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# Morphological variability in tree root architecture indirectly affects coexistence among competitors in the understory

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**Abstract.** Interactions between plants can have strong effects on community structure and function. Variability in the morphological, developmental, physiological, and biochemical traits of plants can influence the outcome of plant interactions and thus have important ecological consequences. However, the ecological ramifications of trait variability in plants are poorly understood and have rarely been tested in the field. We experimentally tested the effects of morphological variation in root architecture of *Quercus douglasii* trees in the field on interactions between understory plants and community composition. Our results indicate that variability among *Q. douglasii* tree root systems initiates a striking reversal in the competitive effects of dominant understory grass species on a less common species. Trees with a deep-rooted morphology facilitated exotic annual grasses and these annual grasses, in turn, competitively excluded the native perennial bunchgrass, *Stipa pulchra*. In contrast, *Q. douglasii* trees with shallow-rooted morphologies directly suppressed the growth of exotic annual grasses and indirectly released *S. pulchra* individuals from competition with these annual grasses. Morphological variation in the root architecture of *Q. douglasii* created substantial conditionality in the outcomes of competition among species which enhanced the potential for indirect interactions to sustain coexistence and increase community diversity.

**Key words:** blue oak; community assembly; competition; facilitation; *Quercus douglasii*; *Stipa pulchra*; trait-mediated indirect interactions.

## INTRODUCTION

Interactions among plant species can have powerful effects on community composition, productivity, and function (Connell 1983, Callaway et al. 1996, Verdú and Valiente Banuet 2008). These interactions can be affected by changes in plant root:shoot ratios, specific leaf area, proportions of fine to coarse roots, biochemistry, and other traits in response to different ecological contexts (Novoplansky 2002, de Kroon et al. 2005, Li et al. 2007). When trait variation affects the way plants interact directly with each other, these interactions can be defined as trait-mediated interactions (Callaway et al. 2003). For example, when the California native shrubs *Haplopappus ericoides* and *H. venetus* var. *seloides* grow in the absence of competition, their root systems are concentrated near the soil surface (D'Antonio and Mahall 1991). However, when competing with the exotic *Carpobrotus edulis* the root systems of *Haplopappus* shift to a much deeper morphology, as they are displaced by the mat-forming exotic (D'Antonio and Mahall 1991). This change in rooting depth by *Haplopappus* suggests that interacting species can exert strong control over the morphology of their competitors; in this case, causing a

change that may result in a trade-off in access to nutrients and water (Ho et al. 2005), but a change that may also allow for continued coexistence between two strongly competing species. Thus, the high degree of trait variability expressed by plants may also have important effects on the way communities assemble, yet the ecological impact of trait variation has rarely been tested in the field (Miner et al. 2005).

Morphological variation may also lead to important trait-mediated *indirect* interactions with other species, and thus, create cascading interactive effects on the structure of communities (Werner and Peacor 2003, Aschehoug and Callaway 2012, Ohgushi et al. 2012). Empirical studies of trait-mediated indirect interactions may yield insight into many different kinds of highly complex ecological interactions, but to date have mostly focused on tri-trophic interactions between plants, consumers, and predators. For example, Schmitz (2008) found that the presence of predators altered the feeding behavior of herbivores in ways that affected the long-term dynamics of the vegetation community and ecosystem function. The change in behavioral response of herbivores to the presence of predators had different direct effects on the dominant plant *Solidago rugosa* and indirectly affected the overall composition of the vegetation community. Surprisingly, despite the high degree of trait variability found in plants and an increasing awareness that indirect interactions among plants may structure communities in important ways

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(Samson and Werk 1986, Aschehoug and Callaway 2012, Metlen et al. 2013), we know of no studies investigating the effects of trait variation on indirect interactions among plants. Here, we explored trait-mediated indirect interactions in the context of morphological variation, plant–plant interactions, and plant community structure.

