
654 CO₂ assimilation in leaves of C-3 species. *Planta* 149, 78-90.

655 Feddes, R.A., Hoff, H., Bruen, M., Dawson, T.E., 2001. Modeling root water uptake in
656 hydrological and climate models. *Bulletin of the American Meteorological Society* 82,
657 2797-2810.

658 Fisher, J.B., Sitch, S., Malhi, Y., Fisher, R.A., Huntingford, C., Tan, S.Y., 2010. Carbon cost of
659 plant nitrogen acquisition: A mechanistic, globally applicable model of plant nitrogen
660 uptake, retranslocation, and fixation. *Global Biogeochem Cycles* 24.

661 Fisk, M.C., Yanai, R.D., Fierer, N., 2010. A molecular approach to quantify root community
662 composition in a northern hardwood forest — testing effects of root species, relative
663 abundance, and diameter. *Can J For Res* 40, 836-841.

664 Fridley, J.D., 2012. Extended leaf phenology and the autumn niche in deciduous forest invasions.
665 *Nature* 485, 359-362.

666 Garrigues, E., Doussan, C., Pierret, A., 2006. Water uptake by plant roots: I – Formation and
667 propagation of a water extraction front in mature root systems as evidenced by 2-D light
668 transmission imaging. *Plant and Soil* 283, 83-98.

669 Gaudinski, J.B., Torn, M.S., Riley, W.J., Dawson, T.E., Joslin, J.D., Majdi, H., 2010. Measuring
670 and modeling the spectrum of fine-root turnover times in three forests using isotopes,
671 minirhizotrons, and the Radix model. *Global Biogeochem Cycles* 24.

672 Gaudinski, J.B., Torn, M.S., Riley, W.J., Swanston, C., Trumbore, S.E., Joslin, J.D., Majdi, H.,
673 Dawson, T.E., Hanson, P.J., 2009. Use of stored carbon reserves in growth of temperate
674 tree roots and leaf buds: analyses using radiocarbon measurements and modeling. *Global
675 Change Biol* 15, 992-1014.

676 Gentine, P., D'odorico, P., Lintner, B., Sivandran, G., Salvucci, G., 2012. Interdependence of
677 climate, soil, and vegetation as constrained by the Budyko curve. *Geophysical Research
678 Letters* 39, L19404.

679 Gessler, A., Schneider, S., Von Sengbusch, D., Weber, P., Hanemann, U., Huber, C., Rothe, A.,
680 Kreutzer, K., Rennenberg, H., 1998. Field and laboratory experiments on net uptake of

681 nitrate and ammonium by the roots of spruce (*Picea abies*) and beech (*Fagus sylvatica*)
682 trees. *New Phytologist* 138, 275-285.

683 Gill, R.A., Jackson, R.B., 2000. Global patterns of root turnover for terrestrial ecosystems. *New*
684 *Phytologist* 147, 13-31.

685 Göransson, H., Wallander, H., Ingerslev, M., Rosengren, U., 2006. Estimating the relative
686 nutrient uptake from different soil depths in *Quercus robur*, *Fagus sylvatica* and *Picea*
687 *abies*. *Plant and Soil* 286, 87-97.

688 Gordon, W.S., Jackson, R.B., 2003. Global Distribution of Root Nutrient Concentrations in
689 Terrestrial Ecosystems. Data set. Available on-line [<http://www.daac.ornl.gov>] from Oak
690 Ridge National Laboratory Distributed Active archive Center, Oak Ridge, Tennessee,
691 U.S.A. .

692 Guo, D., Li, H., Mitchell, R.J., Han, W., Hendricks, J.J., Fahey, T.J., Hendrick, R.L., 2008a. Fine
693 root heterogeneity by branch order: exploring the discrepancy in root turnover estimates
694 between minirhizotron and carbon isotopic methods. *New Phytol* 177, 443-456.

695 Guo, D., Mitchell, R., Hendricks, J., 2004. Fine root branch orders respond differentially to
696 carbon source-sink manipulations in a longleaf pine forest. *Oecologia* 140, 450-457.

697 Guo, D., Xia, M., Wei, X., Chang, W., Liu, Y., Wang, Z., 2008b. Anatomical traits associated
698 with absorption and mycorrhizal colonization are linked to root branch order in twenty-
699 three Chinese temperate tree species. *New Phytol* 180, 673-683.

