EVOLUTIONARY PATTERNS AND BIOGEOCHEMICAL SIGNIFICANCE OF ANGIOSPERM ROOT TRAITS

L. H. Comas,[1,2,]* K. E. Mueller,[1,]† L. L. Taylor,[1,]‡ P. E. Midford,§ H. S. Callahan,‖ and D. J. Beerling‡

*USDA-ARS, Water Management Research, Fort Collins, Colorado 80526, U.S.A.; †Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota 55108, U.S.A.; ‡Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom; §National Evolutionary Synthesis Center, Duke University, Durham, North Carolina 27705, U.S.A.; and ‖Department of Biological Sciences, Barnard College, Columbia University, New York, New York 10027, U.S.A.

On the basis of a synthesis of recent progress in belowground ecology, we advance and discuss a hypothesis that relates root trait evolution to the increased dominance of angiosperms into dry upland habitats and the decline of atmospheric CO_2 concentration that began in the Cretaceous. Our hypothesis is built from examining patterns of fine root adaptations during the Cretaceous, when angiosperms dramatically diversified in association with arbuscular and ectomycorrhizal root-fungal symbionts. We then explore the potential effects of root adaptations and mycorrhizas on the geochemical carbon cycle. On the basis of phylogenetic analyses of root traits among extant plant species, we suggest that angiosperm taxa, which diversified since the early Cretaceous, evolved thinner roots with greater root length per unit of biomass invested (i.e., specific root length [SRL]) than earlier diverging taxa. We suggest that these changes in root morphology were facilitated by a decline in atmospheric CO_2, which likely caused water to become more limiting and nutrients more bound to organic matter. Under these conditions, we suggest that thin roots with long SRL would have allowed plants to more efficiently forage for soil water and nutrients. This assertion is supported by the observation that SRL correlates with greater root length density in soil and increased root capacity to take up water. Simulations indicate that the evolution of angiosperm root systems with greater SRL and ectomycorrhizas during the Cretaceous and Cenozoic substantially increased mineral weathering rates, with a fourfold increase in SRL, equivalent to a quadrupling of atmospheric CO_2 concentration. The hypothesis presented here raises the possibility that plant hydraulic status and nutrient balance together shaped whole-plant growth strategies, with important consequences for the evolution of the biosphere.

Keywords: specific root length, root trait evolution, biogeochemical weathering, EM colonization, AM colonization, nitrogen, carbon dioxide (CO_2), soil.

Introduction

Terrestrial plants, the atmosphere, and the biosphere coevolved over geologic time (Beerling and Berner 2005). Plant functional traits played an important role in this coevolution by controlling plant responses to environmental variation and governing biological impacts on ecosystem processes, such as the sequestration of carbon, cycling of soil nutrients, weathering of minerals, and soil formation (Verboom and Pate 2006). To improve our understanding of plant-biosphere interactions in the past and to better predict the outcome of these interactions in the future, we need to better understand (1) major evolutionary patterns of plant traits, (2) the role and identity of key environmental factors that have shaped these traits, (3) how shifts in root traits correlated with trait shifts in leaves and flowers and with plant nutrient and water requirements, and (4) how different traits and taxa influence ecosystem functioning. Although progress has been made in understanding the functional significance and evolutionary patterns of aboveground plant traits (Reich et al. 2003; Wright et al. 2004; Boyce et al. 2009; Feild et al. 2009; Little et al. 2010), much less is known about the ecological and evolutionary significance of belowground trait variation.

This review focuses specifically on evolutionary patterns of fine root traits of woody forest species and how shifts in the root traits of conifers and angiosperms may have affected biogeochemical processes during the Cretaceous (~145–65 million years ago), a critical time of woody plant and biosphere evolution. We emphasize woody forest species for several reasons. First, several woody plant lineages diversified during the Cretaceous. Second, forests composed of these lineages have played a dominant role in driving terrestrial biogeochemical cycles over this time compared with grasslands and savannas, which are more recent (Beerling and Osborne 2006; Tipple

and Pagani 2007; Strömberg 2011). Third, a broad analysis that includes herbaceous plants is currently hindered in part by methodological issues. Specifically, measurements of trait variation among woody plants have recently focused on the most distal root branches (i.e., ephemeral roots specialized for soil resource acquisition distinct from woody roots), while herbaceous root traits are typically measured on the entire root system, perhaps because there is more overlap among sections of the root system in functions such as soil resource acquisition, transport, anchorage, and storage (perennial herbaceous plants). Other researchers are conducting work with roots of herbaceous annuals and perennials (Grime et al. 1997; Craine et al. 2002; Levang-Brilz and Biondini 2003; Tjoelker et al. 2005; Roumet et al. 2006; Kembel and Cahill 2011), and it may eventually be possible to synthesize data more broadly.

Here, we first provide an overview of fine root morphological and functional traits of woody plants and then evaluate links between fine root morphology, function, and plant growth strategies. These links are critical for interpreting the significance of evolutionary patterns in root traits, which we subsequently explore. Given the paucity of the fossil record for plant roots and mycorrhizas (Peterson 1992), we emphasize phylogenetically informed comparisons of extant taxa as a promising strategy for advancing large-scale ecological understanding (Westoby 2006). Finally, we describe a novel, broad hypothesis that relates root trait evolution to the decline of atmospheric CO_2 concentration that began in the Cretaceous. We consider potential effects of root adaptations on biogeochemical processes during and since the Cretaceous using a combination of theory, observations from modern ecosystems, and simulations of mineral weathering rates (Taylor et al. 2011, 2012). Our overarching aim is to integrate studies of plant traits with ecosystem-scale processes (Allen and Hoekstra 1992) as a necessary step for better understanding the coevolution of plants and the biosphere.

Fine Root Form and Function: A Primer

Short-lived tissues that primarily function in resource acquisition, such as leaves and nonwoody fine roots, represent a considerable plant investment of mineral nutrients and biomass for their construction and maintenance. Recent work has progressed in characterizing fine root systems of woody plants with greater clarity and precision. Fine roots specifically refer to thin and highly branched, distal root clusters that function to forage for and absorb soil resources (Pregitzer 2002; Xia et al. 2010). These nonwoody roots, typically the youngest and thinnest branches (first and second order, counting back from root tips; Pregitzer 2002), are distinct from more conspicuous roots that undergo secondary cambial growth and function for storage and anchorage (Esau 1977; Comas et al. 2002; Pregitzer 2002; Guo et al. 2008). The ephemeral portion of the root systems is comprised of the finest two root branch orders (Xia et al. 2010). Although it is challenging to collect data on this portion of the root system, improved definitions of the fine root system and the standardization of

protocols for appropriate field sampling have allowed for the collection of improved data sets for comparative analyses.

Currently, there are limited data on a broad range of root traits and species to facilitate extensive evaluation. Consequently, key root traits associated with plant growth strategies are poorly resolved. Studies of root functional ecology have emphasized morphological and physiological variables, such as specific root length (SRL; root length per unit biomass) and nitrogen (N) concentration, that reflect resource deployment in fine root tissues (Eissenstat et al. 2000). In principle, SRL is governed by a combination of morphological traits, particularly root diameter and tissue density, that affect the amount of root length deployed per unit root biomass (Fitter 1991). However, thus far, differences in SRL among woody plant species are generally found to be associated with species differences in root diameter rather than tissue density (Comas and Eissenstat 2004, 2009). Certain traits, such as root tissue density and root hair density, may vary less consistently among woody species and be strongly influenced by soil moisture conditions (Comas and Eissenstat 2009; Holdaway et al. 2011; L. H. Comas and H. S. Callahan, personal observation). Other key traits, such as root life span and root length density (RLD) per soil volume, are rarely measured but are central to a plant's ability to forage for soil nutrients. This is partly because it is more time consuming to measure root life span and RLD and because these traits are more difficult to measure at the species level in mixed forests.