*Quercus douglasii* Hook. and Arn. (blue oak) is a winter deciduous oak endemic to California, USA, but very widely distributed within the state (Griffin and Critchfield 1976). Previous work on *Q. douglasii* has shown that it demonstrates strong morphological variation in rooting architecture, making it a model system for investigating trait-mediated interactions in the field. This variation in rooting architecture appears to range between two phenotypic end points: shallow-rooted trees with highly developed fine-root systems in shallow soils (0–50 cm deep) and deep-rooted trees that have few fine roots in shallow soils. Callaway et al. (1991) found that some mature trees expressed very low water potentials over the dry mediterranean climate summers of three different growing seasons (e.g., they did not access a permanent water source). Other trees expressed much higher water potentials during the rainless summers, indicating that they accessed deep water sources. Importantly, the trees with low water potentials developed approximately four to five times more fine-root mass in shallow soils (0–50 cm deep) beneath the canopy than trees with high water potentials (Callaway et al. 1991). This measured variation in root architecture in the field corresponded with controlled experiments of *Q. douglasii* seedlings. In experiments, *Quercus douglasii* seedlings with restricted access to deep stores of water produced roughly twice as many fine lateral roots and more than five times the lateral root mass as seedlings with access to a deep water source (Callaway 1990). Trees exhibiting different rooting phenotypes and water potentials were intermixed on the landscape at the scale of meters, suggesting that these differences were not due entirely to gross microsite differences (Callaway et al. 1991).

Additional experiments found that the two phenotypes did not differ in canopy effects, such as light exposure and temperature, and that soil moisture under the two tree root phenotypes was not significantly different during the understory growing season (Callaway et al. 1991). Although there were differences in understory soil nutrient concentrations between shallow-rooted and deep-rooted trees, these did not result in significant differences in understory plant performance in greenhouse trials (Callaway et al. 1991). However, transplant experiments utilizing root exclosures found that *Bromus diandrus* performance nearly doubled under shallow-rooted trees when seedlings were protected from *Q. douglasii* roots, while exclosures did not change *B. diandrus* performance under deep-rooted trees (Callaway et al. 1991). Further, total productivity under deep-rooted trees was more than three times higher than

under shallow-rooted trees; a striking pattern that remains today. Thus, the morphological variation in root architecture shown by mature *Q. douglasii* in the field appears to have strong, trait-mediated direct effects on understory species (Callaway et al. 1991), which sets the stage for tests of trait-mediated indirect interactions within the understory vegetation community.

The variation in *Q. douglasii* root morphology also correlated with different understory community compositions; the abundance of the native perennial bunchgrass *Stipa* (nee *Nassella*) *pulchra* (Hitche.) Barkworth (purple needle grass) was higher under shallow-rooted trees than deep-rooted trees, but the abundance of European annuals (primarily *Avena fatua* and *Bromus diandrus*), which can competitively exclude other species (Rice and Nagy 2000), was lower (Callaway et al. 1991). Because of this pattern, we hypothesized that morphological variation in *Q. douglasii* root architecture may have strong indirect effects on the way these annual exotic grasses compete with the native *S. pulchra*, thus progressing from an interaction in which understory plant performance is directly affected by tree root morphology to an interaction in which variation in root morphology both directly and indirectly affects understory plant performance.

Here, we build on previous work (Callaway 1990, Callaway et al. 1991) by experimentally investigating interactions in the field where morphological variation in the root architecture of *Q. douglasii* may alter important competitive interactions between exotic annual grasses and *S. pulchra*. Specifically, we tested the hypothesis that *Q. douglasii* trees with shallow-root architectures strongly but indirectly shift competitive outcomes between European annual grasses and *S. pulchra* in favor of *S. pulchra*, while *Q. douglasii* with deep-root architectures strongly facilitate exotic annual grasses, which in turn, competitively exclude *S. pulchra*.

