DISSERTATION

UNDERSTANDING BELOWGROUND DYNAMICS FOR IMPROVED RESTORATION OF ARID ECOSYSTEMS

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ABSTRACT

UNDERSTANDING BELOWGROUND DYNAMICS FOR IMPROVED RESTORATION OF ARID ECOSYSTEMS

Ecological restoration is a key tool for reestablishing biodiversity and ecosystem function to degraded landscapes. Methodological and theoretical approaches from diverse disciplines including community ecology, ecosystem science, and trait-based ecology have greatly advanced the science of Restoration Ecology in recent decades. However, because abiotic (e.g., drought) and biotic stressors (e.g., invasive species) hinder successful restoration, innovative approaches are needed to improve re-vegetation outcomes.

Understanding the combined effects of drought and invasive species on plant community development and soil moisture may provide valuable insight into the mechanisms hindering successful native plant establishment in arid systems. I conducted a four-year field experiment at two sites in Colorado (WGP: Western Great Plains; CD: Cold Desert) to assess the combined effects of drought (66% reduction of ambient growing-season rainfall), invasive annual grass presence (*Bromus tectorum* treatment), and a water-conserving soil amendment on plant establishment and soil moisture at two depths (5 cm and 30 cm). Drought resulted in both higher (WGP site) and lower (CD site) *B. tectorum* cover. As VWC was counter-intuitively higher with drought early in the season at the WGP site, *B. tectorum* may have establishment under particularly favorable conditions before native species became active. In contrast, below average growing-season precipitation combined with drought may have hindered *B. tectorum* establishment at the CD site. At the WGP site, drought reduced seeded forb cover and *B. tectorum* treatment reduced seeded grass cover. This suggests that *B. tectorum* may disproportionately hinder the establishment of morphologically similar species. At the CD site, drought and *B. tectorum* each decreased seeded species to a similar extent. The effects of the soil amendment on seeded species establishment were limited. The effects of *B. tectorum* and drought on soil VWC varied by site and depth. Notably, at the CD site in 2015, *B. tectorum* treatment reduced VWC to a similar magnitude as drought at both 5 cm and 30 cm depth. These results demonstrate that the invasive species and drought can interact with site-specific precipitation patterns to influence plant community development in restored systems.

Trait-based ecology, which aims to link traits, or morphological, physiological, or phenological plant characteristics, with performance and fitness in various environments, has recently been championed as a way to improve restoration outcomes. Most trait-based research focuses on aboveground traits of mature plants. However, root traits of young seedlings may be particularly informative for understanding recruitment patterns because they influence competitive dynamics and stress tolerance. I conducted a greenhouse study to assess the effects of ontogeny (i.e. developmental age) on traits within and among 11 species being developed for re-vegetation of arid ecosystems in the southwestern United States. I measured several leaf and root traits from seedlings at three harvests: 10-days, 24-days, and 42-days old. In addition, using primary component analyses (PCA), I assessed dominant axes of variation in traits at each ontogenetic stage and correlated these axes to future plant growth rate. Differences in median values of most traits were influenced by both species identity and ontogeny. Species hierarchies (i.e. species ranks based on trait values) were stable for most traits, but, in a few cases, species hierarchies varied by ontogenetic stage. Similar correlations and trade-offs among traits were observed at all ontogenetic stages: traits related to resource acquisition and transport (e.g., height, root diameter, seed mass) consistently loaded onto the first PC axis; traits related to tissue construction (e.g., specific root length, root tissue density) loaded onto the second, and traits associated with above and below-ground allocation (e.g., root to shoot ratio, root to shoot area ratio) loaded onto the third. These axes were inconsistently correlated with future growth rate. At the 10-day harvest, only the axis related to tissue construction (high specific leaf area, high specific root length, and low root tissue density) was linked to future growth rate. At the 42-day harvest, all three axes were related to future growth rate. Numerous root traits were consistently correlated to axes related to future growth rate and may be particularly informative for understanding plant strategies at early developmental stages.

A fundamental goal of trait-based ecology, including trait-based restoration, is to link specific traits to community assembly, biodiversity, and ultimately ecosystem function. Despite a growing awareness of the importance of belowground traits on community and ecosystem processes, a synthesis focused on how root traits can inform trait-based restoration is lacking. I reviewed and summarized existing literature focused on root traits in relation to plant performance measures (i.e. survival, establishment, and productivity) important to restoration. I focused my review on studies that related root traits to plant performance under drought, competition (including invasion), and erosion, because these environmental stressors hinder successful restoration in many systems. Numerous studies have linked root traits related to belowground resource acquisition (e.g., root length, rooting depth, specific root length) to drought avoidance (i.e. a plant strategy based on optimizing water uptake to maintain function). Studies relating root traits to drought tolerance (i.e. a plant strategy that allows plants to withstand low levels of tissue dehydration) remain more limited. Similarly, 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 likely decrease resources rapidly to the detriment of neighbors, root traits associated with rapid resource acquisition (e.g., high specific root length, root system extent) may be particularly important for understanding competitive effects. Albeit more limited, research suggests that root traits associated with resource conservation or stress tolerance (e.g., high root tissue density, high root diameter) may elucidate mechanisms related to plants' competitive responses. In the contexts of drought and competition, the response of root traits to the stressor is assessed far more often than the effect of root traits on plant performance measures or ecosystem functions. In contrast, the effects of specific root traits, particularly traits associated with root system extent (e.g., root length, root to shoot ratios) and root strength (i.e. tensile strength) on aggregate and topsoil stability are well documented. Future research that explicitly links root traits to plant

performance is needed to advance trait-based restoration of diverse plant communities and functioning ecosystems.

By considering abiotic and biotic belowground components of restored systems researchers and practitioners may elucidate barriers to native plant establishment and improve revegetation outcomes. I investigated how interactions between drought and invasive species interact to affect abiotic soil condition and restoration outcomes. In addition, through an experimental study and a literature review, I examined how root traits may influence seedling growth and other performance measures. I hope the research presented here will contribute to effective restoration of damaged or degraded ecosystems.

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INTRODUCTION

Low precipitation and soil moisture hinder seedling recruitment and successful plant establishment in many environments including restored dryland systems (Booth et al. 2003, Hardegree et al. 2012, Hardegree et al. 2013, Hardegree et al. 2016). However, because distinct species phenologies may or may not align with seasonal precipitation, impacts of low precipitation on plant establishment may be species or context dependent. Many invasive species have traits that allow them to be successful under changing climates, particularly under scenarios of higher atmospheric CO_2, greater resource availability, and increased global commerce (reviewed in Bradley et al. 2010). The effects of altered precipitation on invasive species success, however, remain more uncertain (Bradley et al. 2010).

Wolkovich and Cleland (2014) suggest that fast growing invasive species and those with high phenological-plasticity (Wainwright and Cleland 2013) are able to track climate changes more closely than native species. This may result in increased invasive species establish during periods of high resource variability but low competition at the beginning and end of growing seasons. Furthermore, when they do successfully establish, invasive species can themselves exert strong influences on vegetation structure and soil hydrological processes (Pyšek et al. 2012). For example, in the western United States (hereafter US) invasion of annual grasses of the *Bromus* genus (*Bromus* hereafter) can lead to loss of deep rooted and fibrous-rooting plant species (Wilcox et al. 2012) and alter the phenology of invaded plant communities (West and Yorks 2006). These changes could in turn influence infiltration and retention of water in specific soil layers to alter the amount of soil moisture available for native species establishment (Booth et al. 2003, Brown et al. 2008, Ryel et al. 2010).

Global climate models largely agree that drylands will experience increased aridity and variability in precipitation in the coming century, but predictions of soil moisture remain uncertain (Burke and Brown 2008, Orlowsky and Seneviratne 2013). This is in part because precipitation and vegetation dynamics in drylands are tightly linked and can independently and synergistically affect soil moisture availability. Directly, increased variability in precipitation or longer and more intense droughts can affect soil moisture. Indirectly, climate-induced changes in vegetation can influence soil moisture availability via altered interception, uptake, and transpiration (Wilson et al. 2018).

While numerous studies have focused on the effects of drought and invasive species on ecosystem and plant community dynamics in intact systems, investigations of drought and invasive species effects on developing plant communities undergoing ecological restoration are limited. Furthermore, no studies have considered the effects of both drought and invasive species on soil moisture simultaneously in a restoration context. Understanding the combined effects of drought and invasive species on plant community development and soil moisture could provide valuable insight into the mechanisms hindering successful native plant establishment in dryland restoration projects that have dismal success rates between 5% and 10% (Kildisheva et al. 2016).

Over the last century and a half, exotic annual *Bromus* species have invaded diverse drylands throughout the western US (Germino et al. 2016). Research has primarily focused on *Bromus tectorum* L. (cheatgrass or downy brome, *B. tectorum* hereafter), a winter annual grass that has invaded over 2 million hectares of drylands in the western US (Bradley and Mustard 2006) since its introduction in the late 1800s (Mack 1981). *B. tectorum's* success largely stems from its life history and phenology, which work together to interfere with native seedling recruitment. Most often, *B. tectorum* germinates in the fall, overwinters as a seedling and rapidly develops roots and shoots (Aguirre and Johnson 1991) before native perennial species become active in the spring. In addition, *B. tectorum* has been shown to increase in abundance when summer soil moisture is low (Bradley et al. 2009) or variable from year to year (Chambers et al. 2007).

While *Bromus* species affect most dryland systems throughout the western US to some degree, distinct eco-regions differ in the extent of invasion as well as their susceptibility to *Bromus* invasion (Chambers et al. 2014). Most studies on *B. tectorum* have focused on its spread and impacts in Cold Desert ecoregions of the western US, primarily the Great Basin (Brooks et al. 2016). Yet, *B. tectorum* readily invades disturbed areas across much of the western US and several modeling (Bradley et al. 2009, Bradley 2010, Abatzoglou and Kolden 2011) and empirical (Prevéy and Seastedt 2014, Prevéy and Seastedt 2015) studies suggest that decreased summer precipitation may result in *B. tectorum* expansion throughout the Western Great Plains (WGP hereafter) and Cold Deserts (CD hereafter) ecoregions outside of the Great Basin. However, many of these studies are conducted in relatively intact systems dominated by plants that can effectively compete with *B. tectorum* (Bradford and Lauenroth 2006). In disturbed areas denuded of established vegetation, precipitation and *B. tectorum* may interact in unique ways to influence plant community dynamics and competition between native species and *B. tectorum*. If it successfully establishes, *B. tectorum* may alter the extent and timing of soil moisture availability (Booth et al. 2003; Ryel et al. 2010; Prevéy and Seastedt 2014) and hinder recruitment of native species that depend on shallow soil moisture for germination (Hardegree et al. 2013, Hardegree et al. 2016), establishment (Harris and Wilson 1970, Aguirre and Johnson 1991, Booth et al. 2003, Humphrey and Schupp 2004), and growth (Ryel et al. 2010).

Fluctuations in seedbed microclimate resulting from variable precipitation may result in conditions that favor *B. tectorum* germination and establishment over that of native species (Roundy et al. 2007, Hardegree et al. 2010, 2013). Restoration ecologists often aim to improve seedbed microclimate and increase the availability of soil resources with soil amendments such as mulch or biochar (e.g., Chambers 2000, Zink and Allen 2003, Beesley et al. 2011). Superabsorbent polymers (SAP) have been used for over 40 years in agricultural settings to increase soil water retention (Hüttermann et al. 2009) but have rarely been used in ecological restoration. They are primarily advertised as a way to improve plant establishment in deficit water conditions as they have been shown to promote crop seedling survival under drought (Akhter et al. 2004, Agaba et al. 2010), improve crop growth under limited irrigation (Hüttermann et al. 1999, Yang et al. 2014), and increase water-holding capacity of soil (Akhter et al. 2004). However, information about their efficacy in natural settings is limited, and effects on plant establishment in restoration projects have been inconsistent (e.g., positive impacts: Rubio et al. 1992, Mangold and Sheley 2007, no effect/variable results: Newhall et al. 2004; Lucero et al. 2010; Garbowski et al. 2019; Johnston and Garbowski 2020). Understanding whether SAP incorporated into the first several centimeters of soil can ameliorate the negative effects of drought and non-native species on native species establishment could provide valuable insight regarding their efficacy in ecological restoration.

We established a study to investigate the interactive effects of growing season (April – September) drought, *B. tectorum* seeding (BRTE hereafter refers to treatment level), and SAP on native plant community development and soil moisture at two climatically distinct dryland sites in Colorado: one within the WGP ecoregion in the northeastern corner of the state and another in the CD ecoregion in the southwestern portion of the state. The WGP and CD sites we selected have similar land use histories and soil moisture and soil temperature regimes, but vary in precipitation seasonality.

Specifically, we aimed to test the following hypotheses:

- Drought will decrease native seeded species cover; increase *B. tectorum* cover; and decrease soil volumetric water content (VWC) at both sites
- BRTE will decrease native seeded species cover. Effects of BRTE will be most pronounced under drought treatments at the CD site at which precipitation is more limited when native species are most active (April-July).
- SAP will ameliorate negative effects of drought and BRTE on native seeded species establishment and will increase soil VWC particularly at shallow soil depths.

MATERIALS AND METHODS

Study Sites

The WGP site is located at a Colorado State University property near Waverly in Larimer County (40°42’30.7’’N, 105°06’24.4’’W, elevation: 1590 m). The WGP site receives approximately 390 mm of precipitation annually with about 270 mm falling during the growing season. The majority of the WGP site’s growing season precipitation (170 mm) falls in the spring and early summer between April and June. The CD site is located at Dry Creek State Wildlife Area in San Miguel County (38°03’25.1’’N , 108°29’59.9’’W) and also receives approximately 390 mm of precipitation annually. Most of the growing season precipitation (160 mm of 220 mm) falls in the late summer and early fall between July and September. These averages were obtained from National Oceanic and Atmospheric Administration stations near each site using data from 1983-2013 (NOAA).

Aside from differences in precipitation seasonality, the CD and WGP sites have similar land use histories, and soil moisture and temperature regimes (Brooks et al. 2016). The WGP site was tilled and seeded with *Agropyron cristatum* (crested wheatgrass) for pasture in the 1950’s or 1960’s and grazed by sheep and cows until about 2000 (personal communication, Nevada Agricultural Experiment Station Associate Professor and State Specialist, Paul Meiman). The CD site was tilled and planted with *Agropyron cristatum* and possibly other pasture grasses in the mid 1950’s, irrigated for several years, and then became fallow. Sheep were then grazed in the area until the late 1970’s, followed by cattle until 2006 (personal communication, Colorado Parks and Wildlife Property Technician, Murphy Jacox). Both sites are characteristic of warm and dry (ustic aridic/aridic) soil temperature and moisture regimes and receive approximately 400 mm of precipitation annually (Lawrimore et al. 2011). Soils at both sites are loams or clay loams with clay content ranging from 23 – 33%. Both sites contain a mixture of native and non-native species. Common species at the WGP site include natives *Aristida purpurea*, *Pascopyrum smithii, Helianthus annuus* and *Cleome serrulata* and non-natives *Agropyron cristatum* and *Convolvulus* *arvensis. B. tectorum* is present at the WGP site but occurs primarily in distinct patches across the landscape. Common species at the CD site include native *Atriplex* shrubs, *Ericameria nauseosa, Chrysothamnus viscidiflorus*, *Artemisia tridentata* Nutt. ssp. *wyomingensis* as well as native grass species *Achnatherum hymenoides, Bouteloua gracilis* and *Pascopyrum smithii.* Common non-native species at the CD site include *B. tectorum*, *Agropyron cristatum*, *Convolvulus arvensis* and *Alyssum simplex*.

Study implementation

Three blocks were designated at each site based on uniform vegetation and minimal slope (<10°). A full factorial design was implemented in each block crossing the following three factors: (1) precipitation [ambient or 66% reduced (drought)]; (2) BRTE treatment (465 *B. tectorum* seeds m^{-2} or none) and; (3) SAP treatment (SAP 25 g m^{-2} or none).

We developed site-specific seed mixes that consisted of native grasses, forbs, and shrubs that were suitable to the climate at each site, present in surrounding areas, and commercially available (Table A.1.1). We used the same number of pure live seeds (PLS) and species in forb, grass, and shrub functional groups for the two seed mixes (46% forbs, 15 species; 22% grasses, 13 species; 32% shrubs, 8 species). A total of 1,200 PLS m^{-2} were broadcast at the WGP site and 1,344 PLS m^{-2} were broadcast at the CD site. A volume sufficient to provide 465 *B. tectorum* seeds m^{-2} was prepared for each BRTE treatment plot. We based density of *B. tectorum* seeds on values reported in similar studies from the region: Johnston and Chapman (2014) reported propagule pressure between 0 and >1,000 seeds m^{-2} at sites in Western Colorado and Concilio et al. (2017) estimated *B. tectorum* densities of about 700 individuals m^{-2} at sites on the Front Range of Colorado. Prolific stands of *B, tectorum* can produce up to 20,000 seeds m^{-2} (Hempy-Mayer and Pyke 2008). We collected *B. tectorum* seeds within 6 km of both study sites and air-dried them in warm, dry conditions without light to after-ripen prior to seeding.

Prior to study implementation we removed sparse woody vegetation with a brush mower and applied glyphosate to remaining vegetation at a rate of 4,480 g ai ha^{-1} two or three times at each site over the course of several weeks. We tilled each experimental block with a rototiller to a depth of 5-10 cm. We undertook these pre-treatment actions to mimic heavy levels of disturbance such as those created by mining or oil and gas extraction. We then applied SAP (Stockosorb 660 Micro, 0.2-0.8 mm, Evonik Industries, Germany) to plots receiving this treatment at a rate of 25 g m^{-2}. We used a SAP application rate that was within the ranges of amounts used in containerized experiments (60 – 600 g m^{-2}; Agaba et al. 2010, Bakass et al. 2002) and agricultural applications (1 – 10 g m^{-2}; Ashkiani et al. 2013, Islam et al. 2011). After broadcasting SAP, we cultivated study areas with a disk harrow to incorporate polymer to 5-10 cm deep. We incorporated broadcast native restoration seeds and *B. tectorum* seeds by hand and light raking. We completed these tasks during recommended seeding periods for the two sites (NRCS 2011) and ahead of the period with highest seasonal precipitation at each site: November/December 2013 at the WGP site and July 2014 at the CD site.

The drought treatment was based on projections of lower summer precipitation in the region (e.g., Archer and Predick 2008, Bradley et al. 2009). The drought we imposed excluded 66% of growing season (April – September) precipitation. We chose this drought scenario because recent research (Knapp et al. 2018) suggests that extreme manipulations of precipitation are needed to accurately assess community and ecosystem responses to climatic events. Although pronounced, in an average precipitation year, this reduction would still result in precipitation amounts falling within the 30-year range of variability for both sites. Rainfall diversion shelters were modified from Yahdjian and Sala (2002). Our modifications included constructing larger shelters (3.6 x 4.4 m) in an “A-frame” design with plastic rain-catchment troughs oriented towards prevailing winds (Fig. A.1.1). We installed plastic flashing around each plot to a depth of 45 cm to limit above- and belowground water movement and root growth between treatment areas and their surroundings. We constructed shelters in April 2014 at the WGP site and June 2014 at the CD site. We deconstructed shelters in late September/early October each year to allow for ambient winter precipitation and reinstalled them during the first two weeks of April each spring.

We measured vegetation cover at peak biomass in late June or early July at both sites each summer from 2014-2017 at the WGP site, and 2015-2017 at the CD site. We measured cover by placing two cover data frames (1.5 x 1 m) with 96 evenly spaced intersections in plots and recorded point intercept cover hits at each intersection point for all canopy layers. Current year *B. tectorum* was recorded even if plants were senescing. Each year, cover data measurement were collected from the same areas within plots. At two of the blocks at each site, we installed soil moisture probes (5TM model probes, Decagon Devices, Pullman WA) in treatment plots to assess effects of treatments on VWC at shallow-depth (5 cm) and mid-depth (30 cm) soils. VWC (m^3 water $m\text{-}^{3}$ soil) was calculated from the permittivity measured by the sensors using the Topp model (Topp et al. 1980). We strung probe cables through PVC piping to prevent weather and animal damage and connected them to data loggers (CR1000 model loggers, Campbell Scientific, Inc., Logan UT) for continuous monitoring of VWC in 2015 and 2016.

Data analyses

We completed all statistical analyses in R (R Core Team, 2017) for each site separately. We used repeated measures linear mixed effects models in the ‘lme4’ package (Bates et al. 2014) to analyze effects of treatments on plant cover for the following functional groups: *B. tectorum,* native seeded species (separated into forbs and grasses when sufficient observations of each permitted individual analyses), non-native annual forb species, and non-native perennial species. In these models, date and treatments were considered fixed effects, and block and plot were considered random effects.

Because of defective sensors and significant rodent damage, soil VWC data from over 25% of sensors was missing. The majority of failures occurred in plots with SAP, preventing us from conducting a repeated measures analysis of soil VWC with SAP plots included. Therefore, we used only data from no-SAP plots for analyses of soil VWC. The sensors we used have manufacturer-specified error of ±1 permittivity. This equates to between 2 and 5% VWC within the range observed in our study according to the Topp model (Topp et al. 1980), therefore differences among treatments that fall within this error should be interpreted with caution. We used repeated measures linear mixed effects models (Bates et al. 2014) with time as the repeated measure to analyze effects of treatment on weekly averages of soil VWC with date and treatments considered fixed effects and block and plot considered random effects. Analyses were completed separately for soil VWC at 5 and 30 cm.

For all models, we examined residual and Q-Q plots to assess homogeneity of variance and normality. Transformations of response variables were performed when needed. Cover values were square root transformed for all functional groups at both sites. To determine differences in response variable means based on treatments, we performed planned contrasts, with Tukey HSD adjustment, using package 'emmeans' (Lenth 2016) on main effects with p-values < 0.05 and all two-way and three-way interactions with p-values < 0.1. Here we discuss treatment interactions with significant effects within a given year. Results of treatment interactions with differences across years are provided in Table A.1.2.

RESULTS

Growing season precipitation (April – September) at the two sites varied considerably from year to year and deviated from 30-year growing season averages (WGP: 270 mm; CD: 220 mm). At the WGP site 227 mm, 375 mm, 154 mm, and 278 mm of precipitation fell during the 2014, 2015, 2016, and 2017 growing seasons, respectively (Fig. A.1.2). A typical precipitation pattern of high rainfall early in the summer was only observed in 2015 and 2016 (Fig. A.1.2). At the CD site 193 mm, 176 mm, and 131 mm of precipitation fell during the 2015, 2016, and 2017 growing seasons, respectively (Fig. A.1.3). At the CD site a typical pattern of high rainfall late in the summer at the CD site was not observed in any year of the study (Fig. A.1.3).

Bromus tectorum and seeded species establishment

BRTE and drought treatments interacted to influence *B. tectorum* cover at both sites. At the WGP site, in the first year post-seeding (2014), *B. tectorum* cover was low (< 2%) and we detected no differences among treatments. In all subsequent years of the study (2015, 2016, 2017), the BRTE treatment resulted in higher *B. tectorum* cover (Fig. 1a; Table 1) but effects depended on drought treatment. In 2015, *B. tectorum* cover was greater only in plots with BRTE and drought compared to no-BRTE plots. In 2016 *B. tectorum* cover was highest in plots with both BRTE and drought treatments and significantly greater than in all other treatment combinations.

At the CD site, *B. tectorum* cover was higher in ambient plots compared to drought plots in the first growing season (2015), but effects of precipitation treatment were not detected in 2016 or 2017 (Fig. 1.2a; Table 1.1). *B. tectorum* cover was higher with the BRTE treatment in both 2015 and 2016, but we detected no effects in the final year of the study (2017) (Fig. 1.2b; Table 1.1). *B. tectorum* cover was unaffected by SAP treatments at either site.

Seeded species cover was influenced by all treatments at the WGP site, but effects depended on year and functional group measured. Seeded forb cover decreased significantly from the first two years of the study to the last two years of the study (Fig. 1.1c; Table 1.1). In the first two years prevalent seeded forbs included *Cleome serrulata*, *Helianthus annuus*, and *Machaeranthera tanacetifolia* and in the last two years *Linum lewisii, Ratibida columnifera* and *Machaeranthera tanacetifolia* were common. Across all years, seeded forb cover was approximately 10% lower in drought plots compared to ambient precipitation plots (Fig. 1.1c; Table 1.1). Overall, seeded grass cover increased through time, but we detected treatment effects only in the final year of the study. In 2017, seeded grass cover was approximately 10% higher in plots without BRTE or drought compared to plots with BRTE (Fig. 1.1.b; Table 1.1). Across years, seeded grass cover was higher in plots with SAP (4.9 ± 1.0 %) compared to plots without SAP (2.2 ± 0.7 %). Dominant grass species at the WGP site included *Pascopyrum smithii*, *Aristida purpurea*, and *Elymus elymoides*.

At the CD site, seeded species cover was low across all years (approximately 5%) and was dominated by forbs (*Helianthus annuus* and *Cleome serrulata*) in the first year and perennial grasses in the later two years, primarily *Bromus carinatus, Pascopyrum smithii,* and *Elymus trachycaulus*. The drought treatment reduced seeded species cover from approximately 8% to 3% (Figs. 1.2e; Table 1.1). Similarly, the BRTE treatment reduced seeded species cover from 8% to 2%. We detected no SAP effects on seeded species at the CD site.

Non-native annual forb cover at the WGP site was lower in plots with BRTE across all years compared to plots without BRTE (Fig. 1.1f; Table 1.1) but was unaffected by drought or SAP treatments (Fig. 1.1e; Table 1.1). Non-native annual forbs were dominated by *Salsola tragus* in 2014, *Bassia scoparia* in 2015, *Lactuca serriola* in 2016 and a diversity of species including *Kochia scoparia, L. serriola, S. tragus* and *Tragopogon dubius* in 2017. Non-native perennial forbs, predominantly *Convolvulus arvensis,* at the WGP site increased from 2014 to 2015 and then decreased for the remainder of the study (Table 1.1; Table A.1.2).

At the CD site in 2015, non-native annual forb cover was lower in drought compared to ambient precipitation plots (Fig. 1.2c; Table 1.1) but differences were not detected in later years. Non-native annual cover at the CD site was dominated by similar species across all years (i.e. *Alyssum simplex*, *Descurainia sophia* and *Sisymbrium altissimum*) and was not affected by BRTE or SAP treatments. Non-native perennial cover at the CD site decreased through time and was dominated by *Convolvulu arvensis* (Table 1.1; Table A.1.2).

Soil volumetric water content

At WGP, drought affected weekly average VWC at 5 cm in both 2015 and 2016, but the magnitude and direction of effects varied over time. At several time points early in the growing season (04-Apr-2015, 11-Apr-2015, 25-Apr-2015, 16-Apr-2016) VWC was higher in drought than ambient precipitation treatments, whereas negative effects were detected later in the season (11-July-2015, 18-July-2015, 14-

May-2016, 21-May-2016) in both years (Figs. 1.3a and 1.3b; Table 1.2), but see previous note on sensor error. In addition, BRTE treatment decreased seasonal VWC at 5 cm in 2016 (Fig. 1.3d; Table 1.2) but not in 2015 (Fig. 1.3c; Table 1.2). At 30 cm, VWC was higher in plots with BRTE and ambient precipitation than in all other treatment combinations in both 2015 and 2016 (Figs. 1.3e and 1.3f; Table 1.2).

At the CD site, BRTE and drought treatments interacted to influence seasonal VWC at 5 and 30 cm in 2015 and at 30 cm in 2015 (Figs. 1.4a - 1.4d; Table 1.2). In 2015, seasonal VWC at 5 cm was higher in plots with ambient precipitation and without BRTE than in all other treatments. In addition, plots with drought and without BRTE had greater seasonal VWC than plots with BRTE (Figure 1.4a; Table 1.2). A similar pattern was observed at 30 cm in 2015: seasonal VWC was higher in plots with ambient precipitation and without BRTE compared to plots with ambient precipitation and BRTE and plot with drought alone (Fig. 1.4c; Table 1.2). In 2016, seasonal VWC at 5 cm was lower in plots with BRTE and drought than all other treatments (Fig. 1.4b; Table 1.2). No treatment effects of VWC at 30 cm depth were detected in 2016 (Fig. 1.4d; Table 1.2).

DISCUSSION

Changes in climate such as lower or more variable precipitation may facilitate the spread of non-native species (Cleland et al. 2007, Abatzoglou and Kolden 2011, Prevéy and Seastedt 2014) and hamper restoration efforts. In our study, drought and the invasive annual grass, *B. tectorum,* interacted to influence restored plant communities and soil moisture.

Bromus tectorum establishment

We hypothesized that drought would result in higher *B. tectorum* cover at both sites, but this trend was observed only at the WGP site in two of the four study years (Fig. 1a). Brooks et al. (2016) suggest that consistent summer precipitation in the WGP results in high competition from native species and unfavorable conditions for *B. tectorum* invasion. If summer precipitation is reduced, *B. tectorum* is predicted to increase in this region (Bradley 2009). The higher cover of *B. tectorum* we observed in drought plots at the WGP site in 2015 and 2016 is consistent with these predictions and other research from the area. In studies investigating the effects of seasonal shifts in precipitation on plant communities along the Front Range of Colorado, Prévey and Seastedt (2014, 2015) observed higher abundance of winter-active, exotic grasses (2014) and higher population growth rate of *B. tectorum* with increased winter precipitation (2015). While our treatment did not alter winter precipitation - all plots in our study received ambient precipitation from October to March - the reduction in summer rainfall in our study resulted in proportionally more rainfall in the winter similar to Prévey and Seastedt (2014, 2015). Because growing season precipitation differed significantly between 2015 and 2016 (375 mm in 2015 vs. 154 mm in 2016) it is likely that proportional changes in seasonal precipitation rather than total precipitation amount resulted in conditions that favored *B. tectorum* establishment over native species establishment.

The imposed summer drought in our study may have created a vacant temporal niche (i.e. a period during which other species are inactive) for *B. tectorum* to exploit before native species became established at the WGP site. Wolkovich and Cleland (2014) suggest that fast growing and plastic species like *B. tectorum* (Mack and Pyke 1983) may be well suited to track changing climate patterns to take advantage of periods of variable resource availability and low competition at the beginning and end of growing seasons. *B. tectorum* can germinate (Hardegree et al. 2013) and elongate roots (Harris 1967) at lower temperatures than many native perennial grass species. Because VWC was counter intuitively higher in drought plots early in the 2015 and 2016 growing seasons, it is possible that *B. tectorum* experienced particularly favorable conditions for growth before native species became active under drought treatment at the WGP site. Furthermore, lower cover of seeded forbs such as *Cleome serrulata* and *Machaeranthera tanacetifolia* in drought treatments and substantial decreases in overall seeded forb cover from 2015 to 2016 may have released *B. tectorum* from competition and allowed it to further increase in cover under drought.

The trend for higher *B. tectorum* in drought plots was limited to the WGP site; at the CD site *B. tectorum* cover was higher in ambient precipitation plots in the first year of the study (Fig. 2a). Reduced rainfall in drought treatments beginning in July 2014 at the CD site may have negatively affected initial *B. tectorum* establishment. Although plant density data were not collected in the fall immediately after seeding (2014), data from 2015 suggest that lower fall establishment of *B. tectorum* may have influenced this pattern. In a companion study, Garbowski et al. (2019) observed lower *B. tectorum* establishment under drought throughout 2015, particularly in the fall (>900 plants m^{-2} compared to < 1 plants m^{-2}). Below average fall precipitation (September – October) in all study years at the CD site may have further hindered *B. tectorum* establishment. Survival and growth after fall germination is imperative for successful *B. tectorum* recruitment (Mack and Pyke 1983, Prevéy and Seastedt 2015, Bishop et al. 2019) and in warmer and drier regions *B. tectorum* often requires favorable environmental conditions or high propagule pressure to successfully establish and persist (Meyer et al. 2001).

Our result of higher *B. tectorum* cover under drought at the WGP site is supported by prior research (Bradley et al. 2009, Chambers et al. 2014, Prevéy and Seastedt 2014), but our finding of lower cover at the CD site suggests that summer drought can also hinder *B. tectorum* establishment. These contrasting results corroborate uncertainty identified in prior studies focused on understanding how precipitation affects *B. tectorum* establishment (Bradley et al. 2009; Chambers et al. 2014).

Seeded species establishment

As hypothesized, seeded species cover was negatively affected by drought and BRTE treatments at both sites, but effects varied by functional group. At the CD site, drought and BRTE treatments had comparable negative effects on seeded species, each decreasing seeded species cover by approximately 5% (Figures 1.2e and 1.2f).

