Getting to the root of restoration: considering root traits for improved restoration outcomes under drought and competition

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A foundational goal of trait-based ecology, including trait-based restoration, is to link specific traits to community assembly, biodiversity, and ecosystem function. Despite a growing awareness of the importance of belowground traits for ecological processes, a synthesis of how root traits can inform restoration of terrestrial plant communities is lacking. We reviewed and summarized existing literature focused on root traits in relation to plant performance measures (i.e. survival, establishment, productivity) in the contexts of drought and competition (including invasion). Root traits related to belowground resource acquisition (e.g. high specific root length, deep roots) are frequently related to drought avoidance (i.e. a plant strategy based on optimizing water uptake to maintain function), whereas studies relating root traits to drought tolerance (i.e. a plant strategy that allows plants to withstand low hydration) remain limited. More studies have linked root traits to plant competitive effects (i.e. the influence a plant has on neighbors) than to competitive responses (i.e. a plant’s ability to resist the effects of neighbors). Because plants with acquisitive traits decrease resources to the detriment of neighbors, root traits associated with rapid resource acquisition (e.g. high specific root length) may be important for understanding competitive effects. Albeit more limited, research suggests root traits associated with resource conservation or stress tolerance (e.g. high root tissue density, high root diameter) may elucidate mechanisms related to competitive responses. Re-vegetation outcomes may be improved by considering root traits, but only if clear links are made between traits and plant performance in varied contexts.

Key words: belowground traits, competition, drought, invasive species, root traits

Conceptual Implications
• Considering root traits in restoration research and practice could improve restoration outcomes. However, because root traits are rarely related to plant performance measures (approximately 20% of reviewed studies), linking root traits to associated ecosystem processes such as productivity remains challenging.
• Restoration projects across varied ecosystems provide ample opportunities to test causal relationships between traits and plant performance.
• Future research that explicitly links root traits to plant performance under various abiotic and biotic stressors is needed to advance trait-based restoration of diverse plant communities and functioning ecosystems. Research that clarifies the influence of individual as well as suites of above- and belowground traits on plant performance would improve restoration outcomes and advance understanding of community assembly processes.
Introduction

Land degradation resulting from anthropogenic and natural impacts extends over 70% of the world’s terrestrial ecosystems and undermines the livelihoods of nearly half of the world’s population (IPBES 2019). Ecological restoration has emerged as a key tool for combating land degradation, enhancing food and water security, and curbing biodiversity loss. Despite substantial growth in the science and practice of ecological restoration over recent decades, restoration efforts rarely result in rapid recovery of ecosystem function (Jones et al. 2018). The lack of a broad conceptual framework to inform restoration at diverse sites and scales (Young et al. 2005) likely contributes to poor re-vegetation outcomes.

Trait-based ecology has also grown rapidly over the last several decades. One of its central goals is to link traits, or morphological, physiological, or phenological plant characteristics, with performance and fitness (Viole et al. 2007). Trait-based approaches have contributed to our understanding of the mechanisms driving community assembly (e.g. HilleRisLambers et al. 2012) and have been extended to explain ecosystem functions and processes (e.g. Suding et al. 2008). Several studies have touted a trait-based approach for improving ecological restoration outcomes (e.g. Funk et al. 2008; Laughlin 2014) and a growing number of empirical studies have linked specific traits to plant establishment, survival, and persistence in restored systems (e.g. Larson et al. 2014; Zirbel & Brudvig 2020).

Identifying traits associated with plant performance under water deficit as well as competition or invasion may be particularly useful for improving restoration outcomes as low soil moisture (e.g. James et al. 2019) and competition from neighbors (e.g. Goldberg 1990) hamper seedling recruitment in many terrestrial systems including restored plant communities. Recent research has linked root traits to stress tolerance (e.g. Kramer-Walter et al. 2016; Bristiel et al. 2019; Harrison & LaForgia 2019), competitive dynamics (e.g. Leger et al. 2019; Foxx & Kramer 2020), and ecosystem functions (Bardgett et al. 2014). A synthesis of how root traits influence plant performance under drought and competition would provide novel insights to trait-based restoration research and practice.