Commonly measured traits of fine roots, such as SRL and root N concentration, closely mirror leaf traits emphasized by studies of functional ecology (e.g., specific leaf area and leaf N concentration; Wright et al. 2004), but roots differ in several ways that add a layer of complexity to discussions of their functional traits and potential trade-offs. First, in the majority of plants, roots form symbioses with one or more types of mycorrhizal fungi that are directly involved in soil resource acquisition, especially of phosphorus (P) and N (Smith and Read 2008). Different types of mycorrhizal fungi, such as ectomycorrhizal and arbuscular mycorrhizal fungi (EM and AM, respectively), also likely exert unique selection pressures on plants—and root traits specifically—because of differences in their own function and morphology (Brundrett 2002; Comas and Eissenstat 2009). Next, while leaf trait evolution is largely driven to maximize carbon (C) fixation while minimizing water loss (Boyce et al. 2009; Feild et al. 2011a), roots provide a wide array of functions, such as direct root uptake of soil resources and support of mycorrhizal fungi, that cannot necessarily be simultaneously maximized (Brundrett 2002). Finally, different strategies are likely required to maximize acquisition of limiting soil resources that differ in spatial distribution and mobility. For example, it has been suggested that immobile nutrients are most effectively foraged by plants supporting mycorrhizal colonization or root hairs and highly branched roots for extensive foraging (Brundrett 2002). In contrast, mobile nutrients and water may be more effectively foraged with increased root surface area and localized proliferation (Robinson et al. 1999; Brundrett 2002). Nonetheless, predictable patterns in root trait variation, reflecting adaptations to selective pressures over geologic time, are expected on the basis of theories of plant strategies related to plant resource acquisition and allocation and are worth exploring.

Optimization of Root Form and Function: Perspectives on Root Trait Adaptation

Root Traits and Plant Growth Strategies

Root morphological traits can vary widely (by a difference of an order of magnitude) among plant species across communities (temperate rainforest chronosequence: Holdaway et al. 2011) as well as within communities (temperate forest: Brundrett and Kendrick 1990; Pregitzer et al. 2002; Withington et al. 2006; Guo et al. 2008; Comas and Eissenstat 2009; tropical forest: St. John 1980; Paz 2003; Zangaro et al. 2007). Variation in root morphology is linked to whole-plant growth strategies (Reich et al. 1998; Comas et al. 2002) that are optimized for success in different environments (Tilman 1988; Lambers and Poorter 1992; Chapin et al. 1993; Westoby 1998; Grime 2001). It has been noted that root diameter is often thinner and SRL greater in angiosperms than in gymnosperms (Reich et al. 1998; Bauhus and Messier 1999; Ostonen et al. 2007; Alvarez-Uria and Körner 2011). However, species of early diverging angiosperm lineages, such as Magnoliids, have coarser roots with lower SRL than gymnosperms (Pregitzer et al. 2002; Comas and Eissenstat 2009). Further, much like specific leaf area, SRL and root diameter may constrain variation in other functional traits—in particular, root physiology and life span—but the nature of trade-offs between morphology and root functions is poorly understood.

Emerging evidence associates root morphology with plant strategies for acquiring limited supplies of water. For example, thinner roots with a reduced cortical area likely have less impedance to water movement (Eissenstat and Achor 1999), and species with thinner roots and longer SRL appear to have greater hydraulic conductivity both within a genus (Huang and Eissenstat 2000; Solari et al. 2006) as well as across broad species comparisons (Rieger and Litvin 1999; Hernández et al. 2009). Among several temperate woody genera—including *Quercus*, *Carya*, *Betula*, *Populus*, and *Aralia*—species with thinner roots and greater SRL were generally associated with more xeric habitats, potentially to abet water uptake (Espeleta and Donovan 2002; L. H. Comas and H. S. Callahan, unpublished data). SRL of species increased as soil moisture decreased across several sites in the Amazon rainforest (Metcalfe et al. 2008). Likewise, roots were thinner and specific root area greater in *Fagus sylvatica* stands in Germany as precipitation declined (Meier and Leuschner 2008). Finally, SRL and hydraulic conductivity were positively related to photosynthetic rates among species adapted to xeric conditions, suggesting that root form and functioning matter for growth when water is limiting (Hernández et al. 2009).

Root morphology, especially SRL, is predicted by theoretical solute transport models to be important for nutrient foraging (Eissenstat and Yanai 1997). Increasing root length and root surface area in soil is more effective for soil nutrient acquisition than simply increased root biomass (Eissenstat 1991; Fitter 1991). Trait patterns revealed in comparative studies generally support this view. For example, fast-growing or early successional species, which theoretically need faster nutrient uptake, were associated with root morphological traits such as longer SRL, thinner root diameters, and, in some cases, low root tissue density (Comas et al. 2002; Paz 2003; Zangaro et al. 2007; Holdaway et al. 2011). Across communities varying in nutrient availability, species adapted to low-nutrient conditions also had thinner roots with longer SRL and greater or insignificantly different root tissue density, potentially enhancing foraging of limited nutrients (Paz 2003; Holdaway et al. 2011).

Longer SRL among contrasting species has been associated with greater metabolic activity and higher rates of nutrient uptake (Comas et al. 2002; Holdaway et al. 2011; but see Comas and Eissenstat 2004) but also higher respiration rates and tissue N concentrations (Comas et al. 2002; Volder et al. 2005). Long SRL among contrasting species has been associated with fast-growing roots (Eissenstat 1991) and shoots (Comas et al. 2002; Nicotra et al. 2002; Comas and Eissenstat 2004), but there are exceptions. Some fast-growing species have short SRL, perhaps due to optimization of root tissue to maximize nutrient uptake through symbiotic interactions with fungi instead of directly through root uptake (Comas et al. 2002; Comas and Eissenstat 2004). Finally, root morphology and physiology have been predicted to vary in concert with root longevity in relation to whole-plant growth strategy, such that investment in roots is optimized relative to resource uptake (Eissenstat and Yanai 1997). However, SRL can be uncoupled to root life span (Withington et al. 2006; Espeleta et al. 2009), for example, when traits such as thickness of outer tangential exodermis walls are more closely associated with root life span than SRL (Withington et al. 2006).

Finally, root morphology can impact the nature of symbioses between plants and mycorrhizal fungi. Thin root diameters and long SRL potentially limit colonization by mycorrhizal fungi, particularly AM fungi, because they have a reduced cortical area per length to support mycorrhizal associations (Baylis 1975; St. John 1980; Graham and Eissenstat 1998; Brundrett 2002). Such relationships have been used to suggest that plants with thick roots and short SRL, which are also associated with slow elongation rates (Eissenstat 1991), are dependent on fungal symbionts for nutrient foraging (Baylis 1972, 1975). However, thin roots with long SRL may have greater surface area per mass to interact with symbiotic fungi and more root length to intersect symbiotic fungi in the soil matrix, as some studies have found greater AM mycorrhizal colonization on thinner roots (Siqueira and Saggin-Junior 2001; Roumet et al. 2006; Zangaro et al. 2007). These studies potentially also reflect the tendency of thinner roots to grow more quickly and be colonized earlier (Roumet et al. 2006), although mycorrhizal colonization rates are presumably regulated by active signaling mechanisms evolved between roots and fungi to control colonization (Graham et al. 1991). EM colonization has rarely been examined in association with root morphology and may be independent of morphological constraints because EM associations form at root tips. Interestingly, L. H. Comas (unpublished data) found less root tip colonization by EM fungi on hosts with thinner root diameter and longer SRL, supporting the hypothesis that hosts with thinner roots and longer SRL may have evolved less dependency on mycorrhizas. That is, if the benefits that plants derive from fungal partners do not compensate for the cost

of supporting them, there may be natural selection for plants to actively downregulate the extent of root colonization.

For several reasons, universal correlations may be unlikely between traits that enhance resource uptake efficiency, such as thin root diameter, longer SRL, low N concentration, and long root life span. First, the number of root traits related to efficient resource allocation suggests that optimal plant investment in absorptive roots can be achieved by several different combinations of trait values. Second, the efficiency of any given trait value or combination of traits also depends on the scope of investment in roots, as reflected by RLD and the extent of soil volume exploited by roots (Eissenstat et al. 2000). In other words, efficiency may be determined not just by the morphological and functional traits of individual fine roots but also by the quantity and spatial extent of root length in soil. Finally, simple predictions of trade-offs among root traits and tissue optimization for resource acquisition are complicated by interactions between fine roots and mycorrhizas.

In summary, a plant's competitive ability for acquiring soil resources is largely determined by the total length and surface area of its roots and mycorrhizas as well as the total volume of soil it can explore. Plant uptake of resources is likely jointly constrained by root morphology, metabolic activity, and root tissue longevity, such that the efficiency gained by one trait (e.g., thin diameter, long SRL, or long life span) could allow for greater investment in root length or mycorrhizal associations. Exploration into these trade-offs has been limited but is crucial for understanding trait patterns. Data from a common garden experiment of temperate trees shows that species with longer SRL (i.e., less biomass investment per unit root length) tend to have greater RLD (fig. 1). Conversely, greater dependence on mycorrhizal fungi for nutrient acquisition could necessitate limits on biomass investments in fine roots, for example, through lower RLD. The form of these trade-offs that is most beneficial to plants (i.e., the optimal combination of root traits) likely depends on the nature of available soil resources, which is a function of climate, soil properties, and biota.