At the WGP site drought reduced seeded forb cover (Figure 1.1c) and BRTE reduced seeded grass cover in ambient precipitation plots (Fig. 1b and 1c). The most abundant native forb species (i.e. *Cleome* *serrulata*, *Helianthus annuus*, *Ratibida columnifera, and Machaeranthera tanacetifolia*) at the WPG site are tap rooted and active late in the growing season. Because they likely depend on soil moisture from deep soil layers, these forbs may have been more impacted by dry conditions at 30 cm depth than shallow rooted grasses. The BRTE treatment reduced cover of morphologically similar native grasses and phenologically similar early-season annual forbs. These results support the general theory of "limiting similarity" under which species with similar resource use strategies compete more strongly than those with dissimilar strategies (Macarthur and Levins 1967, Fargione et al. 2003, Brown and Rice 2009) or phenologies (Funk et al. 2008). As in other studies, our findings suggest strong competitive effects of *B. tectorum* on morphologically similar species (Aguirre and Johnson 1991, Humphrey and Schupp 2004, Yelenik and Levine 2009) and resource partitioning between *B. tectorum* and dissimilar forb species (Sheley and Larson 1994, Parkinson et al. 2013). Our results demonstrate that, in general *B. tectorum* and drought negatively impact native species establishment but specific effects may differ for grasses and forbs. Using forb species with dissimilar morphologies and phenologies from *B. tectorum* may allow for improved restoration outcomes in invaded areas (Barak et al. 2015).

We predicted that SAP would increase seeded species establishment under drought and BRTE treatments at both sites but the SAP treatment did not interact with BRTE or drought treatments. SAP had a positive effect on perennial grasses but only at the WGP site increasing seeded grass cover from 2.2 to 5% across study years. We observed no effect on other functional groups. As SAP was applied to between 5-10 cm depth, fibrous, shallow-rooting grasses may have benefitted more than deeper-rooted forbs or shrubs from SAP addition. Working in similar dryland systems, Johnston and Garbowski (2020) observed increased perennial grass cover with shallowly incorporated SAP but also detected a negative effect of SAP on perennial forbs, which were dominated by taproot-developing species. Even though grass cover is often negatively correlated with *B. tectorum* cover (e.g., Bradford and Lauenroth 2006, Bradley et al. 2009, Chambers et al. 2016), the modest increase in grass cover we observed with SAP at the WGP site did not result in reduced *B. tectorum* cover. Recent research also indicates that in some cases SAP might actually benefit *B. tectorum* (Johnston and Garbowski 2020). The minimal effects of SAP on increased competition from perennial grasses, possible negative effects on seeded forbs, and potential positive effects of SAP on *B. tectorum* make it an unreliable tool for native plant restoration in invaded systems.

Soil volumetric water content

Negative effects of *B. tectorum* on near-surface soil moisture (0 - 30 cm) have been documented in shrublands (Melgoza et al. 1990, Booth et al. 2003a, Kulmatiski et al. 2006, Ryel et al. 2010) and grasslands (Prevéy and Seastedt 2014), but few studies have investigated interactive effects of *B. tectorum* and drought on VWC at various depths. Sensor error, in contrast with statistical error, is rarely explicitly addressed in the ecological literature and differences reported may be within the margin of error of the sensors. Nonetheless, our results suggest that the effects of *B. tectorum* on soil moisture during ecological restoration may be site specific and interact with precipitation to uniquely influence soil VWC at shallow-depth (5 cm) and mid-depth (30 cm).

Shallow-depth (5cm): We predicted that drought would decrease soil VWC at both sites but observed both positive and negative effects of drought in our study. It is likely that lower plant abundance in drought compared to ambient plots early in the season at the WGP site resulted in lower soil water utilization by the plant community and drove the trend for higher VWC at 5 cm. However, because cover measurements were taken only once each year, this interpretation remains speculative.

BRTE treatments resulted in decreased seasonal VWC at 5 cm independently as well as in combination with drought at both sites (Figures 1.3d, 1.4a, and 1.4b). Notably, at the CD site, the BRTE treatment resulted in lower VWC at 5 cm than our imposed drought of 66% reduced growing season precipitation (Fig. 4a). As *B. tectorum* has high transpiration rates (Harris 1967) and shallow roots (Kulmatiski et al. 2006) this result is unsurprising and reflects findings from other studies in dryland communities (Harris 1967, Cline et al. 1977, Booth et al. 2003, Ryel et al. 2010;) but the magnitude in comparison to drought is stark.

Mid-depth (*30 cm*): Although unmeasured, differences in the depth from which *B. tectorum* and other plants utilize soil moisture may have contributed to patterns we observed in VWC at 30 cm at the WGP site: higher VWC in plots with BRTE and ambient precipitation than all other treatment combinations. *B. tectorum* roots are able to grow and access water from >1 m depth (Harris 1967, Leffler et al. 2005) but like many other annual grasses, predominantly utilize water between 0-15 cm soil depth (Kulmatiski et al. 2006, Holmes and Rice 1996). As *B. tectorum* cover in ambient plots with BRTE treatment was much higher compared to plots without BRTE in 2015 (19% vs. 1%) and 2016 (61% vs. 9%), it is possible that competition from *B. tectorum* in ambient plots with BRTE treatment prevented root elongation of native plants into deeper soil layers (Harris 1967) and impeded subsequent water extraction from 30 cm depth. In drought plots, reduced precipitation, which may independently reduce root elongation (Larson and Funk 2016), coupled with higher *B. tectorum* cover may have restricted root growth to shallow soil layers and resulted in low infiltration to 30 cm. At the CD site, higher cover of *B. tectorum* in ambient precipitation plots in 2015 may have resulted in greater utilization of soil moisture at both 5 cm and 30 cm depth at this site. As in prior studies (Harris and Wilson 1970, Booth et al. 2003, Humphrey and Schupp 2004), our results suggest that *B. tectorum* may alter soil moisture conditions to the detriment of newly establishing seedlings, but specific effects on shallow and mid-depth soil layers may depend on growing season precipitation. Isotopic studies that investigate from where establishing invasive and native species extract water could help clarify competitive, albeit indirect, impacts of annual grasses like *B. tectorum* (e.g., Melgoza et al. 1990) on establishing vegetation in restoration settings.

CONCLUSION

Whether low soil moisture is a result of decreased precipitation and/or rapid use by existing vegetation, it hinders plant establishment in restored plant communities. Seedling survival during drought has been linked to plant tolerance of low soil moisture conditions (Ackerly 2004), the ability of seedlings to develop deep roots and access moist soil layers during establishment (Padilla and Pugnaire 2007), and root allocation and morphology (Atwater et al. 2015, Ferguson et al. 2015). Seedling survival in relation to *B. tectorum* competition has been linked to higher root-to-shoot ratios (Rowe and Leger 2010), earlier adult phenology (Rowe and Leger 2010), greater allocation to fine roots (Goergen et al. 2011) and rapid root growth (Leger et al. 2019). While the suites of traits related to survival under drought or invasion can differ greatly from those that confer greatest fitness in ‘stress-less’ environments (Goergen et al. 2011), overlap may exist between traits that promote establishment in drought as well as invaded conditions. As both drought and BRTE treatments in our study decreased soil moisture, it is possible that species that can tolerate low moisture conditions or avoid them by rapidly developing roots to keep pace with seasonal or *B. tectorum* induced soil drying may be best suited to establish under both scenarios. It appears that trait overlap in relation to both stressors seems to be largely related to roots. Thus, additional studies that relate root traits to plant establishment and performance under both of these common stressors may inform species selection for dryland restoration. Further, as precipitation variability is likely to increase under predicted climate scenarios, restoration projects with multiple seeding dates (Bakker et al. 2003, MacDougall et al. 2008) or those that utilize high richness seed mixes with species that emerge under a wide range of conditions (Groves and Brudvig 2019) may offset the negative impacts of planting during particularly dry periods. Additionally, soil amendments such as SAP may improve restoration outcomes, but additional research is needed to discern when application will be beneficial or detrimental and which functional groups are most likely to affected.

Table 1.1: Analysis of variance results for main effects and interactions of *B. tectorum* seeding (BRTE), precipitation (Precip.), and superabsorbent polymer (SAP) treatments and time for cover of different plant functional groups (NN An : Non-native annuals, NN Per : Non-native perennials) at the Western Great Plains and Cold Desert sites. Degrees of freedom (*df*) are for the numerator and denominator.

	Western Great Plains									
	B. tectorum		NN An		NN Per		Seeded Grasses		Seeded Forbs	
	df	F,p	*df*	F,p	*df*	F,p	*df*	F,p	*df*	F,p
Precip.	1,14	1.14,0.3	1,62	2.4,0.13	1,14	0.01,0.91	1,14	2.75,0.12	1,62	9.95,<0.01
BRTE	1,14	87.26,<0.001	1,62	12.99,<0.001	1,14	2.06,0.17	1,14	3.02,0.1	1,62	0.36,0.55
SAP	1,14	2.28,0.15	1,62	0.18,0.67	1,14	3.19,0.1	1,14	6.48,0.02	1,62	2.49,0.12
time	3,48	45.35,<0.001	3,62	16.03,<0.001	3,48	26.78,<0.001[a]	3,48	14.24,<0.001	3,62	19.8,<0.001[a]
Precip.:BRTE	1,14	3.39,0.09	1,62	0.4,0.53	1,14	0.81,0.38	1,14	1.49,0.24	1,62	0.08,0.77
SAP:Precip.	1,14	2.31,0.15	1,62	1.65,0.2	1,14	0.11,0.75	1,14	3.07,0.1	1,62	0.08,0.78
SAP:BRTE	1,14	0.29,0.6	1,62	0.17,0.68	1,14	0.04,0.85	1,14	0,1	1,62	0.46,0.5
Precip.:time	3,48	2.88,0.05	3,62	4.66,<0.01[a]	3,48	0.46,0.71	3,48	2.79,0.05	3,62	0.68,0.57
BRTE:time	3,48	28.8,<0.001	3,62	2.12,0.11	3,48	0.71,0.55	3,48	6.29,<0.01	3,62	0.34,0.8
SAP:time	3,48	1.1,0.36	3,62	0.23,0.87	3,48	1.27,0.3	3,48	0.88,0.46	3,62	0.14,0.93
SAP:Precip.:BRTE	1,14	0.02,0.9	1,62	1.36,0.25	1,14	1.1,0.31	1,14	0.68,0.42	1,62	0.33,0.57
Precip.:BRTE:time	3,48	2.92,0.04	3,62	0.09,0.96	3,48	0.33,0.8	3,48	2.36,0.08	3,62	0.12,0.95
SAP:Precip.:time	3,48	2.22,0.1	3,62	0.13,0.94	3,48	0.16,0.92	3,48	0.7,0.56	3,62	0.24,0.87
SAP:BRTE:time	3,48	0.65,0.59	3,62	1.24,0.3	3,48	0.24,0.87	3,48	1.17,0.33	3,62	0.04,0.99
SAP:Precip.:BRTE:tim	3,48	0.62,0.61	3,62	0.82,0.49	3,48	2.94,0.04	3,48	1.06,0.38	3,62	0.13,0.94

	Cold Desert							
	B. tectorum		NN An		NN Per		Seeded Species	
	df	F,p	*df*	F,p	*df*	F,p	*df*	F,p
Precip.	1,14	4.76,0.05	1,14	6.4,0.02	1,14	0.58,0.46	1,14	4.81,<0.05
BRTE	1,14	24.21,<0.001	1,14	2.67,0.12	1,14	0.06,0.81	1,14	6.26,0.03
SAP	1,14	0.06,0.8	1,14	0.18,0.68	1,14	0.11,0.75	1,14	0.2,0.66
time	2,32	2.87,0.07	2,32	9.41,<0.001[a]	2,32	16.66,<0.001[a]	2,32	2.26,0.12
Precip.:BRTE	1,14	0.05,0.83	1,14	0.07,0.79	1,14	1.55,0.23	1,14	2.91,0.11
SAP:Precip.	1,14	0.3,0.59	1,14	0.4,0.54	1,14	0.17,0.68	1,14	1.8,0.2
SAP:BRTE	1,14	0.58,0.46	1,14	2.51,0.14	1,14	0.76,0.4	1,14	0.49,0.5
Precip.:time	2,32	2.74,0.08	2,32	4.18,0.02[a]	2,32	1.96,0.16	2,32	3.85,0.03[a]
BRTE:time	2,32	5.63,<0.01	2,32	0.02,0.98	2,32	0.08,0.92	2,32	0.07,0.93
SAP:time	2,32	0.35,0.71	2,32	0.19,0.83	2,32	0.15,0.86	2,32	0.11,0.89
SAP:Precip.:BRTE	1,14	0.03,0.86	1,14	0.18,0.68	1,14	0.78,0.39	1,14	0.14,0.72
Precip.:BRTE:time	2,32	2.34,0.11	2,32	0.38,0.69	2,32	0.04,0.96	2,32	0.02,0.98
SAP:Precip.:time	2,32	0.44,0.65	2,32	0.76,0.47	2,32	0.6,0.55	2,32	2.03,0.15
SAP:BRTE:time	2,32	0.64,0.53	2,32	0.1,0.9	2,32	1.02,0.37	2,32	0.06,0.94
SAP:Precip.:BRTE:tim	2,32	0.14,0.87	2,32	0.22,0.81	2,32	1.61,0.22	2,32	1.13,0.34

[a] Results of significant main effects of time and interactions that are not discussed in text are provided in Appendix 1: Table A.1.2

Table 1.2: Analysis of variance results for main effects and interactions of *B. tectorum* seeding (BRTE) and precipitation (Precip.) treatments on weekly soil volumetric water content at 5 cm and 30 cm depth at the Western Great Plains and Cold Desert sites. Degrees of freedom (*df*) are for the numerator and denominator.

	Western Great Plains				Cold Desert			
	5 cm				5 cm			
	2015		2016		2015		2016	
	df	F,p	*df*	F,p	*df*	F,p	*df*	F,p
Precip.	1,101	8.02,<0.01	1,18	5.4,0.03	1,103	3.98,<0.05	1,91	17.61,<0.001
BRTE	1,101	0.03,0.86	1,18	7.63,0.01	1,103	51.84,<0.00	1,91	48.01,<0.001
Time	25,10	67.49,<0.00	20,1	39.35,<0.00	25,10	6.12,<0.001	22,9	1.24,0.23
Precip:BRTE	1,101	2.05,0.16	1,18	0.99,0.33	1,103	9.51,<0.001	1,91	14.38,<0.001
Precip. : time	25,10	2.37,<0.001	20,1	2.77,0.02	25,10	1.29,0.18	22,9	0.92,0.57
BRTE : time	25,10	0.24,>0.99	20,1	0.98,0.52	25,10	0.51,0.97	22,9	0.19,>0.99
Precip : BRTE :	25,10	0.98,0.5	20,1	0.95,0.54	25,10	0.4,0.99	22,9	0.16,>0.99

	Western Great Plains				Cold Desert			
	30 cm				30 cm			
	2015		2016		2015		2016	
	df	F,p	*df*	F,p	*df*	F,p	*df*	F,p
Precip.	1,75	25.31,<0.00	1,41	25.69,<0.00	1,98	1.87,0.17	1,85	2.97,0.09
BRTE	1,75	23.98,<0.00	1,41	7.94,0.01	1,98	0.74,0.39	1,85	0.57,0.45
Time	25,75	4.04,<0.001	20,4	1.99,0.03	25,98	3.99,<0.001	22,8	1.53,0.08
Precip:BRTE	1,75	31.51,<0.00	1,41	28.26,<0.00	1,98	18.45,<0.00	1,85	0.51,0.48
Precip. : time	25,75	0.49,0.98	20,4	0.52,0.94	25,98	0.33,>0.99	22,8	0.33,>0.99
BRTE : time	25,75	0.22,>0.99	20,4	0.15,>0.99	25,98	0.26,>0.99	22,8	0.04,>0.99
Precip : BRTE :	25,75	0.17,>0.99	20,4	0.15,>0.99	25,98	0.22,>0.99	22,8	0.06,>0.99

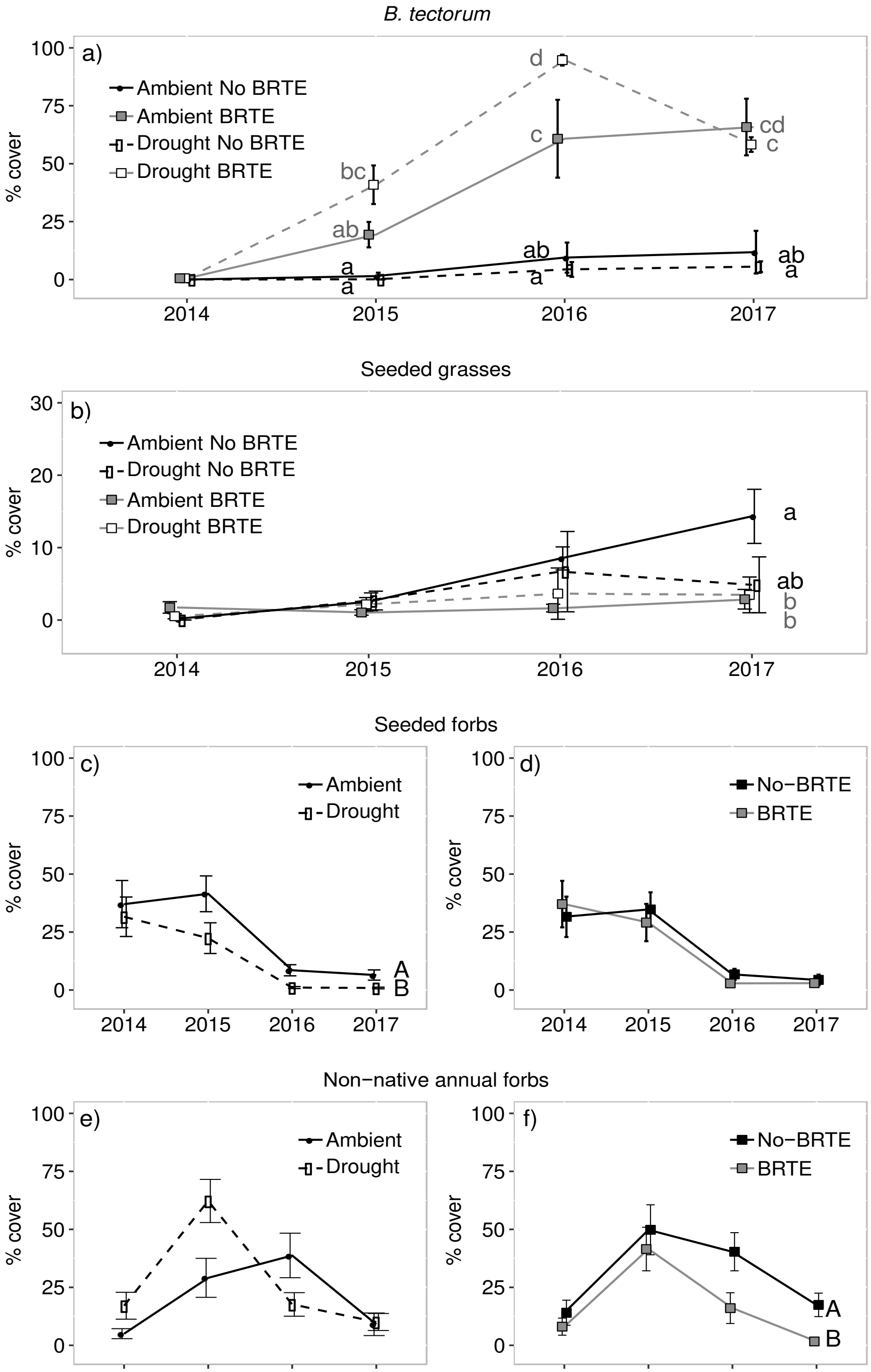

Figure 1.1: a) *B. tectorum* and b) seeded grasses under *B. tectorum* seeding treatment (BRTE) and precipitation treatment (Ambient vs. Drought) at the WGP site. Seeded forbs (panels c and d) and non-native annual forbs (panels e and f) under precipitation (left panels) and BRTE (right panels) treatments at the WGP site. Data are averaged over SAP treatments. Points are means of untransformed data and ± standard error of the mean. Letters denote significant differences between means of transformed data ($p<0.05$) in that year.

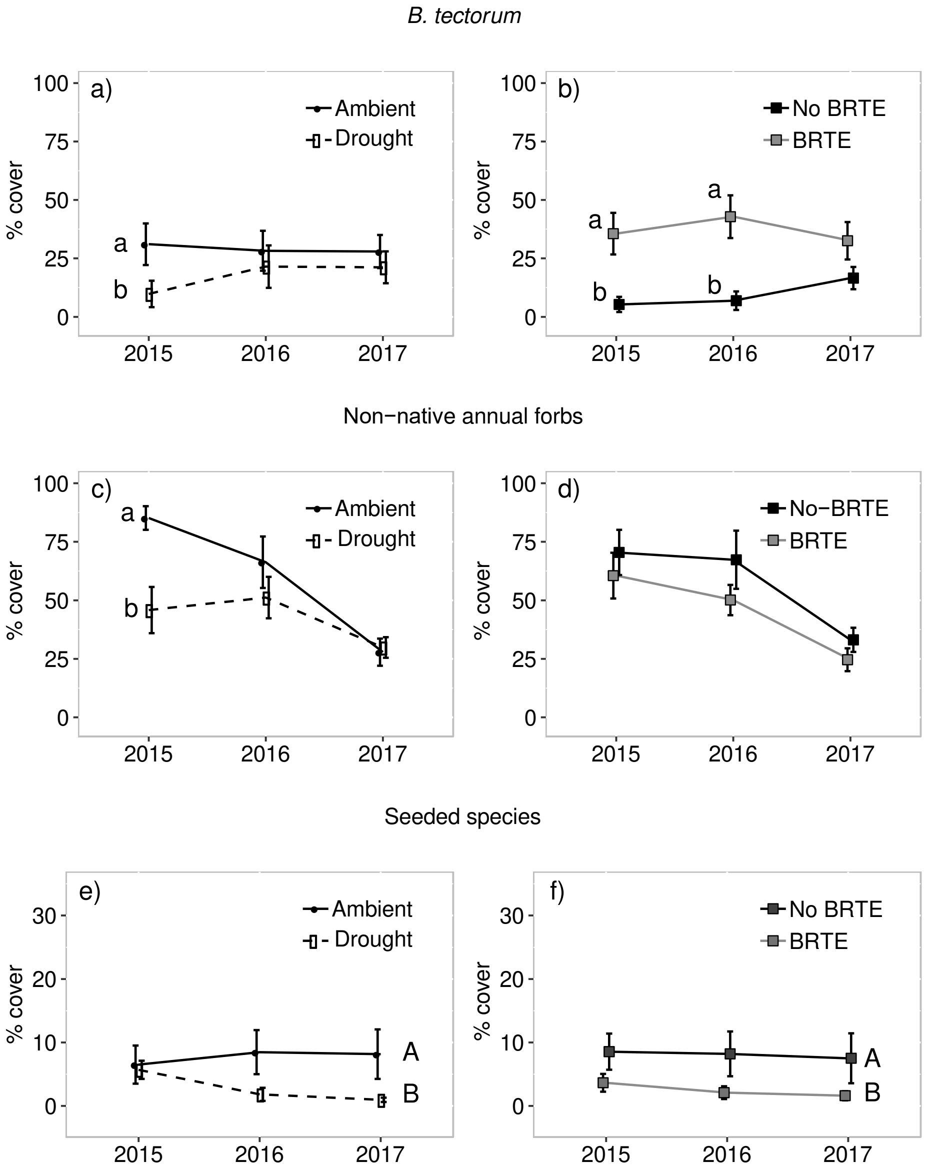

Figure 1.2: a) *B. tectorum* (panels a and b), non-native annual forbs (panels c and d) and seeded species (panels e and f) under precipitation (left panels) and *B. tectorum* seeding (BRTE; right panels) treatments at the CD site. Data are averaged over SAP treatments. Points are means of untransformed data and ± standard error of the mean. Lowercase letters denote significant differences between means in that year and uppercase letters denote significant differences between means across all years at $p<0.05$.

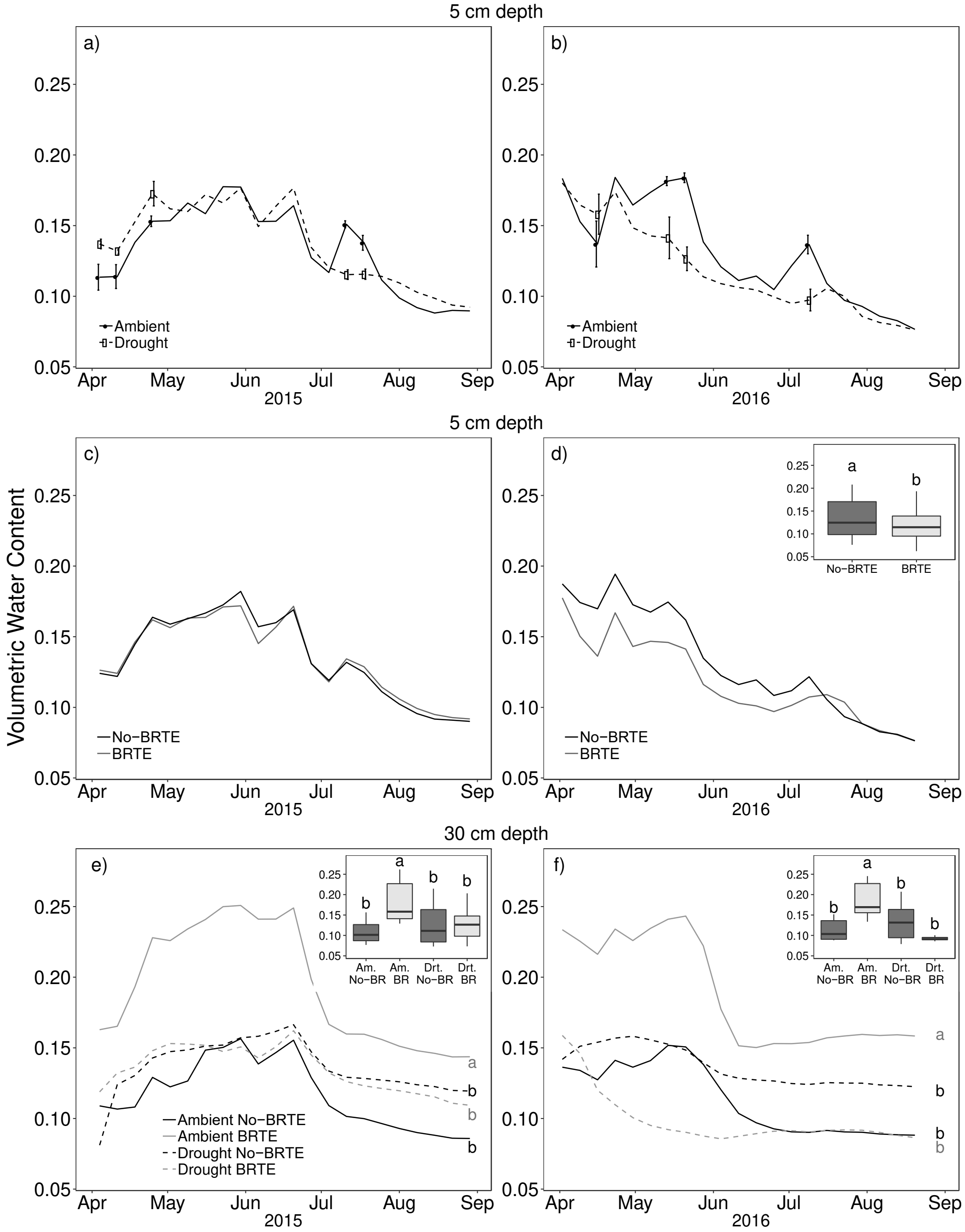

Figure 1.3: Soil volumetric water (VWC) content at 5 cm under precipitation treatment in a) 2015 and b) 2016 at the WGP site. Points are means of weekly VWC ± standard error of the mean at which difference at the $p < 0.05$ level were detected. Soil VWC at 5 cm under *B. tectorum* seeding (BRTE) treatment in c) 2015 and d) 2016. Soil VWC at 30 cm under precipitation and BRTE treatments in e) 2015 and f) 2016. Embedded box-plots show median, first and third quartile, and 95% confidence intervals of seasonal VWC in treatments. Letters denote differences in main effects across the season. Abbreviations for embedded plots are as follow: Am. No-BRTE: Ambient No-BRTE; Am. BRTE: Ambient BRTE; Drt. No-BRTE: Drought No-BRTE; Drt. BRTE: Drought BRTE.

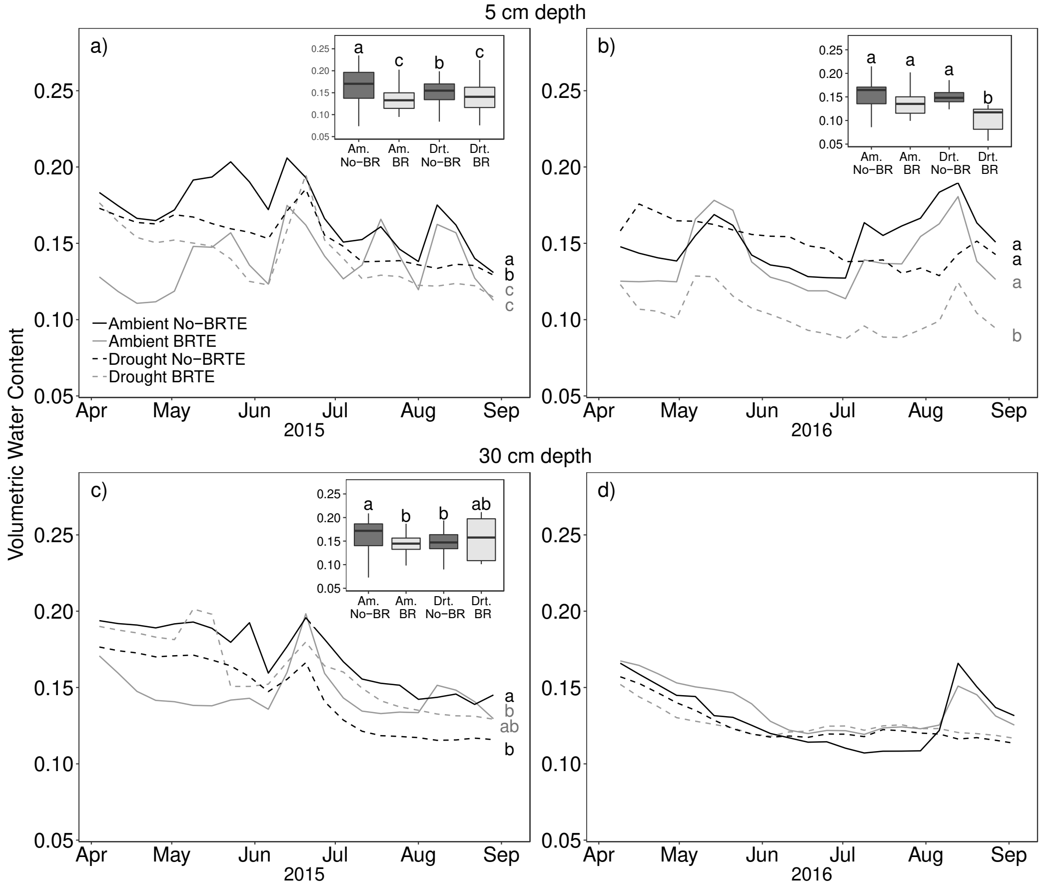

Figure 1.4: Soil volumetric water (VWC) content at 5 cm (panels a and b) and 30 cm (panels c and d) under precipitation and *B. tectorum* seeding (BRTE) treatments in 2015 (left panels) and 2016 (right panels) at the CD site. Embedded box-plots show median, first and third quartile, and 95% confidence intervals of seasonal VWC in treatments. Letters denote differences in main effects across the season. Abbreviations for embedded plots are as follow: Am. No-BRTE: Ambient No-BRTE; Am. BRTE: Ambient BRTE; Drt. No-BRTE: Drought No-BRTE; Drt. BRTE: Drought BRTE.

REFERENCES

Abatzoglou JT, Kolden CA (2011) Climate Change in Western US Deserts: Potential for increased wildfire and invasive annual grasses. Rangeland Ecology & Management 64:471–478. doi: 10.2111/REM-D-09-00151.1

Ackerly D (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecological Monographs 74:25–44. doi: 10.1890/03-4022

Agaba H, Baguma Orikiriza LJ, Osoto Esegu JF (2010) Effects of hydrogel amendment to different soils on plant available water and survival of trees under drought conditions. Clean Soil Air Water 38:328–335. doi: 10.1002/clen.200900245

Aguirre L, Johnson DA (1991) Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. Journal of Range Management 44:347–354.

Akhter J, Mahmood K, Malik KA (2004) Effects of hydrogel amendment on water storage of sandy loam and loam soils and seedling growth of barley, wheat and chickpea. Plant Soil Environment. 50:463-469.