In this review, we synthesize existing research relating root traits to drought and competition/invasion. We focus our discussion on root traits linked to plant performance measures of survival, establishment, and productivity to identify root traits that may improve restoration outcomes in these contexts. In addition, we identify significant gaps in knowledge and describe a research approach that may help researchers and practitioners more effectively apply trait-based approaches to restoration.

Methods

We began our search by identifying appropriate papers in Web of Science (WoS) using key words related to morphological and anatomical root traits and our two stressors of drought and competition. We provided details of the literature search in Supplement S1. Briefly, key words related to drought were “drought,” “precip,” “water availability,” “water deficit” and those related to competition were “invasive” and “compet.” We excluded references from agricultural settings and narrowed results to WoS categories broadly related to ecology or restoration. Studies focused on biological or chemical traits (e.g. mycorrhizal associations, allelopathy) were excluded as the breadth of fields from which they originate made identifying results relevant to restoration difficult. We completed our initial search on 8 November, 2019 and an additional search on 6 August, 2020. This process resulted in 962 references. Of these, papers were considered relevant if the following criteria were met: (1) at least one root trait was measured; (2) the study was conducted in the context of drought or competition/invasion; (3a) for drought studies, traits were measured under multiple levels of water availability (experimentally manipulated or naturally occurring); (3b) for competition/invasion studies, competition or species composition was explicitly manipulated or comparisons between invasives and other groups (i.e. native species or “home” populations) were made. We also included relevant manuscripts from the references of reviewed sources. In total, we completed our review using 161 relevant papers: 89 drought studies and 72 invasion/competition studies (Fig. 1). All papers reviewed are listed in Supplement S1.

We extracted specific details from each relevant reference to quantify and summarize the literature. First, we documented locations, biomes, and functional groups studied. We categorized studies based on functional group (i.e. forb, graminoid, shrub, tree, multiple) or noted if studies were conducted at the community level (i.e. community-weighted means were measured) (Fig. 1). Second, we identified all traits measured in each study: If authors measured multiple traits or distinguished responses among multiple species, we counted each trait and/or species as an individual observation. Third, we determined whether each root trait was considered a dependent or independent variable. If the root trait was considered a dependent variable, we documented the direction of the response in relation to the stressor. If the root trait was considered the independent variable, we noted how it influenced plant performance. We also noted if studies assessed trade-offs among root traits or in relation to aboveground traits. To avoid confusion related to various sources of intraspecific (i.e. within species) trait variation (e.g. plasticity), we limit our discussion of intraspecific differences in traits to those obtained from studies in which authors clearly attribute differences to adaptation (i.e. population- or genotype-level differences). Definitions of the most commonly measured root traits in the papers we reviewed are provided in Table 1.

General Findings

Most of the studies we reviewed were conducted in the Northern Hemisphere and predominantly in temperate and arid biomes (Fig. 1). Root traits were linked to performance measures as independent variables in only approximately 20% of reviewed studies (Figs. 1B, C & 2A, B). In approximately 60% of studies focused on drought and approximately 75% of the studies focused on competition/invasion, root traits were considered dependent variables (Figs. 1B, C & 3A, B). Studies assessing
Root traits for improved restoration

correlations or trade-offs among root traits or in relation to aboveground traits were limited (<25% for drought studies and <5% for competition/invasion studies). Studies conducted in restoration of re-vegetation contexts were also surprisingly rare (<10% of all studies).

Studies of woody vegetation dominated the drought literature (64 woody vs. 25 herbaceous studies). However, because many studies of herbaceous vegetation assessed numerous species, the number of observations was similar between the two groups (Figs. 3A & 3B). Mirroring broader ecological research, most studies we reviewed in the drought category equated “dry” conditions with drought without providing context for this characterization by, e.g. comparing deficit treatments to long-term ranges of variability or standardized climatic index values (Slette et al. 2019). For consistency, we use the term “drought” when discussing studies in which root traits were assessed in relation to water deficit. Allocation traits such as root-to-shoot ratios (RSR) or root mass fractions (RMF) were most frequently measured as response variables in relation to drought and we found relatively more observations of increased versus decreased RSR or RMF in response to drought (Fig. 3A). A similar pattern was reported in a recent meta-analysis (Zhou et al. 2018).