#### MATERIALS AND METHODS

In January 2012, we transplanted *Stipa pulchra* seedlings under mature *Quercus douglasii* trees at Hastings Natural History Reserve in the Santa Lucia Mountains of central California, USA. These seedlings had been grown outdoors in Granite Bay, California, in 125-mL cone-tainers (Stuewe and Sons, Corvallis, Oregon, USA) filled with local soil for ~120 d prior to transplanting. We returned to the original sites of Callaway et al. (1991) and established plots under all 12 deep-rooted trees and six of the shallow-rooted trees used in the original study. We selected six additional shallow-rooted trees based on the distinct leaf morphology described in Callaway and Mahall (1996) and observations of very high fine-root densities in excavations we made in the upper 20 cm of soil under the canopies (Callaway et al. 1991). In addition, we qualitatively assessed both the understory productivity and fine-root mass under all sample trees to ensure

they exhibited the same characteristics as described in Callaway et al. (1991). Our total sample size of trees was 12 deep-rooted trees and 12 shallow-rooted trees. Under each tree, six *S. pulchra* seedlings were planted either directly into the matrix of existing vegetation ( $n = 3$ ) or in the center of a 20 cm diameter removal treatment in which all aboveground biomass of neighbors was removed ( $n = 3$ ). Seedlings received ~500 mL of supplemental water only on day one and two in order to aid establishment. “Uncle Ian’s Mole and Gopher, Deer, Rabbit and Squirrel Repellent” (Ian Enterprises, Woodward, Oregon, USA) and “Deer Off II” (Woodstream Corporation, Lititz, Pennsylvania, USA) were applied equally to all transplanted *S. pulchra* plants to minimize damage by herbivores (i.e., deer and feral pigs), and herbivore damage to surviving plants was minimal. We counted the total number of leaves on all plants after seven weeks, and after 20 weeks of growth, we harvested, dried, and weighed the aboveground biomass of all remaining individuals. At the time of harvest, we also counted the total number of seeds on each plant. To explore whether variation in the root morphology of *Q. douglasii* corresponded with differences in the abundance of *S. pulchra*, we counted the number of *S. pulchra* individuals in three randomly located 60 cm diameter circular plots under each tree.

We used the average of all remaining samples under each individual tree to avoid pseudoreplication and tested for the direct effects of two *Q. douglasii* root morphologies on *S. pulchra* performance and the indirect interactions between *Q. douglasii* and *S. pulchra* as mediated by European annual grasses by comparing total biomass, total leaf number, and seed number of *S. pulchra* plants from either competition or removal treatments under either deep-rooted or shallow-rooted trees and between tree type using a two-way ANOVA with tree root morphology and understory competition as fixed factors (SPSS 20; IBM 2011). Because SPSS does not allow for post-hoc comparison of interaction terms, we also used a one-way ANOVA with four factors and Tukey HSD post-hoc comparisons to determine individual treatment differences (SPSS 20; IBM 2011).

## RESULTS

### Two-way ANOVA results

The fixed effect of tree morphology (deep-rooted or shallow-rooted) was significant for the number of leaves produced by individual *Stipa pulchra* plants ( $P = 0.016$ ), and was marginally significant for average biomass of individual plants ( $P = 0.056$ ), but not significant for the average number of seeds each plant produced ( $P = 0.974$ ). The fixed effect of competition treatment (*S. pulchra* grown with or without neighbors) was significant for average biomass, average number of leaves, and average number of seeds per plant ( $P < 0.001$ ,  $P < 0.001$ ,  $P < 0.001$ , respectively). The interaction term tree

root morphology  $\times$  competition treatment was significant for average individual biomass, the average number of leaves individual plants produced, and the average number of seeds on each plant at time of harvest ( $P < 0.001$ ,  $P < 0.001$ ,  $P < 0.001$ , respectively; Appendix: Table A1).

### One-way ANOVA results

*Relative effects of trees on Stipa pulchra performance.*—*Stipa pulchra* plants grown under shallow-rooted trees without neighbors were significantly more suppressed by competition with trees than *S. pulchra* plants grown under deep-rooted trees without neighbors. *S. pulchra* plants under shallow-rooted trees were smaller, had fewer leaves, and produced less seeds than *S. pulchra* plants grown under deep-rooted trees ( $P < 0.001$ ,  $P < 0.001$ ,  $P < 0.01$ , respectively).

