Commentary

Belowground fine root productivity, traits, and trees

A long-standing debate in plant ecology is how plant diversity – including species richness, functional, and phylogenetic diversity – determines primary productivity aboveground and belowground (Tilman *et al.*, 1997; Cadotte *et al.*, 2009). A leading mechanism linking diversity and productivity posits that diverse assemblages of plants are more likely to complement each other in resource acquiring abilities, leading to greater biomass production than one would expect in low diversity communities, an outcome known as overyielding (Cardinale *et al.*, 2007). Much of our understanding of the relationship between biodiversity and primary productivity comes from grassland communities and experiments. Forest trees are less tractable experimentally for biodiversity productivity studies than grasses and herbs and therefore require observational and correlative studies (Chisholm *et al.*, 2013). Because of this, we know surprisingly little about how long-lived forest trees directly interact with each other belowground and compete for limiting soil resources, and in particular, if they partition space or nutrients to reduce interspecific competition – a classic explanation for species co-existence in diverse communities. Aboveground plant stems are easily measured and identified whereas belowground plant roots are buried, making species interactions and basic patterns of occurrence and co-occurrence difficult to observe. While researchers have used a variety of DNA-based methods to identify roots and explore species interactions and rooting profiles for some time now (Jackson *et al.*, 1999; Hiiesalu *et al.*, 2012) there have been fewer studies done in closed canopy forests (Jones *et al.*, 2011). In this issue of *New Phytologist*, Valverde-Barrantes *et al.* (2014, pp. 731–742) use DNA identification of fine roots to dissect complex belowground interactions in a temperate hardwood forest and test several interrelated hypotheses on the relationship between: belowground species, functional, and phylogenetic diversity; soil resource availability; and productivity.

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In contrast to predictions made by niche partitioning theory, where the expectation would be segregation of root networks due to species-specific competitive dominance in heterogeneous soil, Valverde-Barrantes *et al.* (2014) find little evidence for any species' fine roots dominating high resource patches and competitively excluding less aggressive species. Instead, they find that most of the canopy tree species in their forest behave in largely the same way, with equal fine root proliferation in high resource patches. As a result of this even response to soil fertility, species roots tend to aggregate in nutrient rich soils, resulting in a greater diversity of species within a given patch. They further find that fine root biomass (FRB) and species diversity are greater in these soils. Surprisingly, traits of roots in fertile sites are not those predicted to be associated with competitive ability (e.g. specific root tip abundance and specific root length), but rather those associated with longevity and stress avoidance (root tissue density), implying that tree species adopt a tolerance strategy so that their roots remain in nutrient rich patches over the long run. Moreover, those species present within a nutrient rich patch show functional root traits that are more evenly distributed than one would expect at random, which at first pass suggests some degree of species complementarity. However, in a previous study in the same forest Valverde-Barrantes *et al.* (2013), found that fine root traits were not fixed characteristics of each species, but were instead plastic in response to the species composition of the patch, not levels of soil nutrients, a result reinforced in the present study. Finally, and perhaps most curiously, the residual variation in FRB not explained by soil fertility was positively correlated with increasing phylogenetic distance among co-occurring species within a soil patch better than species richness and trait diversity. These correlations were even stronger when Valverde-Barrantes *et al.* (2014) only examined within habitat variation in FRB and excluded samples that were taken from transitional ecotones. This study is one of the first examples of the power of using DNA approaches to characterize patterns of belowground interactions among co-existing trees to test classical diversity and ecosystem function relationships belowground in forested communities. Their study should fuel further exploration into the relationships between aboveground and belowground diversity, functional traits, and primary productivity, but also open up new approaches to better understand the belowground mechanisms responsible for community assembly and co-existence in diverse plant communities.

Implications for species co-existence and assembly

Species co-existence within diverse assemblages requires that stabilizing mechanisms, including niche segregation and negative density dependent fitness, or equalizing mechanisms, including those that increase competitive equivalence among species, act in ways that reduce the population growth of competitively dominant species (Chesson, 2000). That Valverde-Barrantes *et al.* (2014) found little evidence for competitive dominance but instead symmetrical competition implies that spatial or resource-based segregation based on competitive ability, at least in adult trees, might be of less importance to belowground co-existence than other processes. While it might be tempting to invoke functional equivalence and neutral species behavior (Hubbell, 2005), other findings in this paper suggest that important differences exist among species that might determine patterns of co-existence, mediate competition, and determine species interactions in belowground assemblages.

For example, negative density dependence may be playing a role here. The observation that a significant portion of FRB variation is better explained by the phylogenetic distance among co-occurring species than species richness or functional diversity, suggests that phylogenetic negative density dependence (PNDD), or the lower survival or growth of individuals in neighborhoods composed of phylogenetically related species, is operating belowground and potentially influencing whose roots co-exist in a patch. Conspecific negative density dependence (CNDD), or the decreased survival of individual and conspecific fine roots, could also be occurring, but it is unobservable here given the species level nature of the genetic markers used. However, mixed species composition of soil patches and lack of dominance of any given species is at least consistent with CNDD. That belowground assemblages are phylogenetically over dispersed in high resource patches, suggests competitive exclusion of conspecifics and closely related species could have occurred, leaving species in the same patch that are complementary in their resource use and root traits, or that can become complementary through trait plasticity. Other biotic factors, namely soil pathogens, might also play an indirect role in reducing competition among closely related species. Because the degree of host specificity and pathogenicity tends to decline with increasing phylogenetic distance among hosts (Gilbert & Webb, 2007), this could be one explanation for the correlation between FRB and phylogenetic diversity as phylogenetically diverse assemblages would be less likely to build up populations of shared root pathogens than phylogenetically clustered species assemblages or assemblages dominated by a single species. This result raises the question: do root pathogens indirectly mediate competition within species or between closely related neighboring individuals through CNDD and PNDD processes? Other studies have given some indication that soil microbes play a role in determining the classic pattern of diversity and ecosystem productivity and species co-existence (Maron *et al.*, 2011; Schnitzer *et al.*, 2011). Questions remain, however as to the patterns explored in the Valverde-Barrantes *et al.* (2014) study and how species co-existence and productivity observed belowground scale up to aboveground patterns of species dynamics and productivity across the whole stand. The results of this study clearly indicate that the recent wave of phylogenetic and functional trait studies in community ecology that attempt to infer ecological processes from nonrandom patterns of aboveground species co-occurrences relative to traits and relatedness are potentially ignoring important belowground processes also responsible for diversity maintenance and species co-existence. Given the much greater variety of resources that plants compete for belowground, aboveground patterns are likely to be only part of the story with regards to community assembly and co-existence. As DNA tools for plant and microbial identification continue to be developed and sequencing of environmental samples becomes increasingly accessible, plant interactions occurring in diverse communities just a few centimeters beneath our feet are finally within reach.

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