700 Guswa, A.J., 2008. The influence of climate on root depth: A carbon cost-benefit analysis. *Water*
701 *Resources Research* 44.

702 Harmon, M., 2011. Forest Sector Carbon Calculator Manual-Landcarbon Version 3.0.
703 landcarb.forestry.oregonstate.edu, 1-110.

704 Hendrick, R.L., Pregitzer, K.S., 1992. The Demography of Fine Roots in a Northern Hardwood
705 Forest. *Ecology* 73, 1094-1104.

706 Hendricks, J.J., Hendrick, R.L., Wilson, C.A., Mitchell, R.J., Pecot, S.D., Guo, D., 2006.
707 Assessing the patterns and controls of fine root dynamics: an empirical test and
708 methodological review. *Journal of Ecology* 94, 40-57.

709 Hendricks, J.J., Nadelhoffer, K.J., Aber, J.D., 1993. Assessing the role of fine roots in carbon
710 and nutrient cycling. *TREE* 8, 174.

711 Hildebrandt, A., 2005. *Ecohydrology of a Seasonal Cloud Forest in Dhoofar*, Civil and
712 Environmental Engineering. Massachusetts Institute of Technology, Cambridge.

713 Hopmans, J.W., Bristow, K.L., 2002. Current capabilities and future needs of root water and
714 nutrient uptake modeling. *Advances in Agronomy*, Vol 77 77, 103-183.

715 Hwang, T., Band, L., Hales, T.C., 2009. Ecosystem processes at the watershed scale: Extending
716 optimality theory from plot to catchment. *Water Resources Research* 45.

717 Ingestad, T., Agren, G.I., 1991. The influence of plant nutrition on biomass allocation. *Ecol Appl*
718 1, 168-174.

719 Iversen, C.M., 2010. Digging deeper: fine-root responses to rising atmospheric CO₂
720 concentration in forested ecosystems. *New Phytol* 186, 346-357.

721 Iversen, C.M., Ledford, J., Norby, R.J., 2008. CO₂ enrichment increases carbon and nitrogen
722 input from fine roots in a deciduous forest. *New Phytologist* 179, 837-847.

723 Jackson, R.B., Mooney, H.A., Schulze, E.D., 1997. A global budget for fine root biomass,
724 surface area, and nutrient contents. *Proceedings of the National Academy of Sciences* 94,
725 7362-7366.

726 Jackson, R.B., Moore, L.A., Hoffmann, W.A., Pockman, W.T., Linder, C.R., 1999. Ecosystem
727 rooting depth determined with caves and DNA. *Proceedings of the National Academy of*
728 *Sciences* 96, 11387-11392.

729 Jackson, R.B., Schenk, H.J., Jobbagy, E.G., Canadell, J.G., Colello, G.D., Dickenson, R.E.,
730 Field, C.B., Friedlingstein, P., Heimann, M., Hibbard, K., Kicklighter, D.W., Kleidon, A.,
731 Neilson, R.P., Parton, W.J., Sala, O.E., Sykes, M.T., 2000. Belowground consequences of
732 vegetation change and their treatment in models. *Ecol Appl* 10, 470-483.

733 Jain, A.K., Meiyappan, P., Song, Y., House, J.I., 2013. CO2 emissions from land-use change
734 affected more by nitrogen cycle, than by the choice of land-cover data. *Global Change*
735 *Biology*, n/a-n/a.

736 Jarvis, N.J., 2011. Simple physics-based models of compensatory plant water uptake: concepts
737 and eco-hydrological consequences. *Hydrology and Earth System Sciences* 15, 3431-
738 3446.

739 Javaux, M., Couvreur, V., Vander Borght, J., Vereecken, H., 2013. Root Water Uptake: From
740 Three-Dimensional Biophysical Processes to Macroscopic Modeling Approaches.
741 *Vadose Zone Journal* 12.

742 Johnson, I.R., Thornley, J.H.M., 1987. A Model of shoot: root partitioning with optimal growth.
743 *Annals of Botany* 60, 133-142.