Archer SR, Predick KI (2008) Climate Change and Ecosystems of the Southwestern United States. Rangelands 30(3):23–29. doi: 10.2111/1551-501X(2008)30[23:CCAEOT]2.0.CO;2

Atwater DZ, James JJ, Leger EA (2015) Seedling root traits strongly influence field survival and performance of a common bunchgrass. Basic and Applied Ecology 16:128–140. doi: 10.1016/j.baae.2014.12.004

Ashkiani A, Ghooshchii F, Tohidi-Moghadam HR (2013) Effect of super absorbent polymer on growth, yield components and seed yield of wheat grown under irrigation withholding at different growth stages. Research on Crops 14: 48-53

Bakass M, Mokhlisse A, Lallemant M (2002) Absorption and desorption of liquid water by a superabsorbent polymer: Effect of polymer in the drying of the soil and the quality of certain plants. Journal of Applied Polymer Science, 83: 234–243

Bakker JD, Wilson SD, Christian JM (2003) Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications 13:137–153. doi: 10.1890/1051-0761(2003)013[0137:COGROY]2.0.CO;2

Barak RS, Fant JB, Kramer AT, Skogen KA (2015) Assessing the Value of Potential “Native Winners” for Restoration of Cheatgrass-Invaded Habitat. Western North American Naturalist 75:58–69. doi: 10.3398/064.075.0107

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4 (R package version 1.1-7)[Computer software].

Beesley L, Moreno-Jiménez E, Gomez-Eyles JL (2011) A review of biochars’ potential role in the remediation, revegetation and restoration of contaminated soils. Environmental Pollution 159:3269–3282. doi: 10.1016/j.envpol.2011.07.023

Bishop TBB, Munson S, Gill RA (2019) Spatiotemporal patterns of cheatgrass invasion in Colorado Plateau National Parks. Landscape Ecology 34:925–941. doi: 10.1007/s10980-019-00817-8

Booth MS, Caldwell MM, Stark JM (2003) Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. Journal of Ecology 91:36–48. doi: 10.1046/j.1365-2745.2003.00739.x

Bradford JB, Lauenroth WK (2006) Controls over invasion of *Bromus tectorum*: The importance of climate, soil, disturbance and seed availability. Journal of Vegetation Science 17:693–704. doi: 10.1111/j.1654-1103.2006.tb02493.x

Bradley BA (2010) Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. Ecography 33:198–208. doi: 10.1111/j.1600-0587.2009.05684.x

Bradley BA, Blumenthal DM, Wilcove DS, Ziska LH (2010) Predicting plant invasions in an era of global change. Trends in Ecology and Evolution. 25: 310-318. doi: 10.1016/j.tree.2009.12.003

Bradley BA, Mustard JF (2006) Characterizing the landscape dynamics of an invasive plant and rick of invasion using remote sensing. Ecological Applications 16:1132–1147. doi: 10.1890/1051-0761(2006)016[1132:CTLDOA]2.0.CO;2

Bradley BA, Oppenheimer M, Wilcove DS (2009) Climate change and plant invasions: restoration opportunities ahead? Global Change Biology 15:1511–1521. doi: 10.1111/j.1365-2486.2008.01824.x

Brooks ML, D'Antonio CM, Keeley JE, Belnap J (2016) Exotic annual Bromus invasions: Comparisons among species and ecoregions in the western United States. In: Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US. Springer International Publishing, pp 11–60

Brown CS, Anderson VJ, Claassen VP, et al (2008) Restoration Ecology and invasive plants in the semiarid west. Invasive Plant Science and Management 1:399–413. doi: 10.1614/IPSM-08-082.1

Brown CS, Rice KJ (2009) Effects of belowground resource use complementarity on invasion of constructed grassland plant communities. Biological Invasions 12:1319–1334. doi: 10.1007/s10530-009-9549-6

Burke EJ, Brown SJ (2008) Evaluating uncertainties in the projection of future drought. Journal of Hydrometeorology. 9:292-299. doi: 10.1175/2007JHM929.1

Chambers JC (2000) Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: Implications for restoration. Ecological Applications 10:1400–1413. doi: 10.1890/1051-0761(2000)010[1400:SMASFI]2.0.CO;2

Chambers JC, Bradley BA, Brown CS, DAntonio C (2014) Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17:360–375. doi: 10.1007/s10021-013-9725-5

Chambers JC, Germino MJ, Belnap J (2016) Plant community resistance to invasion by Bromus species: The roles of community attributes, Bromus interactions with plant communities, and Bromus traits. In: Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US. Springer International Publishing, pp 275–304

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes great basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77(1):117–145.

Cleland EE, Chuine I, Menzel A (2007) Shifting plant phenology in response to global change. Trends in Ecology & Evolution 22:357–365. doi: 10.1016/j.tree.2007.04.003

Cline JF, Uresk DW, Rickard WH (1977) Comparison of soil water used by a sagebrush bunchgrass and a cheatgrass community. Journal of Range Management 30: 199-201

Concilio AL, Seastedt TR, Nippert JB (2017) Changing edaphic conditions and exploitation of an expanded phenological niche allows for increased exotic (introduced) plant species dominance. Plant and Soil. 415(1-2):299-315. doi: 10.1007/s11104-016-3167-8

Fargione J, Brown CS, Tilman D (2003) Community assembly and invasion: An experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences 100:8916–8920. doi: 10.1073/pnas.1033107100

Ferguson SD, Leger EA, Li J, Nowak RS (2015) Natural selection favors root investment in native grasses during restoration of invaded fields. Journal of Arid Environments 116:11–17. doi: 10.1016/j.jaridenv.2015.01.009

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology & Evolution 23:695–703. doi: 10.1016/j.tree.2008.07.013

Garbowski M, Brown CS, Johnston DB. Soil amendment interacts with invasive grass and drought to uniquely influence aboveground versus belowground biomass in aridland restoration. Restoration Ecology (In press) doi: 10.1111/rec.13083

Germino MJ, Belnap J, Stark JM, Allen EB, Rau BM (2016) Ecosystem impacts of exotic annual invaders in the genus Bromus. In: Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US. Springer International Publishing, pp 61–95 doi: 10.1007/978-3-319-24930-8_3

Goergen EM, Leger EA, Espeland EK (2011) Native perennial grasses show evolutionary response to *Bromus tectorum* (Cheatgrass) invasion. PLoS ONE 6(3):e18145. doi: 10.1371/journal.pone.0018145

Groves AM, Brudvig LA (2019) Interannual variation in precipitation and other planting conditions impacts seedling establishment in sown plant communities. Restoration Ecology 27:128–137. doi: 10.1111/rec.12708

Hardegree S, Schneider J, Moffet CA (2012) Weather variability and adaptive management for rangeland restoration. Rangelands 34(6):53-56. doi: 10.2111/RANGELANDS-D-12-00048.1

Hardegree SP, Moffet CA, Flerchinger GN, Cho J, Roundy BA, Jones TA, James JJ, Clark PE, Pierson FB (2013) Hydrothermal assessment of temporal variability in seedbed microclimate. Rangeland Ecology and Management 66:127–135. doi: 10.2111/REM-D-11-00074.1

Hardegree SP, Moffet CA, Roundy BA, Jones TA, Novak SJ, Clark PE, Pierson FB, Flerchinger GN (2010) A comparison of cumulative-germination response of cheatgrass (Bromus tectorum L.) and five perennial bunchgrass species to simulated field-temperature regimes. Environmental and Experimental Botany 69:320–327. doi: 10.1016/j.envexpbot.2010.04.012

Hardegree SP, Sheley RL, Duke SE, James JJ, Boehm AR, Flerchinger GN (2016) Temporal variability in microclimatic conditions for grass germination and emergence in the Sagebrush Steppe. Rangeland Ecology and Management 69:123–128. doi: 10.1016/j.rama.2015.12.002

Harris GA (1967) Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecological Monographs 37:89–111. doi: 10.2307/2937337

Harris GA, Wilson AM (1970) Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. Ecology 51:530–534. doi: 10.2307/1935392

Hempy-Mayer K, Pyke DA (2008) Defoliation Effects on *Bromus tectorum* seed production: Implications for grazing. Rangeland Ecology and Management 61: 116-123 doi: 10.2111/07-018.1

Holmes TH, Rice KJ (1996) Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. Annals of Botany 78:233-243 doi: 10.1006/anbo.1996.0117

Hoover DL, Wilcox KR, Young KE (2018) Experimental droughts with rainout shelters: a methodological review. Ecosphere 9:e02088. doi: 10.1002/ecs2.2088

Humphrey LD, Schupp EW (2004) Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. Journal of Arid Environments 58:405–422. doi: 10.1016/j.jaridenv.2003.11.008

Hüttermann A, Orikiriza LJB, Agaba H (2009) Application of superabsorbent polymers for improving the ecological chemistry of degraded or polluted lands. Clean Soil Air Water 37:517–526. doi: 10.1002/clen.200900048

Hüttermann A, Zommorodi M, Reise K (1999) Addition of hydrogels to soil for prolonging the survival of Pinus halepensis seedlings subjected to drought. Soil and Tillage Research 50:295–304. doi: 10.1016/S0167-1987(99)00023-9

Johnston DB, Chapman PL (2014) Rough surface and high-forb seed mix promote ecological restoration of simulated well pads. Invasive Plant Science and Management 7:408–424. doi: 10.1614/IPSM-D-13-00087.1

Johnston, DB, Garbowski M (2020). Responses of Native Plants and Downy Brome to a Water-Conserving Soil Amendment. Rangeland Ecology & Management 73:19-29 doi: 10.1016/j.rama.2019.10.001

Kildisheva OA, Erickson TE, Merritt DJ, Kingsley DW (2016) Setting the scene for dryland restoration: an overview and key findings from a workshop targeting seed-based restoration. Restoration Ecology 24:S36-S42. doi: 10.1111/rec.12392

Knapp AK, Carroll CJW, Griffin-Nolan RJ, Slette IJ, Chaves FA, Baur LE, Felton AJ, Gray JE, Hoffman AM, Lemoine NP, Mao W, Post AK, Smith MD (2018) A reality check for climate change experiments: Do they reflect the real world? Ecology 99: 2145 - 2151 doi: 10.1002/ecy.2474

Kulmatiski A, Beard KH, Stark JM (2006) Exotic plant communities shift water-use timing in a shrub-steppe ecosystem. Plant Soil 288:271–284. doi: 10.1007/s11104-006-9115-2

Larson JE, Funk JL (2016) Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms. New Phytologist 210:827–838. doi:

10.1111/nph.13829

Lawrimore JH, Menne MJ, Gleason BE, Williams CN, Wuertz DB, Vose RS, Rennie J (2011) Global Historical Climatology Network - Monthly (GHCN-M), Version 3. NOAA National Centers for Environmental Information. doi:10.7289/V5X34VDR [July 2014].

Leffler AJ, Peek MS, Ryel RJ, Ivans CY, Caldwell MM (2005) Hydraulic redustrubution through the root systems of senesced plants. Ecology 86:633–642. doi: 10.1890/04-0854

Leger EA, Atwater DZ, James JJ (2019) Seed and seedling traits have strong impacts on establishment of a perennial bunchgrass in invaded semi-arid systems. Journal of Applied Ecology 56:1343–1354. doi: 10.1111/1365-2664.13367

Lenth RV (2016) Least-Squares Means: The R Package lsmeans. Journal of Statistical Software 69:1–33. doi: 10.18637/jss.v069.i01

Lucero ME, Dreesen DR, VanLeeuwen DM (2010) Using hydrogel filled, embedded tubes to sustain grass transplants for arid land restoration. Journal of Arid Environments 74:987–990. doi: 10.1016/j.jaridenv.2010.01.007

Macarthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377–385. doi: 10.1086/282505

MacDougall AS, Wilson SD, Bakker JD (2008) Climatic variability alters the outcome of long-term community assembly. Journal of Ecology 96:346–354. doi: 10.1111/j.1365-2745.2007.01333.x

Mack RN (1981) Invasion of *Bromus tectorum* L. into western north America: An ecological chronicle. Agro-Ecosystems 7:145–165.

Mack RN, Pyke DA (1983) The demography of *Bromus tectorum*: Variation in time and space. The Journal of Ecology 71:69.

Mangold JM, Sheley RL (2007) Effects of soil texture, watering frequency, and a hydrogel on the emergence and survival of coated and uncoated crested wheatgrass seeds. Ecological Restoration 25:6–11. doi: 10.3368/er.25.1.6

Melgoza G, Nowak RS, Tausch R (1990) Soil water exploitation after fire: Competition between Bromus tectorum (Cheatgrass) and two native species. Oecologia 83:7–13.

Meyer SE, Garvin SC, Beckstead J (2001) Factors mediating cheatgrass invasion of intact salt desert shrubland. In: McArthur, E Durant; Fairbanks, Daniel J, comps Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13-15; Provo, UT Proc RMRS-P-21 Ogden, UT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station p 224-232 21:224–232.

Moles AT, Westoby M (2004) Seedling survival and seed size: a synthesis of the literature. Journal of Ecology. 92:372–383.

Newhall RL, Monaco TA, Horton H, Harrison RD, Page RJ (2004) Rehabilitating salt-desert ecosystems following wildfire and wind erosion. Rangelands 26:3–7. doi: 10.2111/1551-501X(2004)26[3:RSEFWA]2.0.CO;2

National Resource Conservation Service Technical Note 59 (2011). Taliga, C. Plant Suitability and Seeding Rates for Conservation Plantings in Colorado. https://www.nrcs.usda.gov/Internet/FSE_PLANTMATERIALS/publications/copmstn10712.pdf

National Oceanic and Atmospheric Administration (NOAA) - National centers for environmental Information. https://www.ncdc.noaa.gov/data-access. Accessed on January 12, 2018.

Orlowsky B, Seneviratne SI (2013) Elusive drought: uncertainty in observed trends and short- and long-term CMIP5 projections. Hydrology and Earth System Sciences 17:1765–1781. doi: 10.3929/ethz-b-000073994

Padilla FM, Pugnaire FI (2007) Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Functional Ecology 21:489–495. doi: 10.1111/j.1365-2435.2007.01267.x

Parkinson H, Zabinski C, Shaw N (2013) Impact of native grasses and cheatgrass (*Bromus tectorum*) on Great Basin forb seedling growth. Rangeland Ecology and Management 66:174–180. doi: 10.2111/REM-D-11-00028.1

Prevéy JS, Seastedt TR (2014) Seasonality of precipitation interacts with exotic species to alter composition and phenology of a semi-arid grassland. Journal of Ecology 102:1549–1561. doi: 10.1111/1365-2745.12320

Prevéy JS, Seastedt TR (2015) Effects of precipitation change and neighboring plants on population dynamics of Bromus tectorum. Oecologia 179:765–775. doi: 10.1007/s00442-015-3398-z

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Montserrat V (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology 18:1725–1737. doi: 10.1111/j.1365-2486.2011.02636.x

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Roundy BA, Hardegree SP, Chambers JC, Whittaker A (2007) Prediction of cheatgrass field germination potential using wet thermal accumulation. Rangeland Ecology and Management 60:613–623. doi: 10.2111/05-206R3.1

Rowe CJ, Leger EA (2010) Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. Evolutionary Applications 4:485–498. doi: 10.1111/j.1752-4571.2010.00162.x

Rubio HO, Wood MK, Cardenas M, Buchanan BA (1992) The effect of polyacrylamide on grass emergence in southcentral New Mexico. Journal of Range Management 45:296. doi: 10.2307/4002981

Ryel RJ, Leffler AJ, Ivans C, et al (2010) Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. Vadose Zone Journal 9:548–13. doi: 10.2136/vzj2010.0022

Sheley RL, Larson LL (1994) Comparative growth and interference between cheatgrass and yellow starthistle seedlings. Journal of Range Management 47:470. doi: 10.2307/4002999

Topp, GC, Davis JL, Annan AP. (1980) Electromagnetic determination of soil water content: measurements in coaxial transmission lines. Water Resources Research, v. 16, No. 3:574-582

Wainwright CE, Cleland EE (2013) Exotic species display greater germination plasticity and higher germination rates than native species across multiple cues. Biological Invasions 15:2253–2264. doi: 10.1007/s10530-013-0449-4

West NE, Yorks TP (2006) Long-term interactions of climate, productivity, species richness, and growth form in relictual sagebrush steppe plant communities. Western North American Naturalist 66:502–526. doi: 10.3398/1527-0904(2006)66[502:LIOCPS]2.0.CO;2

Wilcox BP, Turnbull L, Young MH, William JC, Ravi S, Seyfried MS, Bowling DR, Scott RL, Germino MJ, Caldwell TG, Wainwright J (2012) Invasion of shrublands by exotic grasses: ecohydrological consequences in cold versus warm deserts. Ecohydrology 5:160–173. doi: 10.1002/eco.247

Wilson SD, Schlaepfer DR, Bradford JB, Lauenroth WK, Duniway MC, Hall SA, Jamiyansharav K, Jia G, Lkhagva A, Munson SM, Pyke DA, Tietjen B (2018) Functional group, biomass, and climate change effects on ecological drought in semiarid grasslands. Journal of Geophysical Research Biogeosciences 123:1072–1085. doi: 10.1002/2017JG004173

Wolkovich EM, Cleland EE (2014) Phenological niches and the future of invaded systems with climate change. AoB Plants 6 plu013, doi: 10.1093/aobpla/plu013

Yahdjian L, Sala OE (2002) A rainout shelter design for intercepting different amounts of rainfall. Oecologia 133: 95–101 doi: 10.1007/s00442-002-1024-3

Yang L, Yang Y, Chen Z (2014) Influence of super absorbent polymer on soil water retention, seed germination and plant survivals for rocky slopes eco-engineering. Ecological Engineering 62:27–32. doi: 10.1016/j.ecoleng.2013.10.019

Yelenik SG, Levine JM (2009) Processes limiting native shrub recovery in exotic grasslands after non-native herbivore removal. Restoration Ecology 18:418–425. doi: 10.1111/j.1526-100X.2009.00598.x

Zink TA, Allen MF (2003) The effects of organic amendments on the restoration of a disturbed coastal sage scrub habitat. Restoration Ecology 6:52–58. doi: 10.1046/j.1526-100x.1998.00617.x

CHAPTER 2: ONTOGENY INFLUENCES LEAF AND ROOT TRAITS OF RESTORATION SEEDLINGS

INTRODUCTION

Trait-based plant ecology aims to link species functional traits, or physiological and morphological characteristics of plants, with fitness and performance of species in different environments (Violle et al. 2007). Over the last several decades, trait-based approaches have proven fruitful in advancing our understanding of community assembly or the processes and mechanisms driving community development (e.g., HilleRisLambers 2012, Funk et al. 2016). As restoration is essentially ‘a process of reassembly’ (Funk et al. 2008), trait-based approaches are increasingly being used to elucidate patterns of seedling establishment and survival in restoration studies (e.g., Pywell et al. 2003, Larson et al. 2014, Zirbel and Brudvig 2020).

Despite growing awareness of the importance of belowground traits on competitive dynamics (e.g., Leger et al. 2019) and stress tolerance (e.g., Markesteijn and Poorter 2009, Kramer-Walter et al. 2016, Bristiel et al. 2019), to date, most trait-based studies have focused on aboveground traits. Recent studies have linked root traits such as root length (Harrison and LaForgia 2019, Leger et al. 2019), root mass ratio (RMR) (Ferguson et al. 2015, Leger and Goergen 2017), and root dry matter content (RDMC) (Larson et al. 2020) to seedling establishment and survival. In addition, root tissue density (RTD) has been linked to plant adaptation to low soil nutrients (Kramer-Walter et al. 2017) and moisture (Bristiel et al. 2019, Hanslin et al. 2019). Root traits of young seedlings (<30 days old) (e.g., Rowe and Leger 2010, Larson et al. 2020) as well as older plants (>30 days old) (e.g., Ferguson et al. 2015, Balachowski et al. 2018, Zwicke et al. 2015) have been related to performance in various recruitment settings.

Plant development or ontogeny is an important driver of trait variation (Mason et al. 2013 and Mitchell and Bakker 2014). However, this source of variation is explicitly avoided and rarely considered in trait-based ecology because standard protocols recommend measuring traits from mature individuals (Perez-

Harguindeguy et al. 2016). As young seedlings may be particularly vulnerable to environmental stress (e.g., Leck et al. 2008) and competition (e.g., Gerry and Wilson 1995, Lasky et al. 2015), understanding how traits vary ontogenetically may help elucidate patterns of recruitment and community assembly.

Most studies directly focused on ontogeny (e.g., Niinemets 2004, Niinemets 2005, Mediavilla and Escudero 2009) have used a cross-sectional approach (i.e. plants from different developmental stages are sampled at one time) to assess the influence of developmental age on traits. Results from these studies may confound constitutive ontogenetic influences on traits with environmental or seasonal effects (Cornwell et al. 2006). Research considering the influence of ontogeny on belowground traits is particularly limited (but see Useche and Shipley 2010, Tobner et al. 2013, and Alvarez-Flores et. al 2014 for examples from non-crop species). In the few studies that have linked variation in root traits to ontogeny, trait values were obtained from plants growing in field settings or under variable resource conditions. Therefore, the independent effects of ontogeny on root traits remain largely unexplored. To isolate the influence of ontogeny on plant traits, plants can be grown, measured, and compared at specific developmental stages in controlled and homogenous greenhouse conditions (e.g., Mason et al. 2013).

Identifying correlations and trade-offs among traits along coordinated axes of variation is foundational to understanding plant ecological strategies (e.g., Grime 1997, Garnier et al. 2016). Aboveground, leaf traits fall along a primary axis relating resource acquisition with longevity: on one end of the spectrum are plants with short-lived, fast growing leaves and on the other are plants with long-lived leaves that process resources slowly (i.e. the "Leaf economic spectrum"; Wright et al. 2004). Predictions of the "whole plant economic spectrum" suggest similar correlations among root and shoot traits related to resource acquisition (Reich et al. 2014). Numerous studies have investigated relationships between leaf and root traits (e.g., Ryser 1996, Wahl and Ryser 2000, Craine 2001, Tjoelker et al. 2005) and whole-plant strategies (e.g., Freschet et al. 2010, Reich 2014, de la Riva et al. 2016) but few have considered ontogeny when assessing these relationships (but see Laughlin et al. 2017 and Harrison and LaForgia

2019). Because correlations observed at the seedling stage may differ from those observed at maturity (e.g., Mason et al. 2013, Laughlin et al. 2017, Harrison and LaForgia 2019), understanding how trait correlations change through development is essential for effectively using trait-based approached to understand seedling growth and recruitment.

This study examined ontogenetic patterns in leaf and root traits of eleven grass and forb species being developed for restoration of disturbed ecosystems in the Colorado Plateau region. The desert landscapes of the southwestern United States (US hereafter) are visited by tens of millions of people each year and are expected to experience substantial climate changes in upcoming decades. Because of these ongoing anthropogenic and climate pressures, effective restoration is essential for maintaining the ecosystem services provided by these environments (Winkler et al. 2018). Unfortunately, as in other arid areas, low seedling recruitment may hinder successful re-vegetation outcomes (James et al. 2011). Understanding ontogenetic variation of plants used in restoration may elucidate mechanisms by which young seedlings establish and grow in disturbed, competitive, or stressful conditions.

The specific objectives of this study were to: (1) assess the effects of species identity on leaf and root traits within and among ontogenetic stages (2) assess the effects of ontogenetic stage on leaf and root traits within and among species, (3) compare species hierarchies based on trait values obtained from different ontogenetic stages to those obtained from the TRY database and (4) evaluate shifts in primary axes of trait variation (i.e. coordinated suites of above- and belowground traits) throughout development and relate these axes to future growth. Because seedlings must rapidly accumulate biomass for establishment, subsequent growth, and reproduction, we expected a general shift from traits associated with rapid resource acquisition towards traits associated with resources conservation throughout development (Dayrell et al. 2018).

METHODS

Species selection

We selected species based on recommendations from land managers (Bureau of Land Management, Colorado Parks and Wildlife personal communication) and prior research that identified promising species for restoration in the Colorado Plateau region (Barak et al. 2015). We obtained seeds from the Germplasm Resource Information Network, Chicago Botanic Gardens, the Uncompahgre Partnership, and the Upper Colorado Environmental Plant Center. We obtained between three and five accessions of eleven species primarily from the Asteraceae and Poaceae families. Details for each accession's origin are provided in Tables 2.1 and A.2.1.

Plant growth

We germinated seeds on moist germination paper in incubators at Colorado State University set to 5 °C for 10 hours with no light followed by a gradual increase to 15 °C and light for 14 hours. Between 24 and 48 seeds from a given accession were placed in incubators at the same time. Germinated seedlings were transplanted into containers (Deepots D60, Stuewe & Sons, Inc. D20T) with a 1:1:1 mixture of porous ceramic media (Profile® Greens Grade™), vermiculite (Vigoro), and sand (QUIKRETE) when the radicle was between 2-3 mm long and always within 2 days of germination. Germination and transplanting of accessions were random and staggered over the course of three months (July - September 2017). Between 15 and 20 grams of field soil collected from the Colorado Plateau was added to the top 5 cm of each pot prior to transplanting. To improve establishment, newly transplanted seedlings were placed on a mist bench in the Colorado State University Plant Growth facility and mist watered every 30 minutes for 4 days prior to being moved to ambient greenhouse conditions. Ambient greenhouse temperatures for the duration of the experiment were kept at 18 °C for 12 hours during the day and 13 °C at night with alternating 12 hour light vs. dark.

At transplanting, we randomly assigned plants to a Harvest treatment (10, 24, 42, 84 days after transplanting). On average, 4 plants from each accession were assigned to each harvest for a total of 16 plants grown and measured per accession per time point. We applied Osmocote Plus 15-9-12 9-month slow-release fertilizer with micronutrients (Scotts, Marysville, OH, USA) to the surface of pots when plants were 24 days post transplanting (plants harvested 10 and 24 days after transplanting grew without fertilizer). Seedlings from each accession were grown together in Deepot trays (Stuewe & Sons, Inc. D20T) that were randomly distributed on a single greenhouse bench and randomized every other week. We distributed pots within trays and trays on the greenhouse bench to reduce shading from neighbors. Pots were watered every other day to field capacity over the course of the experiment.

Trait Measurements

Average seed mass for each accession was determined by weighing 4 sets of 10 seeds and averaging to obtain individual seed weights. We measured whole plant (root mass ratio: RMR; root area to shoot area ratio: R_AS_A; height: HT; relative growth rate: RGR), leaf (specific leaf area: SLA; leaf dry matter content: LDMC), and root (specific root length: SRL; root dry matter content: RDMC; root tissue density: RTD; relative root elongation rate: RRER; root diameter: Diam) traits from each plant upon harvest. A description of each trait and how it was calculated is provided in Table 2.2.

Because of the small size of plants, when present, we used all photosynthetic tissues (i.e. cotyledons for forbs and first leaves for grasses) to calculate SLA and LDMC. Similarly, all roots were used to calculate values of root traits. After cutting, fresh leaves were weighed and immediately re-saturated under dark conditions for 24 hours to obtain saturated weights (used to calculate LDMC). We scanned saturated leaves to obtain leaf area using WinRHIZO software (Regent Instruments, Sainte-Foy, Canada). We scanned fresh roots and used WinRHIZO software with a resolution set to 600 dpi to obtain measures of area, length, and volume of fresh roots. These estimates were used to calculate R_AS_A, SRL, RTD, RRER, and root diameter. After scanning, roots were patted dry and weighed to obtain fresh weight. Leaves, roots, and shoots were dried at 60 °C for 48 hours and weighed to obtain dry mass. Fresh and dry weights of roots were used to calculate RDMC.

We calculated growth and root elongation rates between consecutive harvests (0 to 10 days, 10 to 24 days, 24 to 42 days and 42 to 84 days) using averaged values from each accession at each time point. Growth rate and root elongation were estimated relative to initial mass and root length, respectively. We used average seed weight of each accession as the initial weight to obtain RGR between transplanting and the 10-day harvest. Initial root length was set for all species to 3 mm to calculate RRER between transplanting and the 10-day harvest. Averages from 3 to 5 seedlings from each accession were used to calculate accession trait means at each harvest. Because plants from several species were root bound by the 84-day harvest values of leaf and root traits from this time point may be unreliable and are therefor not reported. We did, however, use total plant weight at this final harvest to calculate relative growth rate from 42 to 84 days.

Data analyses

Average trait values for each accession at each harvest were used in all analyses. All values were log transformed prior to analyses. We used a Bayesian random effects model to estimate differences in expected trait values (1) among species across ontogenetic stages, (2) among species within each ontogenetic stage, and (3) among ontogenetic stages within species. We used a Cauchy distribution with mean zero and variance 0.1 as the prior for hyper parameters of each group-level effect. This was done to provide shrinkage, which is a Bayesian method of accounting for multiple comparisons (Gelman et al. 2012). We estimated ontogenetic and species effects by computing the difference between posterior distributions of interest and assessing whether the 95% credible interval of the difference contained zero. We used the same model to compare expected SLA values among species at different time points and values obtained from the TRY database (Kattage et al. 2020).

To assess whether trade-offs among traits were consistent across time points we qualitatively interpreted results of principle components analyses (PCA) (psych package in R; Revelle 2019). Pearson correlations among trait pairs were used to further support interpretation. Pearson correlations were obtained using the “corr.test” and “corr.p” functions with Holm adjustment for multiple comparisons (psych package in R; Revelle 2019). Prior to PCA analyses, traits were examined for linearity and primary component axes were varimax-rotated. We used multiple regression with principle component axes as predictor variables to assess which PC axes were correlated with future growth rate (i.e. from t to t+1). All analyses were completed in R (R Core Team, 2018) and Stan (Stan Development Team, 2018).

RESULTS

Estimates obtained from posterior distributions suggest species and ontogenetic influences on median values for most traits. RTD, RDMC, and root diameter were influenced predominantly by species identity with limited species by ontogeny interactions (Fig. 2.1; Table A.2.2). The perennial grass *M. porteri* had the highest RTD overall (median = 0.10 mg mm^{-3}) and the annual grass *V. octoflora* the lowest RTD (median = 0.04 mg mm^{-3}) (Fig. 2.1f). *V. octoflora* had the highest RDMC (median = 0.13 mg g^{-1}) and the annual forb *H. annuus* had the lowest RDMC (median = 0.08 mg g^{-1}) (Fig. 2.1e). We observed the highest root diameter in the perennial grass *H. comata* (median = 0.38 mm) and lowest root diameter in the perennial grass *M. porteri* (median = 0.20 mm) (Fig. 2.1g). We observed no clear differences between grasses and forbs for these traits and both groups showed considerable variability among species in RTD and root diameter.

Aboveground, differences in median trait values for SLA and LDMC were influenced by both species identity and ontogeny (Fig. 2.1, Table A.2.2). SLA decreased throughout development in *A. tridentata, H. villosa* and *P. patagonica* (Fig. 2.1a). The opposite trend was observed for LDMC, which increased throughout development for the same species in which SLA decreased (Fig. 2.1b). SLA was highest in *V. octoflora* (median = 98.14 mm^2 g^{-1}) and lowest in *M. porteri* (median = 25.42 mm^2 g^{-1}). LDMC was highest in the perennial grass *H. comata* (median = 0.21 mg g^{-1}) and lowest in the annual forb *P. patagonica* (median = 0.10 mg g^{-1}). RGR also varied ontogenetically within most species, generally increasing throughout development (Fig 2.1h).

Belowground, differences in median trait values for SRL and RRER were influenced by both species identity and ontogeny (Fig. 2.1; Table A.2.2). A similar pattern was observed among most species for SRL: SRL increased from the first to second harvest and then decreased from the second to third harvest (Fig. 2.1d). SRL was consistent throughout development in *E. trachycaulus*, *H. villosa*, and *V. octoflora*. The highest SRL was observed in the annual grass, *V. octoflora* (median = 842 m g^{-1}) and the lowest SRL was observed in the perennial grass *H. comata* (median = 155 m g^{-1}). RRER varied ontogenetically in all species, decreasing rapidly between the first and second harvest. Ontogenetic differences in RMR were observed in the annual forb *P. patagonica* and annual grass *V. octoflora*, both of which showed decreasing RMR throughout development (Fig. 2.1c). Species identity, ontogeny nor their interactions influenced R_AS_A (data not shown).

For most traits, species trait hierarchies were consistent at the different ontogenetic stages (Fig 2.2; Table A.2.2). However, we observed deviations from this general pattern for SLA, LDMC, and RRER. For example, LDMC of *H. villosa* was lower than *M. porterii* and *V. octoflora* but only at the 10-day harvest (Table A.2.2). More surprisingly, *M. canescens* had the lowest RRER at the 10-day harvest and the highest RRER at the 24-day harvest. Comparisons of seedling values to those obtained from the TRY database were limited to SLA for a subset of species: SLA values for *H. villosa*, and *M. canescens* were unavailable through TRY. We observed differences among seedling and TRY values for SLA in *P. patagonica*, *H. comata* and *V. octoflora* (Table A.2.3). For these species, SLA values obtained from the TRY database were lower than those we measured, and differences between TRY and seedling values were greatest for 10-day old seedlings and progressively decreased through development (Fig 2.2; Table A.2.3).