### Phylogenetic Patterns of Root Trait Variation

Because of the scarcity of fossil roots and mycorrhizas during the Cretaceous, the geologic record has not produced a detailed picture of root trait evolution during the most important period of angiosperm diversification. A powerful approach to filling this knowledge gap is to examine trait variation among living plants in the context of their phylogenetic history (Peterson 1992). The emerging pattern from phylogenetic analyses of extant angiosperms and gymnosperms suggests that basal angiosperms had relatively coarse roots and short SRL but that angiosperm lineages diversifying more recently during the Cretaceous had finer roots (Comas and Eissenstat 2009; L. H. Comas and H. S. Callahan, unpublished data; figs. 2, 3). However, this evolutionary interpretation necessitates the assumption that trait differences among extant species mirror the patterns of their ancestors, which should be tested with fossil evidence when available (Feild et al. 2011b).
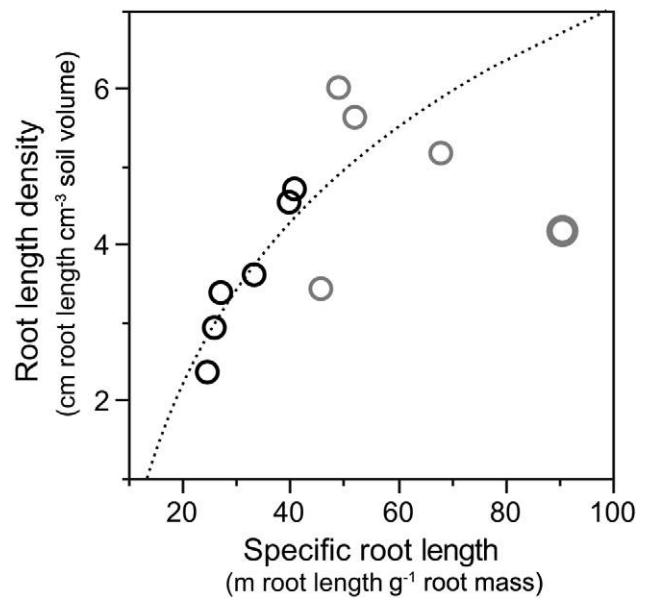
Fig. 1 Relationship between specific root length (SRL) and root length density (RLD) in soil of first- and second-order terminal roots from 11 temperate forest trees grown in a common garden in central Poland (Withington et al. 2006). Species represented include five hardwoods (gray circles; *Acer pseudoplatanus* L., *Acer platanoides* L., *Fagus sylvatica* L., *Quercus robur* L., and *Tilia cordata* Mill.) and six conifers (black circles; *Abies alba* Mill., *Larix decidua* Mill., *Picea abies* (L.) Karst., *Pinus nigra* Arnold, *Pinus sylvestris* L., and *Pseudotsuga menziesii* (Mirbel) Franco). The dotted line indicates RLD as a function of ln-transformed SRL, excluding one point (*F. sylvatica*; thick gray circle; $R^2 = 0.69$, $P < 0.05$). A logarithmic fit that includes *F. sylvatica* was also significant ($R^2 = 0.41$, $P < 0.05$). Consistent with this relationship and the relationship between root diameter and SRL, root diameter was also negatively correlated with RLD ($R^2 = 0.37$, $P < 0.05$; data not shown).

Baylis (1972, 1975) first suggested that recent plant radiations resulted in species evolving thinner roots and long root hairs. He hypothesized that this evolutionary pattern was driven by benefits of less dependency on mycorrhizas, which require substantial C support of fungi by plants (Peng et al. 1993; Graham and Eissenstat 1998). This hypothesis was founded on weak projections of root trait patterns (extrapolated from Magnoliid vs. grass root traits) and a simplistic view of plant-fungal interactions but has inspired investigations into root trait patterns. Baylis partially supported his hypotheses with observations that extant species that are nonmycorrhizal or facultatively mycorrhizal have thin roots with dense numbers of thin root hairs (Baylis 1972, 1975). These observations have been supported by others, although nonmycorrhizal or facultatively mycorrhizal plants are often special cases, limited either to a few rare cases of plants adapted to extreme habitats—such as Cyperaceae and Proteacea—or to short-lived herbaceous vegetation, such as Brassicaceae (Peat and Fitter 1993; Lambers et al. 2008; Brundrett 2009).

Pregitzer et al. (2002) reported large interspecific variation in root morphology among nine North American species and, consistent with the suggestions of Baylis, noted an evo-
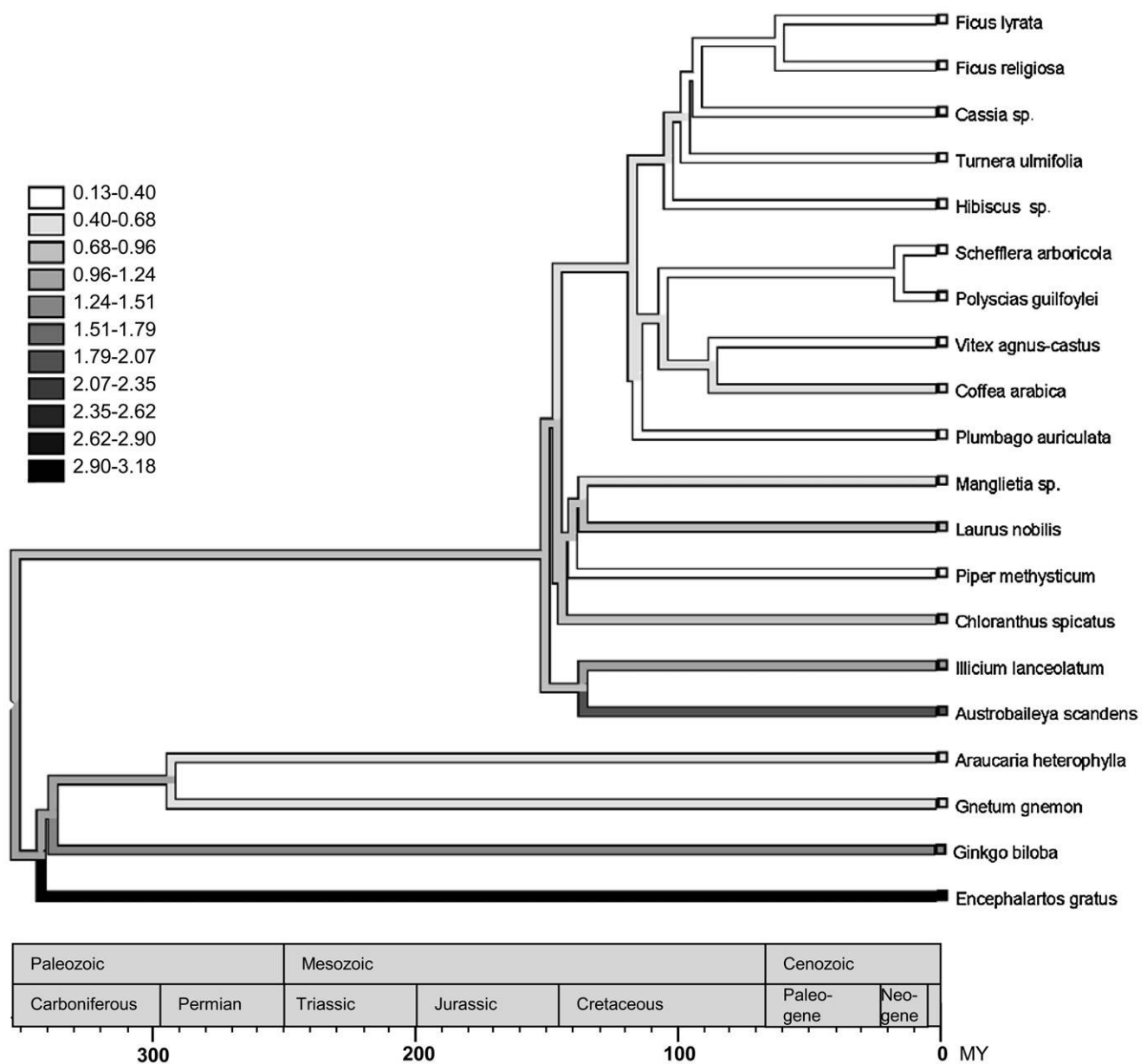
Fig. 2 Diameter (mm) of roots functioning in soil resource acquisition (i.e., clusters of first- and second-order root tips) reconstructed along phylogenetic lines among 20 tropical and subtropical angiosperms and some of their nearest extant nonseed plant lineages. The phylogenic tree is based on recent analyses of plant taxa, with branch lengths indicating proximity of relationships in units of millions of years, as estimated with maximum likelihood methods (Wikstrom et al. 2001; Magallon and Sanderson 2005). Species include 16 angiosperms (*Austrobaileya–Ficus*) and four nonangiosperm seed plants. Branch color indicates root diameter of each species and node, with values at nodes estimated with squared-change parsimony (Mesquite 2.75; Maddison and Maddison 2010).