*Effects of understory competition on Stipa pulchra performance.*—*Stipa pulchra* plants grown under deep-rooted trees were significantly suppressed by understory competition with other species ( $P < 0.001$ ). The dry biomass of plants grown alone was more than six times greater ( $1.59 \pm 0.13$  g; shown are all means  $\pm$  SE) than plants grown with neighbors ( $0.22 \pm 0.04$  g). In addition, when the number of leaves on individual plants were counted after seven weeks of growth, plants without neighbors had significantly more leaves ( $30.40 \pm 2.39$ ) than plants that were exposed to understory competition ( $9.26 \pm 1.42$ ,  $P < 0.001$ ). At the time of harvest, the average number of seeds per plant was 18 times greater for plants grown without neighbors ( $18.29 \pm 2.52$ ) vs. plants with neighbors ( $1.01 \pm 0.91$ ,  $P < 0.001$ ; Fig. 1).

In contrast, *S. pulchra* plants grown under shallow-rooted trees were not affected by understory competition. We found no significant differences in dry weight biomass ( $P = 1.00$ ), leaf number ( $P = 0.947$ ) or the average number of seeds per plant at the time of harvest ( $P = 0.990$ ; Fig. 1) between individuals that had all neighbors removed and individuals in competition with neighbors.

*Interaction of tree morphology and understory competition on Stipa pulchra performance.*—*Stipa pulchra* plants grown under deep-rooted trees with neighbors were significantly more suppressed by the combination of competition with trees and other understory species. *Stipa pulchra* plants were smaller, tended to have fewer leaves, and produced fewer seeds than *S. pulchra* plants grown under shallow-rooted trees with neighbors ( $P < 0.005$ ,  $P < 0.079$ ,  $P < 0.011$ , respectively).

*Abundance of Stipa pulchra under trees.*—We randomly sampled the existing vegetation under trees for the abundance of *Stipa pulchra* individuals. The average number of individual *S. pulchra* plants was roughly 10 times greater under shallow-rooted trees ( $1.00 \pm 0.22$ ) than under deep-rooted trees ( $0.08 \pm 0.06$ ,  $P < 0.001$ ; Appendix: Fig. A1).

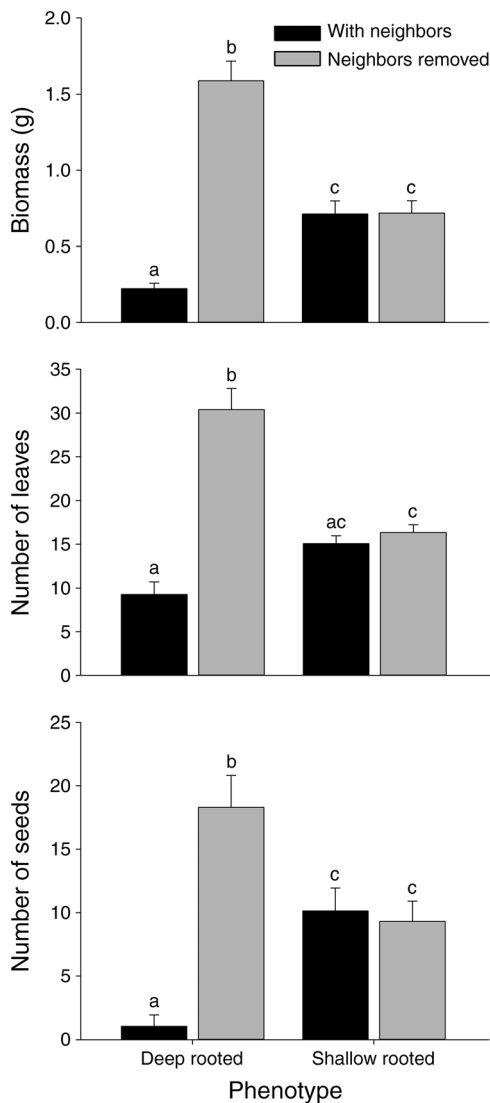


FIG. 1. Biomass, leaf number, and seed number of *Stipa pulchra* planted under *Quercus douglasii* trees with phenotypes of either shallow roots or deep roots. *Stipa pulchra* were planted with all neighbors removed in a 20 cm diameter centered on the target plant or with neighbors left intact. Error bars represent +SE, and different letters above the bars denote a significant difference between the means ( $P < 0.05$ ).

