

## Species variability in the relative strength of intraspecific and interspecific interactions

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### Abstract

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Understanding cases in restoration and in agriculture in which species diversity improves productivity and ecosystem functioning is crucial due to the need to restore degraded habitat and improve crop productivity for a growing human population. Reaching these diversity benefits is likely influenced by the dynamic of less negative interspecific than intraspecific interactions that promote diversity. But further testing is needed to understand the relationship of intraspecific- relative to interspecific interactions. Here I used seedlings from three native and one introduced species used in restoration in the western United States in pairwise interaction combinations and found that the study species varied in shoot biomass in response to interaction treatments of the control, intraspecific, and interspecific interactions ( $R^2 = 0.7$ ,  $p < 0.001$ ), and that intraspecific interactions were more negative than interspecific interactions for four of five of the pairings. Overall, as shoot mass size differences increased between interspecific neighbors, interactions became more positive ( $R^2 = 0.6$ ,  $p < 0.001$ ). These findings point to variability in species responses in whether the focal species compete more intensely with conspecific or heterospecific neighbors and indicates the need for more careful selection of interacting species for meeting both agricultural and restoration goals.

### Keywords

ex-situ, forbs, interactions, native plants, shoot mass

### Introduction

Intercropping species has been used in agriculture towards sustainable fertilizer use and in wild plant restoration to restore diversity and capture biodiversity ecosystem functions. Diversity benefits in both systems have been well characterized and include greater above and belowground productivity, reduced invasibility by invasive plant species, reduced diseases occurrence, and greater diversity of pollinators (EBELING et al., 2008; KNOPS et al., 1999; RAVENEK et al., 2014). The benefit of mixing species is predicated on non-overlapping use of resources, or even complementarity in niche space and resource use (CARDINALE et al., 2007; FARGIONE and TILMAN, 2005) that results in reduced competition between species and improved growth. As an example, MAKUMBA et al. (2009) showed that corn-*Gliricidia* intercropping roots occupied differing rooting depths allowing for

corn to acquire nutrients nearer to the surface not contested by *Gliricidia*.

The dynamic of less negative interspecific interactions is an important component for diversity and coexistence between species (CHESSON, 2000). Another critical component to species coexistence that promotes these less negative interspecific interactions is the relationship between how negative interspecific interactions are compared to intraspecific interactions. Under this coexistence framework, intraspecific interactions should be more negative than interspecific interactions for long-term coexistence because conspecifics require more similar resources than they do with interspecific neighbors (CHESSON, 2000; HILLERISLAMBERS et al., 2012; MAYFIELD and LEVINE, 2010). The resulting intense intraspecific competition functions to limit the species' own population growth and promotes diversity. ADLER et al. (2018) demonstrated this relationship using a meta-analy-

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Table 1. Plant species and their interaction combinations with sample sizes for each treatment. Sample size varied due to germination response and seedling mortality.

Pairing	Interaction type	Sample size
<i>Helianthus annuus</i>	Control	5
<i>Linum perenne</i>		3
<i>Pascopyrum smithii</i>		4
<i>Helianthus annuus</i> vs. <i>Helianthus annuus</i>	Intraspecific	11
<i>Linum perenne</i> vs. <i>Linum perenne</i>		6
<i>Pascopyrum smithii</i> vs. <i>Pascopyrum smithii</i>		5
<i>Helianthus annuus</i> vs. <i>Linum perenne</i>	Interspecific	4
<i>Linum perenne</i> vs. <i>Helianthus annuus</i>		4
<i>Linum perenne</i> vs. <i>Pascopyrum smithii</i>		9
<i>Pascopyrum smithii</i> vs. <i>Linum perenne</i>		9
<i>Pascopyrum smithii</i> vs. <i>Achillea millefolium</i>		5

sis of phenomenological interaction experiments in which intraspecific competition largely was more intense than interspecific competition. However, other studies have shown variability in whether plants compete more intensely with interspecific neighbors (CRUZ et al., 2020; LI et al., 2020). Furthermore, the difference in plant size is important to determining interaction outcomes and can produce a hierarchy of inferior and superior competitors (KEDDY et al., 2002); this may influence the relative strength of interspecific and intraspecific interactions. Taken together, the variable nature of the directionality of intraspecific and interspecific interactions indicates a need to evaluate groupings of species and how size differences influence these relationships. This has not been commonly done for species used in restoration.