lutionary pattern across conifer, magnoliid, and eudicot clades for roots to have evolved greater SRL and decreased diameter. Examining root morphology across a broader taxonomic range of species (25 temperate woody taxa) within the same forest community, Comas and Eissenstat (2009) found a 10-fold difference in SRL among angiosperms spanning ~140 million years of species diversification. Across a broader phylogeny in a data set of 20 tropical and subtropical species sampled from plants in botanical collections, an evolution-

ary pattern was found of first- and second-order roots becoming thinner as seed plants diverged from basal lineages (e.g., cycads, gnetophytes, *Gingko*) through recent angiosperm clades (figs. 2, 3). Among angiosperms alone, this data set showed a 20-fold difference in SRL, spanning the same interval of diversification. In several cases, root diameter of basal angiosperms overlapped with basal seed plant lineages (Comas and Eissenstat 2009; L. H. Comas and H. S. Callahan, unpublished data; figs. 2, 3). Within temper-
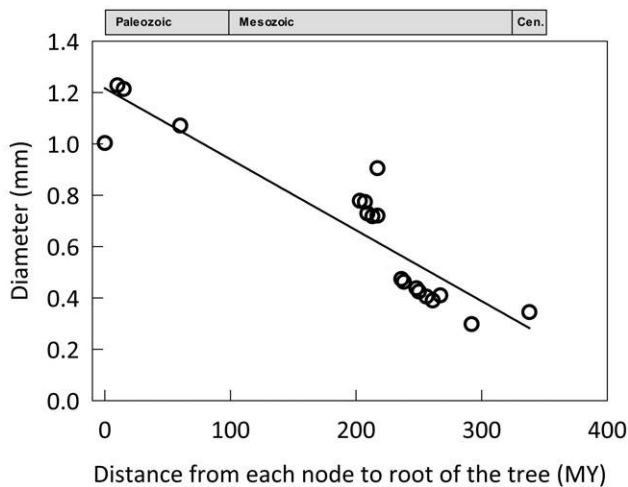
Fig. 3 Reconstructed root diameter as a function of time in millions of years from each node to the root of the phylogenetic tree for the 20 tropical and subtropical species in fig. 2. Points represent the 19 nodes among the 20 species. The root of the tree is 0. The solid line indicates a significant decrease in root diameter with time from the root of the tree ($R^2 = 0.83$, $P < 0.001$).

ate forest communities, recently diverged lineages were not uniformly fine rooted but included some species with coarser roots (Comas and Eissenstat 2009; L. H. Comas and H. S. Callahan, unpublished data). Interestingly, these species often had other strategies for competing for resources, such as allelopathy in *Juglans nigra* (Comas and Eissenstat 2009). Recently diverged angiosperm lineages also include species with some of the finest roots that exist, such as ericaceous plants that have roots finer than human hair (Valenzuela-Estrada et al. 2008).

Interactions among Woody Root Traits, Environmental Change, and Biogeochemical Processes since the Early Cretaceous

Several woody plant taxa—including some of the best-studied taxa with respect to root traits, such as temperate tree species—diversified during the late Cretaceous and subsequently rose to dominance (Wing and Boucher 1998). We present a hypothesis for how environmental change shaped root trait evolution during the Cretaceous and the potential implications of these trait shifts. We base the hypothesis on the theoretical framework outlined above as well as observations of how current plants and ecosystems respond to environmental change. We then use a model to evaluate the potential effects of root diameter and SRL on chemical mineral weathering and the effect of different atmospheric CO_2 concentrations

Natural Selection of Woody Root Traits in the Context of Paleoenvironmental Change

How might the evolution of thinner roots, higher SRL, and EM associations have been related to climatic changes occur-

ring during the Cretaceous? We hypothesize that one important effect on root trait evolution was the long-term drop in atmospheric CO_2 concentration that began during the Cretaceous and continued until ~20 million years ago (Royer 2006; Fletcher et al. 2008). This decline in CO_2 concentration would have increased substrate limitation of photosynthesis. In angiosperms, this constraint on photosynthesis may have been partly alleviated by the evolution of progressively higher leaf stomatal and vein densities to allow greater rates of leaf CO_2 uptake (Beerling and Franks 2010; Brodribb and Feild 2010; Feild et al. 2011a). To support the greater water losses required to achieve high leaf vein density and photosynthetic rates as CO_2 concentration potentially declined, selection would likely favor evolution of root traits that maximized water uptake and transport by roots while minimizing energetic investment in root construction and maintenance. In this context, thin roots with greater SRL could have been advantageous compared with thick, dense roots by enabling plants to efficiently increase the volume of soil that could be explored (i.e., RLD; fig. 1) and the hydraulic conductance of root systems (Eissenstat and Achor 1999; Rieger and Litvin 1999; Huang and Eissenstat 2000; Solari et al. 2006; Hernández et al. 2009).

Advancements in water acquisition and transport may have allowed early angiosperms to escape the wet habitats of their ancestors and diversify into more xeric and open habitats previously dominated by ferns and lycophytes (Feild and Arens 2007). Changes in belowground traits may have occurred in conjunction with aboveground traits, such as increases in leaf photosynthetic capacity (Boyce et al. 2009; Feild et al. 2009; Brodribb and Feild 2010). Species with thinner roots and longer SRL may be more competitive in novel habitats (i.e., be more weedy), especially if coevolved mycorrhizal fungi are absent or limited. Weedy herbaceous species have been associated with longer SRL than nonweedy species (Wright et al. 1999). Nonmycorrhizal or facultatively mycorrhizal species can be associated with highly disturbed habitats that can limit the development of extensive mycorrhizal networks (Malloch et al. 1980; Fitter and Moyersoen 1996; Brundrett 2002).

Declining CO_2 concentration from the Cretaceous onward could have favored evolution of thin roots with long SRL as a result of its indirect effects on soil nutrient availability. As climate cooled with the long-term decline in CO_2 concentration (Royer 2006; Fletcher et al. 2008), reductions in soil organic matter decomposition rates may have increasingly slowed release of N and P, decreasing the availability to plants (Kirschbaum 1995; Näsholm et al. 1998; Smith and Read 2008, p. 536). Such a pattern is evident across modern forests: nitrate, the most mobile form of soil N, is typically most abundant in the tropics, but ammonium and organic N become increasingly abundant and nitrate becomes scarce as one moves poleward (Read and Perez-Moreno 2003). When immobile and organic N sources are relatively abundant, plants with traits that facilitated EM fungal associations and efficient soil exploration—that is, thin, highly branched roots—would likely have a superior capacity for N acquisition and growth. Variation in root morphology across modern environmental gradients suggests that long SRL is beneficial where nutrients limit plant growth, such as at high latitudes

and sites with nutrient-poor soils (Ostonen et al. 2007; Alvarez-Uria and Körner 2011; Holdaway et al. 2011), but more studies are needed to verify these patterns.