Similar numbers of studies focused on root trait responses of herbaceous (n = 41 references) and woody (n = 31 references) species to competition (Figs. 1A & 3C, D). However, of the 21 studies that linked root traits to plant performance in relation to competition only one considered woody species. Overall, most competition/invasion studies assessed impacts of interspecific competition. Responses of RSR or RMF to competition were most frequently measured but responses were inconsistent (Figs. 3C & 3D). Over 30% of the studies in the competition/invasion category were comparative and reported differences in traits among specific groups, but few quantified the effects of competition on root traits or the effects of root traits on plant performance (Fig. 3C & 3D). Fourteen studies (approximately 20%) focused on invasive species.

Figure 1. (A) Locations of studies linking root traits to drought (orange symbols) and competition/invasion (black symbols). Symbols for functional groups studied are as follow: community (i.e. traits measured at the community level (+), multiple species (*), forb (☐), graminoid (●), shrub (◼), and tree (Δ). Lower panels display (B) drought and (C), competition/invasion studies overlaid on Whittaker Biomes. Symbols indicate whether root traits were considered independent (☐) or dependent (●) variables in studies.
Table 1. Most commonly measured root traits from 161 studies included in this review. * Root biomass was considered a trait in many of the studies we reviewed. However, for consistency with the definition provided in Violle et al. (2007) we consider biomass only a dependent variable (i.e. response trait) not an independent variable.

| Trait                                   | Abbreviation | Definition                                      |
|-----------------------------------------|--------------|-------------------------------------------------|
| Rooting Depth                           | Depth        | Average diameter of roots | Max rooting depth or 95% rooting depth |
| Root biomass*                           | Biomass      | Belowground biomass per plant                   |
| Root length                             | Length       | Total length of roots per plant                 |
| Root length density                     | RLD          | Length of roots per soil volume                 |
| Root elongation rate                    | RER          | Increase in root length/time                    |
| Root-to-shoot ratio/mass fraction       | RSR/RMF      | Ratio of dry root mass to dry shoot mass or total plant mass |
| Root tissue density                     | RTD          | Root dry mass/root volume                       |
| Specific root length                    | SRL          | Root length/root volume                         |

Drought

Global climate models largely agree that ecosystems around the world will experience more frequent extreme events such as drought and increased variability in inter- and intra-annual precipitation in the coming century (Dai 2011). Lower precipitation or increased variability in soil moisture may disrupt the development of restored plant communities because many species require specific weather patterns for germination, establishment, and persistence (e.g. Moles & Westoby 2004).

A comprehensive trait-based framework characterizing unique plant strategies for coping with drought has recently been refined (Volaire 2018). However, understanding of how root traits fit into these broad categories remains rudimentary, even though morphological root traits are likely key components of drought avoidance and tolerance strategies (Volaire 2018). An avoidance strategy is based on optimizing water uptake belowground to maintain leaf water potential, turgor, and function aboveground (e.g. Comas et al. 2013; Volaire 2018). Plants may grow deep roots or increase root surface area to maximize water uptake and avoid water stress. In contrast, drought-tolerant plants are able to withstand low hydation and survive, albeit at the cost of reduced growth (Volaire 2018).

Here, we discuss several root traits linked to increased establishment, survival, or productivity under water-deficit conditions and relate them to drought avoidance and tolerance strategies.

Rooting Depth and Root Elongation Rate

Traits associated with drought avoidance via increased rooting depth or root elongation rate (RER) were often identified as key determinants of plant performance under drought. Deep roots improve plant survival during drought by providing plants access to moisture from deep soil layers (e.g. Padilla & Pugnaire 2007; Harrison & LaForgia 2019). Similarly, plants with high RER may be able to quickly access unexploited soil moisture to optimize water uptake. Studies have linked RER to higher drought survival in trees (e.g. Horton & Clark 2001; Stella & Battles 2010) and herbaceous species (e.g. Pérez-Ramos et al. 2012).