744 Kashian, D.M., Romme, W.H., Tinker, D., Turner, M.G., Ryan, M.G., 2013. Post-fire changes in
745 forest carbon storage over a 300-year chronosequence of *Pinus contorta*-dominated
746 forests. *Ecol Monog* 83, 49-66.

747 Keane, R.E., Loehman, R.A., Holsinger, L.M., 2011. The FireBGCv2 Landscape Fire Succession
748 Model: A Research Simulation Platform for Exploring Fire and Vegetation Dynamics.
749 US Department of Agriculture, Forest Service, Rocky Mountain Research Station.

750 Kleidon, A., Heimann, M., 1998. A method of determining rooting depth from a terrestrial
751 biosphere model and its impacts on the global water and carbon cycle. *Global Change*
752 *Biology* 4, 275–286.

753 Kulmatiski, A., Beard, K., 2012. Root niche partitioning among grasses, saplings, and trees
754 measured using a tracer technique. *Oecologia*, 1-13.

755 Kulmatiski, A., Beard, K.H., Verweij, R.J.T., February, E.C., 2010. A depth-controlled tracer
756 technique measures vertical, horizontal and temporal patterns of water use by trees and
757 grasses in a subtropical savanna. *New Phytologist* 188, 199-209.

758 Lai, C., Katul, G., 2000. The dynamic role of root-water uptake in coupling potential to actual
759 transpiration. *Advances in Water Resources* 23, 427-439.

760 LeBauer, D.S., Wang, D., Richter, K.T., Davidson, C.C., Dietze, M.C., 2013. Facilitating
761 feedbacks between field measurements and ecosystem models. *Ecol Monog* 83, 133-154.

762 Lee, E.H., Tingey, D.T., Beedlow, P.A., Johnson, M.G., Burdick, C.A., 2007. Relating fine root
763 biomass to soil and climate conditions in the Pacific Northwest. *Forest Ecology and*
764 *Management* 242, 195-208.

765 Levis, S., Bonan, G.B., Vertenstein, M., Oleson, K.W., 2004. The Community Land Model's
766 Dynamic Global Vegetation Model (CLM-DGVM): Technical Description and User's
767 Guide. NCAR Tech. Note TN-459, 1-50.

768 Li, L.H., Wang, Y.P., Yu, Q., Pak, B., Eamus, D., Yan, J.H., van Gorsel, E., Baker, I.T., 2012.
769 Improving the responses of the Australian community land surface model (CABLE) to
770 seasonal drought. *Journal of Geophysical Research-Biogeosciences* 117.

771 Lucash, M.S., Eissenstat, D.M., Joslin, J.D., McFarlane, K.J., Yanai, R.D., 2007. Estimating
772 nutrient uptake by mature tree roots under field conditions: challenges and opportunities.
773 *Trees-Structure and Function* 21, 593-603.

774 Lucash, M.S., Yanai, R.D., Joslin, J.D., 2008. Nutrient uptake by intact and disturbed roots of
775 loblolly pine seedlings. *Environ. Exp. Bot.* 64, 15-20.

776 Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B.A., McMurtrie,
777 R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D., Field, C.B., 2004.
778 Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon
779 dioxide. *BioScience* 54, 731-739.

780 Malhi, Y., Doughty, C., Galbraith, D., 2011. The allocation of ecosystem net primary
781 productivity in tropical forests. *Philosophical Transactions of the Royal Society B:*
782 *Biological Sciences* 366, 3225-3245.

783 Manabe, S., 1966. Climate and Ocean Circulation .I. Atmospheric Circulation and Hydrology of
784 Earths Surface. *Mon Weather Rev* 97, 739-774.

785 Matamala, R., Gonzalez-Meler, M.A., Jastrow, J.D., Norby, R.J., Schlesinger, W.H., 2003.
786 Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science*
787 302, 1385-1387.

788 McCormack, M.L., Adams, T.S., Smithwick, E.A.H., Eissenstat, D.M., *in press*. Variability in
789 root production, phenology, and turnover rate among 12 temperate tree species. *Ecology*.

790 McCormack, M.L., Eissensat, D.M., Prasad, A., Smithwick, E.A.H., 2013. Regional scale
791 patterns of fine root lifespan and turnover under current and future climate. *Global*
792 *Change Biol* 19, 1697-1708.