Although some slight departures were observed in relation to specific trait loadings on primary component axes at different time points, qualitative interpretation of PCAs (Fig 2.3; Table 2.3) suggest similar trade-offs among traits at all ontogenetic stages. When assessing PCA results, we chose to retain the first three axes in all three cases as together they accounted for >60% of the variation in the data at all time points. Here we discuss traits with loadings >|0.6| on rotated component axes (RC).

Height, root diameter, and seed mass consistently loaded onto RC1 and explained 31%, 27% and 27% of the variation in data at the first, second, and third ontogenetic stages, respectively. RRER and LDMC were also positively correlated with RC1 at the first and third harvests, respectively. These traits can all be interpreted in relation to resource acquisition and transport. The second and third axes explained the same amount of variation at each ontogenetic stage: 22% at the first, 18% at the second, and 20% at the third. SRL and RTD loaded onto RCs consistently, representing an axis related to tissue quality (species with low SRL tended to have high RTD). R_AS_A ratio and RMR were consistently loaded onto RCs, reflecting an axis related to above- vs. belowground allocation.

Only RC2 (tissue quality axis: RTD, SRL, SLA) was positively correlated with future growth (assessed as relative growth rate from t to t + 1) at the first ontogenetic stage and explained 23% of the variation in RGR ($R^2 = 0.23$; p = <0.001; model: RGR = -2.08 + RC2 (0.86)). At the second harvest, the relationship between all three RCs and future growth was marginally significant (p = <0.1) and together RCs explained 18 % of the variation in future RGR. At the third harvest, all three RCs were retained (p = <0.05) and together explained 32% of the variation in future RGR ($R^2 = 0.32$; p<0.001; model: RGR = -0.1332 + RC1 (-0.49) + RC2 (0.34) + RC3 (0.33)).

Several traits were correlated at all ontogenetic stages (supported by Pearson correlation coefficients; Table 2.4). Consistent positive correlations were found between shoot height and seed mass, shoot height and root diameter, and root diameter and seed mass. RTD and SRL were consistently negatively correlated. Overall, more and stronger correlations among traits were observed at the 10-day and 42-day harvest compared to the 24-day harvest.

DISCUSSION

Ontogenetic effects on traits

Most of the traits we measured varied by species and observed differences aligned with expectations of the “whole-plant economic spectrum” (WPES) (Reich et al. 2014). In general, species with “fast” strategies had traits associated with rapid resource acquisition and non-persistent tissues and those with “slow” strategies had traits associated with resource conservation. For example, the annual grass *V. octoflora* had the highest values of SLA and SRL and lowest value of RTD. In contrast, the perennial grasses, *H. comata* and *M. porteri* had relatively low values of SLA and SRL and the highest values of LDMC and RTD, respectively. These results align with conclusions from numerous studies documenting trait variation along the WPES in mature plants (e.g., Pérez-Ramos et al. 2012, de la Riva et al., 2016) as well as findings from a recent study documenting variation along the WPES in 4-day-old seedlings (Larson et al. 2020). Species identity did not affect RMR, RGR, and RRER when values were averaged over all ontogenetic stages. However, differences were observed at distinct ontogenetic stages for these traits. This result underscores the importance of explicitly considering ontogeny when assessing interspecific trait variation. Further, given the numerous differences in specific traits related to “fast vs. slow” strategies among species, it is surprising that interspecific differences in RGR were overall limited and only observed at the first two harvests.

Identifying species and ontogenetic differences in RGR could elucidate mechanisms driving seedling recruitment and community assembly (Lasky et al. 2015). This is because early size advantages can influence competitive outcomes (e.g., Gerry and Wilson 1995, Goldberg 1996, Reichmann et al. 2016) or access to resources at later developmental stages (e.g., Padilla and Pugnaire 2007). Across herbaceous plant taxa, the greatest growth rates are observed in the first weeks following germination after which RGR usually decreases (e.g., Grime and Hunt 1975, Hunt and Lloyd 1987). In line with these general trends, we observed increasing RGR throughout development with the greatest increases observed between the first and second harvests for most species. Albeit few and limited to the first two ontogenetic stages, when differences in RGR were observed, values among species varied by an order of magnitude. For example, at the 10-day harvest *V. octoflora* had a RGR of 0.0032 mg day $^{-1}$ whereas *M.*

porterii had a growth rate of 0.033 mg day $^{-1}$. Despite its initial low growth rate, *V. octoflora* had the greatest RGR of all species at the second and third harvest. Because we accounted for initial seed and plant weight in our calculation of RGR, variation among species likely resulted from differences in traits measured in this study (e.g., SLA, SRL) or unmeasured traits such as net assimilation rate (e.g., Hunt and Cornelissen 1997, Shipley 2006) or photosynthetic nitrogen use efficiency (Reichmann et al. 2016) that have been liked to RGR at early developmental stages. Although additional research in more natural settings is needed, identifying interspecific differences in RGR among species is essential to understanding community assembly processes that influences restoration outcomes.

As in several other studies focused on aboveground traits (e.g., Mason et al. 2013, Mitchell and Bakker 2014), we observed that the effect of ontogeny on SLA and LDMC varied by species. In line with our expectation of a shift from an acquisitive to conservative strategy throughout development, SLA generally decreased and LDMC increased from the first to third sampling date. However, these differences were only significant in three species. Similar findings have been reported from numerous studies of woody species and more limited investigations of herbaceous species (e.g., Niimemets et al. 2004, Niimemets et al. 2005, Jullien et al. 2009, Mason et al. 2013, Dayrell et al. 2018). Because of SLA's central role in the "leaf-economic-spectrum" (Wright et al. 2004) and its consistent relationship to growth rate (e.g., Lambers and Poorter 1992, Walters et al. 1993, Grime et al.1997), even relatively minor changes at the seedling stage may influence community dynamics. For example, Reichmann et al. (2016) found that differences in SLA of young seedlings (<17 days old) allowed an invasive grass to rapidly acquire aboveground biomass and outcompete natives. As ontogenetic differences in SLA and LDMC were observed in the same three species, it is possible that these two traits are reliably coordinated in species that alter leaf construction during early development.

Mirroring aboveground results, the effects of ontogeny on root traits were species and trait specific. We observed considerable ontogenetic differences within species for SRL and RRER whereas differences in RDMC, RTD, and root diameter were predominantly influenced by species identity. Touted as the belowground analogue to SLA (Eissenstat et al. 2000), SRL reflects the absorptive capacity of roots per unit biomass invested. Paralleling our expectations of aboveground acquisition traits, we expected SRL to decrease through development. However, we observed an initial increase from the 10-day to the 24-day harvest followed by a decrease in SRL at the 42-day harvest in eight of the 11 species we measured. Because seedlings were grown without fertilizer until the 24-day harvest, it is possible that increased SRL in the early stages of our study resulted from root adjustments to low nutrient conditions (e.g., Fort, Jouany & Cruz 2014, Chieppa et al. 2019). After slow-release fertilizer was added at the 24-day harvest, nutrient limitation may have been alleviated resulting in a subsequent decrease in SRL.

Because we calculated RRER between time points relative to initial root length, our measure essentially estimated how quickly new roots were produced *per unit initial* root length. Growth rate is often measured relative to initial biomass but few examples exist in relation to root elongation. We observed a considerable decrease in RRER from the first harvest compared to the later two harvests in all species. Rapid root growth at the earliest developmental stages is essential for anchoring plants to substrates and for acquisition of nutrients and moisture (Leck et al. 2008). In arid systems, seedlings that rapidly elongate roots may be able to access stable sources of soil moisture to increase establishment and survival (Padilla and Pugnaire 2007, Harrison and LaForgia 2019). Furthermore, because RER has been linked to aboveground seedling growth under variable moisture conditions (Larson and Funk 2016), it may be particularly informative for understanding growth strategies of young plants in arid systems.

As RDMC and RTD have both been linked with conservative resource use strategies (e.g., Perez-Ramos et. al 2012, Kramer-Walter 2016, Roumet et al. 2016) we expected both traits to increase with ontogenetic development. However, we observed limited variation in these traits related to ontogeny. RTD has been linked to plant tolerance to low resource conditions (Kramer-Walter et al. 2016, Bristiel et al. 2019) and RGR (Wahl and Ryser 2000) and RDMC has been linked to seedling survival after drought (Zwicke et al. 2015) as well as plant community resilience to weather extremes (de la Riva 2017). Because of their relative ontogenetic stability and potential links to community dynamics, future research focused on these traits may clarify patterns of seedling establishment and survival in climatically variable or resource limited systems.

Species hierarchies at different ontogenetic stages and comparisons to TRY

Interspecific differences in trait values are used to explain numerous community and ecosystem processes (McGill et al. 2006, Suding et al. 2008). However, because ontogeny may influence interspecific trait variation and associated community dynamics (e.g., Parish and Bazzaz 1985, Poorter 2007, Spasojevic et al. 2014), species relationship may depend on when plants are measured. In our study, species hierarchies were consistent for most traits at the different ontogenetic stages. However, interspecific differences in RRER and SLA varied considerably depending on which ontogenetic stage data were collected from or if trait values were obtained from the TRY database (SLA only).

The SLA values we obtained from greenhouse grown seedlings were, in general, higher than those obtained from the TRY database. As SLA values from the TRY database were primarily taken from mature field grown individuals, these patterns may result from ontogenetically based differences in SLA or from contrasting greenhouse and field environments. Several studies have documented higher SLA values of plants grown under optimal greenhouse conditions compared to field settings (Garnier and Freijsen 1994, Poorter and De Jong 1999, Poorter et al. 2016) likely resulting from lower light levels and higher temperatures in greenhouses than in field conditions. Regardless of the underlying reason of these incongruences, if SLA and RRER influence community assembly and species interactions, trait-based predictions may differ depending on when plants are measured. When making comparisons among species *across* time points (e.g., *A. tridentata* at 10-days to *V. octoflora* at 24-days), many pair-wise differences were observed (data not shown). Such differences in ontogeny among species are expected in natural conditions because seeds germinate and seedlings emerge and initiate growth at different times. Decoupling ontogenetic-based differences in SLA and other traits from those that are seasonally or phenologically based may provide a more mechanistic understanding of various community assembly processes such as priority effects (i.e. the benefits a species gains by initiating growth before co-occurring species) or competitive hierarchies (i.e. competitive outcomes determined by differences in competition-related traits).

Trait correlations and trade-offs

Despite considerable ontogenetic variation in some traits, PCA results from different ontogenetic stages were relatively similar suggesting consistent patterns in variation throughout early development. Similarly, several pairwise correlations were observed at every ontogenetic stage. However, some of the relationships we observed do not reflect prevalent patterns observed in mature plants.

Seed mass and plant height were consistently positively related in both PCA and pairwise correlations. This was surprising because seed mass and height are generally considered components of different plant strategies (Westoby 1998): plant height at maturity is related to competitive ability (e.g., Westoby 1998, Keddy and Shipey 1989, Kunstler et al. 2016) whereas seed mass is related to dispersal and seedling survival (e.g., Jakobsson and Eriksson 2000, Moles and Westoby 2004). Because the official handbook for measurement of plant traits (Perez-Harguindeguy et al. 2016) recommends that measurements of height be obtained from herbaceous plants “toward the end of the growing season”, the relationship we observed in our study may not reflect predominant patterns in the literature. However, several other studies specifically focused on seedling dynamics have, in fact, found correlations between seed mass and seedling size (Jakobsson and Eriksson 2000) as well as height (Seiwa and Kikuzawa 1991, Seiwa and Kikuzawa 1996). This discrepancy highlights the importance of reconsidering accepted patterns in trait variation at different ontogenetic stages. Further, as patterns observed early in development have cascading effects on trait variation at later stages (Jakobsoson and Eriksson 2000), understanding these shifts is imperative for elucidating patterns in seedling recruitment and subsequent impacts on community assembly (Lasky et al. 2015, Harrison and LaForgia 2019).

In both PCA and independent pairwise correlations, SRL and RTD were negatively associated at every ontogenetic stage in our study. This result aligns (Holdaway et al. 2011, Kong et al. 2014) and conflicts (Craine et al. 2001, Kramer-Walter et al. 2016) with earlier studies. In studies that found the two traits uncorrelated (Craine et al. 2001, Kramer-Walter et al. 2016), RTD and SRL were measured on mature plants growing along or originating from gradients of nutrient availability. In these studies, RTD tended to increase with decreasing soil fertility. Similarly, Bristeil et al. (2019) found high RTD in grass populations originating from low moisture environments. It is possible that decoupled RTD and SRL in these studies resulted from either plastic responses or evolutionary adaptations to low resource conditions. In fact, Bristeil et al. (2019) found plants with high RTD and high SRL (a trait combination that maximizes both resource acquisition and stress tolerance) were well suited to cope with drought. Although plants grew without fertilizer until the 24-day harvest, resources limitation in our study was likely minimal. Therefore, it is possible that SRL and RTD remained coordinated because roots were not required to adjust RTD to low-resources. Furthermore, early seedling root anatomy may have influenced the relationship between SRL and RTD. The proportion of stele (xylem and phloem vessels) in the root and the proportion of cell wall of the stele (Wahl and Ryser 2000) are key constituents of RTD. As both of these anatomical root features are likely underdeveloped at early ontogenetic stages (Campilho et al. 2009), roots of young seedlings may lack the specific root components (numerous phloem and xylem vessels) that results in high RTD. Longer-term studies that control for ontogeny and resources may clarify conditions and developmental stages under which RTD and SRL are or are not correlated.

Root diameter and height were also correlated at every ontogenetic stage in our study. Although Wahl and Ryser (2000) identified a correlation between root cross-sectional area and height over 20 years ago, this relationship has received much less attention than other trait associations over the last two decades. Wahl and Ryser (2000) found that larger root diameters were characterized by large xylem vessel diameters that were essential for high transport capacity in roots of large plants (Wahl and Ryser 2000).

This same relationship may be essential for seedling growth in the early stages of development when rapid increases in height are imperative for survival.

Traits related to tissue construction (high SRL and SLA, low RTD) were most strongly correlated to future growth rate at the earliest developmental stage. This suggests that very young seedlings of the species we studied may all assume a “fast strategy” based on quickly acquiring the resources needed for subsequent growth in the first few days after germination. The species we studied have been identified as promising candidates for restoration of arid ecosystems and were obtained from the same eco-region. Therefore, they may be characterized by similar traits that confer success in restoration settings (Pywell et al. 2003, Biondini 2007): in this case, rapid resource acquisition at early developmental stages. Additional data from a more random sample of species would provide information about whether this trend is apparent across diverse species. At later stages, all PC axes were related to future growth suggesting more diverse growth strategies. Despite significant correlations, PC axes accounted for a relatively small proportion of variation in future RGR at each developmental stage (between 18 and 32%) suggesting unmeasured traits also influenced growth at the seedling stage.

CONCLUSION

We observed considerable ontogenetic variation in several leaf and root traits of eleven species being developed for restoration of arid ecosystems in the southwestern US. Our approach of measuring traits from seedlings grown in controlled greenhouse settings allowed us to isolate ontogenetic effects on traits from environmental or seasonal effects. However, additional research in field settings is needed to assess whether similar patterns would be observed in more stressful conditions. Research focused on suites of traits related to abiotic and biotic stress tolerance at the seedling stage may be particularly informative for improving restoration outcomes.

Low and variable precipitation (Hardegree et al. 2018) as well as invasive species competition (Brown et al. 2008) hinder successful restoration of arid ecosystems throughout the western US. However, studies focused on how ontogenetic differences in traits influence competitive dynamics (e.g., Lasky et al. 2015) and drought tolerance (e.g., Harris and LaForgia 2019) remain rare. Explicitly testing the effects of developmental stage and associated trait values on community assembly processes will be crucial for effectively applying trait-based approaches to restoration of arid ecosystems.

Table 2.1: Species, abbreviations, growth forms and number of accessions included in the study (n = 51). Per. stands for perennial; An. for annual; Bi. for biennial.

Species	Abbreviation	Growth Form	Family	Number
Achillea millefolium	ACMI	Per. Forb	Asteraceae	3
Artemisia tridentata	ARTR	Per. Shrub	Asteraceae	6
Elymus trachycaulus	ELTR	Per. Grass	Poaceae	4
Helianthus annuus	HEAN	An. Forb	Asteraceae	4
Hesperostipa comata	HECO	Per. Grass	Poaceae	5
Heterotheca villosa	HEVI	Per. Forb	Asteraceae	4
Machaeranthera canescens	MACA	Bi. Forb	Asteraceae	6
Muhlenbergia porteri	MUPO	Per. Grass	Poaceae	3
Packera multilobata	PAMU	Per. Forb	Asteraceae	5
Plantago patagonica	PLPA	An. Forb	Plantaginaceae	6
Vulpia octoflora	VUOC	An. Grass	Poaceae	5

Table 2.2: Traits measured in the study.

Trait	Abbr.	Units	Definition
Seed mass	SMass	mg	Weight of individual seeds
Relative growth rate	RGR	mg mg^{-1}	Mass$_{(t)}$ - Mass$_{(t-1)}$ / Mass $_{(t-1)}$ × days
Root mass ratio	RMR	unitless	Root dry mass/Total plant dry mass
Root area to shoot area ratio	R_AS_A	unitless	Root area/Shoot area
Height	HT	cm	Natural plant height
Leaf dry matter content	LDM	mg g^{-1}	Leaf dry mass/fresh mass
Specific leaf area	SLA	mm^2 g^{-1}	Leaf area/leaf dry mass
Relative root elongation	RRER	cm cm^{-}1	Root length$_{(t)}$ - Root length$_{(t-1)}$ / Root length $_{(t-1)}$ × days
Root diameter	Diam.	mm	Average root diameter
Root dry matter content	RDM	mg g^{-1}	Root dry mass/fresh mass
Root tissue density	RTD	mg mm^{-3}	Root dry mass/volume
Specific root length	SRL	m g^{-1}	Root length/dry mass

Table 2.3: Results of principle components analyses of the trait correlation matrix at 10-days, 24-day, and 42-day harvests. All variables were log-transformed prior to analyses. Eigenvectors >|0.6| are in bold. Total variance explained by each rotated component (RC) is provided in the var.exp. row of the table.

	10-day PCA			24-day PCA			42-day PCA		
	RC1	RC2	RC	RC1	RC2	RC3	RC1	RC2	RC3
SLA	0.09	**0.87**	0.04	-0.27	-0.36	-0.29	-0.12	-0.18	**0.88**
LDMC	0.32	-	0.52	0.46	0.40	0.36	**0.75**	0.32	-0.10
HT	**0.85**	0.14	0.31	**0.83**	0.13	-0.03	**0.85**	0	-0.07
RASA	0.03	-	**0.71**	0	**0.81**	-0.23	-0.12	**0.78**	-0.16
RDMC	-0.09	-	**0.76**	0.08	-0.07	**0.67**	0.51	0.57	0.16
RMR	0.13	0.47	**0.72**	-0.07	**0.61**	0.19	-0.07	**0.92**	-0.11
RTD	-0.32	**-**	0.54	-0.31	0.19	**0.85**	-0.24	0.4	**-0.79**
Diam	**0.79**	-	-	**0.9**	-0.23	-0.06	**0.75**	-0.21	-0.12
RER	**0.90**	0.18	0.15	0.03	**0.73**	0.04	0.02	-0.08	-0.21
SRL	-0.34	**0.78**	-	-0.53	-0.08	**-0.7**	-0.36	-0.12	**0.84**
S.Mass	**0.93**	-	-	**0.89**	0.04	0.11	**0.83**	-0.21	-0.09
var.exp.	0.31	0.22	0.22	0.27	0.18	0.18	0.27	0.2	0.2

Table 2.4: Pearson correlations of traits at 10-day, 24-day and 42-day harvests. Correlations with Holm adjusted p-values <0.05 are in bold.

10-day trait correlations

	SLA	LDMC	HT	RASA	RDMC	RMR	RTD	Diam	RRER	SRL	Smass
SLA	1										
LDMC	-0.3623	1									
HT	0.1658	0.4162	1								
RASA	-0.1369	0.3709	0.3341	1							
RDMC	-0.1373	0.4112	0.0259	0.2874	1						
RMR	**0.4892**	0.092	0.281	0.3192	**0.4492**	1					
RTD	**-0.5136**	0.3477	-0.1909	0.4145	**0.5571**	0.0608	1				
Diam	-0.0209	0.2154	0.4302	-0.1242	-0.0457	0.0043	-0.2168	1			
RRER	0.1533	0.2611	**0.8269**	0.0825	0.0247	0.2906	-0.3362	**0.551**	1		
SRL	**0.5051**	-0.3676	-0.1599	-0.0489	-0.3238	0.0385	**-0.593**	**-0.4904**	-0.1327	1	
SMass	-0.0283	0.1875	**0.7362**	-0.0329	-0.1615	-0.0562	-0.2002	**0.7441**	**0.7759**	-0.4251	1

24-day trait correlations

	SLA	LDMC	HT	RASA	RDMC	RMR	RTD	Diam	RRER	SRL	Smass
SLA	1										
LDMC	**-0.4764**	1									
HT	-0.1702	0.3957	1								
RASA	-0.2988	0.197	0.0347	1							
RDMC	0.0237	**0.4492**	0.1391	-0.0926	1						
RMR	0.2758	0.1337	0.0246	**0.4486**	0.204	1					
RTD	-0.2613	0.0536	-0.2356	-0.0694	0.322	0.2572	1				
Diam	-0.0544	0.2755	**0.6169**	-0.1475	0.0453	-0.1196	-0.3663	1			
RRER	-0.1983	0.2556	0.1788	0.2817	-0.1412	0.3306	0.2291	-0.1394	1		
SRL	0.3689	-0.3144	-0.3355	0.0771	-0.264	-0.1955	**-0.5337**	**-0.4653**	-0.1203	1	
SMass	-0.1847	0.2805	**0.686**	0.0216	0.0402	0.1115	-0.0921	**0.7871**	0.0496	**-0.6355**	1

42-day trait correlations

	SLA	LDMC	HT	RASA	RDMC	RMR	RTD	Diam	RRER	SRL	Smass
SLA	1										
LDMC	-0.3453	1									
HT	-0.1337	**0.6066**	1								
RASA	-0.319	0.0881	-0.0777	1							
RDMC	-0.0333	**0.507**	0.3041	0.1128	1						
RMR	-0.157	0.1467	-0.0071	**0.7811**	0.3725	1					
RTD	**-0.68**	0.0516	-0.1444	0.3211	0.0577	0.4407	1				
Diam	-0.1065	0.344	**0.542**	-0.062	0.1813	-0.1311	-0.2871	1			
RRER	-0.1416	-0.1245	0.0726	0.1747	-0.0744	0.0302	-0.087	0.2859	1		
SRL	**0.6873**	-0.2905	-0.3525	-0.0748	-0.2006	-0.2416	**-0.6449**	-0.3755	-0.1133	1	
SMass	-0.1206	**0.5085**	**0.6493**	-0.153	0.1971	-0.2219	-0.1636	**0.6207**	-0.0878	**-0.3077**	1

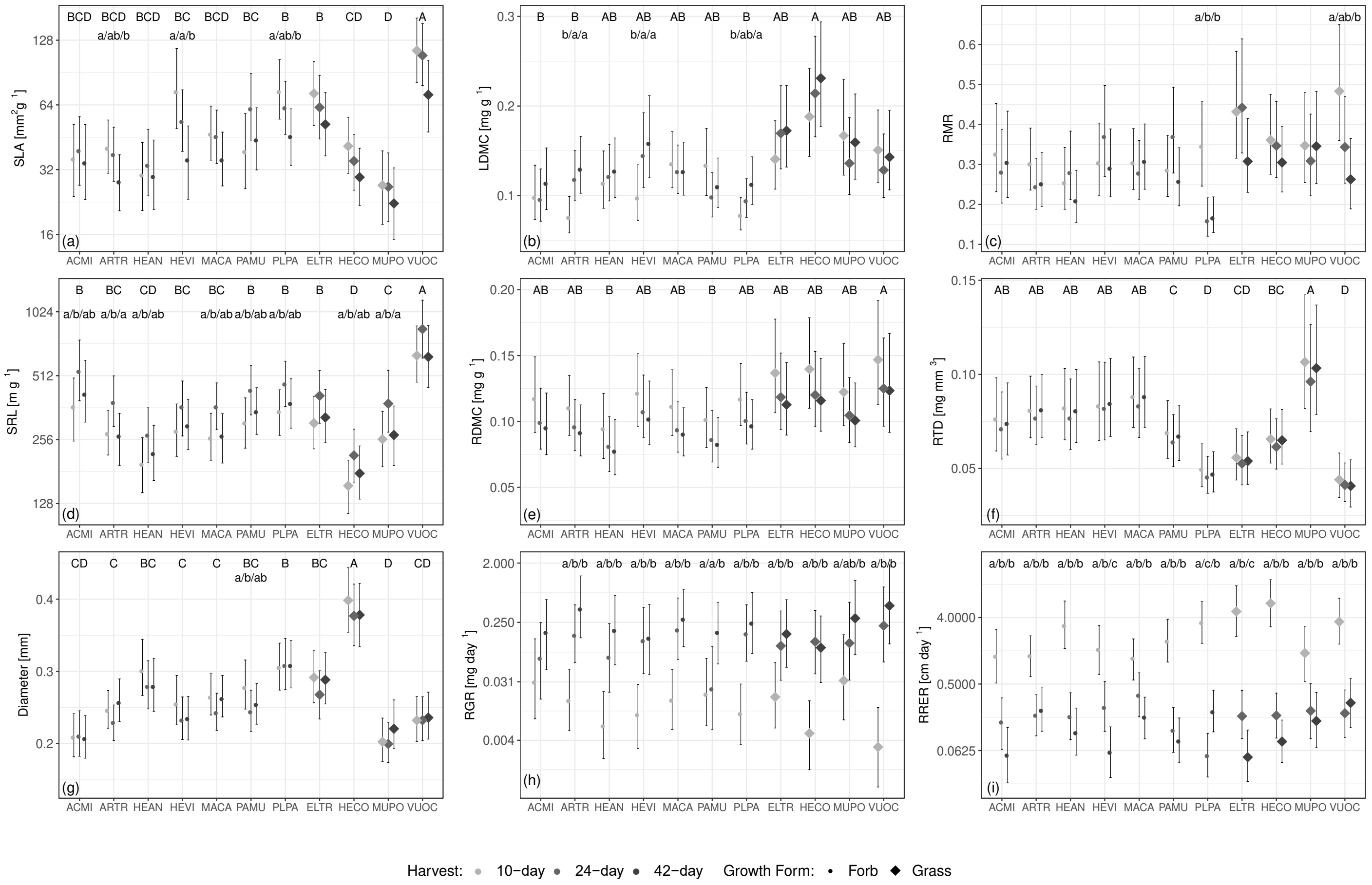

Figure 2.1: Estimates of median trait values and 95% credible intervals (CI) obtained from posterior distributions. Capital letters denote differences in medians among species across all ontogenetic stages. Lowercase letters denote difference among ontogenetic stages within a species. Species abbreviations are as follow: ACMI: *Achillea millefolium*; ARTR: *Artemisia tridentata*; HEAN: *Helianthus annuus*; HEVI: *Heterotheca villosa*; MACA: *Machaeranthera canescens*; PAMU: *Packera multilobata*; PLPA: *Plantago patagonica*; ELTR: *Elymus trachycaulus*; HECO: *Hesperostipa comata*; MUPO: *Muhlenbergia porteri*; VUOC: *Vulpia octoflora.* Trait abbreviations are as follow: SLA: specific leaf area; LDMC: leaf dry matter content; RMR: root mass ratio; SRL: specific root length; RDMC: root dry matter content; RTD: root tissue density; RGR: relative growth rate; RRER: relative root elongation rate

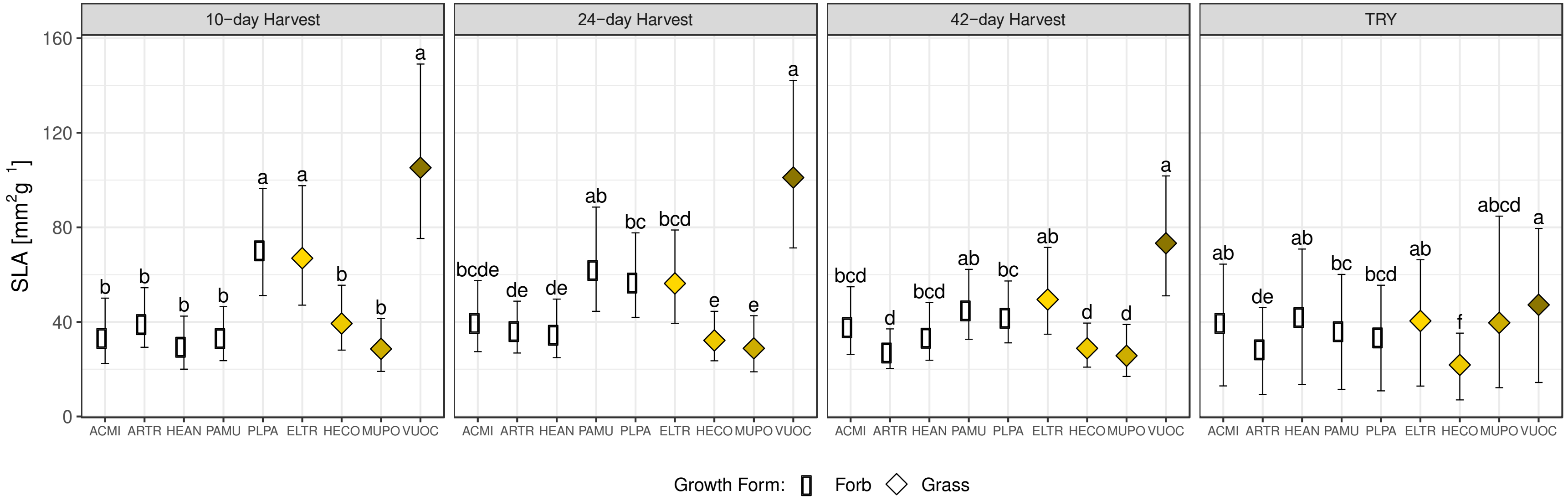

Figure 2.2: Estimates of median specific leaf area (SLA) values and 95% credible intervals obtained from posterior distributions at each harvest and from the TRY database. Letters denote difference among species within ontogenetic stage. Differences were determined by assessing whether the 95% CI of the difference between given groups contained zero. Species abbreviations are as follow: ACMI: *Achillea millefolium*; ARTR: *Artemisia tridentata*; HEAN: *Helianthus annuus*; HEVI: *Heterotheca villosa*; MACA: *Machaeranthera canescens*; PAMU: *Packera multilobata*; PLPA: *Plantago patagonica*; ELTR: *Elymus trachycaulus*; HECO: *Hesperostipa comata*; MUPO: *Muhlenbergia porteri*; VUOC: *Vulpia octoflora*

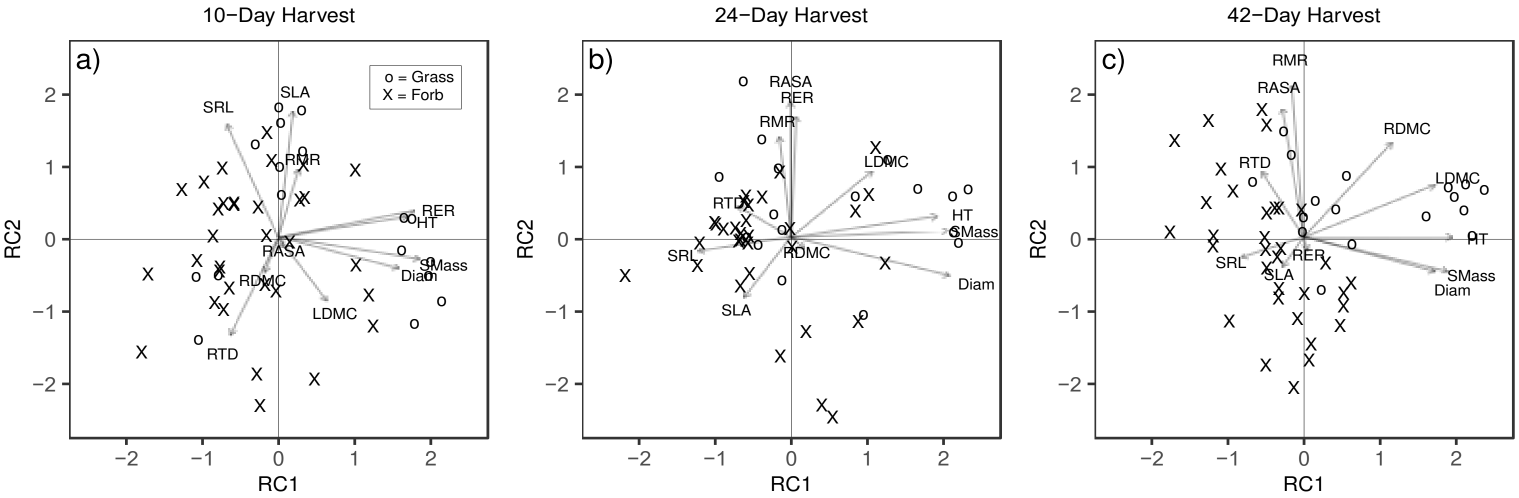

Figure 2.3: The first two varimax-rotated principle components (RC) plotted for traits measured at 10-day, 24-day, and 42-day harvests. "X" symbols represent forbs and "o" symbols represent grasses. Trait abbreviations are as follow: Diam: root diameter, HT: height; LDMC: leaf dry matter content; RASA: root area to shoot area ratio; RDMC: root dry matter content; RER: relative root elongation rate; RMR: root mass ratio; RTD: root tissue density; SLA: specific leaf area; SMass: seed mass, SRL: specific root length.