Novel EM associations in the Mesozoic likely also benefited plant nutrient acquisition in ecosystems where substantial proportions of nutrients were bound to organic matter. It is well established that the original state of mycorrhizal status in vascular plants was AM (Brundrett 2009). Although mycorrhizal formations of basal angiosperms are a big unknown, the majority of extant vascular plants form AM, with EM associations evolving independently in at least 12 lineages that include species dominant in many important ecosystems today (Brundrett 2009). It has been suggested that EM associations evolved in concert with leaf traits, promoting slower leaf litter decomposition (Cornelissen et al. 2001). Regardless, because EM fungi have a greater ability to take up organic compounds (at least relative to AM) and translocate N from EM hyphae to roots (Read and Perez-Moreno 2003; Chapman et al. 2006), EM associations are thought to be advantageous when organic-bound nutrients are relatively abundant (Malloch et al. 1980; Brundrett 2002). There is also evidence that EM fungi, relative to AM fungi, stimulate soil organic matter degradation (Brzostek and Finzi 2011) and net N mineralization (i.e., release of inorganic N from organic N sources; Phillips and Fahey 2006). Additional advantages that EM fungi can contribute to their hosts are that they tend to develop more extensive hyphal networks in soil that remain active longer into the season (Querejeta et al. 2007). Finally, EM fungi have several traits that likely enhanced weathering rates relative to AM, which may have led to competitive advantages of EM over AM hosts if nutrients freed during the weathering process stimulated plant growth (Taylor et al. 2009).

## Effects of Root and Mycorrhizal Fungal Coevolution on Mineral Weathering

An important long-term sink for atmospheric CO_2 concentration is the release of calcium and magnesium during chemical weathering of two common silicate rocks, granite and basalt. Weathering increases the continental fluxes of calcium and magnesium released from silicate rocks into the oceans to form marine carbonates and remove CO_2 from the atmosphere (Berner 2004). Plants enhance silicate rock weathering by the activities of fine roots and mycorrhizal hyphae, which increase the acidity of soil in the rhizosphere through respiration, nutrient uptake, and exudation of organic acids (Jones 1998; Casarin et al. 2003; Taylor et al. 2009). Furthermore, fine root and fungal activities associated with forest soils promote the production of pedogenic clay minerals and reduce soil erosion (Pate and Verboom 2009; Verboom et al. 2010). Because pH is one of the most important drivers of chemical weathering, rhizosphere soil should experience higher weathering rates than soil without roots or hyphae. Thus, the influences of SRL and mycorrhizal fungi on the nature and extent of the rhizosphere in soils are potentially important controls on mineral weathering rates and subsequent feedbacks on atmospheric CO_2 concentration in the long term.

It has long been assumed that the spread of angiosperms contributed to a decline in atmospheric CO_2 concentration during the late Cretaceous (Volk 1989; Berner and Kothavala 2001). Taylor et al. (2009) suggested that the spread of ectomycorrhizal interactions in both angiosperm and gymnosperm trees provided a plausible alternative—or even complementary—mechanism for enhancing weathering over the same period. This hypothesis was later supported by process-based modeling of the effects of plants and mycorrhiza on terrestrial weathering regimes through the Cretaceous (Taylor et al. 2011, 2012). Here, we employ the same root-mycorrhizal fungal model in a sensitivity analysis to explore the effects of evolutionary changes in root traits on silicate rock weathering (basalt and granite; figs. 2, 3). Because there are many uncertainties in modeling, including the paucity of data on roots and fungi of the Cretaceous, our results should be considered illustrative rather than definitive. Nevertheless, process-based modeling provides an indication of the relative importance of root traits for influencing this key control point on the long-term geochemical carbon cycle.

We model acidification of the rhizosphere as being ultimately controlled by the net primary production of vegetation, with the total influence of plants being dependent on the spatial extent of their rooting systems in soil (Taylor et al. 2011, 2012). Roots and hyphae are treated as cylinders, with root diameter, total length, and CO_2 concentration given as input parameters. In this simple geochemical model, there is no attempt to link fine root or mycorrhizal hyphal traits to plant physiology. Rather, the aim of this modeling is to investigate theoretical weathering effects attributable to different root traits. Holding climate, vegetation, root biomass, and AM colonization constant, we estimated the effects of changes in RLD and diameter on weathering of basalt and granite under both contemporary and Cretaceous CO_2 concentrations (fig. 4). To test the sensitivity of the model to root length in soil (fig. 4A, 4C), assuming strict covariance between SRL and RLD (fig. 1), we varied SRL over the range observed by Comas and Eissenstat (2009) while holding fine root diameter constant at 0.58 mm, the mean value for forests (Jackson et al. 1997). To assess whether root morphology—specifically diameter—could influence weathering rates independently of RLD (i.e., assuming RLD is insensitive to root diameter), we varied diameter over the range observed by Comas and Eissenstat (2009; fig. 4B, 4D) while holding RLD constant by constraining SRL at 36 m/g, derived from average forest RLD (Jackson et al. 1997) and biomass scaled from Norby et al. (2004). Our results demonstrate that changes in root morphology are likely to influence weathering rates through their potential effect on RLD (as shown in fig. 1). Variations in root diameter per se have minor effects on weathering rates (at constant RLD and biomass; fig. 4), whereas changes in RLD exert much stronger effects (at constant diameter or tissue density and biomass). Weathering rates on basalt were higher than those on granite because basalt is easier to weather and is richer in calcium and magnesium than granite.

We also investigated potential effects of evolutionary shifts in EM colonization on basalt and granite weathering by broad-leaved deciduous tree species (fig. 5). We found that
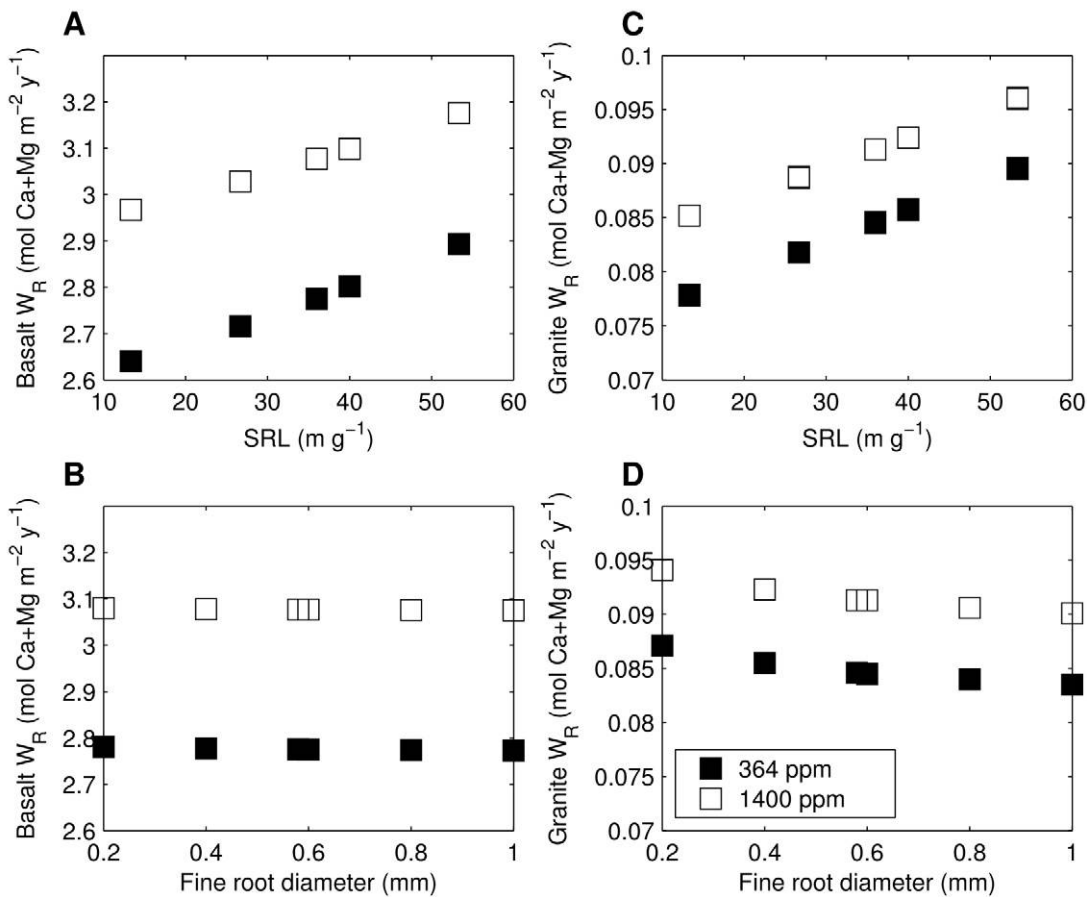
Fig. 4 Weathering of basalt (*A*, *B*) and granite (*C*, *D*) as a function of specific root length (SRL), with diameter held constant at 0.58 mm (*A*, *C*), and of fine root diameter, with SRL held constant at 36 m g^{-1} (*B*, *D*). These simulations show model sensitivity to independent model parameters of SRL and diameter. Values for diameter and SRL when constant were averages across temperate and tropical trees from the literature (Jackson et al. 1997). Range in root length density (RLD) used in the model was 2.0–8.0 km m^{-2} land for temperate and tropical trees (Jackson et al. 1997). RLD was converted to SRL assuming a standing fine root biomass of 150 g m^{-2} land. Open symbols indicate elevated CO$_2$ (1400 ppm); solid symbols indicate ambient CO$_2$ (364 ppm).

modeled weathering rates on both basalt and granite soils were sensitive to variations between the nonmycorrhizal state (0%) up to 100% EM colonization (fig. 5*A*, 5*B*). Similar results are obtained if the proportion of EM vegetation relative to AM vegetation is considered (fig. 5*C*, 5*D*), representing the evolution and spread of EM hosts at the expense of AM hosts in the Mesozoic. Small differences between the nonmycorrhizal (fig. 5*C*) and AM (fig. 5*D*) weathering (below 5% EM) are observed on granite but not basalt. The shapes of these curves are a complex function of geochemical controls on soil solution pH, which effectively dictate that EM colonization rates under ~30% are not associated with large increases in weathering rates.