793 McCulley, R.L., Jobbagy, E.G., Pockman, W.T., Jackson, R.B., 2004. Nutrient uptake as a
794 contributing explanation for deep rooting in arid and semi-arid ecosystems. *Oecologia*
795 141, 620-628.

796 McMurtrie, R.E., Iversen, C.M., Dewar, R.C., Medlyn, B.E., Näsholm, T., Pepper, D.A., Norby,
797 R.J., 2012. Plant root distributions and nitrogen uptake predicted by a hypothesis of
798 optimal root foraging. *Ecology and Evolution* 2, 1235-1250.

799 Medvigy, D., Wofsy, S.C., Munger, J.W., Hollinger, D.Y., Moorcroft, P.R., 2009. Mechanistic
800 scaling of ecosystem function and dynamics in space and time: Ecosystem Demography
801 model version 2. *J. Geophys. Res.* 114.

802 Metherell, A.K., Harding, L.A., Cole, C.V., William, J., 2010. CENTURY Soil Organic Matter
803 Model Environment Technical Documentation. Colorado State University.

804 Milchunas, D.G., 2009. Estimating Root Production: Comparison of 11 Methods in Shortgrass
805 Steppe and Review of Biases. *Ecosystems* 12, 1381-1402.

806 Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future:
807 Managing in the face of uncertainty. *Ecol Appl* 17, 2145-2151.

808 Mommer, L., Wagemaker, C.A.M., De Kroon, H., Ouborg, N.J., 2008. Unravelling below-
809 ground plant distributions: a real-time polymerase chain reaction method for quantifying
810 species proportions in mixed root samples. *Molecular Ecology Resources* 8, 947-953.

811 Mote, P.W., Parson, E.A., Hamlet, A.F., Ideker, K.N., Keeton, W.S., Lettenmaier, D.P., Mantua,
812 N.J., Miles, E.L., Peterson, D.W., Peterson, D.L., Slaughter, R., Snover., A.K., 2003.

813 Preparing for climatic change: The water, salmon, and forests of the Pacific Northwest.
814 Climatic Change 61, 45-88.

815 Nadelhoffer, K.J., 2000. The potential effects of nitrogen deposition on fine-root production in
816 forest ecosystems. *New Phytol* 147, 131-139.

817 Nadezhdina, N., Ferreira, M., Silva, R., Pacheco, C., 2008. Seasonal variation of water uptake of
818 a *Quercus suber* tree in Central Portugal. *Plant and Soil* 305, 105-119.

819 Neumann, R.B., Cardon, Z.G., 2012. The magnitude of hydraulic redistribution by plant roots: a
820 review and synthesis of empirical and modeling studies. *New Phytologist* 194, 337-352.

821 Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E., McMurtrie, R.E., 2010. CO₂
822 enhancement of forest productivity constrained by limited nitrogen availability.
823 *Proceedings of the National Academy of Sciences* 107, 19368-19373.

824 Oleson, K.W., Lawrence, D.M., Bonan, G.B., Flanner, M.G., Kluzek, E., Lawrence, P.J., Levis,
825 S., Swenson, S.C., Thornton, P.E., Dai, A., 2010. Technical Description of version 4.0 of
826 the Community Land Model (CLM) Rep., 257 pp. National Center for Atmospheric
827 Research, Boulder, CO.

828 Ollinger, S.V., Aber, J.D., Reich, P.B., Freuder, R.J., 2002. Interactive effects of nitrogen
829 deposition, tropospheric ozone, elevated CO₂ and land use history on the carbon
830 dynamics of northern hardwood forests. *Global Change Biology* 8, 545-562.

831 Öpik, M., Zobel, M., Cantero, J., Davison, J., Facelli, J., Hiiesalu, I., Jairus, T., Kalwij, J.,
832 Koorem, K., Leal, M., Liira, J., Metsis, M., Neshataeva, V., Paal, J., Phosri, C., Põlme,
833 S., Reier, Ü., Saks, Ü., Schimann, H., Thiéry, O., Vasar, M., Moora, M., 2013. Global
834 sampling of plant roots expands the described molecular diversity of arbuscular
835 mycorrhizal fungi. *Mycorrhiza*, 1-20.