To understand intraspecific relative to interspecific interaction relationships of species may improve long-term planting aims and thus requires testing for implementation. So, here I used seedlings from three native and one introduced species used in restoration in the western United States to test the relationship of intraspecific relative to interspecific interactions, as seedlings can be more sensitive to competition (FOSTER, 1999; JAMES et al., 2011). I grouped plants in pairwise interaction treatments in a growth chamber to evaluate the strength of these relationships using aboveground plant size and shoot size differences because the difference in plant biomass can determine competitive outcomes and coexistence (ABBOTT and STACHOWICZ, 2016; KEDDY et al., 2002). I hypothesized that 1) shoot mass varies between neighbor pairs and interaction type (intraspecific and interspecific pairings); 2) intraspecific interactions will be more negative than interspecific interactions for all species pairs; and 3) interaction intensity will vary with neighbor shoot difference and be moderated by interaction type.

## Materials and methods

### Species and population sources

Species were selected using the Utah's Watershed Restoration Initiative restoration (Utah's Watershed Restoration Initiative) species list to determine species that were highly seeded per acre in restorations and likely to be seeded together. I used four plant species: one perennial grass *Pascopyrum smithii* (purchased; Central Milling Wheatland, UT, USA), and three forb species *Helianthus annuus* (wild collected by the Seeds of Success program, which uses stan-

dardized seed collection protocols (HAIDET and OLWELL, 2015), Colorado, USA); *Achillea millefolium* (purchased, Ranier Seeds, WA, USA); and an introduced species, *Linum perenne* (purchased, Ranier Seeds, WA, USA).

### Propagation and study design

I grew seedlings at the Chicago Botanic Garden (Glencoe, IL, USA) from July to October 2016. On 13 July 2016, I surface sterilized 80 seeds per species with 3% bleach solution for 30 seconds followed by a deionized water rinse for 1 minute. Next, I placed 40 seeds per species on each of two 90 mm diameter petri dishes filled with 1.5% solidified agar for cold moist stratification at 3 °C in a refrigerator until I observed germination consisting of emergence of the radicle. Germination response and survivorship varied by species and influenced the resulting sample sizes possible for each treatment group and possible treatment combinations for analyses. I checked germination three times weekly and moved germinants to watered, randomized cone-tainers (Stuewe and Sons, Tangent, OR, USA) in a growth chamber at 25 °C/15 °C day/night with a 14 hour/10 hour photoperiod 15%/6% relative humidity on a 12-h day/night cycle. Two germinants were planted into cone-tainer (2.54 cm diameter × 12.1 cm; Stuewe and Sons, Tangent, OR USA) for the inter- and intraspecific treatments after being filled with commercial sand and 4 cm square veil at the bottom of cone-tainers to stabilize the soil. One germinant was planted for the control group. Germinants were planted between 27 July 2016 and 31 August 2016 with neighbors planted simultaneously. Plants were grown together for eight weeks and harvested between 14 September and 17 October 2016. I applied Murashige-Skoog (Sigma Aldrich, MO, USA) half strength nutrients (4g L<sup>-1</sup>) every two weeks and watered plants every three days. I removed plants from cone-tainers but was unable to disentangle roots from the mesh and harvested shoots. Shoot biomass was then placed plants in envelopes to in an herbarium drier at 95 °C for one week prior to weighing.

I used eleven interaction treatments across three focal species (*H. annuus*, *L. perenne*, and *P. smithii*) to assess the strength of intraspecific relative to interspecific interactions (Table 1). Plants were grown singly for the control group and at a density of two plants per cone-tainer for both the intraspecific and interspecific interactions. Intraspecific interactions had two seedlings of the same species and interspecific interactions contained one seedling of each paired species.

## Data calculations

I collected shoot mass of all individuals after harvesting and square root transformations of shoot mass to meet assumptions of normality. I used log response ratio (lnRR) as

$$\lnRR = \log(\bar{x}_{\text{treatment}} / \bar{x}_{\text{reference group}})$$

as a metric of interaction intensity (HEDGES et al., 1999) and calculated lnRR on shoot mass to address whether intraspecific interactions will be more negative than interspecific interactions, with the interspecific treatment mean compared to the intraspecific treatment mean. I then used the lnRR to calculate the average percent difference between growth of the focal plant with a heterospecific compared to a conspecific neighbor as,

$$\text{Percent difference} = 100\% \times e^{\lnRR} - 1$$

following Pustejovsky (PUSTEJOVSKY, 2018). Positive percentage points indicate that conspecific interactions were more negative than heterospecific interactions, whereas negative values denote more negative heterospecific interactions. I also calculated the lnRR at the individual-level for all treatments, as the log of the individual value divided by the control group mean. This value represents the proportional size difference between plants in the treatment of interest to the reference group. Negative values denote competition, zero denotes neutral interactions (or even a signal of interactions that cannot be identified through this approach), and positive values denote facilitation or positive interactions (HEDGES et al., 1999; SUDING et al., 2003). I calculated the hierarchical shoot mass difference to address the hypothesis on size differences using the equation,

$$t_a - t_b$$

where  $t_a$  is the mass of the focal plant and  $t_b$  is the mass of non-focal neighbor plant (FORT et al., 2014; KRAFT et al., 2014; KUNSTLER et al., 2012). I made one calculation for each pot between plant pairs on untransformed data for shoot mass. Shoot mass distances close to zero indicate the neighbor traits were similar, whereas non-zero values indicate trait differences relative to the focal and non-focal plant.