We further investigated how high atmospheric CO$_2$ concentrations that prevailed during the Cretaceous (Fletcher et al. 2008) when angiosperm trees diversified might affect biological weathering by roots and both types of mycorrhizal fungi (AM and EM). An elevated atmospheric CO$_2$ concentration (1400 ppm CO$_2$) increased forest net primary production by 22% (from 5.8 to 7.11 Mg C ha^{-1} yr^{-1}) and reduced rhizosphere pH by 0.1–0.3 pH units as a result of the increased nu-

trient uptake by roots and mycorrhizal fungi required to support the higher net primary production. This resulted in a marked increase in basalt and granite weathering rates across the modeled range of root morphology and EM colonization compared with contemporary CO$_2$ concentration (figs. 4, 5). It is striking that quadrupling RLD via changes in root morphology and quadrupling atmospheric CO$_2$ concentration have similar effects on weathering rates, indicating that root morphology could be an important, previously unrecognized driver of weathering and therefore drawdown of CO$_2$.

Conclusions

Root trait patterns of extant woody angiosperms suggest that root adaptations accompanied the diversification and subsequent rise of angiosperms since the early Cretaceous. If fine root and mycorrhizal adaptations during the Cretaceous mirrored trait differences found in their extant relatives, root trait shifts likely allowed these angiosperms to forage for soil water and nutrients more effectively. The evolution of thinner
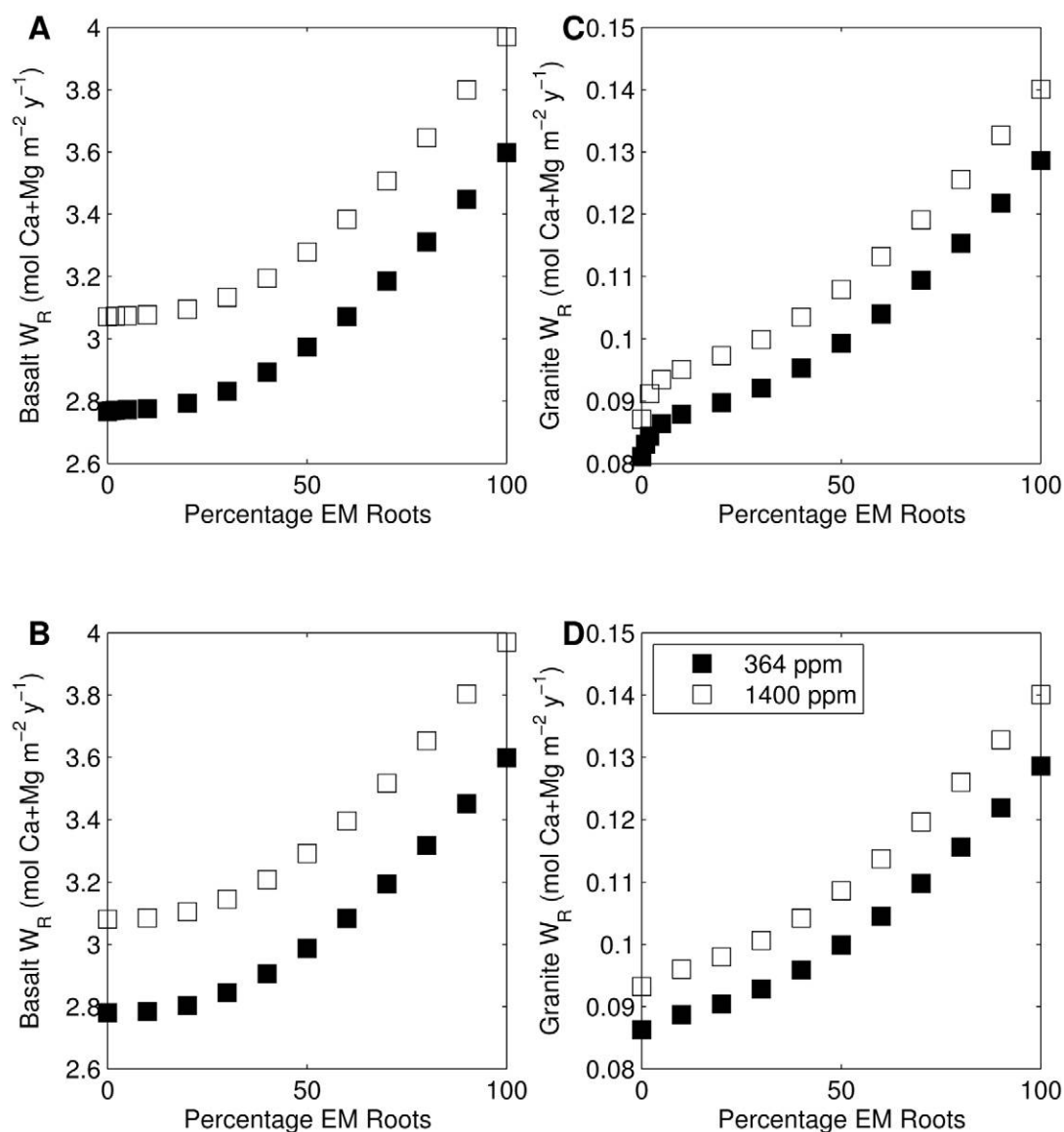
Fig. 5 Impact of percent colonization of root tips by ectomycorrhizal fungi on weathering rates of basalt (*A*, *B*) and granite (*C*, *D*). In *A* and *C*, roots uncolonized by ectomycorrhizal (EM) fungi are assumed to be nonmycorrhizal, while in *B* and *D*, roots uncolonized by EM are assumed to be colonized by arbuscular mycorrhizal (AM) fungi. Root diameter was set at 0.58 mm, and at 0% EM colonization, total length was set at 5400 m m^{-3} soil. The length of EM hyphae extending beyond the root surface in the top layer of soil was 125 m cm^{-3} soil at 100% EM root tip colonization, and in *B* and *D*, the length of AM was 5 cm cm^{-3} soil when EM colonization was 0% (Klironomos et al. 1997; Taylor et al. 2011). Symbols indicate CO$_2$ concentrations as in fig. 4.

roots with longer SRL—and presumably high root hydraulic capacity—in extant nonbasal angiosperm clades is consistent with evolution of high leaf vein density and photosynthetic capacity of these plants. The combination of plant traits (high SRL, high root and leaf hydraulic capacity) may have been critical for expansion into novel habitats that were drier or more open. Root trait shifts associated with this angiosperm rise to dominance could have accelerated mineral weathering, complementing the faster growth rate of angiosperms and the increased requirement of angiosperms for soil nutrients. It is also possible that the long-term decline in atmospheric CO$_2$

concentration beginning in the Cretaceous, coupled with a cooling climate, was a critical factor in shaping the evolution of root traits and selected for finer diameter roots with longer SRL to facilitate root foraging for nutrients as nutrient became increasingly retained in organic matter. These hypotheses are supported by general patterns of fine root diameter of plant species becoming finer, moving from basal to more recently diverged lineages over a broad phylogenetic range of angiosperms and their nearest nonseed plant relatives. Support for these hypotheses can also be found in observations of root trait variation across environmental gradients, which indicate

that fine roots of plants adapted to nutrient-poor conditions, drier sites, and higher latitudes also tend to be thinner with greater SRL. However, given the scarcity of data on root morphology and the fact that many environmental factors change along gradients of fertility and water availability, further data and controlled studies are needed to evaluate the hypotheses and generalizations reported here.