REFERENCES

Alvarez-Flores R, Winkel T, Degueldre D, Del Castillo C, Joffre R (2013) Plant growth dynamics and root morphology of little-known species of Chenopodium from contrasted Andean habitats. Botany 92:101–108. doi: 10.1139/cjb-2013-0224

Balachowski JA, Volaire FA (2018) Implications of plant functional traits and drought survival strategies for ecological restoration. Ecology 55:631-640. doi: 10.1111/1365-2664.12979

Barak RS, Fant JB, Kramer AT, Skogen KA (2015) Assessing the value of potential "Native Winners" for restoration of cheatgrass-invaded habitat. Western North American Naturalist 75:58–69. doi: 10.3398/064.075.0107

Biondini M (2007) Plant diversity, production, stability, and susceptibility to invasion in restored northern tall grass prairies (United States). Restoration Ecology 15:77–87. doi: 10.1111/j.1526-100X.2006.00192.x

Bristiel P, Roumet C, Violle C, Volaire F (2019) Coping with drought: root trait variability within the perennial grass *Dactylis glomerata* captures a trade-off between dehydration avoidance and dehydration tolerance. Plant and Soil 434:327–342. doi: 10.1007/s11104-018-3854-8

Brown CS, Anderson VJ, Claassen VP, et al (2008) Restoration ecology and invasive plants in the Semiarid West. Invasive Plant Science and Management 1:399–413. doi: 10.1614/IPSM-08-082.1

Campilho A, Lindgren O, Helariutta Y (2018) Vascular morphogenesis during root development. In: Root Development, Annual Plant Review Book series. Vol. 37. Blackwell Publishing doi: 10.1002/9781119312994.apr0397

Chieppa J, Nielsen UN, Tissue DT, Power SA (2019) Drought and phosphorus affect productivity of a mesic grassland via shifts in root traits of dominant species. Plant and Soil 444:457–473. doi: 10.1007/s11104-019-04290-9

Cornwell WK, Schwilk DW, Ackerly DD (2006) A trait-based test for habitat filtering: convex hull volume. Ecology 87:1465–1471. doi: 10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

Craine JM, Froehle J, Tilman DG, et al (2001) The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. Oikos 93:274–285. doi: 10.1034/j.1600-0706.2001.930210.x

Dayrell RLC, Arruda AJ, Pierce S, et al (2018) Ontogenetic shifts in plant ecological strategies. Functional Ecology 32:2730–2741. doi: 10.1111/1365-2435.13221

de la Riva EG, Lloret F, Perez-Ramos IM, et al (2017) Importance of functional diversity in the stability of Mediterranean shrubland communities after the impact of extreme climatic events. Journal of Plant Ecology 10: 281-293 doi: 10.1093/jpe/rtw027

de la Riva EG, Tosto A, Perez-Ramos IM, et al (2016) A plant economics spectrum in Mediterranean forests along environmental gradients: is there coordination among leaf, stem and root traits? Journal of Vegetation Science 27:187–199. doi: 10.1111/jvs.12341

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Building roots in a changing environment: implications for root longevity. New Phytologist 147:33–42. doi: 10.1046/j.1469-8137.2000.00686.x

Ferguson SD, Leger EA, Li J, Nowak RS (2015) Natural selection favors root investment in native grasses during restoration of invaded fields. Journal of Arid Environments 116:11–17. doi: 10.1016/j.jaridenv.2015.01.009

Fort F, Cruz P, Jouany C (2014) Hierarchy of root functional trait values and plasticity drive early-stage competition for water and phosphorus among grasses. Functional Ecology 28:1030–1040. doi: 10.1111/1365-2435.12217

Freschet GT, Cornelissen JHC, Van Logtestijn RSP, Aerts R (2010) Evidence of the "plant economics spectrum" in a subarctic flora. Journal of Ecology 98:362–373. doi: 10.1111/j.1365-2745.2009.01615.x

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology & Evolution 23:695–703. doi: 10.1016/j.tree.2008.07.013

Funk JL, Larson JE, Ames GM, et al (2016) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biological Reviews 1–18. doi: 10.1111/brv.12275

Garnier E, Freijsen AHJ (1994) On ecological inference from laboratory experiments conducted under optimum conditions. A whole plant perspective on carbon-nitrogen interactions 267–292.

Garnier E, Navas ML, Grigulis K (2016) Plant Functional Diversity: Organism traits, community structure, and ecosystem properties. Oxford Scholarship Online. doi: 10.1093/acprof:oso/9780198757368.001.0001

Gelman A, Hill J, Masanao Y. (2012) Why we (usually) don't have to worry about multiple comparisons. Journal of Research on Educational Effectiveness 5: 189-211 doi: 10.1080/19345747.2011.618213

Gerry AK, Wilson SD (1995) The Influence of initial size on the competitive responses of six plant species. Ecology 76:272–279. doi: 10.2307/1940648

Goergen EM, Leger EA, Espeland EK (2011) Native perennial grasses show evolutionary response to Bromus tectorum (cheatgrass) invasion. PLoS ONE 6:e18145. doi: 10.1371/journal.pone.0018145

Goldberg D (1996) Competitive ability: definitions, contingency and correlated traits. Philosophical Transitions of the Royal Society. Biological sciences. 351:1377–1385. doi: 10.1098/rstb.1996.0121

Grime JP, Hunt R (1975) Relative Growth-Rate: Its range and adaptive significance in a local flora. The Journal of Ecology 63:393. doi: 10.2307/2258728

Grime JP, Thompson K, Hunt R, et al (1997) Integrated screening validates primary axes of specialisation in plants. Oikos 79:259. doi: 10.2307/3546011

Hanslin HM, Bischoff A, Hovstad KA (2019) Root growth plasticity to drought in seedlings of perennial grasses. 1–18. doi: 10.1007/s11104-019-04117-7

Hardegree SP, Abatzoglou JT, Brunson MW, et al (2018) Weather-centric rangeland revegetation planning. Rangeland Ecology & Management 71:1–11. doi: 10.1016/j.rama.2017.07.003

Harrison S, LaForgia M (2019) Seedling traits predict drought-induced mortality linked to diversity loss. Proceedings of the National Academy of Sciences 116:5576–5581. doi: 10.1073/pnas.1818543116

HilleRisLambers J, Adler PB, Harpole WS, et al (2012) Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology Evolution and Systematics 43:227–248. doi: 10.1146/annurev-ecolsys-110411-160411

Holdaway RJ, Richardson SJ, Dickie IA, et al (2011) Species- and community-level patterns in fine root traits along a 120,000-year soil chronosequence in temperate rain forest. Journal of Ecology 99:954–963. doi: 10.1111/j.1365-2745.2011.01821.x

Hunt R, Cornelissen JHC (1997) Components of relative growth rate and their interrelations in 59 temperate plant species. New Phytologist 135:395–417. doi: 10.1046/j.1469-8137.1997.00671.x

Hunt R, Lloyd PS (2008) Growth and partitioning. New Phytologist 106:235–249. doi:10.1111/j.1469-8137.1987.tb04692.x

Jakobsson A, Eriksson O (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. Oikos 88:494–502. doi: 10.1034/j.1600-0706.2000.880304.x

James JJ, Svejcar TJ, Rinella MJ (2011) Demographic processes limiting seedling recruitment in arid grassland restoration. Journal of Applied Ecology 48:961–969. doi: 10.1111/j.1365-2664.2011.02009.x

Keddy PA, Shipley B (1989) Competitive hierarchies in herbaceous plant communities. Oikos 54:234. doi: 10.2307/3565272

Kong D, Ma C, Zhang Q, Li L, Chen X, Zeng H, Guo D (2014) Leading dimensions in absorptive root trait variation across 96 subtropical forest species. New Phytologist 203:863–872. doi: 10.1111/nph.12842

Kramer-Walter KR, Bellingham PJ, Millar TR, et al (2016) Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. Journal of Ecology 104:1299–1310. doi: 10.1111/1365-2745.12562

Kunstler G, Falster D, Coomes DA, et al (2016) Plant functional traits have globally consistent effects on competition. Nature 529:204–207. doi: 10.1038/nature16476

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological causes and ecological consequences. Advances in Ecological Research 23:187-261 doi: 10.1016/S0065-2504(08)60148-8

Larson JE, Anacker BL, Wanous S, Funk JL (2020) Ecological strategies begin at germination: Traits, plasticity and survival in the first 4 days of plant life. Functional Ecology. doi: 10.1111/1365-2435.13543

Larson JE, Funk JL (2016) Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms. New Phytologist 210:827–838. doi: 10.1111/nph.13829

Larson JE, Sheley RL, Hardegree SP, Doescher PS, James JJ (2014) Seed and seedling traits affecting critical life stage transitions and recruitment outcomes in dryland grasses. Journal of Applied Ecology 52:199–209. doi: 10.1111/1365-2664.12350

Lasky JR, Bachelot B, Muscarella R, et al (2015) Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. Ecology 96:2157–2169. doi: 10.1890/14-1809.1

Laughlin DC (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. Ecology Letters 17:771–784. doi: 10.1111/ele.12288

Leck MA, Parker VT, Simpson RL, Simpson RS (2008) Seedling ecology and evolution. Cambridge University Press.

Leger EA, Atwater DZ, James JJ (2019) Seed and seedling traits have strong impacts on establishment of a perennial bunchgrass in invaded semi-arid systems. Journal of Applied Ecology 97:311-325. doi: 10.111/1365-2664.13367

Markesteijn L, Poorter L (2009) Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. Journal of Ecology 97:311–325. doi: 10.1111/j.1365-2745.2008.01466.x

Mason CM, McGaughey SE, Donovan LA (2013) Ontogeny strongly and differentially alters leaf economic and other key traits in three diverse Helianthus species. Journal of Experimental Botany 64:4089–4099. doi: 10.1093/jxb/ert249

McGill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21:178–185. doi: 10.1016/j.tree.2006.02.002

Mediavilla S, Escudero A (2009) Ontogenetic changes in leaf phenology of two co-occurring Mediterranean oaks differing in leaf life span. Ecological Research 24:1083–1090. doi: 10.1007/s11284-009-0587-4

Mitchell RM, Bakker JD (2014) Intraspecific Trait Variation Driven by Plasticity and Ontogeny in Hypochaeris radicata. PLoS ONE 9:e109870–8. doi: 10.1371/journal.pone.0109870

Moles AT, Westoby M (2004) Seedling survival and seed size: a synthesis of the literature. Journal of Ecology 92:372–383. doi: 10.1111/j.0022-0477.2004.00884.x

Niinemets U (2005) Key Plant structural and allocation traits depend on relative age in the perennial herb *Pimpinella saxifraga*. Annals of Botany. doi: 10.1093/aob/mci180

Niinemets U (2004) Adaptive adjustments to light in foliage and whole-plant characteristics depend on relative age in the perennial herb *Leontodon hispidus*. New Phytologist162:683–696. doi: 10.1111/j.1469-8137.2004.01071.x

Padilla FM, Pugnaire FI (2007) Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Functional Ecology 21:489–495. doi: 10.1111/j.1365-2435.2007.01267.x

Parish JAD, Bazzaz FA (1985) Ontogenetic niche shifts in old-field annuals. Ecology 66:1296–1302. doi: 10.2307/1939182

Perez-Harguindeguy N, Diaz S, Garnier E, et al (2013) New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany doi: 10.1071/BT12225

Perez-Ramos IM, Roumet C, Cruz P, Blanchard A, Autran P, Garnier E (2012) Evidence for a “plant community economics spectrum” driven by nutrient and water limitations in a Mediterranean rangeland of southern France. Journal of Ecology 100:1315–1327. doi: 10.1111/1365-2745.12000

Poorter H, Fiorani F, Pieruschka R, et al (2016) Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. New Phytologist 212:838–855. doi: 10.1111/nph.14243

Poorter H, Jong RD (1999) A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. New Phytologist 143:163–176. doi: 10.1046/j.1469-8137.1999.00428.x

Poorter L (2015) Are species adapted to their regeneration niche, adult niche, or both? The American Naturalist 169:433–442. doi: 10.1086/512045

Pywell RF, Bullock JM, Roy DB, Warman L, Walker KJ, Rothery P (2003) Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40:65–77. doi: 10.1046/j.1365-2664.2003.00762.x

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Reich PB (2014) The world-wide “fast-slow” plant economics spectrum: a traits manifesto. Journal of Ecology 102:275–301. doi: 10.1111/1365-2745.12211

Reichmann LG, Schwinning S, Polley HW, Fay PA (2016) Traits of an invasive grass conferring an early growth advantage over native grasses. Journal of Plant Ecology 9:672–681. doi: 10.1093/jpe/rtw014

Roumet C, Birouste M, Picon-Cochard C, et al (2016) Root structure-function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. New Phytologist 210:815–826. doi: 10.1111/nph.13828

Rowe CLJ, Leger EA (2010) Competitive seedlings and inherited traits: a test of rapid evolution of Elymus multisetus (big squirreltail) in response to cheatgrass invasion. Evolutionary Applications. 4:485–498. doi: 10.1111/j.1752-4571.2010.00162.x

Ryser P (1996) The importance of tissue density for growth and life span of leaves and roots: A comparison of five ecologically contrasting grasses. Functional Ecology 10:717. doi: 10.2307/2390506

Seiwa K, Kikuzawa K (2011) Phenology of tree seedlings in relation to seed size. Canadian Journal of Botany 69:532–538. doi: 10.1139/b91-072

Seiwa K, Kikuzawa K (1996) Importance of seed size for the establishment of seedlings of five deciduous broad-leaved tree species. Vegetatio 123:51–64. doi: 10.1007/BF00044887

Shipley B (2006) Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. Functional Ecology 20:565–574. doi: 10.1111/j.1365-2435.2006.01135.x

Spasojevic MJ, Yablon EA, Oberle B, Myers JA (2014) Ontogenetic trait variation influences tree community assembly across environmental gradients. Ecosphere 5:1–20. doi: 10.1890/ES14-000159.1

Suding KN, Lavorel S, Chapin FS, et al (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14:1125-1140 doi: 10.1111/j.1365-2486.2008.01557.x

Stan Development Team (2018) Stan Modeling Language Users Guide and Reference Manual, Version 2.18.0. http://mc-stan.org

Tjoelker MG, Craine JM, Wedin D, Reich PB, Tilman D (2005) Linking leaf and root trait syndromes among 39 grassland and savannah species. New Phytologist 167:493–508. doi: 10.1111/j.1469-8137.2005.01428.x

Tobner CM, Paquette A, Messier C (2013) Interspecific coordination and intraspecific plasticity of fine root traits in North American temperate tree species. Frontiers in Plant Science doi: 10.3389/fpls.2013.00242

Useche A, Shipley B (2010) Plasticity in relative growth rate after a reduction in nitrogen availability is related to root morphological and physiological responses. Annals of Botany 106(4) 617-625 doi: 10.1093/aob/mcq144

Wahl S, Ryser P (2000) Root tissue structure is linked to ecological strategies of grasses. New Phytologist 148:459–471. doi: 10.1046/j.1469-8137.2000.00775.x

Walters MB, Kruger EL, Reich PB (1993) Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic considerations. Oecologia 96:219–231. doi: 10.1007/BF00317735

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199:213–227. doi: 10.1023/A:1004327224729

Winkler DE, Backer DM, Belnap J, et al (2018) Beyond traditional ecological restoration on the Colorado Plateau. Restoration Ecology 26:1055–1060. doi: 10.1111/rec.12876

Wright IJ, Reich PB, Westoby M, et al (2004) The worldwide leaf economics spectrum. Nature 428: 821-827 doi: 10.1038/nature02403

Zirbel CR, Brudvig LA (2020) Trait-environment interactions affect plant establishment success during restoration. Ecology 101:23. doi: 10.1002/ecy.2971

Zwicke M, Picon-Cochard C, Morvan-Bertrand A, et al (2015) What functional strategies drive drought survival and recovery of perennial species from upland grassland? Annals of Botany 116:1001–1015. doi: 10.1093/aob/mcv037

CHAPTER 3: GETTING TO THE ROOT OF RESTORATION: CONSIDERING ROOT TRAITS FOR IMPROVED RESTORATION OUTCOMES [1]

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 the last few decades, restoration efforts rarely result in rapid recovery of ecosystem function (Jones et al. 2018) and re-vegetation success rates are often as low as 5-10% (Kildisheva et al. 2016). The lack of a broad conceptual framework that informs restoration at diverse sites and scales (Young et al. 2005) likely contributes to these poor outcomes.

Trait-based ecology has also grown rapidly over the last several decades. A central goal of trait-based ecology is to link traits or, morphological, physiological, or phenological plant characteristics, with performance and fitness (Violle et al. 2007). Trait-based approaches have contributed to our understanding of the mechanisms driving community assembly (e.g., HilleRisLambers 2012, Funk et al. 2016) and have been extended to explain ecosystem processes with the "response and effect" framework (Lavorel and Garnier 2002, Suding et al. 2008). Under this framework traits are categorized into two groups: those that predict species responses to environmental change (response traits) and those that influence ecosystem processes (effect traits). Several authors 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., Pywell et al. 2003, Larson et al. 2014, Zirbel and Brudvig 2020).

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[1] This chapter contains published work from: Garbowski M, Avera B, Bertram JH, Courkamp JS, Gray J, Hein KM, Lawrence R, McIntosh M, McClelland S, Post AK, Slette IJ, Winkler DE, Brown CS. Getting to the root of restoration: Considering root traits for improved restoration outcomes under drought and competition. Restoration Ecology. doi: 10.1111/rec.13291

Identifying traits associated with plant performance under drought, competition and invasion, as well as soil erosion may be particularly useful for improving restoration outcomes. This is because low soil moisture (e.g., Moles and Westoby 2004, Hardegree et al. 2012) and competition from neighbors (e.g., Goldberg 1990, Brown et al. 2008) hamper seedling recruitment in many contexts including restoration. In addition, land and soil degradation resulting from erosion may preclude the development of healthy plant communities due to loss of nutrients (e.g., Lü et al. 2007), native seeds (e.g., Cerdá and García-Fayos 1997, Chambers 2000), and soil structure (e.g., Pimentel et al. 1995). Root traits have been linked to stress tolerance (e.g., Kramer-Walter 2016, Bristiel et al. 2019, Harrison and LaForgia 2019), competitive dynamics (e.g., Leger et al. 2019), and ecosystem functions including soil stability (e.g., Rillig et al. 2014, Vannoppen et al. 2015, Bardgett et al. 2016) yet remain understudied in comparison to their aboveground counterparts.

In this review we synthesize research relating root traits to drought, competition/invasion, and erosion. We specifically 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 areas threatened by the above-mentioned environmental pressures. Finally, we describe a research approach that may help researchers and practitioners more effectively apply trait-based approaches in restoration research and planning.

METHODS

We reviewed primary literature focused on morphological and anatomical root traits related to environmental stressors of drought, invasion and/or competition, and two components of soil erosion - topsoil stability and aggregate stability. We began our search by identifying appropriate papers in Web of Science (WoS) using key words related to root traits and our three environmental stressors. To restrict our results to those obtained from non-cultivated plants, we excluded references from agricultural settings. We further refined our search by narrowing results to WoS categories broadly related to ecology or restoration (e.g., ecology, environmental engineering, biodiversity conservation). Studies focused on biological or chemical traits (e.g., mycorrhizal associations, allelopathy) were excluded. We chose to omit these papers because the breadth and diversity of fields from which these studies originate made identifying results relevant to restoration difficult. Appendix 3 provides details of keywords used at each stage of the initial literature search. This processes resulted in 1,017 references (completed in November 2019). Of these, papers were considered relevant if the following criteria were met: (1) a root trait had to be measured (i.e. papers that eluded to root traits without measuring them were excluded); (2) the study had to have been conducted in the context of one of our three restoration categories (drought, invasion/competition, soil stability); (3) for drought studies, water availability had to be manipulated in experimental studies or the study had to have been conducted in the context of a naturally occurring drought (i.e. either intra-annual or inter-annual); (4) for invasion/competition studies, competition had to be explicitly manipulated (i.e. studies that focused solely on coexistence or resource partitioning were excluded). We also added relevant manuscripts from the references sections of reviewed sources. This processes resulted in 203 relevant papers across all categories (86 in the drought, 69 in the invasion/competition, 48 in soil erosion).

Once we identified relevant studies, we extracted specific details from each reference to address our overarching goal of identifying root traits related to plant performance in stressful conditions that hider restoration outcomes. First, we identified all traits measured in each study. In studies that measured multiple traits, each trait was counted as an individual observation. Second, we determined whether the root trait was considered a response or predictor variable in each case. If the root trait was considered a response variable, we documented the direction of the response in relation to the environmental stressor. If the root trait was considered the predictor variable, we noted how it influenced performance measures. Definitions of the most commonly measured root traits are provided in Table 3.1.

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, IPCC 2013). 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 (e.g., Moles and Westoby 2004, Hardegree et al. 2010, Hardegree 2013). After germination, vulnerable young seedlings must overcome environmental stressors such as drought to successful establish and persist in plant communities (e.g., Leishman and Westoby 1994, Asay et al. 2001, Engelbrecht et al. 2005). Even though a comprehensive trait-based framework characterizing unique plant strategies for coping with drought has recently been developed (Volaire 2018), our understanding of how root traits fit into these broad categories remains rudimentary.

Morphological root traits are likely key components of dehydration avoidance and tolerance strategies (Volaire 2018). The avoidance strategy is based on optimizing water uptake belowground to maintain leaf water potential, turgor, and function aboveground (Comas et al. 2013, Volaire 2018). In addition to aboveground responses, plants may grow deep roots or increase root surface area to maximize water uptake and avoid water stress. In contrast, dehydration tolerance is based on maximizing survival at the expense of reduced growth (Volaire 2018). Among other physiological characteristics, plants employing a tolerance strategy may have high root tissue density (RTD) and root to shoot ratios (RSR or RMF: root mass fraction) (Bristiel et al. 2019). Here we discuss several root traits related to these two strategies that have been linked to increased establishment, survival, or biomass production under drought.

Root traits were categorized as dependent variables in 51 (60%) of the reviewed papers and were linked to performance measures as independent variables in 18 (21%) references. Root traits were considered both dependent and independent variables in the remaining or studies were focused on correlations among traits in relation to drought. Allocation traits (RSR or RMF) and root biomass were most frequently measured in relation to drought (Fig. 3.1). We observed few clear patterns in the direction of response of root traits to moisture deficit, but general trends suggest increased RSR/RMF and decreased overall root biomass under water-limited conditions. Similar patterns were reported in a recent meta-analysis (Zhou et al. 2018). In many cases, drought had no effect on root traits. We focus our discussion on the traits that were explicitly linked to performance under water-deficit conditions rather than on the response of root traits to drought (recently reviewed in Zhou et al. 2018).

Rooting depth and root elongation rate (RER)

Traits associated with desiccation avoidance via increased rooting depth or RER were often identified as key determinants of plant performance under drought. Just as for mature plants (Canadell and Zedler 1995, Lloret et al. 1999), the primary mechanism by which deep roots improve seedling survival during drought is by providing plants access to moisture from deeper soil layers (Reader et al. 1993, Padilla and Pugnaire 2007, Harrison and LaForgia 2019). With access to stable soil moisture, plants can maintain water uptake (Ehleringer and Dawson 1992) and avoid dehydration (Volaire 2018). Similarly, plant with high RER may be able to quickly use unexploited soil moisture to optimize water uptake. Studies have linked RER to higher drought survival in trees (e.g., Horton and Clark 2002, Stella and Battles 2012) and herbaceous species (e.g., Perez-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 a small 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 that survived at the highest rates employed strategies of rapid resource acquisition (deep roots and rapid shoot elongation) during favorable spring conditions with both dehydration avoidance (i.e., root elongation and maintenance of leaf water content) and tolerance (i.e., high fructan content in roots, high leaf meristem water content, cell membrane stability) strategies during the drought period. In other studies, researchers found that a dehydration 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 and trade-offs is foundational to understanding plant strategies for coping with environmental stress (Grime et al. 1997, Garnier et al. 2016). Yet, we found few studies that assessed trait-correlations in relation to drought, particularly at the seedling stage.

By assessing multiple traits at once, researchers may be able to identify whether individual traits or suites of traits are responsible for 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 other traits and a reliable predictor of plant growth under a gradient of moisture conditions. Similarly, Harrison and LaForgia (2019) found greater root length at the seedling stage resulted in lower plant mortality of annual grassland species during drought. However, in this study, root length was uncorrelated with other traits and seedling traits were only weakly correlated with adult traits. As demonstrated by this study, pinpointing relevant developmental stages at which specific traits (or combinations of traits) influence performance will be essential for making accurate predictions of how plant communities will respond to environmental stressors such as drought. Further, because seeds used in restoration projects are often produced in agronomic settings with abundant resources, future studies that assess coordination among multiple traits under adequate as well as limited resource conditions (e.g., Freschet et al. 2015, Ren et al. 2019) may be particularly informative for identifying species with appropriate strategies for establishing and persisting in drought-threatened systems.

Root biomass and allocation

Together, root biomass and the allocation measures (RSR/RMF) were most frequently related to performance. We found relatively more observations of increased versus decreased RSR or RMF (Fig.

3.2) in response to drought that in some cases were further related to performance measures. Positive effects of high RSR or RMF on performance measures have been documented in woody (e.g., Leiva and Fernández-Alés 1998, Stella and Battles 2012, Lloret et al. 1999) as well as herbaceous (e.g., Bristiel et al. 2019, Peralta et al. 2019, Hanslin et al. 2019) species. These results align with expectations of the functional equilibrium theory that suggests plants adjust biomass allocation to access resources that are most limiting to growth (Brouwer 1963). 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 (e.g., Craine et al. 2009, Poorter et al. 2012).

Although evidently important, measures of biomass fractions may obscure important changes in other root traits under drought. This is because root mass may remain constant while root length or diameter changes. Whether root biomass changes in coordination with traits towards drought avoidance (e.g., increased root length and higher specific root length (SRL)) or tolerance (e.g., increased RTD) strategies may be species (Olmo et al. 2014, Peralta et al. 2019), population (Corcuera et al. 2012, Bristiel et al. 2019), or drought specific (Poorter et al. 2012, Zwicke 2015). For example, working with grass seedlings, Hanslin et al. (2019) found that rooting depth and root morphology (root length and number of higher-order roots) responded to drought, while root biomass and allocation remained relatively constant. These coordinated changes align with a drought avoidance strategy despite no observed changes in biomass allocation. In contrast, working with the perennial grass, *Dactylis glomerata*, Bristiel et al. (2019) found the diameter and RTD of deep roots better explained drought tolerance than rooting depth or biomass allocation. Interestingly, in this study, the most drought tolerant populations combined thin roots with high RTD. This intermediate strategy likely promoted both extensive soil exploration as well as high tolerance to drought. Because of 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. This is surprising because drought avoidance traits may not always predict long-term survival under drought (Lopez-Iglesias et al. 2014). We believe that lesser-studied traits, specifically those related to drought tolerance (e.g., 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 for advancing our understanding of plant tolerance to drought. This is 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 and Ryser 2000), it is independent of acquisitive root traits such as SRL in the belowground trait-economic spectrum (Kramer-Walter et al. 2016), and consistently reflects adaptation to low soil resources (nutrients: Kramer-Walter et al. 2016, moisture: Bristiel et al. 2019, Hanslin et al. 2019). Species with high RTD are often slow growing but may be better able to resist root cavitation due to smaller but more numerous xylem vessels (Wahl and Ryser 2000, Pratt et al. 2007). As vulnerability to root cavitation is often greater than stem xylem cavitation (e.g., Wahl and Ryser 2000, Zhou et al. 2013), research focused on the relationship of root anatomy to drought tolerance could further inform how seedlings cope with drought.

Root traits and 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 traits 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 and Pugnaire 2007). In fact, eight of the twelve studies that linked rooting depth or RER to 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 and Bradford 2009), these traits may have limited influence on plant performance. Rather, traits related to recovery after drought such rapid root development after periods of low soil moisture (e.g., Jupp and Newman 1987, Huang et al. 1997) or high levels of water-soluble carbohydrates in roots (Jiang and Huang 2000) might better predict plant performance in pulse systems.

In addition to precipitation quantity and seasonality, soil texture soil will also affect moisture availability at a given restoration site. In general, finer textured soils (i.e. loamy/clayey) have higher water holding capacity that coarse-textured (i.e. sandy) soils but also hold water more tightly, i.e., at lower water potentials (Jury and Horton 2004). While several studies have linked root traits of established vegetation to soil texture and precipitation (e.g., Sperry and Hacke 2002, Kulmatiski and Beard 2013), 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 soil moisture regimes will be essential for reassembling plant communities capable of 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, Grime 1977, Tilman 1985). The impacts of shoot and root competition have been studied extensively in isolation (e.g., Clements et al. 1939, McPhee and Aarssen 2001) as well as together (e.g., Cahill 1999, Cahill 2002, Bartelheimer et al. 2010) and have been discussed in several reviews (e.g., Wilson 1988, Coomes et al. 2000) and a recent meta-analysis (Kiaer et al. 2013). The importance of competition in restoration has primarily been highlighted in the context of invasion (Funk et al. 2008), which is a leading concern in re-vegetation projects (Brown et al. 2008).

A plant's competitive ability has traditionally been described by two components: competitive effect and competitive response (Goldberg 1990, Goldberg 1996). Competitive effect is defined as a plant's ability to influence the growth of a neighboring plant whereas competitive response is defined as a plant's ability to resist the effects of neighbors. Although a consistent relationship between competitive effect and response would simplify our understanding of competitive dynamics, studies correlating the two components have been inconsistent; positive (e.g., Wilson and Keddy 1986, Goldberg and Fleetwood 1987), uncorrelated (e.g., Cahill et al. 2005, Gibson et al. 2017), and negative (e.g., Wang et al. 2010) relationships have been identified. Although traits may serve as proxies for competitive abilities (e.g., Wilson and Keddy 1986, Keddy et al. 2002), limited studies have explicitly related the two. Investigations relating root traits to competitive abilities are especially rare even though competition for nutrients and water influences plant interactions (e.g., Belcher et al. 1995, Schwinning et al. 2017).

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 (Fig. 3.2 inset). 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 that can be used to improve plant establishment and persistence in restoration of lands susceptible to competition from aggressive or invasive plant species.

Root traits were identified as dependent variables in the majority (76%) of the studies related to competition or invasion and were related to competitive ability or performance about 20% of the time. Most studies were conducted under altered resources (e.g., light, water, nutrients) and were focused on the impacts of interspecific (between or among species) competition. Aboveground biomass was most frequently used to assess performance of competing species. Many studies were comparative and reported differences in traits among specific groups (e.g., root traits of invasive compared to native species) but did not quantify the effects of competition on root traits. 14 studies compared root traits of invasive species in the introduced range to those from native range populations or co-occurring non-invasive species. Only a few studies assessed trait correlations in relation to competition (e.g., Semchenko et al. 2018 and Wang et al. 2010). As most studies investigated at least two species and measured more than one root trait, we identified over 450 root trait measurements related to competition in our survey (Fig 3.2). RSR/RMF, root biomass and SRL were most frequently measured (Fig. 3.2). Few traits responded consistently to competition but general trends for decreased root biomass and root length were common (Fig. 3.2). RSR/RMF, root biomass, and root length were frequently related to plant performance under competition (Fig. 3.2 inset).

Root to shoot ratio and root mass fraction

Allocation measures (i.e. RSR, RMF) were most often related to competitive abilities, establishment, and productivity (Fig 3.2 inset). However, the direction and effect of RSR/RMF on competitive ability or performance varied by species and environmental context. For example, working with the perennial grass *Elymus multisetus,* Rowe et al. (2011) observed both increased tolerance to (competitive response) and suppression of (competitive effect) the invasive annual grass *Bromus tectorum* in plants with higher root to shoot ratios. Similarly, when assessing plant establishment in areas invaded by *B. tectorum,* Leger et al. (2017) found higher rates of survival among individuals of two perennial grass species originating from populations with relatively high RSR. Importantly, both of these 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 about 100 years (Mack 1981), the difference in allocation and associated competitive ability between these groups demonstrates that competition can result in adaptation over short timescales. However, such evolutionary responses related to allocation do not always result in improved competitive ability. Gibson et al (2017) and Ferguson et al. (2015) both 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, especially in seedlings (Gedroc et al. 1996). Therefore, a species' ability to respond to competition by increasing or decreasing investment in root biomass may influence its competitive ability or survival in competitive settings. For example, in a study comparing competitive interactions between a xeric (*Scleropogon breviolius*) and mesic (*Sporobolus airoides*) grass, Novoplansky and Goldberg (2001) found opposite patterns in allocation in relation to interspecific competition for the two species: *S. breviolius* increased and *S. airoides* decreased its RSR. Because *S. brevoilius* seedlings had high RSR as a result of competition, they also were better able to tolerate subsequent drought. However, in a study of competitive dynamics between exotic Johnson grass (*Sorghum halepense*) and several native grass species, a lower RSR at the juvenile stage allowed Johnson grass 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 relation to competition may be species- and context specific.