Despite mounting evidence for a positive effect of deep roots and high RER on plant performance under drought, each of these traits may be only part of a broader plant strategy for coping with water limitation. For example, in a study of perennial grassland species, Zwicke et al. (2015) observed a positive correlation between maximum rooting depth before drought and plant survival. However, species with the highest rates of survival employed strategies related to rapid resource acquisition (i.e. deep roots and rapid shoot elongation) during favorable spring conditions with either drought avoidance (i.e. root elongation and maintenance of leaf water content) or tolerance (i.e. high fructan content in roots, high leaf meristem water content, cell membrane stability) strategies during a subsequent controlled drought period. In studies of woody vegetation, researchers found that a drought avoidance strategy based solely on maximizing water uptake via deep roots did not result in lower levels of drought-induced xylem cavitation in dryland shrubs (Hacke et al. 2000) or plant survival in Mediterranean woody species (Lopez-Iglesias et al. 2014). Rather, species that maximized water uptake while also decreasing transpiration via lower leaf area and higher water use efficiency were most likely to resist drought-induced cavitation (Hacke et al. 2000) or survive drought (Lopez-Iglesias et al. 2014). Identifying such trait correlations, interactions, and trade-offs is foundational to understanding plant strategies for coping with environmental stress (e.g. Garnier et al. 2016); yet, limited studies include root traits in their assessments of trait-correlations in relation to drought.

By assessing multiple traits simultaneously, researchers may be able to identify whether individual traits or suites of traits explain plant survival and performance under drought. For example, working with seedlings from sage scrub ecosystems, Larson and Funk (2016) found RER to be consistently correlated with numerous other traits (i.e. specific root length: SRL, RMF, root diameter, nitrogen uptake) and a reliable predictor of plant growth under a gradient of moisture conditions. Similarly, Harrison and LaForgia (2019) found greater rooting depth (measured as the maximum length of a tap root) at the seedling stage resulted in lower plant mortality of annual grassland species during drought. However, unlike results related to RER found by Larson and Funk (2016), Harrison and LaForgia (2019) found that rooting depth was uncorrelated with other traits. Harrison and LaForgia (2019) also observed seedling traits to be only weakly correlated with adult traits. These results demonstrate the importance of pinpointing relevant developmental stages at which specific traits or trait combinations influence plant performance and highlight how trait correlations may vary by environmental context.

Allocation

Positive effects of high RSR or RMF on performance measures under drought have been documented in woody (e.g. Stella & Battles 2010) and herbaceous (e.g. Bristiel et al. 2019; Hanslin et al. 2019) species. By investing more in roots relative to aboveground tissues, plants may be able to increase water uptake...
while decreasing transpiration during periods of water stress. However, because root mass or allocation measures may remain constant while root length, diameter, or architecture changes, shifts in allocation may not clearly align with avoidance or tolerance strategies. For instance, working with the perennial grass, *Dactylis glomerata*, Bristiel et al. (2019) found the most drought-tolerant population combined thin roots with high root tissue density (RTD). This intermediate strategy likely promotes both extensive soil exploration as well as high tolerance to drought. Given the coordinated changes observed in numerous traits related to root biomass, measures of dry mass fractions should be coupled with measures of root morphology or architecture to better understand composite belowground strategies to drought (Comas et al. 2013).

**Drought Tolerance Traits**

Our review suggests that morphological root traits related to drought tolerance are studied less frequently than those related to drought avoidance. We believe that lesser-studied traits,
specifically those related to drought tolerance, such as RTD or plant hydraulic function (e.g. root xylem vessel area, root cavitation resistance) (Griffin-Nolan et al. 2018), warrant further study in ecological contexts. RTD may be particularly informative because its constituents (proportion of stele in root, proportion of cell wall in the stele, number of xylem vessels) are directly related to water transport and growth rate (Wahl & Ryser 2000), it is independent of acquisitive root traits such as SRL in the belowground trait-economic spectrum (Kramer-Walter et al. 2016), and it consistently reflects adaptation to low soil resources (nutrients: Kramer-Walter et al. 2016; moisture: Bristiel et al. 2019; Hanslin et al. 2019).