836 Orwin, K.H., Kirschbaum, M.U.F., St John, M.G., Dickie, I.A., 2011. Organic nutrient uptake by
837 mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment.
838 Ecology Letters 14, 493-502.

839 Ostonen, I., Lõhmus, K., Pajuste, K., 2005. Fine root biomass, production and its proportion of
840 NPP in a fertile middle-aged Norway spruce forest: Comparison of soil core and
841 ingrowth core methods. Forest Ecology and Management 212, 264-277.

842 Park, B., Yanai, R., Fahey, T., Bailey, S., Siccama, T., Shanley, J., Cleavitt, N., 2008. Fine Root
843 Dynamics and Forest Production Across a Calcium Gradient in Northern Hardwood and
844 Conifer Ecosystems. Ecosystems 11, 325-341.

845 Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across
846 natural systems. Nature 421, 37-42.

847 Parton, W.J., Hanson, P.J., Swanston, C., Torn, M., Trumbore, S.E., Riley, W., Kelly, R., 2010.
848 ForCent model development and testing using the Enriched Background Isotope Study
849 experiment. Journal of Geophysical Research 115, G04001.

850 Pitman, A.J., 2003. The evolution of, and revolution in, land surface schemes designed for
851 climate models. International Journal of Climatology 23, 479-510.

852 Poorter, H., Nagel, O., 2000. The role of biomass allocation in the growth response of plants to
853 different levels of light, CO₂, nutrients and water: a quantitative review. Australian
854 Journal of Plant Physiology 27, 595-607.

855 Pregitzer, K.S., 2002. Fine roots of trees – a new perspective. New Phytologist 154, 267-270.

856 Pregitzer, K.S., Laskowski, M.J., Burton, A.J., Lessard, V.C., Zak, D.R., 1998. Variation in
857 sugar maple root respiration with root diameter and soil depth. Tree Phys 18, 665-670.

858 Proe, M.F., Midwood, A.J., Craig, J., 2000. Use of stable isotopes to quantify nitrogen,
859 potassium and magnesium dynamics in young Scots pine (*Pinus sylvestris*). *New*
860 *Phytologist* 146, 461-469.

861 Richardson, A.D., Anderson, R.S., Arain, M.A., Barr, A.G., Bohrer, G., Chen, G.S., Chen, J.M.,
862 Ciais, P., Davis, K.J., Desai, A.R., Dietze, M.C., Dragoni, D., Garrity, S.R., Gough,
863 C.M., Grant, R., Hollinger, D.Y., Margolis, H.A., McCaughey, H., Migliavacca, M.,
864 Monson, R.K., Munger, J.W., Poulter, B., Raczka, B.M., Ricciuto, D.M., Sahoo, A.K.,
865 Schaefer, K., Tian, H.Q., Vargas, R., Verbeeck, H., Xiao, J.F., Xue, Y.K., 2012.
866 Terrestrial biosphere models need better representation of vegetation phenology: results
867 from the North American Carbon Program Site Synthesis. *Global Change Biology* 18,
868 566-584.

869 Robinson, D., 2004. Scaling the depths: Below-ground allocation in plants, forests and biomes.
870 *Functional Ecology* 18, 290-295.

871 Santantonio, D., Hermann, R.K., Overton, W.S., 1977. Root biomass studies in forest
872 ecosystems. *Pedobiologia* 17, 1-31.

873 Schaefer, K., Collatz, G.J., Tans, P., Denning, A.S., Baker, I., Berry, J., Prihodko, L., Suits, N.,
874 Philpott, A., 2008. Combined Simple Biosphere/Carnegie-Ames-Stanford Approach
875 terrestrial carbon cycle model. *J Geophys Res-Biogeophys* 113.

876 Scheller, R.M., Hua, D., Bolstad, P.V., Birdsey, R.A., Mladenoff, D.J., 2011. The effects of
877 forest harvest intensity in combination with wind disturbance on carbon dynamics in
878 Lake States Mesic Forests. *Ecological Modelling* 222, 144-153.

879 Scheller, R.M., Kretchun, A.M., Tuyl, S.V., Clark, K.L., Lucash, M.S., Hom, J., In press.
880 Divergent carbon dynamics under climate change in the New Jersey Pine Barrens, USA.
881 Ecosphere.