Acknowledgments

Literature Cited

Allen TFH, TW Hoekstra 1992 Towards a unified ecology. Columbia University Press, New York.

Alvarez-Uria P, C Körner 2011 Fine root traits in adult trees of evergreen and deciduous taxa from low and high elevation in the Alps. Alp Bot 121:107–112.

Bauhus J, C Messier 1999 Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada. Can J For Res 29:260–273.

Baylis GTS 1972 Fungi, phosphorus, and evolution of root systems. Search 3:257–259.

——— 1975 The Magnolioid mycorrhiza and mycotrophy in root systems derived from it. Pages 373–389 in RE Sanders, B Mosse, PB Tinker, eds. Endomycorrhizas. Academic Press, London.

Beerling DJ, RA Berner 2005 Feedbacks and the coevolution of plants and atmospheric CO_2. Proc Natl Acad Sci USA 102: 1302–1305.

Beerling DJ, PJ Franks 2010 The hidden cost of transpiration. Nature 464:495–496.

Beerling DJ, CP Osborne 2006 The origin of the savanna biome. Glob Change Biol 12:2023–2031.

Berner RA 2004 The Phanerozoic carbon cycle: CO_2 and O_2. Oxford University Press, Oxford.

Berner RA, Z Kothavala 2001 GEOCARB III: a revised model of atmospheric CO_2 over Phanerozoic time. Am J Sci 301:182–204.

Boyce CK, TJ Brodribb, TS Feild, MA Zwieniecki 2009 Angiosperm leaf vein evolution was physiologically and environmentally transformative. Proc Biol Sci 276:1771–1776.

Brodribb TJ, TS Feild 2010 Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. Ecol Lett 13:175–183.

Brundrett MC 2002 Coevolution of roots and mycorrhizas of land plants. New Phytol 154:275–304.

——— 2009 Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320:37–77.

Brundrett MC, B Kendrick 1990 The roots and mycorrhizas of herbaceous woodland plants. 2. Structural aspects of morphology. New Phytol 114:469–479.

Brzostek ER, AC Finzi 2011 Substrate supply, fine roots, and temperature control proteolytic enzyme activity in temperate forest soils. Ecology 92:892–902.

Casarin V, C Plassard, G Souche, JC Arvieu 2003 Quantification of oxalate ions and protons released by ectomycorrhizal fungi in rhizosphere soil. Agronomie 23:461–469.

Chapin FS, K Autumn, F Pugnaire 1993 Evolution of suites of traits in response to environmental stress. Am Nat 142:S78–S92.

Chapman SK, JA Langley, SC Hart, GW Koch 2006 Plants actively control nitrogen cycling: uncorking the microbial bottleneck. New Phytol 169:27–34.

Comas LH, TJ Bouma, DM Eissenstat 2002 Linking root traits to potential growth rate in six temperate tree species. Oecologia 132: 34–43.

Comas LH, DM Eissenstat 2004 Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. Funct Ecol 18:388–397.

——— 2009 Patterns in root trait variation among 25 co-existing North American forest species. New Phytol 182:919–928.

Cornelissen JHC, R Aerts, B Cerabolini, MJA Werger, MGA van der Heijden 2001 Carbon cycling traits of plant species are linked with mycorrhizal strategy. Oecologia 129:611–619.

Craine JM, D Tilman, D Wedin, P Reich, M Tjoelker, J Knops 2002 Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. Funct Ecol 16:563–574.

Eissenstat DM 1991 On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. New Phytol 118:63–68.

Eissenstat DM, DS Achor 1999 Anatomical characteristics of roots of citrus rootstocks that vary in specific root length. New Phytol 141:309–321.

Eissenstat DM, CE Wells, RD Yanai, JL Whitbeck 2000 Building roots in a changing environment: implications for root longevity. New Phytol 147:33–42.

Eissenstat DM, RD Yanai 1997 The ecology of root lifespan. Adv Ecol Res 27:1–60.

Esau K 1977 Anatomy of seed plants. Wiley, New York.

Espeleta JF, LA Donovan 2002 Fine root demography and morphology in response to soil resources availability among xeric and mesic sandhill tree species. Funct Ecol 16:113–121.

Espeleta JF, JB West, LA Donovan 2009 Tree species fine-root demography parallels habitat specialization across a sandhill soil resource gradient. Ecology 90:1773–1787.

Feild TS, NC Arens 2007 The ecophysiology of early angiosperms. Plant Cell Environ 30:291–309.

Feild TS, TJ Brodribb, A Iglesias, DS Chatelet, A Baresch, GR Upchurch, B Gomez, et al 2011a Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution. Proc Natl Acad Sci USA 108:8363–8366.

Feild TS, DS Chatlet, TJ Brodribb 2009 Ancestral xerophobia: a hypothesis on the whole plant ecophysiology of early angiosperms. Geobiology 7:237–264.

Feild TS, GR Upchurch, DS Chatelet, TJ Brodribb, KC Grubbs, M-S Samain, S Wanke 2011b Fossil evidence for low gas exchange capacities for early Cretaceous angiosperm leaves. Paleobiology 37: 195–213.

Fitter AH 1991 The ecological significance of root system architec-

ture: an economic approach. Pages 229–243 *in* D Atkinson, ed. Plant and root growth: an ecological perspective. Blackwell Science, London.

Fitter AH, B Moyersoen 1996 Evolutionary trends in root-microbe symbioses. Philos Trans R Soc B 351:1367–1375.

Fletcher BJ, SJ Brentnall, CW Anderson, RA Berner, DJ Beerling 2008 Atmospheric carbon dioxide linked with Mesozoic and early Cenozoic climate change. Nat Geosci 1:43–48.

Graham JH, DM Eissenstat 1998 Field evidence for the carbon cost of citrus mycorrhizas. New Phytol 140:103–110.

Graham JH, DM Eissenstat, DL Drouillard 1991 On the relationship between a plant's mycorrhizal dependency and rate of vesicular-arbuscular mycorrhizal colonization. Funct Ecol 5:773–779.

Grime JP 2001 Plant strategies, vegetation processes, and ecosystem properties. Wiley, New York.

Grime JP, K Thompson, R Hunt, JG Hodgson, JHC Cornelissen, IH Rorison, GAF Hendry, et al 1997 Integrated screening validates primary axes of specialization in plants. Oikos 79:259–281.

Guo DL, MX Xia, X Wei, WJ Chang, Y Liu, ZQ Wang 2008 Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. New Phytol 180:673–683.

Hernández EI, A Vilagrosa, JG Pausas, J Bellot 2009 Morphological traits and water use strategies in seedlings of Mediterranean coexisting species. Plant Ecol 207:233–244.

Holdaway RJ, SJ Richardson, IA Dickie, DA Peltzer, DA Coomes 2011 Species- and community-level patterns in fine root traits along a 120,000-year soil chronosequence in temperate rain forest. J Ecol 99:954–963.

Huang B, DM Eissenstat 2000 Root plasticity in exploiting water and nutrient heterogeneity. Pages 111–133 *in* R Wilkinson, ed. Plant-environment interactions. Marcel Dekker, New York.

Jackson RB, HA Mooney, ED Schulze 1997 A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci USA 94:7362–7366.

Jones DL 1998 Organic acids in the rhizosphere: a critical review. Plant Soil 205:25–44.

Kembel SW, JF Cahill Jr 2011 Independent evolution of leaf and root traits within and among temperate grassland plant communities. PLoS ONE 6:e19992.

Kirschbaum MUF 1995 The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biol Biochem 27:753–760.

Klironomos JN, MC Rillig, MF Allen, DR Zak, M Kubiske, KS Pregitzer 1997 Soil fungal-arthropod responses to *Populus tremuloides* grown under enriched atmospheric CO_2 under field conditions. Glob Change Biol 3:473–478.

Lambers H, H Poorter 1992 Inherent variation in growth-rate between higher-plants: a search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261.

Lambers H, JA Raven, GR Shaver, SE Smith 2008 Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol 23:95–103.

Levang-Brilz N, ME Biondini 2003 Growth rate, root development and nutrient uptake of 55 plant species from the Great Plains grasslands, USA. Plant Ecol 165:117–144.

Little SA, SW Kembel, P Wilf 2010 Paleotemperature proxies from leaf fossils reinterpreted in light of evolutionary history. PLoS ONE 5:e15161.