Root Traits and Precipitation Patterns/Soil Moisture Regimes

Precipitation seasonality at specific restoration sites may modify the influence of certain root traits on plant performance. For example, avoidance traits such as maximum rooting depth or high RER may be important for seedling establishment and survival in Mediterranean climates in which soil moisture progressively decreases from shallow to deep layers throughout the dry season (e.g. Padilla & Pugnaire 2007). Indeed, eight of the 12 studies that linked rooting depth or RER to improved performance measures were conducted in or with species from Mediterranean climates. However, in pulse precipitation systems characterized by small and intermittent precipitation events that result in fluctuating soil moisture conditions across all soil depths (Lauenroth & Bradford 2009), these traits may have negligible influence on plant performance. Rather, traits related to recovery after drought such as rapid root development after periods of low soil moisture (e.g. Huang et al. 1997) or high levels of water-soluble carbohydrates in roots (Jiang & Huang 2000) might better predict plant performance in pulse systems.

In addition to precipitation quantity and pattern, soil texture will also affect moisture availability at a given restoration site. In general, fine-textured soils (i.e. high loam or clay content) have higher water holding capacity than coarse-textured (i.e. sandy) soils but also hold water more tightly (i.e. at lower water potentials; Jury & Horton 2004). While several studies...
have linked root traits of established vegetation to soil texture and precipitation (e.g. Sperry & Hacke 2002), few studies have considered combined effects of soil texture and precipitation on seedling establishment or survival (but see Eckhart et al. 2017).

Research focused on understanding how root traits interact with site-specific and appropriately characterized precipitation regimes will be essential for reassembling plant communities capable of establishing and persisting under various drought scenarios.

**Competition and Invasion**

For nearly a century, ecologists have recognized competition for resources as a primary mechanism defining the assembly and structure of plant communities (e.g. Clements et al. 1929). A plant’s competitive ability has traditionally been described by two components: competitive effect and competitive response (Goldberg 1990). Competitive effect is defined as a plant’s ability to influence the growth of neighboring plants, whereas competitive response is defined as a plant’s ability to resist the effects of neighbors. Studies looking for associations between the two components have been inconsistent; relationships have been defined as positive (e.g. Goldberg & Fleetwood 1987), uncorrelated (e.g. Gibson et al. 2018), and negative (e.g. Wang et al. 2010).

Here, we discuss morphological root traits explicitly linked to competitive ability (competitive effect and competitive response), survival, establishment, and productivity of plants in competitive situations. Because only one study linked root traits to the performance of woody plants under competition, we focus our discussion on herbaceous species. In addition, we briefly discuss how root traits relate to two prevalent hypotheses of plant competition (limiting similarity vs. competitive hierarchies), and review trends associated with root traits of invasive species despite limited information available on this topic. We focus on these aspects of root traits related to competition to highlight traits with the potential to improve plant establishment and persistence in restoration of lands susceptible to competition from weedy or invasive plant species, which are leading concerns in re-vegetation projects (e.g. Brown et al. 2008; Funk et al. 2008).

**Allocation**

Allocation measures (i.e. RSR, RMF) were most often related to competitive abilities, establishment, and productivity (Fig. 2B). However, the direction and effect of RSR/RMF on competitive ability or performance varied by species and environmental context. For example, working with different populations of the perennial grass *Elymus multisetus*, Rowe and Leger (2010) observed both increased suppression of (competitive effect) and tolerance to (competitive response) the invasive annual grass *Bromus tectorum* in plants with high RSR. Similarly, when assessing plant establishment in areas invaded by *B. tectorum*, Leger and Goergen (2017) found higher rates of survival among individuals of two perennial grass species originating from populations with relatively high RSR. Importantly, both studies compared individuals from populations that were either “experienced” or “naïve” to *B. tectorum* competition. As *B. tectorum* has only been present in the western United States for approximately 150 years (Mack 1981), the difference in allocation and associated competitive ability between these groups demonstrates that plants can adapt to competition over short timescales. However, such evolutionary responses related to allocation do not always result in improved competitive ability. Gibson et al. (2018) and Ferguson et al. (2015) observed higher RSR in experienced populations of the perennial grasses *Pseudoroegneria spicata* and *Elymus elymoides* in relation to competition from the invasive aster *Centaurea stoebe* and *B. tectorum*, respectively. However, in both cases, no effects of RSR on either competitive effect or response were detected.