882 Schenk, H.J., 2008. The Shallowest Possible Water Extraction Profile: A Null Model for Global
883 Root Distributions. *Vadose Zone Journal* 7, 1119-1124.

884 Schenk, H.J., Jackson, R.B., 2002. The global biogeography of roots. *Ecol Monog* 72, 311-328.

885 Schnepf, A., Roose, T., Schweiger, P., 2008a. Growth model for arbuscular mycorrhizal fungi.
886 *Journal of the Royal Society Interface* 5, 773-784.

887 Schnepf, A., Roose, T., Schweiger, P., 2008b. Impact of growth and uptake patterns of
888 arbuscular mycorrhizal fungi on plant phosphorus uptake—a modelling study. *Plant and*
889 *Soil* 312, 85-99.

890 Schymanski, S.J., Sivapalan, M., Roderick, M.L., Beringer, J., Hutley, L.B., 2008. An
891 optimality-based model of the coupled soil moisture and root dynamics. *Hydrology and*
892 *Earth System Sciences Discussions* 5, 51-94.

893 Schymanski, S.J., Sivapalan, M., Roderick, M.L., Hutley, L.B., Beringer, J., 2009. An
894 optimality-based model of the dynamic feedbacks between natural vegetation and the
895 water balance. *Water Resources Research* 45.

896 Sharp, R.E., Davies, W.J., 1985. Root growth and water uptake by maize plants in drying soil.
897 *Journal of Experimental Botany* 36, 1441-1456.

898 Shevliakova, E., Pacala, S.W., Malyshev, S., Hurtt, G.C., Milly, P.C.D., Caspersen, J.P.,
899 Sentman, L.T., Fisk, J.P., Wirth, C., Crevoisier, C., 2009. Carbon cycling under 300 years
900 of land use change: Importance of the secondary vegetation sink. *Global Biogeochemical*
901 *Cycles* 23.

902 Simunek, J., Hopmans, J.W., 2009. Modeling compensated root water and nutrient uptake. *Ecol*
903 *Model* 220, 505-521.

904 Sivandran, G., Bras, R.L., 2013. Dynamic root distributions in eco-hydrological modeling: A
905 case study at Walnut gulch experimental watershed. *Water Resources Research* In press.

906 Sivandran, G., L.Bras, R., 2012. Identifying the optimal spatially and temporally invariant root
907 distribution for a semiarid environment. *Water Resources Research* 48.

908 Smit, A.L., Bengough, A.G., Engels, C., van Noordwijk, M., Pellerin, S., van de Geijn, S.C.,
909 2000. *Root methods: a handbook*. Springer.

910 Smith, S., Read, D., 2008. *Mycorrhizal Symbiosis*. Elsevier, NY, NY.

911 Smithwick, E.A.H., Eissensat, D.M., Lovett, G.M., Bowden, R.D., Rustad, L.E., Driscoll, C.T.,
912 2013. Root stress and nitrogen deposition: Consequences and research priorities. *New*
913 *Phytol* 197, 1697-1708.

914 Soethe, N., Lehmann, J., Engels, C., 2006. The vertical pattern of root and nutrient uptake at
915 different altitudes of a south Ecuadorian montane forest. *Plant and Soil* 286, 287-299.

916 Steinaker, D.F., Wilson, S.D., Peltzer, D.A., 2010. Asynchronicity in root and shoot phenology
917 in grasses and woody plants. *Global Change Biol* 16, 2241-2251.

918 Stover, D.B., Day, F.P., Butnor, J.R., Drake, B.G., 2007. Effect of elevated CO₂ on coarse-root
919 biomass in Florida scrub detected by ground-penetrating radar. *Ecology* 88, 1328-1334.

920 Thornton, P.E., Lamarque, J.F., Rosenbloom, N.A., Mahowald, N.M., 2007. Influence of carbon-
921 nitrogen cycle coupling on land model response to CO₂ fertilization and climate
922 variability. *Global Biogeochemical Cycles* 21.

923 Tian, H., Melillo, J.M., Lu, C., Kicklighter, D.W., Liu, M., Ren, W., Xu, X., Chen, G., Zhang,
924 C., Pan, S., 2011. China's terrestrial carbon balance: Contributions from multiple global
925 change factors.