Maddison WP, DR Maddison 2010 Mesquite: a modular system for evolutionary analysis. Version 2.74. http://mesquiteproject.org.

Magallon SA, MJ Sanderson 2005 Angiosperm divergence times: the effect of genes, codon positions, and time constraints. Evolution 59:1653–1670.

Malloch DW, KA Pirozynski, PH Raven 1980 Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (a review). Proc Natl Acad Sci 77:2113–2118.

Meier IC, C Leuschner 2008 Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. Glob Change Biol 14:2081–2095.

Metcalfe DB, P Meir, LEOC Aragão, ACL Costa, AP Braga, PHL Gonçalves, J Athaydes Silva Junior, et al 2008 The effects of water availability on root growth and morphology in an Amazon rainforest. Plant Soil 311:189–199.

Näsholm T, A Ekblad, A Nordin, R Giesler, M Högberg, P Högberg 1998 Boreal forest plants take up organic nitrogen. Nature 392:914–916.

Nicotra AB, N Babicka, M Westoby 2002 Seedling root anatomy and morphology: an examination of ecological differentiation with rainfall using phylogenetically independent contrasts. Oecologia 130:136–145.

Norby RJ, J Ledford, CD Reilly, NE Miller, EG O'Neill 2004 Fine-root production dominates response of a deciduous forest to atmospheric CO_2 enrichment. Proc Natl Acad Sci USA 101:9689–9693.

Ostonen I, Ü Püttsepp, C Biel, O Alberton, MR Bakker, K Lõhmus, H Majdi, D Metcalfe, et al 2007 Specific root length as an indicator of environmental change. Plant Biosyst 141:426–442.

Pate JS, WH Verboom 2009 Contemporary biogenic formation of clay pavements by eucalypts: further support for the phytotarium concept. Ann Bot 103:673–685.

Paz H 2003 Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. Biotropica 35:318.

Peat HJ, AH Fitter 1993 The distribution of arbuscular mycorrhizas in the British flora. New Phytol 125:845–854.

Peng SB, DM Eissenstat, JH Graham, K Williams, NC Hodge 1993 Growth depression in mycorrhizal citrus at high phosphorus supply: analysis of carbon costs. Plant Physiol 101:1063–1071.

Peterson RL 1992 Adaptations of root structure in relation to biotic and abiotic factors. Can J Bot 70:661–675.

Phillips RP, TJ Fahey 2006 Tree species and mycorrhizal associations influence the magnitude of rhizosphere effects. Ecology 87:1302–1313.

Pregitzer KS 2002 Fine roots of trees: a new perspective. New Phytol 154:267–273.

Pregitzer KS, JL DeForest, AJ Burton, MF Allen, RW Ruess, RL Hendrick 2002 Fine root architecture of nine North American trees. Ecol Monogr 72:293–309.

Querejeta JI, LM Egerton-Warburton, MF Allen 2007 Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California oak savanna. Soil Biol Biochem 39:409–417.

Read DJ, J Perez-Moreno 2003 Mycorrhizas and nutrient cycling in ecosystems: a journey towards relevance? New Phytol 157:475–492.

Reich PB, MG Tjoelker, MB Walters, DW Vanderklein, C Bushena 1998 Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. Funct Ecol 12:327–338.

Reich PB, IJ Wright, J Cavender-Bares, JM Craine, J Oleksyn, M Westoby, MB Walters 2003 The evolution of plant functional variation: traits, spectra, and strategies. Int J Plant Sci 164(suppl):S143–S164.

Rieger M, P Litvin 1999 Root system hydraulic conductivity in species with contrasting root anatomy. J Exp Bot 50:201–209.

Robinson D, A Hodge, BS Griffiths, AH Fitter 1999 Plant root proliferation in nitrogen-rich patches confers competitive advantage. Proc R Soc B 266:431–435.

Roumet C, C Urcelay, S Diaz 2006 Suites of root traits differ between annual and perennial species growing in the field. New Phytol 170: 357–368.

Royer DL 2006 CO_2-forced climate thresholds during the Phanerozoic. Geochim Cosmochim Acta 70:5665–5675.

Siqueira JO, OJ Saggin-Junior 2001 Dependency on arbuscular mycorrhizal fungi and responsiveness of some Brazilian native woody species. Mycorrhiza 11:245–255.

Smith SE, DJ Read 2008 Mycorrhizal symbiosis. Academic Press, Cambridge.

Solari LI, F Pernice, TM DeJong 2006 The relationship of hydraulic conductance to root system characteristics of peach (*Prunus persica*) rootstocks. Physiol Plant 128:324–333.

St. John TV 1980 Root size, root hairs and mycorrhizal infection: a re-examination of Baylis' hypothesis with tropical trees. New Phytol 84:483–487.

Strömberg CAE 2011 Evolution of grasses and grassland ecosystems. Annu Rev Earth Planet Sci 39:517–544.

Taylor LL, SA Banwart, JR Leake, DJ Beerling 2011 Modeling the evolutionary rise of the ectomycorrhiza on subsurface weathering environments and the geochemical carbon cycle. Am J Sci 311: 369–403.

Taylor LL, SA Banwart, PJ Valdes, JR Leake, DJ Beerling 2012 Evaluating the effects of the co-evolution of terrestrial ecosystems, climate and CO_2 on continental weathering over geological time: a global-scale process-based approach. Philos Trans R Soc B 367: 565–582.

Taylor LL, JR Leake, J Quirk, K Hardy, SA Banwart, DJ Beerling 2009 Biological weathering and the long-term carbon cycle: integrating mycorrhizal evolution and function into the current paradigm. Geobiology 7:171–191.

Tilman D 1988 Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, NJ.

Tipple, BJ, M Pagani 2007 The early origins of terrestrial C_4 photosynthesis. Annu Rev Earth Planet Sci 35:435–461.

Tjoelker MG, JM Craine, D Wedin, PB Reich, D Tilman 2005 Linking leaf and root trait syndromes among 39 grassland and savannah species. New Phytol 167:493–508.

Valenzuela-Estrada LR, V Vera-Caraballo, LE Ruth, DM Eissenstat 2008 Root anatomy, morphology, and longevity among root orders in *Vaccinium corymbosum* (Ericaceae). Am J Bot 95:1–9.

Verboom WH, JS Pate 2006 Bioengineering of soil profiles in semiarid ecosystems: the "phytotarium" concept. A review. Plant Soil 289:71–102.

Verboom WH, JS Pate, M Aspandiar 2010 Neoformation of clay in lateral root catchments of mallee eucalypts: a chemical perspective. Ann Bot 105:23–36.

Volder A, DR Smart, AJ Bloom, DM Eissenstat 2005 Rapid decline in nitrate uptake and respiration with age in fine lateral roots of grape: implications for root efficiency and competitive effectiveness. New Phytol 165:493–501.

Volk T 1989 Rise of angiosperms as a factor in long-term climatic cooling. Geology 17:107–110.

Westoby M 1998 A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199:213–227.

——— 2006 Phylogenetic ecology at world scale, a new fusion between ecology and evolution. Ecology 87:S163–S165.

Wikstrom N, V Savolainen, MW Chase 2001 Evolution of the angiosperms: calibrating the family tree. Proc R Soc B 268: 2211–2220.

Wing SL, LD Boucher 1998 Ecological aspects of the cretaceous flowering plant radiation. Annu Rev Earth Planet Sci 26:379–421.

Withington JM, PB Reich, J Oleksyn, DM Eissenstat 2006 Comparisons of structure and life span in roots and leaves among temperate trees. Ecol Monogr 76:381–397.

Wright IJ, PB Reich, M Westoby, DD Ackerly, Z Baruch, F Bongers, J Cavender-Bares, T Chapin, et al 2004 The worldwide leaf economics spectrum. Nature 428:821–827.

Wright SR, MW Jennette, HD Coble, TW Rufty 1999 Root morphology of young *Glycine max*, *Senna obtusifolia*, and *Amaranthus palmeri*. Weed Sci 47:706–711.

Xia MX, DL Guo, KS Pregitzer 2010 Ephemeral root modules in *Fraxinus mandshurica*. New Phytol 188:1065–1074.

Zangaro W, FR Nishidate, J Vandresen, G Andrade, MA Nogueira 2007 Root mycorrhizal colonization and plant responsiveness are related to root plasticity, soil fertility and successional status of native woody species in southern Brazil. J Trop Ecol 23:53.