In the above-mentioned studies, differences in allocation measures were likely due to constitutive genetic differences among populations and species. However, biomass allocation can be highly plastic, particularly at the seedling stage (Gedroc et al. 1996) and a species’ ability to respond to competition by adjusting allocation may influence its competitive ability. For example, in a study comparing competitive interactions between a xeric (*Scleropogon breviro lis*) and mesic (*Sporobolus airoides*) grass, Novoplansky and Goldberg (2001) found opposite patterns of allocation in relation to interspecific competition for the two species. Because *Scleropogon breviro lis* seedlings had high RSR resulting from competition, they were better able to tolerate subsequent drought. However, in a study of competitive dynamics between exotic Johnsongrass (*Sorghum halepense*) and native grass species, a lower RSR at the juvenile stage allowed Johnsongrass to quickly develop aboveground tissues and outcompete native species via increased competition for light (Schwinning et al. 2017). These studies demonstrate that the effects of root allocation on plant performance in response to competition may be species and context specific. Furthermore, as changes in allocation may result from ontogeny (e.g. Gedroc et al. 1996) or plant size (Cahill 2003), results should be interpreted with caution and future research should aim to isolate responses in allocation due to competition from confounding factors.

Several less-studied root traits warrant discussion due to their reported links to plant performance in competitive settings. We discuss these in the contexts of competitive effects and competitive responses because root traits associated with these aspects of competitive ability may differ (e.g. Wang et al. 2010; Semchenko et al. 2018).

**Competitive Effect Traits**

Root traits associated with rapid resource acquisition, such as high SRL and total root length, may be particularly important for understanding species’ competitive effects, as plants with acquisitive traits likely deplete resources rapidly to the detriment of neighboring plants (i.e. exploitative competition) (Goldberg 1990). In the studies we reviewed, SRL was positively correlated with competition intensity (Bennett et al. 2016) and was linked to superior competitors in comparative studies (Mommer et al. 2011; Collins et al. 2016; but see Goodwin
et al. 1999). Although high SRL may improve a plant’s competitive effect, influences on performance measures may be context specific. For example, Rolhauser et al. (2019) found that high SRL was negatively related to competitive effect, likely due to interactions with pulse moisture regimes. Root length (Gordon & Rice 1993; Leger & Goergen 2017) and root area (Wang et al. 2010), both traits related to resource acquisition, have also been linked to species competitive effects but results are limited to only a few studies.

**Competitive Response Traits**

Root traits associated with resource conservation may be especially relevant for deciphering species’ competitive responses. For example, in a study assessing the establishment and performance of forbs and woody species in competition with grass and forb competitors, low SRL (i.e. the conservative end of the SRL axis) was positively linked to survival and competitive response (Zangaro et al. 2016). Similarly, working with herbaceous species, Semchenko et al. (2018) found species best suited to tolerate competition had deep roots, low SRL, and minimal branching. High root diameter, which may be indicative of more stress-tolerant and long-lived roots, was also positively related to species’ competitive responses in grasses (Rowe & Leger 2010). Of the few times that RTD was assessed, it was unaffected by competition (Hajek et al. 2014), was positively correlated with species competitive response (Bennett et al. 2016; Zangaro et al. 2016), and was characteristic of inferior “effect” competitors (Semchenko et al. 2018). Given that RTD is independent from acquisitive belowground traits such as SRL (Kramer-Walter et al. 2016) and has been linked to adaptation to low-resource environments, it may also be indicative of stress tolerance induced by competition.

Traits related to root architecture (e.g. number of root tips, branching, forking) have been linked to both species’ competitive effect and response. For example, Leger and Goergen (2017) and Foxx and Kramer (2020) observed higher survival of perennial grass individuals with high numbers of root tips in competition with B. tectorum. The degree of root branching/forking has been linked to both increased (Rowe & Leger 2010) and decreased (Semchenko et al. 2018) competitive tolerance. Albeit few, these significant but contrasting results relating root architecture to competitive dynamics highlight their potential relevance for future study.