Although examining levels of plasticity may inform understanding of competitive dynamics as demonstrated by the studies mentioned, it may not always result in altered competitive ability (e.g., Reynolds & Antonio 1996, Cahill 2003). In addition, changes in allocation may result from ontogeny (Gadroc et al. 1996, Muller et al. 2000) or plant size (Cahill 2003) rather than adaptive or plastic responses to competition. Therefore, results should be interpreted with caution and future research should aim to isolate responses in allocation due to direct competition from other influences such as nutrient or water limitation or ontogeny.

Root biomass

Unlike aboveground competition that is largely size-asymmetric (i.e. the preemption of light by larger plants improves subsequent light capture resulting in competitive exclusion of smaller individuals), belowground competition is primarily size symmetric (i.e. competition is roughly proportional to root size) (Schwinning and Weiner 1998). Because of this, root biomass is tightly correlated with belowground competition experienced by neighboring plants (e.g., Cahill and Casper 2000). Increased competitive effects resulting from high root biomass have been documented in wetlands (Gaudet and Keddy 1988), grasslands/prairies (Cahill and Casper 2000, Wang et al. 2010, Semchenko et al. 2018) and savannah systems (Pillay and Ward 2014). Although there is general support for higher competitive effects with greater root biomass, specific trends may be species or system specific. For example, Pillay and Ward (2014) observed a positive correlation between root biomass and competitive effect in mesic (dry) but not humid (wet) savannah trees. This suggests that traits related to resource acquisition may be particularly important in environments where resource preemption and competition for belowground resources determines competitive outcomes. Because measures of allocation or root biomass may mask changes in other root traits (see Drought section), researchers would benefit from studying them in conjunction with traits associated with architecture or morphology to better understand how composite belowground strategies influence competitive dynamics.

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

Competitive effect traits

In addition to high root biomass and RSR/RMF, root traits associated with rapid resource acquisition such as SRL and total root length may be particularly important for understanding species' competitive effects. This is because plants with acquisitive traits likely decrease 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), negatively related to survival and competitive response (Zangaro et al. 2016, Semchenko et al. 2018), and was linked to both superior (Mommer et al. 2011, Collins et al. 2016) and inferior (Goodwin et al. 1999) competitors in comparative studies. Further, in a study assessing the establishment and performance of forbs and woody species in competition with aggressive grass and forb competitors, SRL was negatively linked to survival and competitive response in almost all cases (Zangaro 2016). Although high SRL may improve a plants' competitive effect, specific effects on performance measures may context specific. For example, Rolhauser et al. (2018) found that SRL was negatively related to competitive effect, likely due to interactions with 'pulse' moisture regimes. Root length (Gordon and Rice 1993, Leger et al. 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. Semchenko et al. (2018) found that 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, is also positively related to species' competitive responses (Rowe et al. 2011, Zangaro et al. 2016). Of the few times that RTD was assessed, it was unaffected by competition (Hajek et al. 2018), showed a positive relationship to competitive response (Bennett et al. 2016, Zangaro et al. 2016), and was characteristic of inferior "effect" competitors (Semchenko et al. 2018). Because RTD is independent from acquisitive belowground traits such as SRL (Kramer-Walter et al. 2016) and has been linked to adaptation to low resources environments (nutrients: Kramer-Walter et al. 2016, moisture: Bristiel et al. 2019, Hanslin et al. 2019), 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 et al. (2017) found higher survival of individuals with a high number of root tips in areas invaded by *B. tectorum* but observed no effect of root tips on survival in non-invaded areas. The degree of root branching/forking has been linked to both increased (Rowe et al. 2011) 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. In restoration projects where seeds or seedlings are introduced into sites denuded of existing vegetation (i.e. similar to early successional communities), root traits related to competitive effects may exert strong influence on community assembly. Similarly, in areas dominated by weedy species, plants with traits related to competitive effects may promote 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 and Goldberg 2001). In these cases, using species with traits related to competitive response may promote establishment and persistence.

Limiting similarity vs. Competitive hierarchies

Much research on plant competition is based on the common assumption that similar species compete more strongly than dissimilar ones (i.e. limiting similarity or competition-niche similarity hypothesis, MacArthur and Levins 1967). This assumption has been expanded in trait-based ecology by quantifying species similarity based on traits related to competition (e.g., resource acquisition, shade tolerance) (e.g., Goldberg 1996, Kunstler et al. 2012). Two trait-based hypotheses have been developed to frame competitive dynamics. Under the “Competition-trait similarity hypothesis” (Kunstler et al. 2012), competitive interactions among species with large differences in mean values of traits related to competition are predicted to be weaker than for individuals with more similar trait values. In contrast, under the “Competitive ability hierarchy hypothesis” (Grime 2006, Mayfield and Levine 2010), competitive outcomes result from hierarchical differences in species’ competitive abilities. Under this framework, competition intensity is predicted to increase as the distance in trait values related to competition among species increases. A few recent studies have tested these hypotheses in relation to root traits of competing species.

In a study comparing grasses with acquisitive vs. conservative resource use strategies, hierarchical trait difference in SRL, root phosphorus use efficiency, and root length density (RLD) better predicted competition intensity than trait similarity in non-limiting resource environments (Fort et al. 2013). Similarly, working with common, rare, and native species, Feng and van Kleunen (2016) observed that a target plant experienced stronger competition when, among other traits, it had a higher RSR and its neighbors a lower RSR. Competitive dynamics resulting from trait hierarchies have also been demonstrated in studies of aboveground traits (e.g., Kunstler 2012, Herben and Goldberg 2014, Funk and Wolf 2016) suggesting they may be important drivers of competition above- as well as belowground. However, competition may be influenced by both competitive hierarchies and limiting similarity if they act on different traits. In a study of competition in diverse herbaceous mixtures, competitive hierarchies dominated aboveground competition (i.e. higher specific leaf area than neighbors provided a competitive advantage), whereas limiting similarity influenced competition belowground (i.e. species with similar SRL competed more strongly and those that increased root diameter relative to neighbors experienced less competition) (Bennett et al. 2016). Furthermore, in line with the limiting similarity hypothesis, Burns and Strauss (2012) documented decreased competition in multi-species assemblages resulting from divergence in RSR among competitors that, in turn, resulted in increased aboveground productivity. As research directly testing how competitive-hierarchies and/or limiting-similarity influence belowground competitive dynamics is rare, future studies that identify situations in which one is more important than the other could greatly advance our understanding of plant interactions and potentially 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 and Osborn 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 15 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 natives species or "home" populations to which they are compared (few "no difference" classifications in Fig. 3.3). Allocation measures (RSR/RMF) were most often measured, and higher and lower values were common between invasives and compared groups (i.e. native and "home" populations). If belowground traits of invasive species mirror patterns found for aboveground traits, it is likely that successful invaders in high-resource environments will possess root traits associated with rapid resource acquisition (e.g., high SRL, root area, root length), whereas, successful invaders in low-resource environments may possess traits related to either resource acquisition or conservation (Funk 2013, Giora and Osborn 2014). This remains a largely unexplored area of research.

TOPSOIL AND AGGREGATE STABILTY

Vegetation has long been used to improve soil stability and prevent erosion. The specific effects of roots on water-induced erosion have recently been reviewed by Gyssels et al. 2005 and Vannoppen et al. 2015. In addition, Rillig et al. (2014) have concisely described key root traits related to soil aggregation. Here, we briefly summarize findings from these earlier reviews and discuss developments from the last several years related to the effects of specific root traits on two soil characteristics related to erosion: topsoil and aggregate stability. We do not discuss literature related to slope stability but direct readers to Reubens et al. 2007 and Stokes et al. 2009 for comprehensive reviews on this topic.

Erosion resulting from concentrated flow is most often measured in terms of soil detachment rates or soil erodibility, which are related through the following equation: $D_r = K_c (\tau - \tau_{cr})^b$ where D_r (kg m $^{-2}$ s^{-1}) is detachment rate, K_c (s m^{-1}) is soil erodibility, τ and τ_{cr} are the average and critical flow shear stress for soil detachment, and b is an exponent related to soil properties (Knapen et al. 2007). Soil detachment or erosion occurs when the forces resulting from flowing or falling water surpass thresholds of resistance between soil particles (Knapen et al. 2007).

Roots can help mitigate soil detachment and erosion through their influence on soil cohesion (a component of soil shear strength) or aggregate stability (i.e. the ability to resist disintegration under force). Roots add to soil cohesion through their ability to withstand tension. As roots extend through the soil matrix, they reinforce soil to increase its shear strength (e.g., Wu 1976, Pollen and Simon 2005). The contribution of roots to soil shear strength is quantified in terms of root cohesion. Roots may enhance the formation or stabilization of soil aggregates in several ways. First, roots may compress or entangle soil particles to promote aggregate formation (e.g., Tisdall and Oades 1982, Six et al. 2004). Second, organic residues from roots entering the soil via root sloughing or dieback may serve as food sources for microbes that secrete organic polymers and bind particles together (e.g., De Gryze et al. 2005, Cosentino et al. 2006). Finally, root exudates may bind together soil particles to promote aggregate formation or stabilization (Rillig et al. 2014). Recent studies have identified several root traits as important contributors to soil stability via their effects on soil cohesion and aggregate stability.

We identified 47 references for which root traits were related to topsoil or aggregate stability and in almost all cases root traits were considered explanatory (i.e. independent) variables in relation to soil stability.

Root (mass) density, root length density (RLD), and root area ratio (RAR)

Root traits that characterize the overall size of root systems such as RD (kg m^{-3}), root length (m), RLD (km m^{-3}), and RAR (m^2 m^{-3}) are most often related to both aggregate stability and soil cohesion (Fig. 3.4) (Rillig et al. 2014, Vannoppen et al. 2015).

The influence of roots on soil aggregate stability is related to root system extent largely because expansive root systems interact with more soil particles. Greater aggregate stability has been linked to root biomass (e.g., Mardhiah et al. 2014, Podwojewski et al. 2014, Blankinship 2016), root density (e.g., Demenois et al. 2018a), root length (e.g., Jastrow et al. 1998, Gould et al. 2016) and RLD (e.g., Li et al. 2015, Vergani and Graf 2016). However, recent research suggests that roots may have variable effects on aggregates of different sizes and specific effects may be context dependent.

Two recent studies (Blankinship et al. 2016, Poirier et al. 2018), found that plant roots predominantly influenced the formation and stabilization of macroaggregates (>250 um). Specifically, Poirier et al. 2018 found that graminoid species with dense root networks (i.e. high RLD) were about three times more efficient at promoting macroaggregation per unit biomass compared to woody and non-woody dicots with less extensive root systems. However, while the total mass of macroaggregates was greater under graminoid species compared to woody and non-woody dicots in this study, individual macroaggregates had lower diameter. Similarly, Jastrow et al. (1998) found a positive association between small macroaggregates and the RLD of very fine roots (<0.2mm) suggesting that root systems characterized by many very fine roots may limit the development of very large macroaggregate (but see Demenois et al. 2018a). Together these results highlight how plants with different root traits may uniquely influence aggregates of different sizes.

The effects of traits related to root system extent on soil aggregation may depend on successional stage or plant community diversity. Recent studies from systems including fluvial islands (Mardhiah et al. 2014), Mediterranean shrublands (Erktan et al. 2016), and the tropics (Demenois et al. 2018b) have found a general trend for greater aggregate stability at later successional stages. Yet, the effects of root traits on aggregation were not consistently related to a particular successional stage: Erktan et al. (2016) found root traits to be most important in the initial stages of succession whereas Mardhiah et al. (2014) observed the greatest influence at later successional stages. As succession underpins many restoration efforts (e.g., Hobbs et al. 2007), understanding how the influence of root traits on soil properties changes through time is essential for restoring soils and their associated functions. In addition, in a couple of studies (Pohl et al. 2010, Gould et al. 2016) the effects of RLD on aggregate stability were modified by community diversity. Future studies that identify how different ecosystem attributes modify interactions among root traits, soil aggregation, and ecosystem services (e.g. soil erosion, carbon sequestration, soil biodiversity) would be particularly beneficial for guiding restoration practice.

Traits related to greater root system extent (RD, RL, RLD) have frequently been related to reduced erosion by water. In a meta-analysis of 36 studies, Vannoppen et al. (2015) found that both high RD and RLD reduced soil detachment resulting from concentrated flow. In this meta-analysis and several other studies (e.g., Burylo et. al 2012, De Baets et al. 2007, De Baets 2010), authors found RLD better-explained soil detachment rates than RD. This is because fine roots (i.e. fibrous root systems) have high root to soil contact area and are more effective at reducing soil erosion than a few thick roots (i.e. tap roots) (e.g., De Baets et al. 2007, De Baets 2010, Zhang et al. 2014, Zhong et al. 2016). Similarly, Adhikari et al. (2013) and Burylo et al. (2011) found that species with high RAR had the greatest positive influence on soil stability of stream banks and mountain slopes. Although it may seem obvious that a more extensive root system would lead to greater soil stability, other root traits may modify this general pattern.

Tensile strength

Root tensile strength is a mechanical trait that is calculated as the force required to break a root divided by the cross-sectional area of a root (e.g. Bischetti et al. 2005). It has been used extensively in models relating roots to soil shear strength (e.g. Wu et al. 1979, Pollen and Simon 2005) and numerous studies have found a non-linear inverse relationship between root tensile strength and root diameter such that smaller roots have higher tensile strength per unit area compared to larger roots (e.g. Genet et al. 2005, De Baets et. al 2008, Burylo et al. 2014). Because of this relationship, root cohesion resulting from many thin roots is greater than cohesion resulting from a few thick roots. Despite this general relationship, the effect of tensile strength on soil erosion may be modified by root traits related to architecture and extent. For example, working with riparian shrubs, Adhikari et al. (2013) found that species with moderate tensile strength and high RAR were more effective at stabilizing soils along riverbanks than species with the high tensile strength but low RAR. Relatedly, De Baets et al. (2008) found that differences in soil shear strength varied by depth at which roots of different species were most prevalent: high tensile strength graminoid species influenced soil cohesion at 0-10 cm whereas effects of shrubs dominated at deeper soil depths. As erosion processes may vary at small spatial scales (Ghestem et al. 2014) and the influence of root traits on soil stability may be influenced by soil type (Vannoppen 2017), considering the effects of root traits in relation to site- and location-specific erosion threats will likely result in the most effective species selection for restoration projects focused on erosion reduction.

FUTURE DIRECTIONS FOR IMPROVED TRAIT-BASED RESTORATION

We argue that to more effectively utilize trait-based approaches in ecological restoration, more research is needed that explicitly links traits to performance measures and identifies the effects of specific traits on ecosystem processes and functions. In the vast majority of studies related to soil stability, root traits are used as independent (i.e. effect traits) rather than dependent (response traits) variables. Because of this, specific traits (e.g. RLD and tensile strength) have been identified as key contributors to soil stability, an important ecosystem service. In contrast, root traits were considered response traits in most studies related to drought and competition and were rarely related to performance measures such as survival or growth rate. While this “response-centered” approach highlights how environmental stressors affect traits, it does little to elucidate which traits are important for species establishment and persistence in stressful conditions or which traits will influence key ecosystem processes. We believe a two-tiered research agenda that combines a vital-rates approach with a greater focus on effect-traits is needed to advance trait-based restoration.

Several authors have argued that linking individual traits to population-level fitness components (i.e. vital rates; e.g., survival, growth rate, reproductive output) is imperative for reliable trait-based predictions of population, community, and ecosystem dynamics (e.g., Violle et al. 2007, Laughlin and Messier 2015). Focusing on survival/establishment and individual growth rates as proxies of fitness may be particularly tangible and informative in restoration contexts. By understanding how traits influences critical life stage transitions at the seedling stage (James et al. 2011, Larson et al. 2014), researchers and practitioners may gain insight into longer-term patterns of community development (e.g., Harrison and LaForgia 2019). However, because specific trait values are unlikely to improve survival or growth in all environments (e.g., Laughlin et al. 2018), understanding how traits affect performance under various abiotic and biotic conditions is essential for identifying widespread vs. context specific effects. As ecological restoration is undertaken in a diversity of systems and conditions, ample opportunities exist to test causal relationships between traits, plant performance, and fitness in restoration settings.

In water-limited systems, identifying how specific traits influence performance measures under different types of moisture deficit may improve source and species selection for ecosystem-specific restoration. Mirroring broader ecological research (Slette et al. 2019), most studies we reviewed equated “dry” conditions with drought without providing context for this characterization by, for example, comparing deficit treatments to long-term ranges of variability or standardized climatic index values. Because of this, elucidating general trends and patterns remains difficult. Studies that assess the effectiveness of root traits along gradients of precipitation or under various drought scenarios (e.g., moderate vs. severe drought; pulse vs. press drought; e.g., Zwicke et al. 2015, Padilla et al. 2013) would inform the development of ecosystem-specific seed mixes capable of persisting under various types of moisture deficit.

In the contexts of competition and invasion, focusing on causal relationships between traits and performance measures may be most informative if considered within the response-effect framework. Resource-mediated plant competition has been used to explain competitive dynamics for decades (e.g. Gaudet and Keddy 1988, Goldberg et al. 1990, Casper and Jackson 1997). Yet, 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 (i.e. leaf water potential, height, rooting depth) related to resource depletion to both competitive effect and competitive response. By adopting this framework and extending results to survival and growth, researchers may reveal more generalizable patterns of competition than can be gleaned from pairwise competition studies. For example, the exotic annual species *Bromus rubens, Schismus spp.,* and *Erodium cicutarium* all increase biomass in high-nitrogen environments to the detriment of co-occurring native species (Brooks et al. 2003). Determining if similar traits are responsible for these increases would provide a trait-based explanation to this pattern. If consistent effects on nutrient and moisture resources were identified, species with appropriate traits could be selected for restoration. Appropriate traits would likely relate to competitive effects geared at suppressing neighbors via rapid resource acquisition or competitive responses associated with tolerance of low nutrient and moisture levels (Schemenko et al. 2017).

Once links between traits and performance in various abiotic and biotic situations are established, restoration projects can be designed to target specific ecosystem processes or functions (Laughlin 2014). However, to move towards this goal, appropriate statistical methods and considerable amounts of data will be needed to estimate direct and indirect relationships among traits and environmental variables. Structural equation modeling may be a particularly useful tool for quantifying these relationships as it enables researchers to test both direct and indirect casual relationships among variables (Grace 2006). Structural equation modeling has been used to link traits to ecosystem services in undisturbed systems (e.g., Bowker et al. 2010, Lavorel and Grigulis 2012, Lavorel et al. 2013, Bu et al. 2019), but it is rarely used in restoration research.

CONCLUSION

In this review we highlight the numerous ways that root traits can inform restoration research and practice. We specifically identify root traits that have been linked to performance measures of survival, establishment, and growth in environments threatened by drought, competition, and erosion. Root traits related to belowground resource acquisition (e.g., root length, rooting depth, SRL) are frequently linked to drought avoidance whereas root traits related to drought tolerance and hydraulic functional remain understudied. Similarly, studies linking root traits to plant competitive effects abound, whereas studies focused on root traits related to competitive response are more limited. Root traits associated with rapid resource acquisition (e.g., high SRL, root length, root system extent) are most often related to competitive effects. Albeit more limited, research suggests that root traits associated with resource conservation or stress tolerance (e.g., high RTD, high root diameter) may elucidate mechanisms related to competitive response. In the contexts of drought and competition, the responses of root traits to environmental stressors are assessed far more often than the effects of root traits on plant performance measures. In contrast, the effects of specific root traits such as root length and root tensile strength on topsoil and aggregate stability are well documented.

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 environmental stress. Second, determining which traits or suites of traits best predict plant performance at different ontogenetic stages may improve predictions of how plant communities will develop under various abiotic and biotic stressors. Third, tests of causal relationships among traits, performance measures, and ecosystem processes across diverse systems are needed to effectively apply trait-based approaches to ecological restoration. Restoration ecology provides opportunities to test these relationships and to contribute to the vast amounts of data that will be needed to move the field forward. With increasing global awareness of the importance of restoration for environmental and human well being (UNEA, 2019), and increasing amounts of publicly available trait data from the TRY (Kattage et al. 2020) and Fine-Root Ecology (Iversen et al. 2018) databases, we trust researchers and practitioners can get to the root of one of the world's most pressing challenges: restoring the world's damaged and degraded ecosystems.

Table 3.1: Most commonly encountered root traits in our review.

Trait	Abbreviation	Definition
Root biomass		Belowground biomass per plant
Root length		Total length of roots per plant
Rooting depth		Max rooting depth or 95% rooting depth
Root (mass) density		Belowground biomass per soil volume
Root mass ratio/fraction	RMR/RMF	Root dry mass/total plant mass
Root length density	RLD	Length of roots per soil volume
Root elongation rate	RER	Increase in root length/time
Root dry matter content	RDMC	Root dry mass/fresh mass
Root tissue density	RTD	Root dry mass/ root volume
Specific root length	SRL	Root length/dry mass
Tensile strength		Breaking force/cross sectional area

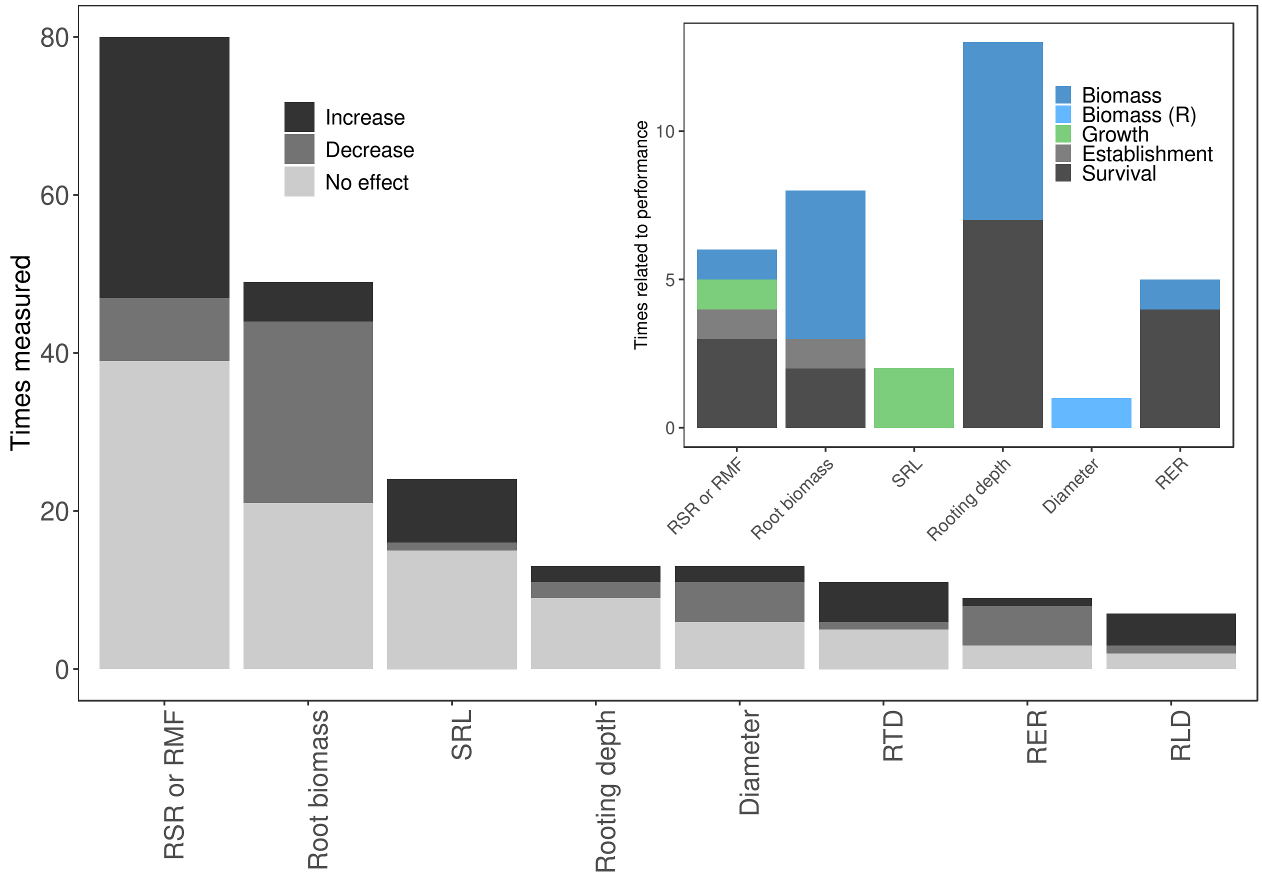

Figure 3.1: Main figure: Number of times traits were measured in relation to drought in reviewed studies (n = 86 references). All individual trait measurements were included if reported by authors (i.e. several trait measurements from a single study may contribute to the count reported here). Shading indicates whether drought resulted in an increase (darkest grey), decrease (medium grey), or no effect (light grey) on the specific root trait (x-axis). Inset: Number of times traits were related to performance measures under water-limited conditions. Colors refer to specific performance measures: biomass (blue), growth (green), and survival/establishment (grey). “Biomass” includes total and aboveground biomass, “Biomass (R)” stands for “recovery biomass” and “Growth” includes measures of growth rate and growth potential (a measure of growth under resource abundant conditions). Abbreviations are as follow: RSR: root to shoot ratio; RMF: Root mass fraction; SRL: specific root length; RTD: root tissue density; RER: root elongation rate; RLD: root length density.

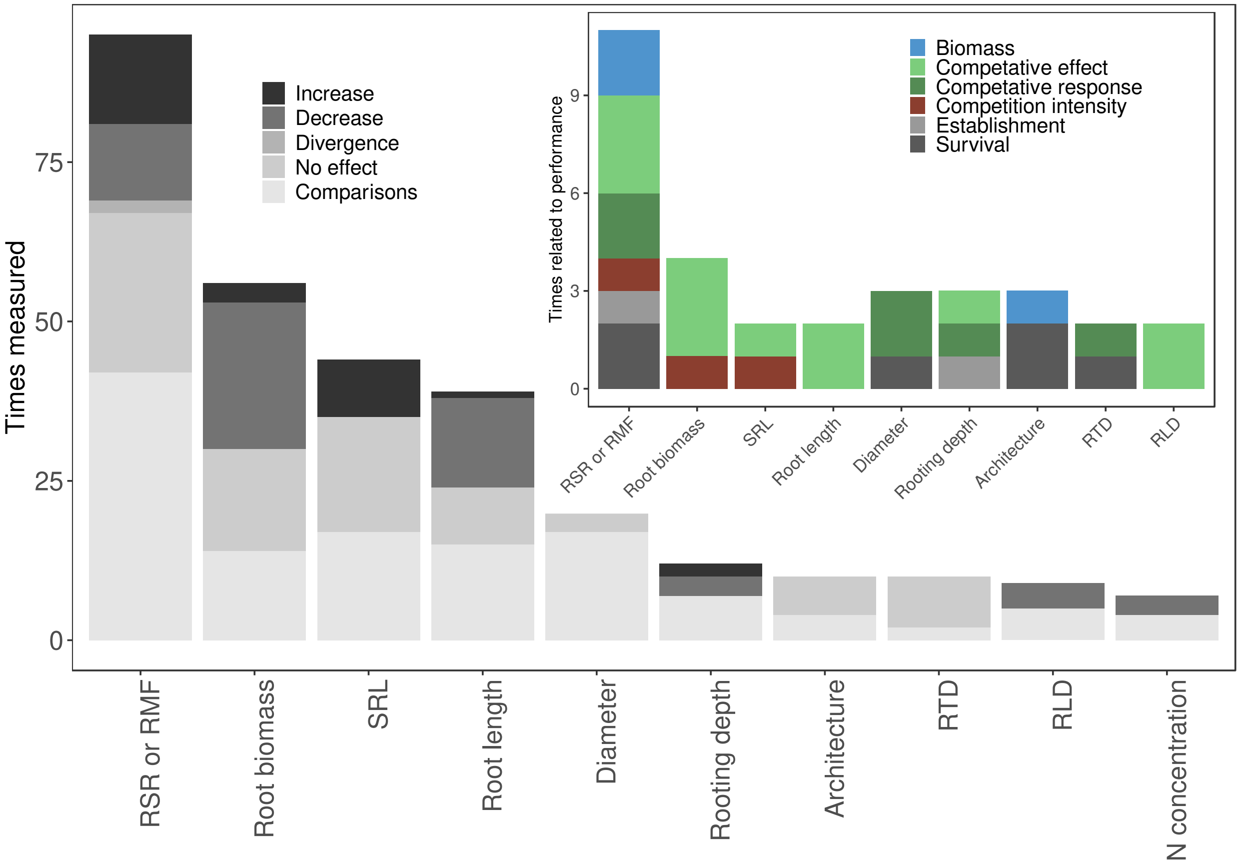

Figure 3.2: Main figure: Number of times traits were measured in relation to invasion or competition in reviewed studies (n = 69 references). All individual trait measurements were included if reported by authors (i.e. several trait measurements from a single study may contribute to the count reported here). Shading indicates whether competition resulted in an increase (darkest grey), decrease (medium-dark grey), divergence (medium grey) or no effect (medium-light grey) on traits. Comparative studies (i.e. those that compared traits among specific groups such as invasive vs. native species) are depicted in the lightest grey. Inset: Number of times traits were related to performance measures in competitive conditions. Colors refer to specific performance measures: biomass (blue), competitive effect (light green), competitive response (dark green), competition intensity (dark red), establishment (light grey), survival (dark grey). Abbreviations are as follow: RSR: root to shoot ratio; RMF: Root mass fraction; SRL: specific root length; RTD: root tissue density; RER: root elongation rate; RLD: root length density, N concentration: nitrogen concentration.

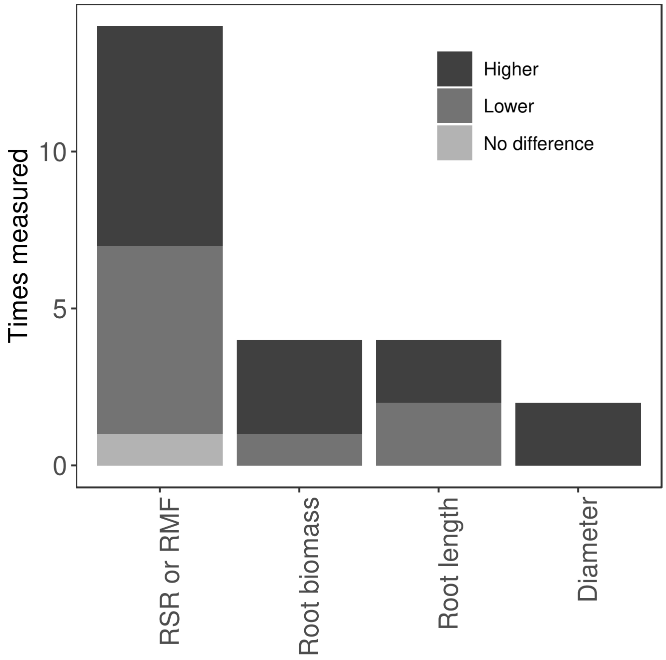

Figure 3.3: Number of times traits of invasive species were compared to either the same species in its home range or non-invasive species (n = 15 references). All individual trait measurements were included if reported by authors (i.e. several trait measurements from a single study may contribute to the count reported here). Shading indicates whether the invasive species possessed traits that had values that were higher (darkest grey), lower (medium grey), or similar (lightest grey) to "home" or native species. Abbreviations are as follow: RSR: root to shoot ratio; RMF: Root mass fraction.