#### DISCUSSION

We found that morphological variation in *Quercus douglasii* root architecture had substantial direct and indirect effects on the performance of the native perennial bunchgrass *Stipa pulchra* in the understory plant community. When growing without neighbors, under deep-rooted trees, *S. pulchra* plants were more than twice as big as when growing without neighbors under shallow-rooted trees. This suggests that *Q. douglasii* root morphology exerts powerful direct effects on the performance of *S. pulchra*, a finding that is consistent with other studies (Callaway et al. 1991).

Previous studies have shown that trees with a deep-rooted morphology strongly facilitate exotic annual grasses (Callaway et al. 1991), leading to understory productivity being twice that of the surrounding grasslands and more than three times the understory productivity of shallow-rooted trees; a striking pattern which remains today (R. M. Callaway, *personal observation*). Here, we found that exotic annual grasses growing under deep-rooted trees have strong, exclusionary effects on *S. pulchra*, decreasing individual biomass by >85% and reducing seed output by 95%. In contrast, exotic annual grasses growing under shallow-rooted trees had no effect on *S. pulchra*. Our experimental results are also consistent with the patterns of abundance for *S. pulchra* in the understory: Shallow-rooted trees had far more individual *S. pulchra* plants in the understory community than deep-rooted trees (Appendix: Fig. A1). Importantly, our results reveal that *Q. douglasii* had powerful indirect effects on both the performance and persistence of *S. pulchra* in the understory that appear to be driven by variation in *Q. douglasii* root architecture (Fig. 2). To our knowledge, this is the first experimental test of a trait-mediated indirect interaction among plants, and our results suggest that the indirect effects of morphological variation in plants may be an important factor in determining both plant community dynamics and long-term community composition.

An important limitation of our study is that the evaluation of the effects of morphological variation of mature oak trees was in the field, and as a consequence, we could not experimentally induce variation in the root morphology of *Q. douglasii*. Instead, our study builds on previously published studies suggesting that the variation in root architecture is in response to water availability in the environment (Callaway 1990, Callaway et al. 1991, Callaway and Mahall 1996), although we can't rule out genetic differences. A second limitation of our study is that we cannot eliminate the possibility that the indirect interactions we hypothesize to be caused by variation in root architecture are instead caused by differences in microsites occupied by deep-rooted vs. shallow-rooted trees. Further, we did not replicate the studies performed by Callaway et al. (1991), which established root-mediated competition between *Q. douglasii* and understory plants as the primary determinant of understory productivity. As a consequence, we cannot rule out that the same site factors that determine differences in *Q. douglasii* root phenotype also cause differences in the way the annual grasses interact with *S. pulchra* in our study. However, since we utilized a large proportion of the same study trees and the patterns of understory productivity appeared similar to work presented in Callaway et al. (1991), it is likely that root-mediated interactions are an important aspect of our results. Further, the close proximity of many individuals, spatial mixing of the two root phenotypes at the scale of meters, and the very

strong correlation of understory effects with the edges of the tree canopies (Callaway et al. 1991) suggests that abiotic microsite differences are not likely to explain our results.