Both competitive effect and response traits likely influence community assembly during restoration, but their relative importance may vary depending on context or particular restoration goals. At sites denuded of existing vegetation (i.e. similar to early-successional communities), root traits related to competitive effects may exert a strong influence on community assembly. Similarly, in areas dominated by weedy species, plants with traits related to competitive effects may promote the suppression of aggressive competitors (Funk et al. 2008). However, in these situations assessing competitive hierarchies and their consequences (discussed below) may be necessary to better predict competitive outcomes. In projects where seedlings need to establish among existing vegetation, competitive effects of young seedlings on established plants are likely to be irrelevant (Howard & Goldberg 2001) and using species with traits related to competitive response may improve establishment.

**Limiting Similarity Versus Competitive Hierarchies**

Two trait-based hypotheses have been developed to frame competitive dynamics. The “competition-trait similarity hypothesis” (e.g. Kunstler et al. 2012) is a trait-based extension of the limiting similarity or competition-niche similarity hypothesis (MacArthur & Levins 1967). Under this framework, competition is expected to be strongest between species with similar mean values of traits related to competition. In contrast, the “competitive ability hierarchy hypothesis” (e.g. Kunstler et al. 2012) predicts stronger competition between species with large differences in mean values of traits related to competition. Under this framework, competitive outcomes result from hierarchical differences in species’ competitive abilities.

Several recent studies have tested these hypotheses in relation to root traits of competing species. In a study comparing grasses with acquisitive versus conservative resource-use strategies, hierarchical trait difference in SRL, root phosphorus use efficiency, and root length density better-predicted competition intensity than trait similarity in non-limiting resource environments (Fort et al. 2014). Similarly, working with common, rare, and non-native species, Feng and van Kleunen (2016) observed that a target plant experienced stronger competition when, among other traits, it had higher RSR and its neighbors lower RSR. Competitive dynamics resulting from trait hierarchies have also been demonstrated in studies of aboveground traits (e.g. Kunstler et al. 2012; Funk & Wolf 2016), suggesting that they may be important drivers of competition above- as well as belowground. However, in support of the limiting similarity hypothesis, Burns and Strauss (2012) documented decreased competition in multi-species assemblages resulting from divergence in RSR among competitors, which subsequently resulted in increased aboveground productivity. Competition may be influenced by both competitive hierarchies and limiting similarity if they act on different traits. For example, working with diverse herbaceous mixtures, Bennett et al. (2016) observed prevalent competitive hierarchies aboveground (i.e. higher specific leaf area enhanced competitive abilities), whereas limiting similarity influenced competition belowground (i.e. similar SRL increased competition and divergence in root diameter decreased competition). Direct tests of how these two hypotheses influence belowground competitive dynamics are rare, but could advance understanding of plant interactions to improve restoration outcomes.

**Invasive Root Traits**

Although aboveground traits of invasive and non-invasive species have been compared in empirical studies (e.g. Funk 2008), meta-analyses (van Kleunen et al. 2010), and reviews (Gioria & Osborne 2014), differences in root traits between the two groups have rarely been measured and have
not been quantified. Identifying patterns is difficult as we found only 14 studies that explicitly compared root traits between invasive and non-invasive species. The only obvious trend is that, in most cases, root traits of invasive species differ from the native species or “home” populations to which they are compared (Fig. 4). Allocation measures (RSR/RMF) were most often measured, and higher and lower values were reported for invasives compared to non-invasives or “home” populations. If belowground traits of invasive species mirror patterns found for aboveground traits, it is likely successful invaders in high-resource environments will possess root traits associated with rapid resource acquisition, whereas successful invaders in low-resource environments may possess traits related to either resource acquisition or conservation (e.g. Funk 2013; Gioria & Osborne 2014). This remains a largely unexplored area of research.