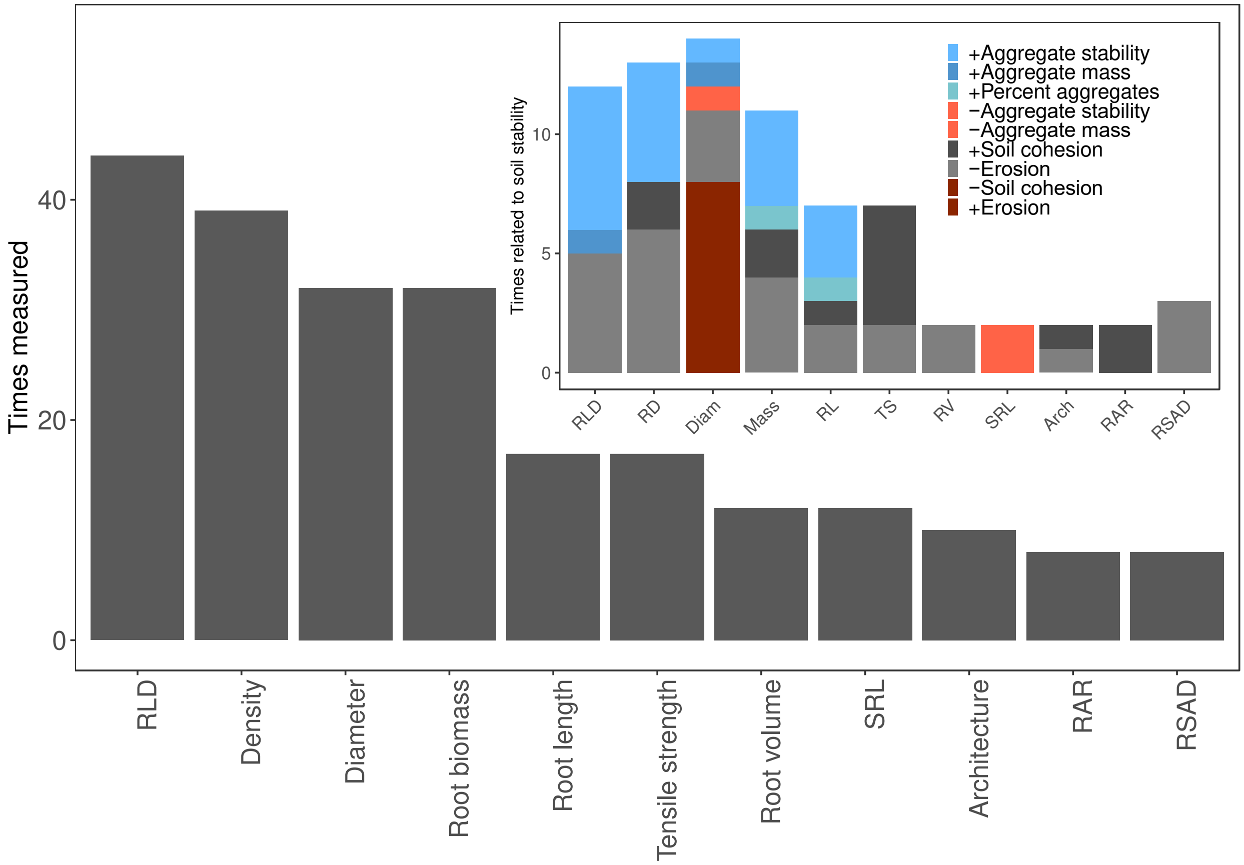

Figure 3.4: Main figure: Number of times traits were measured in relation to topsoil or aggregate stability in reviewed studies (n = 48 references). All individual trait measurements were included if reported by authors (i.e. several trait measurements from a single study may contribute to the count reported here). Inset: Number of times traits were related to components of soil stability in the reviewed studies. Colors are related to components of soil stability as follow: positive relationships to aggregate stability are depicted in shades of blue; negative relationships to aggregate stability are depicted in light red; positive relationships to soil cohesion or negative relationships to soil erosion are depicted in shades of grey; and negative relationships to soil cohesion or positive relationships to soil erosion are depicted in dark red. Abbreviations are as follow: RLD: root length density, RD/Density: root mass density, Diam: diameter, Mass: Root biomass; RL: root length; TS: tensile strength; RV: root volume; SRL: specific root length, Arch: Architecture (number of root tips or branches); RAR: root area ratio; RSAD: root surface area density.

REFERENCES

Adhikari AR, Gautam MR, Yu Z, et al (2013) Estimation of root cohesion for desert shrub species in the Lower Colorado riparian ecosystem and its potential for streambank stabilization. Ecological Engineering 51:33–44. doi: 10.1016/j.ecoleng.2012.12.005

Allen DC, Cardinale BJ, Thompson TW (2016) Plant biodiversity effects in reducing fluvial erosion are limited to low species richness. Ecology 97:17–24. doi: 10.1890/15-0800.1

Asay KH, Horton WH, Jensen KB, Palazzo AJ (2011) Merits of native and introduced Triticeae grasses on semiarid rangelands. Canadian Journal of Plant Science 81:45–52. doi: 10.4141/P99-131

Bardgett RD, Mommer L, De Vries FT (2014) Going underground: root traits as drivers of ecosystem processes. Trends in Ecology & Evolution 29:692–699. doi: 10.1016/j.tree.2014.10.006

Bartelheimer M, Gowing D, Silvertown J (2010) Explaining hydrological niches: the decisive role of below-ground competition in two closely related Senecio species. Journal of Ecology 98:126–136. doi: 10.1111/j.1365-2745.2009.01598.x

Belcher JW, Keddy PA, Twolan-Strutt L (1995) Root and shoot competition intensity along a soil depth gradient. The Journal of Ecology 83:673.

Bennett JA, Riibak K, Tamme R, et al (2016) The reciprocal relationship between competition and intraspecific trait variation. Journal of Ecology 104:1410–1420. doi: 10.1111/1365-2745.12614

Bischetti GB, Chiaradia EA, Simonato T, et al (2007) Root strength and root area ratio of forest species in Lombardy (Northern Italy). In: Eco-and Ground Bio-Engineering: The Use of Vegetation to Improve Slope Stability, 2nd edn. Springer, Dordrecht, Dordrecht, pp 31–41

Blankinship JC, Fonte SJ, Six J, Schimel JP (2016) Plant versus microbial controls on soil aggregate stability in a seasonally dry ecosystem. Geoderma 272:39–50. doi: 10.1016/j.geoderma.2016.03.008

Bloom AJ, Chapin SF, Mooney HA (1985) Resource limitation in plants-an economic analogy. Annual Reviews in Ecology and Systematics 16:363-692 doi: 10.1146/annurev.es.16.110185.002051

Bowker MA, Maestre FT, Escolar C (2010) Biological crusts as a model system for examining the biodiversity–ecosystem function relationship in soils. Soil Biology and Biochemistry 42:405–417. doi: 10.1016/j.soilbio.2009.10.025

Bristiel P, Roumet C, Violle C, Volaire F (2019) Coping with drought: root trait variability within the perennial grass *Dactylis glomerata* captures a trade-off between dehydration avoidance and dehydration tolerance. Plant Soil 434:327–342. doi: 10.1007/s11104-018-3854-8

Brooks ML (2003) Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. Journal of Applied Ecology 40:344–353. doi: 10.1046/j.1365-2664.2003.00789.x

Brouwer R (1983) Functional equilibrium: sense or nonsense? Netherlands Journal of Agricultural Sciences 31:335–348

Brown CS, Anderson VJ, Claassen VP, et al (2008) Restoration ecology and invasive plants in the semiarid west. Invasive Plant Science and Management 1:399–413. doi: 10.1614/IPSM-08-082.1

Bu W, Huang J, Xu H, et al (2019) Plant functional traits are the mediators in regulating effects of abiotic site conditions on aboveground carbon stock-evidence from a 30 ha tropical forest plot. Frontiers in Plant Science 9:25. doi: 10.3389/fpls.2018.01958

Burns JH, Strauss SY (2012) Effects of competition on phylogenetic signal and phenotypic plasticity in plant functional traits. Ecology 93:S126–S137. doi: 10.1890/11-0401.1

Burylo M, Dutoit T, Rey F (2014) Species traits as practical tools for ecological restoration of marly eroded lands. Restoration Ecology 22:633–640. doi: 10.1111/rec.12113

Burylo M, Hudek C, Rey F (2011) Soil reinforcement by the roots of six dominant species on eroded mountainous marly slopes (Southern Alps, France). CATENA 84:70–78. doi: 10.1016/j.catena.2010.09.007

Burylo M, Rey F, Mathys N, Dutoit T (2012) Plant root traits affecting the resistance of soils to concentrated flow erosion. Earth Surface Processes and Landforms 37:1463–1470. doi: 10.1002/esp.3248

Burylo M, Rey F, Roumet C, et al (2009) Linking plant morphological traits to uprooting resistance in eroded marly lands (Southern Alps, France). Plant Soil 324:31–42. doi: 10.1007/s11104-009-9920-5

Cahill JF (1999) Fertilization effects on interactions between above- and belowground competition in an oil field. Ecology 80:466–480. doi: 10.1890/0012-9658(1999)080[0466:FEOIBA]2.0.CO;2

Cahill JF, Casper BB (2000) Investigating the relationship between neighbor root biomass and belowground competition: field evidence for symmetric competition belowground. Oikos 90:311–320. doi: 10.1034/j.1600-0706.2000.900211.x

Cahill JF (2002) Interactions between root and shoot competition vary among species. Oikos 99:101–112. doi: 10.1034/j.1600-0706.2002.990111.x

Cahill JF (2003) Lack of relationship between below-ground competition and allocation to roots in 10 grassland species. Journal of Ecology 91: 532:540 doi: 10.1046/j.1365-2745.2003.00792.x

Cahill JF, Kembel SW, Gustafson DJ (2005) Differential genetic influences on competitive effect and response in *Arabidopsis thaliana*. Journal of Ecology 93:958–967. doi: 10.1111/j.1365-2745.2005.01013.x

Canadell J, Zedler PH (1995) Underground structures of woody plants in Mediterranean ecosystems of Australia, California, and Chile. In: Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia. Springer, New York, NY, New York, NY, pp 177–210

Cerdà A, García-Fayos P (1997) The influence of slope angle on sediment, water and seed losses on badland landscapes. Geomorphology 18:77–90. doi: 10.1016/S0169-555X(96)00019-0

Chambers JC (2000) Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: Implications for restoration. Ecological Applications 10:1400–1413. doi: 10.1890/1051-0761(2000)010[1400:SMASFI]2.0.CO;2

Clements FE, Weaver JE, Hanson HC (1929) Plant competition: an analysis of community functions. Carnegie institution of Washington.

Collins CG, Wright SJ, Wurzburger N (2016) Root and leaf traits reflect distinct resource acquisition strategies in tropical lianas and trees. Oecologia 180:1037–1047. doi: 10.1007/s00442-015-3410-7

Comas L, Becker S, Cruz VMV, et al (2013) Root traits contributing to plant productivity under drought. Frontiers in Plant Science 4:1–16. doi: 10.3389/fpls.2013.00442

Coomes DA, Grubb PJ (2000) Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. Ecological Monographs 70:171-207. doi: 10.1890/0012-9615(2000)070[0171:IORCIF]2.0.CO;2

Corcuera L, Gil-Pelegrín E, Notivol E (2012) Differences in hydraulic architecture between mesic and xeric Pinus pinaster populations at the seedling stage. Annals of Botany. doi: 10.1093/treephys/tps103

Cosentino D, Chenu C, Le Bissonnais Y (2006) Aggregate stability and microbial community dynamics under drying–wetting cycles in a silt loam soil. Soil Biology and Biochemistry 38:2053–2062. doi: 10.1016/j.soilbio.2005.12.022

Craine JM (2009) Resource strategies of wild plants. Princeton University Press.

Dai A (2011) Drought under global warming: a review. Wiley Interdisciplinary Reviews: Climate Change 2:45–65. doi: 10.1002/wcc.81

De Baets S, Poesen J (2010) Empirical models for predicting the erosion-reducing effects of plant roots during concentrated flow erosion. Geomorphology 118:425–432. doi: 10.1016/j.geomorph.2010.02.011

De Baets S, Poesen J, Knapen A, Galindo P (2007) Impact of root architecture on the erosion-reducing potential of roots during concentrated flow. Earth Surface Processes and Landforms 32:1323–1345. doi: 10.1002/esp.1470

De Baets S, Poesen J, Reubens B, et al (2008) Root tensile strength and root distribution of typical Mediterranean plant species and their contribution to soil shear strength. Plant and Soil 305:207–226. doi: 10.1007/s11104-008-9553-0

De Gryze S, Six J, Brits C, Merckx R (2005) A quantification of short-term macroaggregate dynamics: influences of wheat residue input and texture. Soil Biology and Biochemistry 37:55–66. doi: 10.1016/j.soilbio.2004.07.024

Demenois J, Carriconde F, Bonaventure P, et al (2018a) Impact of plant root functional traits and associated mycorrhizas on the aggregate stability of a tropical Ferralsol. Geoderma 312:6–16. doi: 10.1016/j.geoderma.2017.09.033

Demenois J, Rey F, Ibanez T, et al (2018b) Linkages between root traits, soil fungi and aggregate stability in tropical plant communities along a successional vegetation gradient. Plant and Soil 424:319–334. doi: 10.1007/s11104-017-3529-x

Eckhart VM, Howland MR, Jennison K, et al (2017) Contrasting soil-texture niches facilitate coexistence of two congeneric plants that differ in competitive ability. AoB PLANTS 9: plx066; doi: 10.1093/aobpla/plx066

Ehleringer JR, Dawson TE (1992) Water uptake by plants: perspectives from stable isotope composition. Plant Cell Environ 15:1073–1082. doi: 10.1111/j.1365-3040.1992.tb01657.x

Engelbrecht BMJ, Kursar TA, Tyree MT (2005) Drought effects on seedling survival in a tropical moist forest. Trees 19:312–321. doi: 10.1007/s00468-004-0393-0

Erktan A, Cécillon L, Graf F, et al (2016) Increase in soil aggregate stability along a Mediterranean successional gradient in severely eroded gully bed ecosystems: combined effects of soil, root traits and plant community characteristics. Plant and Soil 398:121–137. doi: 10.1007/s11104-015-2647-6

Feng Y, van Kleunen M (2016) Phylogenetic and functional mechanisms of direct and indirect interactions among alien and native plants. Journal of Ecology 104:1136–1148. doi: 10.1111/1365-2745.12577

Ferguson SD, Leger EA, Li J, Nowak RS (2015) Natural selection favors root investment in native grasses during restoration of invaded fields. Journal of Arid Environments 116:11–17. doi: 10.1016/j.jaridenv.2015.01.009

Fort F, Cruz P, Jouany C (2014) Hierarchy of root functional trait values and plasticity drive early-stage competition for water and phosphorus among grasses. Functional Ecology 28:1030–1040. doi: 10.1111/1365-2435.12217

Freschet GT, Swart EM, Cornelissen JHC (2015) Integrated plant phenotypic responses to contrasting above- and below-ground resources: key roles of specific leaf area and root mass fraction. New Phytologist 206:1247–1260. doi: 10.1111/nph.13352

Freschet GT, Valverde-Barrantes OJ, Tucker CM, et al (2017) Climate, soil and plant functional types as drivers of global fine-root trait variation. Journal of Ecology 105:1182–1196. doi: 10.1111/1365-2745.12769

Funk JL (2013) The physiology of invasive plants in low-resource environments. Conservation Physiology 1:1 cot 026 doi: 10.1093/conphys/cot026

Funk JL (2008) Differences in Plasticity between invasive and native plants from a low resource environment. Journal of Ecology 96:1162–1173. doi: 10.2307/20143564

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology & Evolution 23:695–703. doi: 10.1016/j.tree.2008.07.013

Funk JL, Larson JE, Ames GM, et al (2016) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biological Reviews 1–18. doi: 10.1111/brv.12275

Funk JL, Wolf AA (2016) Testing the trait-based community framework: Do functional traits predict competitive outcomes? Ecology 97:2206–2211. doi: 10.1002/ecy.1484

Garnier E, Navas ML, Grigulis K (2016) Plant Functional Diversity: Organism traits, community structure, and ecosystem properties. Oxford Scholarship Online. doi: 10.1093/acprof:oso/9780198757368.001.0001

Gaudet CL, Keddy PK (1988) A comparative approach to predicting competitive ability from plant traits. Nature 334: 242-243

Gedroc JJ, McConnaughay KDM, Coleman JS (1996) Plasticity in Root/Shoot Partitioning: Optimal, Ontogenetic, or Both? Functional Ecology 10:44. doi: 10.2307/2390260

Genet M, Stokes A, Salin F, et al (2005) The influence of cellulose content on tensile strength in tree roots. Plant and Soil 278:1–9. doi: 10.1007/s11104-005-8768-6

Ghestem M, Cao K, Ma W, et al (2014) A Framework for identifying plant species to be used as "ecological engineers" for fixing soil. PLoS One. 10.1371/journal.pone.0095876

Gibson A, Nelson CR, Atwater DZ (2018) Response of bluebunch wheatgrass to invasion: Differences in competitive ability among invader-experienced and invader-naïve populations. Functional Ecology 32:1857–1866. doi: 10.1111/1365-2435.13090

Gioria M, Osborne BA (2014) Resource competition in plant invasions: emerging patterns and research needs. Frontiers Plant Science 5:445. doi: 10.3389/fpls.2014.00501

Goldberg D (1990) Components of resource competition in plants. In: Perspectives on plant competition. Elsevier Inc.

Goldberg D (1996) Competitive ability: definitions, contingency and correlated traits. Philosophical Transitions of the Royal Society. Biological sciences. 351:1377–1385. doi: 10.1098/rstb.1996.0121

Goldberg DE, Fleetwood L (1987) Competitive effect and response in four annual plants. The Journal of Ecology 75:1131. doi: 10.2307/2260318

Goodwin JR, Doescher PS, Eddleman LE, Zobel DB (1999) Persistence of Idaho Fescue on degraded sagebrush-steppe. Journal of Range Management 52:187. doi: 10.2307/4003515

Gordon DR, Rice KJ (1993) Competitive effects of grassland annuals on soil water and Blue Oak (*Quercus Douglasii*) seedlings. Ecology 74:68–82. doi: 10.2307/1939502

Gould IJ, Quinton JN, Weigelt A, et al (2016) Plant diversity and root traits benefit physical properties key to soil function in grasslands. Ecology Letters 19:1140–1149. doi: 10.1111/ele.12652

Griffin-Nolan RJ, Bushey JA, Carroll CJW, et al (2018) Trait selection and community weighting are key to understanding ecosystem responses to changing precipitation regimes. Functional Ecology 32:1746–1756. doi: 10.1111/1365-2435.13135

Grime JP (1979) Plant strategies and vegetation processes. John Wiley and Sons, Inc.

Grime JP, Thompson K, Hunt R, et al (1997) Integrated screening validates primary axes of specialisation in plants. Oikos 79:259. doi: 10.2307/3546011

Grime JP (2006) Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. Journal of vegetation science 17:255–260. doi: 10.1111/j.1654-1103.2006.tb02444.x

Gyssels G, Poesen J, Bochet E, Li Y (2016) Impact of plant roots on the resistance of soils to erosion by water: a review:. Progress in Physical Geography 29:189–217. doi: 10.1191/0309133305pp443ra

Hacke UG, Sperry JS, Pittermann J (2000) Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. Basic and Applied Ecology 1:31–41. doi: 10.1078/1439-1791-00006

Hajek P, Hertel D, Leuschner C (2014) Root order- and root age-dependent response of two poplar species to belowground competition. Plant and Soil 377:337–355. doi: 10.1007/s11104-013-2007-3

Hanslin HM, Bischoff A, Hovstad KA (2019) Root growth plasticity to drought in seedlings of perennial grasses. Plant and Soil 440:551–568. doi: 10.1007/s11104-019-04117-7

Hardegree S, Schneider J, Moffet CA (2012) Weather variability and adaptive management for rangeland restoration. Rangelands 34:53-56. doi: 10.2111/RANGELANDS-D-12-00048.1

Hardegree SP, Moffet CA, Flerchinger GN, et al (2013) Hydrothermal Assessment of Temporal Variability in Seedbed Microclimate. Rangeland Ecology & Management 66:127–135. doi: 10.2111/REM-D-11-00074.1

Hardegree SP, Moffet CA, Roundy BA, et al (2010) A comparison of cumulative-germination response of cheatgrass (Bromus tectorum L.) and five perennial bunchgrass species to simulated field-temperature regimes. Environmental and Experimental Botany 69:320–327. doi: 10.1016/j.envexpbot.2010.04.012

Harrison S, LaForgia M (2019) Seedling traits predict drought-induced mortality linked to diversity loss. Proceedings of the National Academy of Sciences 116:5576–5581. doi: 10.1073/pnas.1818543116

Herben T, Goldberg DE (2014) Community assembly by limiting similarity vs. competitive hierarchies: testing the consequences of dispersion of individual traits. Journal of Ecology 102:156–166. doi: 10.1111/1365-2745.12181

HilleRisLambers J, Adler PB, Harpole WS, et al (2012) Rethinking community assembly through the lens of coexistence theory. Annual Reviews in Ecology Evolution and Systematics 43:227–248. doi: 10.1146/annurev-ecolsys-110411-160411

Hobbs RJ, Walker LR, Walker J (2007) Integrating Restoration and Succession. In: Linking Restoration and Ecological Succession. Springer, New York, NY, New York, NY, pp 168–179

Horton JL, Clark JL (2001) Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings. Forest Ecology and Management 140:239–247. doi: 10.1016/S0378-1127(00)00314-5

Howard TG, Goldberg DE (2001) Competitive response hierarchies for germination, growth, survival and their influence on abundance. Ecology 82:979–990. doi: 10.1890/0012 9658(2001)082[0979:CRHFGG]2.0.CO;2

Huang B, Duncan RR, Carrow RN (1997) Drought-resistance mechanisms of seven warm-season Turfgrasses under surface soil drying: I. Shoot Response. Crop Science 37:1858–1863. doi: 10.2135/cropsci1997.0011183X003700060032x

IPBES (2019) Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Global Assessment Report on Biodiversity and Ecosystem Services.

Iversen CM, Powell AS, McCormack ML, et al (2018) Fine-Root Ecology Database (FRED): A Global Collection of Root Trait Data with Coincident Site, Vegetation, Edaphic, and Climatic Data, Version 2. Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. Access on-line at: https://doi.org/10.25581/ornlsfa.012/1417481.

Jastrow JD, Miller RM, Lussenhop J (1998) Contributions of interacting biological mechanisms to soil aggregate stabilization in restored prairie. Soil Biology and Biochemistry 30:905–916. doi: 10.1016/S0038-0717(97)00207-1

Jiang Y, Huang B (2000) Effects of drought or heat stress alone and in combination on Kentucky Bluegrass. Crop Science 40:1358–1362. doi: 10.2135/cropsci2000.4051358x

Jones HP, Jones PC, Barbier EB, et al (2018) Restoration and repair of Earth's damaged ecosystems. Proceedings of the Royal Society B: Biological Sciences 285:20172577. doi: 10.1098/rspb.2017.2577

Jupp AP, Newman EI (1987) morphological and anatomical effects of severe drought on the roots of *Lolium perenne* L. New Phytologist 105:393–402. doi: 10.1111/j.1469-8137.1987.tb00876.x

Jury WA, Horton R (2004) Soil physics. John Wiley and Sons, Inc. Hoboken, New Jersey.

Kattge, J, Bönisch, G, Díaz, S, et al. (2020). TRY plant trait database - enhanced coverage and open access

Keddy P, Nielsen K, Weiher E, Lawson R (2002) Relative competitive performance of 63 species of terrestrial herbaceous plants. Journal of vegetation Science 13:5–16. doi: 10.1111/j.1654-1103.2002.tb02018.x

Kildisheva OA, Erickson TE, Merritt DJ, et al (2016) Setting the scene for dryland restoration: an overview and key findings from a workshop targeting seed enablement technologies. Restoration Ecology 24: 35-42 doi: doi.org/10.1111/rec.12392

Kiær LP, Weisbach AN, Weiner J (2013) Root and shoot competition: a meta-analysis. Journal of Ecology 101:1298–1312. doi: 10.1111/1365-2745.12129

Knapen A, Poesen J, Govers G, et al (2007) Resistance of soils to concentrated flow erosion: A review. Earth-Science Reviews 80:75–109. doi: 10.1016/j.earscirev.2006.08.001

Köcher P, Horna V, Beckmeyer I, Leuschner C (2012) Hydraulic properties and embolism in small-diameter roots of five temperate broad-leaved tree species with contrasting drought tolerance. Annals of Forest Science 69:693–703. doi: 10.1007/s13595-012-0189-0

Kramer-Walter KR, Bellingham PJ, Millar TR, et al (2016) Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. Journal of Ecology 104:1299–1310. doi: 10.1111/1365-2745.12562

Kulmatiski A, Beard KH (2013) Woody plant encroachment facilitated by increased precipitation intensity. Nature Climate Change 3: 833–837 doi: doi.org/10.1038/nclimate1904

Kunstler G, Lavergne S, Courbaud B, et al (2012) Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. Ecology Letters 15:831–840. doi: 10.1111/j.1461-0248.2012.01803.x

Larson JE, Funk JL (2016) Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms. New Phytologist 210:827–838. doi: 10.1111/nph.13829

Larson JE, Sheley RL, Hardegree SP, et al (2014) Seed and seedling traits affecting critical life stage transitions and recruitment outcomes in dryland grasses. Journal of Applied Ecology 52:199–209. doi: 10.1111/1365-2664.12350

Lauenroth WK, Bradford JB (2009) Ecohydrology of dry regions of the United States: precipitation pulses and intraseasonal drought. Ecohydrology 2: 173–181.

Laughlin DC (2014) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. Ecology Letters 17:771–784. doi: 10.1111/ele.12288

Laughlin DC, Messier J (2015) Fitness of multidimensional phenotypes in dynamic adaptive landscapes. Trends in Ecology & Evolution 30:487–496. doi: 10.1016/j.tree.2015.06.003

Laughlin DC, Strahan RT, Adler PB, Moore MM (2018) Survival rates indicate that correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits. Ecol Letters 21:411–421. doi: 10.1111/ele.12914

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16:545–556. doi: 10.1046/j.1365-2435.2002.00664.x

Lavorel S, Grigulis K (2012) How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. Journal of Ecology 100:128–140. doi: 10.1111/j.1365-2745.2011.01914.x

Lavorel S, Storkey J, Bardgett RD, et al (2013) A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. Journal of vegetation science 24:942–948. doi: 10.1111/jvs.12083

Leger EA, Atwater DZ, James JJ (2019) Seed and seedling traits have strong impacts on establishment of a perennial bunchgrass in invaded semi-arid systems. Journal of Applied Ecology 56:1343–1354. doi: 10.1111/1365-2664.13367

Leger EA, Goergen EM (2017) Invasive *Bromus tectorum* alters natural selection in arid systems. Journal of Ecology 105:1509–1520. doi: 10.1111/1365-2745.12852

Leishman MR, Westoby M (1994) The role of seed size in seedling establishment in dry soil conditions -- experimental evidence from semi-arid species. The Journal of Ecology 82:249. doi: 10.2307/2261293

Leiva MJ, Fernández-Alés R (1998) Variability in seedling water status during drought within a *Quercus ilex subsp. ballota* population, and its relation to seedling morphology. Forest Ecology and Management 111:147–156. doi: 10.1016/S0378-1127(98)00320-X

Li Q, Liu G, Zhang Z, et al (2015) Effect of root architecture on structural stability and erodibility of topsoils during concentrated flow in hilly Loess Plateau. Chinese Geographical Science 25:757–764. doi: 10.1007/s11769-014-0723-0

Lloret F, Casanovas C, Penuelas J (1999) Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. Functional Ecology 13:210–216. doi: 10.1046/j.1365-2435.1999.00309.x

Lopez-Iglesias B, Villar R, Poorter L (2014) Functional traits predict drought performance and distribution of Mediterranean woody species. Acta Oecologica 56:10–18. doi: 10.1016/j.actao.2014.01.003

Lü Y, Fu B, Chen L, et al (2016) Nutrient transport associated with water erosion: progress and prospect:. Progress in Physical Geography 31:607–620. doi: 10.1177/0309133307087085

Macarthur R, Levins R (1967) The Limiting Similarity, Convergence, and Divergence of Coexisting Species. The American Naturalist 101:377–385. doi: 10.1086/282505

Mack RN (1981) Invasion of *Bromus tectorum* L. into western north America: An ecological chronicle. Agro-Ecosystems 7:145–165.

Mardhiah U, Caruso T, Gurnell A, Rillig MC (2014) Just a matter of time: Fungi and roots significantly and rapidly aggregate soil over four decades along the Tagliamento River, NE Italy. Soil Biology and Biochemistry 75:133–142. doi: 10.1016/j.soilbio.2014.04.012

Mayfield MM, Levine JM (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085–1093. doi: 10.1111/j.1461-0248.2010.01509.x

McPhee CS, Aarssen (2001) The separation of above-and below-ground competition in plants a review and critique of methodology. Plant Ecology 152: 119-136 doi: 10.2307/20051026

Moles AT, Westoby M (2004) Seedling survival and seed size: a synthesis of the literature. Journal of Ecology 92:372–383. doi: 10.1111/j.0022-0477.2004.00884.x

Mommer L, Visser EJW, van Ruijven J, et al (2011) Contrasting root behaviour in two grass species: a test of functionality in dynamic heterogeneous conditions. Plant and Soil 344:347–360. doi: 10.1007/s11104-011-0752-8

Müller I, Schmid B, Weiner J (2000) The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. Perspectives in Plant Ecology, Evolution and Systematics 3:115-127 doi: 10.1078/1433-8319-00007

Novoplansky A, Goldberg D (2001) Interactions between neighbour environments and drought resistance. Journal of Arid Environments 47:11–32. doi: 10.1006/jare.2000.0701

Olmo M, Lopez-Iglesias B, Villar R (2014) Drought changes the structure and elemental composition of very fine roots in seedlings of ten woody tree species. Implications for a drier climate. Plant and Soil 384:113–129. doi: 10.1007/s11104-014-2178-6

Ostonen I, Püttsepp Ü, Biel C, et al (2007) Specific root length as an indicator of environmental change. Plant Biosystems 141:426–442. doi: 10.1080/11263500701626069

Padilla FM, de Dios Miranda J, Pugnaire FI (2007) Early root growth plasticity in seedlings of three Mediterranean woody species. Plant and Soil 296:103–113. doi: 10.1007/s11104-007-9294-5

Padilla FM, Pugnaire FI (2007) Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Functional Ecology 21:489–495. doi: 10.1111/j.1365-2435.2007.01267.x

Padilla FM, Aarts BHJ, Roijendijk YOA et al (2013) Root plasticity maintains growth of temperate grassland species under pulsed water supply. Plant and Soil 369:377-386

Peralta AML, Sánchez AM, Luzuriaga AL, et al (2019) Evidence of functional species sorting by rainfall and biotic interactions: A community monolith experimental approach. Journal of Ecology 107:2772–2788. doi: 10.1111/1365-2745.13210

Pérez-Ramos IM, Roumet C, Cruz P, et al (2012) Evidence for a “plant community economics spectrum” driven by nutrient and water limitations in a Mediterranean rangeland of southern France. Journal of Ecology 100:1315–1327. doi: 10.1111/1365-2745.12000

Pillay T, Ward D (2014) Competitive effect and response of savanna tree seedlings: comparison of survival, growth and associated functional traits. Journal of vegetation science 25:226–234. doi: 10.1111/jvs.12075

Pimentel D, Harvey C, Resosudarmo P, et al (1995) Environmental and economic costs of soil erosion and conservation benefits. Science 267:1117–1123. doi: 10.1126/science.267.5201.1117

Podwojewski P, Grellier S, Mthimkhulu S, Titshall L (2014) How tree encroachment and soil properties affect soil aggregate stability in an eroded grassland in South Africa. Soil Science Society of America Journal 78:1753–1764. doi: 10.2136/sssaj2013.12.0511

Pohl M, Graf F, Buttler A, Rixen C. (2012) The relationship between plant species richness and soil aggregate stability can depend on disturbance. Plant and Soil. 355:87–102 doi: 10.1007/s11104-011-1083-5

Poirier V, Roumet C, Angers DA, Munson AD (2018) Species and root traits impact macroaggregation in the rhizospheric soil of a Mediterranean common garden experiment. Plant and Soil 424:289–302. doi: 10.1007/s11104-017-3407-6

Pollen N, Simon A (2005) Estimating the mechanical effects of riparian vegetation on stream bank stability using a fiber bundle model. Water Resources Research 41:55. doi: 10.1029/2004WR003801

Pollen-Bankhead N, Simon A (2010) Hydrologic and hydraulic effects of riparian root networks on streambank stability: Is mechanical root-reinforcement the whole story? Geomorphology 116:353–362. doi: 10.1016/j.geomorph.2009.11.013

Poorter H, Niklas KJ, Reich PB, et al (2011) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytologist 193:30–50. doi: 10.1111/j.1469-8137.2011.03952.x

Pywell RF, Bullock JM, Roy DB, et al (2003) Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40:65–77. doi: 10.1046/j.1365-2664.2003.00762.x

Reader RJ, Jalili A, Grime JP, et al (1993) A comparative study of plasticity in seedling rooting depth in drying soil. The Journal of Ecology 81:543.