The link between morphological variation in *Q. douglasii*, the environment, and the effect of this variation on both direct and indirect plant–plant interactions helps to fill a gap in our understanding of how plant communities assemble. There are two general, but contrasting, theories for how plant species may assemble into communities as a result of competition among plants. The first proposes that plant communities are competitively transitive in nature (Goldsmith 1978, Mitchley and Grubb 1986, Keddy and Shipley 1989). In other words, all species in a given pool, or community, can be ranked in a linear competitive hierarchy, or “pecking order,” which provides a predictive tool for community organization. An important limitation of hierarchical assembly rules is that indirect interactions are not included, and thus, there can be no trait-mediated indirect interactions in the theory. Instead, the crucial prediction of hierarchical assembly rules is that communities will consistently move towards dominance by the best competitor in the hierarchy unless interrupted by nonequilibrium forces such as disturbance or herbivory. The second body of theory poses that plants may exhibit non-transitive or nonhierarchical assembly rules as they form communities (May and Leonard 1975, Buss and Jackson 1979, Petraitis 1979). Whereas hierarchical organization is best described mathematically as  $A > B > C$ , nonhierarchical organization occurs when loops form in the hierarchy such as  $A > B$ ,  $B > C$ , but  $C > A$ . This results in species C having an indirect positive effect on species B through a direct negative effect on species A. Given the right starting point, a simple loop within a suite of competing species can result in a perpetually shifting state in which species coexist indefinitely in the absence of abiotic heterogeneity or nonequilibrium processes (Karlson and Jackson 1981, Bronstein et al. 2004, Laird and Schamp 2006, Kaur et al. 2009). Importantly, in nonhierarchical systems, indirect interactions are the central rule of the predictive model that creates the opportunity for trait-mediated indirect interactions to be included within the existing conceptual framework. Here we show that the indirect effects of *Q. douglasii* are important in determining *Stipa pulchra* persistence in the understory community, and as such, our results demonstrate the importance of including indirect interactions in models of community assembly.

Further, most theory for how plants interact is built on the construct, or at least the implicit assumption, that plants are “fixed” in their competitive abilities. However, we found that morphological variation in *Q. douglasii* created tremendous conditionality in the outcomes of competition among species and greatly enhanced the potential for indirect interactions to sustain coexistence and increase community diversity.

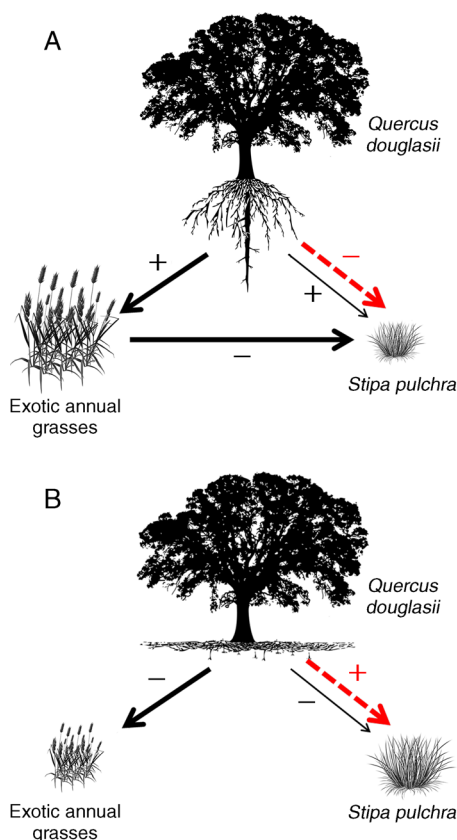


FIG. 2. Conceptual diagram of interactions among understory species determined by the root morphology of *Quercus douglasii*. Solid lines represent direct interactions between species, and red dashed lines represent the trait-mediated indirect effects of *Q. douglasii* on *Stipa pulchra*. Panel (A) depicts the strong facilitative (plus sign) effect of deep-rooted *Q. douglasii* on exotic annual grasses and the concomitant suppression of *S. pulchra* by these annuals. Panel (B) depicts the suppressive effect (minus sign) of *Q. douglasii* on understory species and how this indirectly facilitates *S. pulchra*.

As a consequence, theory for how plant communities assemble that does not incorporate complex suites of direct and indirect interactions and conditionality driven by *variation* in traits rather than just a trait mean is likely to be incomplete.

Conditionality in interactions between plants, consumers, and predators has been shown to have important effects on ecosystem processes (Schmitz 2008, Ohgushi et al. 2012). Here, we extend this to suggest that morphological variation in plants can have powerful effects on plant community dynamics and structure. The emerging study of trait-mediated indirect interactions among plants may provide insight into how plants coexist and assemble into communities.

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## SUPPLEMENTAL MATERIAL

## Appendix

Detailed results of two-way ANOVA model and figure of reproductive output results ([Ecological Archives E095-153-A1](#)).