926 Tierney, G.L., Fahey, T.J., 2002. Fine root turnover in a northern hardwood forest: a direct
927 comparison of the radiocarbon and minirhizotron methods. *Canadian Journal of Forest
928 Research-Revue Canadienne De Recherche Forestiere* 32, 1692-1697.

929 Tjoelker, M.G., Craine, J.M., Wedin, D., Reich, P.B., Tilman, D., 2005. Linking leaf and root
930 trait syndromes among 39 grassland and savannah species. *New Phytologist* 167, 493-
931 508.

932 Treseder, K.K., Balser, T.C., Bradford, M.A., Brodie, E.L., Dubinsky, E.A., Eviner, V.T.,
933 Hofmockel, K.S., Lennon, J.T., Levine, U.Y., MacGregor, B.J., Pett-Ridge, J., Waldrop,
934 M.P., 2012. Integrating microbial ecology into ecosystem models: challenges and
935 priorities. *Biogeochem* 109, 7-18.

936 Treseder, K.K., Turner, K.M., Mack, M.C., 2007. Mycorrhizal responses to nitrogen fertilization
937 in boreal ecosystems: potential consequences for soil carbon storage
938 doi:10.1111/j.1365-2486.2006.01279.x. *Global Change Biol* 13, 78-88.

939 Vadeboncoeur, M.A., Hamburg, S.P., Yanai, R.D., 2007. Validation and refinement of allometric
940 equations for roots of northern hardwoods. *Canadian Journal of Forest Research* 37,
941 1777-1783.

942 Vargas, R., 2009. On the fate of old stored carbon after large-infrequent disturbances in plants.
943 *Plant signaling & behavior* 4, 617-619.

944 Vogt, K.A., Vogt, D.J., Bloomfield, J., 1998. Analysis of some direct and indirect methods for
945 estimating root biomass and production of forests at an ecosystem level. *Plant and Soil*
946 200, 71-89.

947 Wan, C.G., Yilmaz, I., Sosebee, R.E., 2002. Seasonal soil-water availability influences
948 snakeweed, root dynamics. *Journal of Arid Environments* 51, 255-264.

949 Wang, D., LeBauer, D., Dietze, M.C., 2012. Predicting yields of short-rotation hybrid poplar
950 (*Populus* spp.) for the contiguous US through model-data synthesis. *Ecol Appl.*

951 Withington, J.M., Reich, P.B., Oleksyn, J., Eissenstat, D.M., 2006. Comparisons of structure and
952 life span in roots and leaves among temperate trees. *Ecological Monographs* 76, 381-397.

953 Wolf, A., Ciais, P., Bellassen, V., Delbart, N., Field, C.B., Berry, J.A., 2011. Forest biomass
954 allometry in global land surface models. *Global Biogeochem Cycles* 25.

955 Xia, M., Guo, D., Pregitzer, K.S., 2010. Ephemeral root modules in *Fraxinus mandshurica*. *New*
956 *Phytol* 188, 1065-1074.

957 Yanai, R.D., Fisk, M.C., Fahey, T.J., Cleavitt, N.L., Park, B.B., 2008. Identifying roots of
958 northern hardwood species: patterns with diameter and depth. *Can J For Res* 38, 2862-
959 2869.

960 Yang, H., Auerswald, K., Bai, Y., Han, X., 2011. Complementarity in water sources among
961 dominant species in typical steppe ecosystems of Inner Mongolia, China. *Plant and Soil*
962 340, 303-313.

963 Yuan, Z.Y., Chen, H.Y.H., 2012. A global analysis of fine root production as affected by soil
964 nitrogen and phosphorus. *Proceedings of the Royal Society B: Biological Sciences* 279,
965 3796-3802.

966 Zaehle, S., Friend, A.D., 2010. Carbon and nitrogen cycle dynamics in the O-CN land surface
967 model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates.
968 *Global Biogeochem Cycles* 24.

969 Zeng, X.B., 2001. Global vegetation root distribution for land modeling. *Journal of*
970 *Hydrometeorology* 2, 525-530.

971 Zhu, B., Cheng, W., 2011. Rhizosphere priming effect increases the temperature sensitivity of
972 soil organic matter decomposition. *Global Change Biology* 17, 2172-2183.

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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.