Ren GQ, Li Q, Li Y, et al (2019) The enhancement of root biomass increases the competitiveness of an invasive plant against a co-occurring native plant under elevated nitrogen deposition. Flora 261:151486. doi: 10.1016/j.flora.2019.151486

Reubens B, Poesen J, Danjon F, et al (2007) The role of fine and coarse roots in shallow slope stability and soil erosion control with a focus on root system architecture: a review. Trees 21:385–402. doi: 10.1007/s00468-007-0132-4

Reynolds HL, D Antonio C (1996) The ecological significance of plasticity in root weight ratio in response to nitrogen: Opinion. Plant and Soil 185:75–97. doi: 10.1007/BF02257566

Rillig MC, Aguilar-Trigueros CA, Bergmann J, et al (2015) Plant root and mycorrhizal fungal traits for understanding soil aggregation. New Phytologist 205:1385–1388. doi: 10.1111/nph.13045

Rowe CLJ, Leger EA (2010) Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. Evolutionary Applications 4:485–498. doi: 10.1111/j.1752-4571.2010.00162.x

Schwinning S, Meckel H, Reichmann LG, et al (2017) Accelerated development in Johnsongrass seedlings (*Sorghum halepense*) suppresses the growth of native grasses through size-asymmetric competition. PLoS ONE 12:e0176042. doi: 10.1371/journal.pone.0176042

Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113:447–455. doi: 10.1007/s004420050397

Semchenko M, Lepik A, Abakumova M, Zobel K (2018) Different sets of belowground traits predict the ability of plant species to suppress and tolerate their competitors. Plant and Soil 424:157–169. doi: 10.1007/s11104-017-3282-1

Six J, Bossuyt H, Degryze S, Denef K (2004) A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. Soil and Tillage Research 79:7–31. doi: 10.1016/j.still.2004.03.008

Sperry JS, Hacke UG (2002) Desert shrub water relations with respect to soil characteristics and plant functional type. Funct Ecol 16:367–378. doi: 10.1046/j.1365-2435.2002.00628.x

Stella JC, Battles JJ (2010) How do riparian woody seedlings survive seasonal drought? Oecologia 164:579–590. doi: 10.1007/s00442-010-1657-6

Stokes A, Atger C, Bengough AG, et al (2009) Desirable plant root traits for protecting natural and engineered slopes against landslides. Plant and Soil 324:1–30. doi: 10.1007/s11104-009-0159-y

Suding KN, Lavorel S, Chapin FS, Cornelissen JHC, Díaz S, Garnier E, Goldberg D, Hooper DU, Jackson ST, Navas M (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14:1125-1140 doi: 10.1111/j.1365-2486.2008.01557.x

Tilman D (1985) The Resource-Ratio Hypothesis of Plant Succession. The American Naturalist 125:827–852. doi: 10.1086/284382

Tisdall JM, Oades JM (1982) Organic matter and water stable aggregates in soils. Journal of Soil Science 33: 141-163. doi: 10.1111/j.1365-2389.1982.tb01755.x

UNEA (2019). United Nations Environment Agency, Press Release, March 1, 2019. New UN Decade on Ecosystem Restoration offers unparalleled opportunity for job creation, food security and addressing climate change. https://www.unenvironment.org/news-and-stories/press-release/new-un-decade-ecosystem-restoration-offers-unparalleled-opportunity

van Kleunen M, Weber E, Fisher M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13: 235–245 doi: 10.1111/j.1461-0248.2009.01418.x

Vannoppen W, Vanmaercke M, De Baets S, Poesen J (2015) A review of the mechanical effects of plant roots on concentrated flow erosion rates. Earth-Science Reviews 150:666–678. doi: 10.1016/j.earscirev.2015.08.011

Vergani C, Graf F (2016) Soil permeability, aggregate stability and root growth: a pot experiment from a soil bioengineering perspective. Ecohydrology 9: 830–842.

Violle C, Garnier E, Lecoeur J, et al (2009) Competition, traits and resource depletion in plant communities. Oecologia 160:747–755. doi: 10.1007/s00442-009-1333-x

Violle C, Navas ML, Vile D, et al (2007) Let the concept of trait be functional! Oikos 116: 882-892 doi:

Volaire F (2018) A unified framework of plant adaptive strategies to drought: Crossing scales and disciplines. Global Change Biology 259:660–10. doi: 10.1111/gcb.14062

Wahl S, Ryser P (2000) Root tissue structure is linked to ecological strategies of grasses. New Phytologist 148:459–471. doi: 10.1046/j.1469-8137.2000.00775.x

Wang P, Stieglitz T, Zhou DW, Cahill JF (2010) Are competitive effect and response two sides of the same coin, or fundamentally different? Functional Ecology 24:196–207. doi: 10.1111/j.1365-2435.2009.01612.x

Wilson JB (1988) Shoot competition and root competition. The Journal of Applied Ecology 25:279.

Wilson SD, Keddy PA (1986) Species competitive ability and position along a natural stress/disturbance gradient. Ecology 67:1236–1242. doi: 10.2307/1938679

Wu TH (1976) Investigation of landslides on prince of Wales Island, Alaska. Ohio State University

Young TP, Petersen DA, Clary JJ (2005) The ecology of restoration: historical links, emerging issues and unexplored realms. Ecology Letters 8:662–673. doi: 10.1111/j.1461-0248.2005.00764.x

Zangaro W, Lescano LEAM, Matsuura EM, et al (2016) Differences between root traits of early- and late-successional trees influence below-ground competition and seedling establishment. Journal of Tropical Ecology 32:300–313. doi: 10.1017/S0266467416000274

Zhang C-B, Chen L-H, Jiang J (2014) Why fine tree roots are stronger than thicker roots: The role of cellulose and lignin in relation to slope stability. Geomorphology 206:196–202. doi: 10.1016/j.geomorph.2013.09.024

Zhong RH, He XB, Bao YH, et al (2016) Estimation of soil reinforcement by the roots of four post-dam prevailing grass species in the riparian zone of Three Gorges Reservoir, China. Journal of Mountain Science 13:508–521. doi: 10.1007/s11629-014-3397-2

Zhou G, Zhou X, Nie Y, et al (2018) Drought-induced changes in root biomass largely result from altered root morphological traits: Evidence from a synthesis of global field trials. Plant Cell Environment 41:2589–2599. doi: 10.1111/pce.13356

Zhou H, Chen Y, Li W, Ayup M (2013) Xylem hydraulic conductivity and embolism in riparian plants and their responses to drought stress in desert of Northwest China. Ecohydrology 6:984–993. doi: 10.1002/eco.1412

Zirbel CR, Brudvig LA (2020) Trait-environment interactions affect plant establishment success during restoration. Ecology 101:23. doi: 10.1002/ecy.2971

Zwicke M, Picon-Cochard C, Morvan-Bertrand A, et al (2015) What functional strategies drive drought survival and recovery of perennial species from upland grassland? Annals of Botany 116:1001–1015. doi: 10.1093/aob/mcv037

APPENDIX 1: INVASIVE ANNUAL GRASS INTERACTS WITH DROUGHT TO INFLUENCE PLANT COMMUNITIES AND SOIL MOISTURE IN DRYLAND RESTORATION

Table A.1.1: Seed mixes for the Western Great Plains and Cold Desert study sites.

Western Great Plains			Cold Desert		
Genus	Species	PLS Seeds m^{-2}	Genus	Species	PLS Seeds
		Shrubs			
Amelanchier	*alnifolia*	48	*Artemisia*	*nova*	48
Artemisia	*ludoviciana*	48	*Artemisia*	*tridentata*	192
Artemisia	*frigida*	48	*Atriplex*	*canescens*	48
Atriplex	*canescens*	48	*Atriplex*	*confertifolia*	48
Cercocarpus	*montanus*	48	*Chrysothamnus*	*viscidiflorus*	48
Ericameria	*nauseosa*	48	*Ephedra*	*viridis*	48
Krascheninnikovia	*lanata*	48	*Ericameria*	*nauseosa*	48
Yucca	*glauca*	48	*Krascheninnikovia*	*lanata*	48
		Grasses			
Aristida	*purpurea*	24	*Achnatherum*	*hymenoides*	24
Achnatherum	*hymenoides*	24	*Bouteloua*	*gracilis*	24
Bouteloua	*curtipendul*	24	*Bromus*	*carinatus*	24
Bouteloua	*dactyloides*	12	*Elymus*	*elymoides*	24
Bouteloua	*gracilis*	24	*Elymus*	*trachycaulus*	12
Elymus	*elymoides*	12	*Hesperostipa*	*comata*	24
Elymus	*trachycaulu*	24	*Koeleria*	*macrantha*	24
Hesperostipa	*comata*	12	*Leymus*	*cinereus*	12
Koeleria	*macrantha*	24	*Pascopyrum*	*smithii*	12
Nassella	*viridula*	24	*Pleuraphis*	*jamesii*	24
Panicum	*virgatum*	24	*Poa*	*fendleriana*	12
Pascopyrum	*smithii*	12	*Poa*	*secunda*	24
Schizachyrium	*scoparium*	24	*Sporobolus*	*cryptandrus*	24
		Forbs			
Achillea	*millefolium*	24	*Achillea*	*millefolium*	48
Cleome	*serrulata*	24	*Balsamorhiza*	*saggitata*	36
Dalea	*purpurea*	36	*Cleome*	*serrulata*	36
Eriogonum	*umbellatum*	48	*Erigeron*	*speciosus*	36
Hedysarum	*boreale*	36	*Eriogonum*	*umbellatum*	48
Helianthus	*annuus*	48	*Hedysarum*	*boreale*	48
Heterotheca	*villosa*	48	*Helianthus*	*annuus*	36
Linum	*lewisii*	48	*Heterotheca*	*villosa*	48
Lupinus	*argenteus*	48	*Linum*	*lewisii*	48
Machaeranthera	*tanacetifolia*	36	*Oenothera*	*pallida*	24
Oenothera	*speciosa*	24	*Oenothera*	*caespitosa*	24
Penstemon	*angustifoliu*	48	*Penstemon*	*cyanocaulis*	24
Ratibida	*columnifera*	12	*Penstemon*	*comarrhenus*	36
Thelesperma	*filifolium*	36	*Penstemon*	*palmerii*	36
Verbesina	*encelioides*	36	*Penstemon*	*strictus*	24

Table A.1.2: Means and standard error (SE) of the mean for interactions of *B. tectorum* seeding (BRTE), precipitation (Precip.) super-absorbent polymer (SAP) treatments and time for percent cover of different functional groups at the Western Great Plains and Cold Desert sites. Letters denote Tukey differences for means contrasts with p-values <0.05.

Western Great Plains						
BRTE	Precip.	SAP	time	mean	se	Tukey
Seeded forbs						
			2014	34.33	6.51	a
			2015	31.94	5.36	a
			2016	4.82	1.42	b
			2017	3.69	1.24	b
Non-native annuals						
	Ambient		2014	5.03	2.14	a
	Drought		2014	17.1	5.78	abc
	Ambient		2015	29.12	8.4	bcd
	Drought		2015	62.24	9.3	d
	Ambient		2016	38.76	9.59	cd
	Drought		2016	17.66	5.08	abc
	Ambient		2017	9.07	4.87	ab
	Drought		2017	10.07	3.67	abc
Non-native perennials						
			2014	6.86	1.92	a
			2015	47.2	7.94	c
			2016	14.93	2.98	b
			2017	20.99	3.14	b
Cold Desert						
Seeded species						
	Ambient		2015	6.47	3.01	a
	Drought		2015	5.64	1.4	ab
	Ambient		2016	8.46	3.48	ab
	Drought		2016	1.82	1.03	b
	Ambient		2017	8.16	3.9	ab
	Drought		2017	0.95	0.34	ab
Non-native perennials						
			2015	20.73	2.32	
			2016	24.77	4.56	
			2017	6.45	1.24	

Figure A.1.1: Rainfall exclusion shelter used to impose drought treatments on plots.

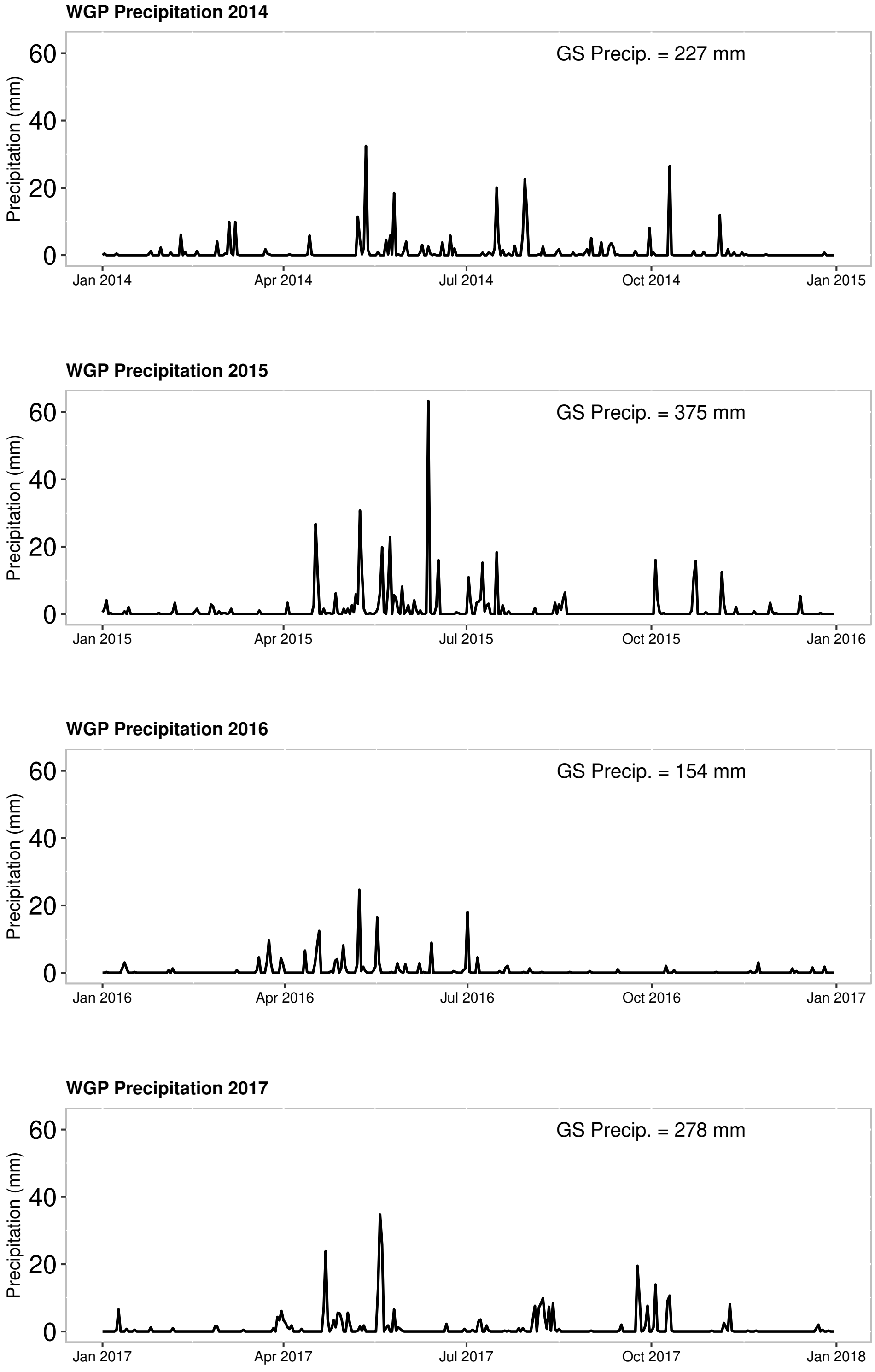

Figure A.1.2: Annual precipitation at the Western Great Plains (WGP) site throughout study years. GS Precip. stands for growing season precipitation (April 1 – Sep 30) of each year. Precipitation data were obtained from a station at the site.

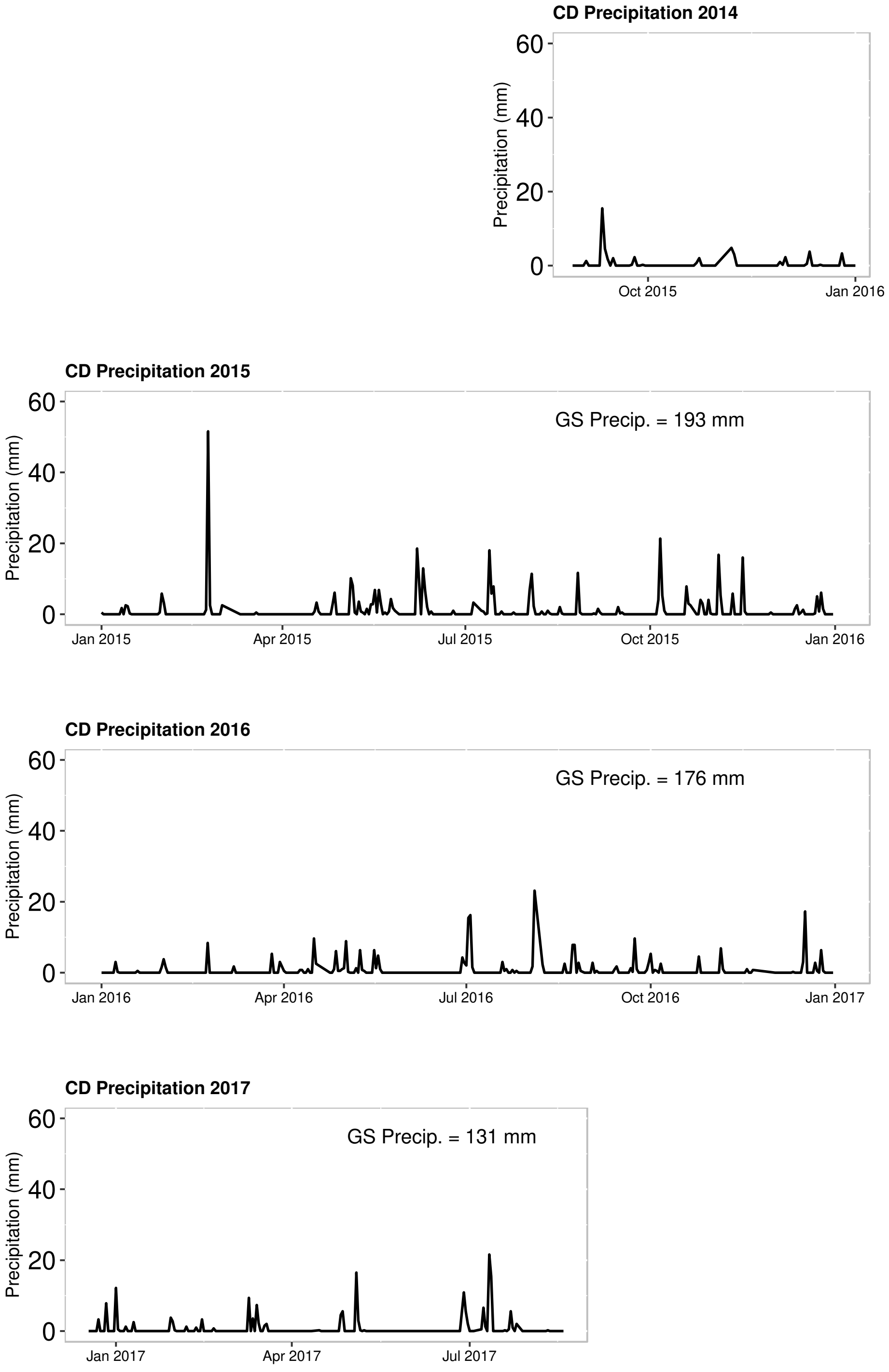

Figure A.1.3: Annual precipitation at the Cold Desert (CD) site throughout study years. GS Precip. stands for growing season precipitation (April 1 – Sep 30) of each year. Precipitation data were obtained from the Redvale NOAA weather station (Station ID: GHCND:US1COSM0010) which is located about 20 km south-west of the study site.

APPENDIX 2: ONTOGENY INFLUENCES LEAF AND ROOT TRAITS OF RESTORATION SEEDLINGS

Table A.2.1: Species with accession numbers (AcNum) of sources used in the study. Information provided by the Germplasm Resources Information Network, Chicago Botanic Gardens, and the Upper Colorado Plant Materials Center.

Species	AcNum	Coordinates		Species	AcNum	Coordinates	
Achillea millefolium	NM930N-25	35.86646	-106.6857	*Machaeranthera canescens*	NM930N-106	35.96817	-107.22121
Achillea millefolium	UT931-146	41.94972	-113.34694	*Machaeranthera canescens*	NM930N-62	36.60836	-107.6772
Achillea millefolium	CP2-126	40.06627	-112.65762	*Machaeranthera canescens*	UT933-282	38.53059	-111.94972
Artemisia tridentata	PSSL-379	39.27436	-112.39891	*Machaeranthera canescens*	UT080-193	40.064978	-109.290653
Artemisia tridentata	UT933-293	37.89199	-111.46527	*Machaeranthera canescens*	CP1-157	37.39383	-109.89788
Artemisia tridentata	UT060-34	38.297058	-109.40074	*Machaeranthera canescens*	PSSL-214	37.75111	-113.77272
Artemisia tridentata	PSSL-385	37.73702	-113.72483	*Muhlenbergia porteri*	AZ040-37	32.97421	-109.63735
Artemisia tridentata	PSSL-391	38.06763	-112.96172	*Muhlenbergia porteri*	AZ040-33	32.3442	-110.23776
Artemisia tridentata	UT933-295	38.21344	-111.99722	*Muhlenbergia porteri*	AZ040-48	31.68657	-110.18779
Elymus trachycaulus	LLPMC-5	35.66973	-106.74295	*Packera multilobata*	AZ932-79	35.15194	-111.74638
Elymus trachycaulus	UT933-339	39.13694	-111.48361	*Packera multilobata*	UT933-362	38.5075	-111.44027
Elymus trachycaulus	UT933-383	37.57111	-112.80916	*Packera multilobata*	UT060-10	38.53856	-109.83993
Elymus trachycaulus	UT933-330	38.04555	-112.18527	*Packera multilobata*	UT060-44	37.557572	-109.731633
Helianthus annuus	AZ040-209	32.58275	-109.50922	*Packera multilobata*	UT060-11	38.596764	-109.28685
Helianthus annuus	UT060-16	38.94887	-109.27236	*Packera multilobata*	UT030-228	37.27402	-112.258
Helianthus annuus	UT080-188	40.15247	-109.6255	*Plantago patagonica*	AZ040-203	34.968	-110.29501
Helianthus annuus	UT030-213	37.45394	-111.82855	*Plantago patagonica*		Unknown	Unknown
Hesperostipa comata	CP1-13	35.07588	-111.61441	*Plantago patagonica*	UT080-156	40.24813	-109.42438
Hesperostipa comata	UT933-27	38.6425	-111.84444	*Plantago patagonica*	CP1-149	37.84591	-111.35508
Hesperostipa comata	CP2-86	38.71756	-110.7356	*Plantago patagonica*	UT931-593	38.84798	-110.21712
Hesperostipa comata	CP2-62	39.17724	-110.47451	*Plantago patagonica*	CP2-70	37.13345	-112.60287
Hesperostipa comata	UT040-13	37.4815	-112.66208	*Vulpia octoflora*	AZ930-50	33.40208	-113.05036
Heterotheca villosa	CP1-58	35.11533	-111.65944	*Vulpia octoflora*	CP2-63	39.17516	-110.8015
Heterotheca villosa	CP1-29	38.61725	-108.30169	*Vulpia octoflora*	UT060-3	38.641089	-109.7477
Heterotheca villosa	NM930N-84	36.82336	-107.50986	*Vulpia octoflora*	CP2-68	38.63238	-109.80499
Heterotheca villosa	NM930N-4	36.82336	-107.50986	*Vulpia octoflora*	CP2-69	37.11391	-112.6091

Table A.2.2: Estimates of median trait values obtained from posterior distributions. Letters in the Dif (Difference) columns denote differences in among species at each ontogenetic stage (i.e. down columns). Species abbreviations are: AC: *Achillea millefolium*; AR: *Artemisia tridentata*; EL: *Elymus trachycaulus*; HN: *Helianthus annuus*; HC: *Hesperostipa comata*; HV: *Heterotheca villosa*; MA: *Machaeranthera canescens*; MU: *Muhlenbergia porteri*; PA: *Packera multilobata*; PL: *Plantago patagonica*; VU: *Vulpia octoflora*

	SLA						LDMC						RMR					
Speci	10-day	Dif	24-day	Dif	42-day	Dif	10-day	Dif	24-day	Dif	42-day	Dif	10-day	Dif	24-day	Dif	42-day	Dif
AC	35.88	cd	39.29	cd	34.43	bc	0.10	bc	0.10	c	0.11	bc	0.33	abc	0.28	bc	0.31	ab
AR	40.41	cd	37.60	d	28.07	c	0.08	c	0.12	bc	0.13	bc	0.30	bc	0.24	c	0.25	ab
EL	72.34	ab	62.33	bc	51.94	ab	0.14	ab	0.17	ab	0.17	ab	0.43	ab	0.44	a	0.31	ab
HN	30.33	d	33.59	d	29.83	c	0.11	b	0.12	bc	0.13	bc	0.25	c	0.28	bc	0.21	bc
HC	41.13	bc	35.07	d	29.52	c	0.19	a	0.21	a	0.23	a	0.36	abc	0.35	abc	0.30	ab
HV	73.64	ab	53.58	bcd	35.53	bc	0.10	bc	0.15	bc	0.16	ab	0.30	bc	0.37	ab	0.29	ab
MA	46.96	bc	45.71	bcd	35.57	bc	0.14	ab	0.13	bc	0.13	bc	0.30	bc	0.28	bc	0.31	a
MU	27.06	d	26.63	d	22.29	c	0.17	a	0.14	bc	0.16	ab	0.35	abc	0.31	abc	0.35	a
PA	38.90	cd	61.60	bc	43.96	ab	0.13	ab	0.10	c	0.11	c	0.29	b	0.37	a	0.26	ab
PL	73.65	a	62.04	b	45.61	ab	0.08	c	0.09	c	0.11	c	0.35	abc	0.16	d	0.17	c
VU	114.56	a	108.64	a	71.31	a	0.15	a	0.13	bc	0.14	b	0.48	a	0.34	a	0.26	ab
	SRL						RDMC						RTD					
Speci	10-day	Dif	24-day	Dif	42-day	Dif	10-day	Dif	24-day	Dif	42-day	Dif	10-day	Dif	24-day	Dif	42-day	Dif
AC	365.76	b	537.98	b	420.33	b	0.12	abc	0.10	ab	0.10	ab	0.08	ab	0.07	ab	0.07	ab
AR	273.75	bc	383.43	bc	267.31	bc	0.11	abc	0.10	ab	0.09	ab	0.08	ab	0.08	ab	0.08	ab
EL	306.06	b	411.82	b	325.64	b	0.14	ab	0.12	a	0.11	a	0.06	cd	0.05	cd	0.05	cd
HN	196.10	cd	269.85	cd	220.79	cd	0.09	c	0.08	b	0.08	b	0.08	ab	0.08	ab	0.08	ab
HC	155.27	d	215.76	d	177.64	d	0.14	a	0.12	a	0.12	a	0.07	bc	0.06	bc	0.06	bc
HV	280.75	bc	366.48	bc	297.56	bc	0.12	abc	0.11	ab	0.10	ab	0.08	ab	0.08	ab	0.08	ab
MA	261.50	bc	365.21	bc	266.80	bc	0.11	abc	0.09	ab	0.09	ab	0.09	ab	0.08	ab	0.09	ab
MU	257.24	c	378.30	c	269.28	c	0.12	abc	0.10	ab	0.10	ab	0.11	a	0.10	a	0.10	a
PA	306.98	b	438.31	b	347.12	b	0.10	bc	0.09	b	0.08	b	0.07	c	0.06	c	0.07	c
PL	346.36	b	470.45	b	379.47	b	0.12	abc	0.10	ab	0.10	ab	0.05	d	0.05	d	0.05	d
VU	637.06	a	848.44	a	628.23	a	0.15	ab	0.12	a	0.12	a	0.04	d	0.04	d	0.04	d
	Root Diameter						RGR						RRER					
Speci	10-day	Dif	24-day	Dif	42-day	Dif	10-day	Dif	24-day	Dif	42-day	Dif	10-day	Dif	24-day	Dif	42-day	Dif
AC	0.21	e	0.21	de	0.21	e	0.0308	a	0.0714	ab	0.1766	a	1.19	de	0.15	abc	0.05	d
AR	0.25	de	0.23	de	0.26	cd	0.0162	ab	0.1582	a	0.4017	a	1.21	de	0.19	ab	0.22	ab
EL	0.29	bc	0.27	bc	0.29	bc	0.0182	ab	0.1093	ab	0.1663	a	4.84	ab	0.18	ab	0.05	d
HN	0.30	b	0.28	bc	0.28	bc	0.0067	ab	0.0738	ab	0.1894	a	3.15	abcd	0.18	ab	0.11	abcd
HC	0.40	a	0.38	a	0.38	a	0.0051	b	0.1267	ab	0.1026	a	6.24	a	0.19	ab	0.08	cd
HV	0.26	cd	0.23	cde	0.23	dc	0.0098	ab	0.1321	ab	0.1434	a	1.47	cde	0.24	ab	0.06	d
MA	0.26	bcd	0.24	cd	0.26	bcd	0.0165	ab	0.1944	a	0.2817	a	1.12	e	0.36	a	0.18	abc
MU	0.20	e	0.20	e	0.22	de	0.0325	a	0.1207	ab	0.2881	a	1.32	cde	0.22	ab	0.16	abcd
PA	0.28	bc	0.24	c	0.25	cd	0.0203	ab	0.0243	b	0.1783	a	1.92	bcde	0.12	b	0.08	bcd
PL	0.31	b	0.31	b	0.31	b	0.0101	ab	0.1675	a	0.2441	a	3.41	abcd	0.05	c	0.21	abc
VU	0.23	de	0.23	cde	0.24	cde	0.0032	b	0.2222	a	0.4482	a	3.51	abc	0.20	ab	0.28	a

Table A.2.3: Estimates of median trait values obtained from posterior distributions using data from each harvest and values obtained from the TRY database. Letters in Dif. (Difference) columns denote differences in medians among ontogentic stages for each species (i.e. down columns). Species abbreviations are as follow: ACMI: *Achillea millefolium*; ARTR: *Artemisia tridentata*; ELTR: *Elymus trachycaulus*; HEAN: *Helianthus annuus*; HECO: *Hesperostipa comata*; HEVI: *Heterotheca villosa*; MACA: *Machaeranthera canescens*; MUPO: *Muhlenbergia porteri*; PAMU: *Packera multilobata*; PLPA: *Plantago patagonica*; VUOC: *Vulpia octoflora*

	ACMI		ARTR		ELTR		HEAN		HECO		MUPO		PAMU		PLPA		VUOC	
Harvest	Med	D	Med	D	Med	D	Med	D	Med	D	Med	D	Med	D	Med	D	Med	D
24-day	39.42	a	36.74	a	56.11	a	35.02	a	32.25	ab	29.05	a	62.26	b	57.12	ab	101.27	a
42-day	38.01	a	27.59	a	49.37	a	34.00	a	29.12	ab	25.59	a	45.03	ab	42.01	b	73.18	ab
TRY	39.55	a	28.68	a	39.94	a	41.75	a	21.43	b	39.38	a	35.98	ab	33.48	b	46.49	b

APPENDIX 3: GETTING TO THE ROOT OF RESTORATION: CONSIDERING ROOT TRAITS FOR IMPROVED RESTORATION OUTCOMES

The following keywords were used to compile a list of manuscripts from Web of Science (Thomson Reuters, Manhattan, NY, USA):

"root trait*" OR "below-ground trait*" OR "morphological root trait*" OR "anatomical root trait*"OR "root system morphology" OR "specific root length" OR "SRL" OR "specific root area" OR "SRA" OR "root to shoot" OR "root to shoot ratio" OR "root:shoot ratio" OR "root mass fraction" OR "RMF" OR "root mass ratio" OR "RMR" OR "root tip*" OR "root fork*" OR "root branch*" OR "root diameter" OR "mean root diameter" OR "root cross sectional area" OR "fine root*" OR "coarse root*" OR "fine root allocation" OR "coarse root allocation" OR "root* depth" OR "root length density" OR "root tissue density" OR "root dry matter content" OR "root nitrogen" OR "root elongation rate") AND “drought” OR “precip*” OR "water-availability" OR drought OR “invasi*” OR “compet*” OR “erosi*” OR “soil stabil*” OR “aggregate stabil*”

The following words were used to exclude papers from non-relevant categories:

agri* OR crop* OR agron* OR bean* OR fruit OR "rice" OR "corn" OR "maize" OR "zea" OR pea* OR tomat* OR "sorghum" OR "salvia" OR "arabidopsis" OR citrus OR nut* OR "banana" OR "wheat" OR cereal* OR grain* OR viti* OR "grape*" OR "ornamental" OR "education" OR "tourism" OR "learning" OR "toxicology" OR "ecotoxicology" OR "phytoremediation" OR "toxic*" OR "mycorrhi*" OR "allelopath*" OR "genet*"

Results were further limited to the following Web of Science categories:

“Ecology” OR "Engineering, Environmental" OR "Evolutionary Biology" OR "Biodiversity Conservation" OR "soil science" OR "plant science" OR "environmental science" OR "environmental studies" OR "forestry”