**Future Directions for Improved Trait-Based Restoration**

To more effectively utilize trait-based approaches in ecological restoration, additional research is needed that explicitly links root traits to performance measures and identifies the effects of specific traits on ecosystem processes. Recent studies focused on specific ecosystem processes such as soil stability, and carbon or nutrient cycling have identified such links. For example, tensile strength and root length density have been identified as key contributors to topsoil (Vannoppen et al. 2015) and aggregate (Rillig et al. 2015) stability. Similarly, root traits related to metabolic function have been linked to nutrient cycling and those related to architecture and lifespan have been linked to carbon cycling (Bardgett et al. 2014). We believe a two-tiered research agenda focused on how traits influence vital rates (e.g. survival, growth rate, reproductive output) and ecosystem processes are needed to advance trait-based restoration.

Several authors have argued that linking individual traits to population-level fitness components or vital rates is imperative for reliable trait-based predictions of population, community, and ecosystem dynamics (e.g. Violle et al. 2007; Laughlin & Messier 2015). By understanding how traits influence growth rates and critical life stage transitions (i.e. germination, emergence, establishment, survival) (e.g. Larson et al. 2014; James et al. 2019), researchers and practitioners may gain insight into longer-term patterns of community development and associated ecosystem processes. However, understanding how traits affect performance under various abiotic and biotic conditions is essential for identifying widespread versus context-specific patterns because specific trait values are unlikely to improve survival or growth in all environments (Laughlin et al. 2018). As land degradation extends across varied ecosystems, ample opportunities exist to test causal relationships between traits, plant performance, and fitness in distinct systems undergoing ecological restoration. Brief descriptions of methods used for assessing the influence of root traits on plant performance are provided in Table 2.

Identifying how specific traits influence performance measures under different types of moisture deficit may improve species or population selection for ecosystem-specific restoration. As most “drought” conditions in the studies we reviewed were not contextualized in relation to broader patterns, identifying general trends remains difficult. Studies relating root traits to plant performance along gradients of precipitation or under various drought scenarios (e.g. Padilla et al. 2013; Zwicke et al. 2015) would improve restoration of ecosystems threatened by distinct forms of drought.

In the contexts of competition and invasion, understanding how specific traits influence resource depletion may elucidate causal relationships between traits and competitive outcomes. Resource-mediated plant competition has been used to explain competitive dynamics for decades (e.g. Gaudet & Keddy 1988; Goldberg 1990); however, few studies empirically link traits to competitive dynamics via their effects on resource depletion (Violle et al. 2009 and references therein). Violle et al. (2009) outline a framework relating instantaneous measures of traits to resource depletion and competitive ability. Adopting this framework and extending results to survival and growth may reveal more generalizable patterns of competition than can be gleaned from pairwise competition studies. Once links between traits and performance in various environments are established, restoration projects can be designed to target specific ecosystem processes or functions (Laughlin 2014).
traits associated with resource conservation or stress tolerance often related to competitive effects and research suggests root traits related to drought avoidance and drought tolerance are most commonly linked to drought avoidance, whereas root traits related to drought tolerance remain understudied. Studies linking root traits to competitive response are more limited. Root traits associated with rapid resource acquisition are most often related to competitive effects and research suggests root traits associated with resource conservation or stress tolerance may influence competitive response.

Several research avenues would advance trait-based approaches to ecological restoration. First, research focused on how coordinated suites of traits influence plant performance is needed to understand composite plant strategies for coping with abiotic and biotic stress. Second, determining which traits or suites of traits best predict plant performance at different ontogenetic stages may improve predictions of how individual plants and plant communities will respond to stress. Third, tests of causal relationships among traits, performance measures, and ecosystem processes across varied systems are needed to effectively apply trait-based approaches to ecological restoration. Restoration ecology provides abundant opportunities to test these relationships. With increasing global awareness of the importance of restoration for environmental and human well-being (UNEA 2019), and increasing publicly available trait data from the TRY (Kattge et al. 2020), Fine-Root Ecology (Iversen et al. 2018), and Global Root Traits (Guerrero-Ramirez et al. 2020) databases, we trust researchers and practitioners can get to the root of one of the world’s most pressing challenges, restoring its damaged and degraded ecosystems.

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Supporting Information
The following information may be found in the online version of this article:

Supplement S1. Details of the literature search.