## Analyses

All analyses were carried out in R (R CORE TEAM, 2021). To assess hypothesis one that shoot mass varies between neighbor pairs and interaction type (control, intraspecific and interspecific treatments) I used a linear model to compare shoot mass as the response, and the maximal models contained the additive terms 'interaction type' and 'species identity' of the interaction pair nested in interaction type. To address whether intraspecific interactions is more negative than interspecific interactions for all species pairs, I compared the percent change for focal species in intraspecific compared to interspecific interactions. And lastly, I tested whether interaction intensity varies with neighbor shoot difference and whether it was moderated by interaction type and focal species using a linear model with interaction intensity modeled with shoot mass difference and the additive terms of 'interaction type' and 'focal species'. For hypotheses one and two, I selected the best fit model using the "stepAIC" function in the MASS package (VENABLES and RIPLEY, 2002) which selects models with the lowest Akaike Information Criterion (AIC) value. Next, I performed correlation tests and associated significance tests for all 6 combinations of relationships in hypothesis three using the "cor.test" function in the stats package (R CORE TEAM, 2021) to assess the relationships.

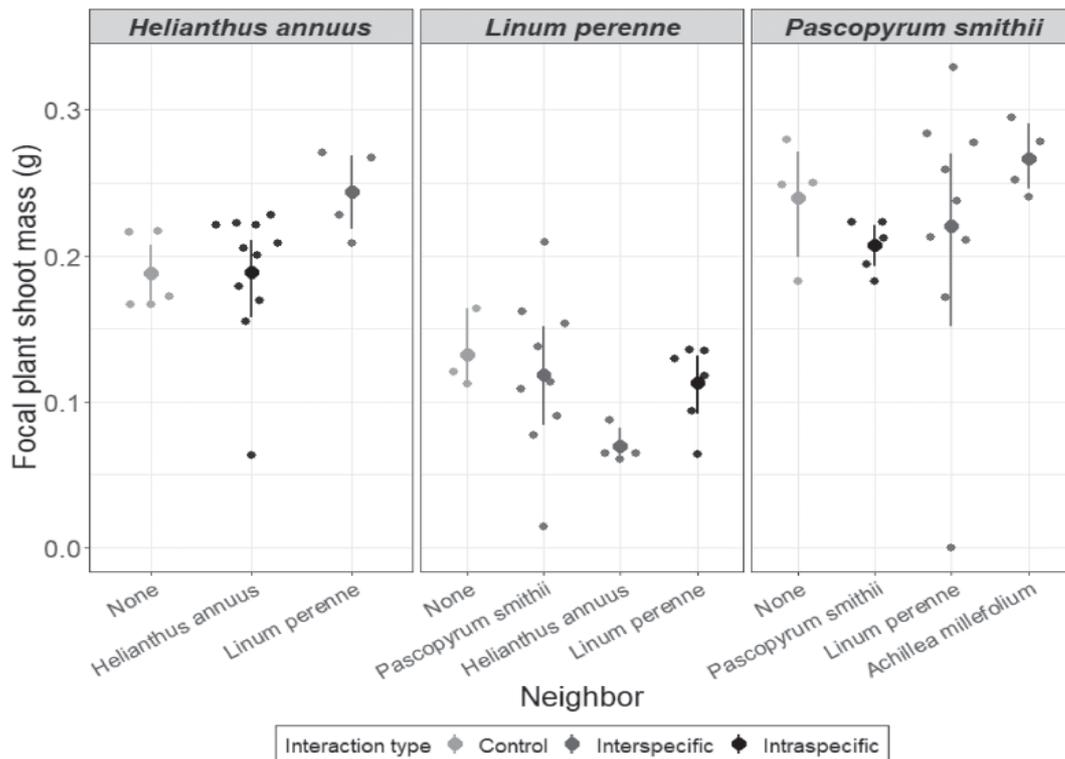


Fig. 1. Species shoot mass mean and 95% confidence intervals for all interaction treatments.

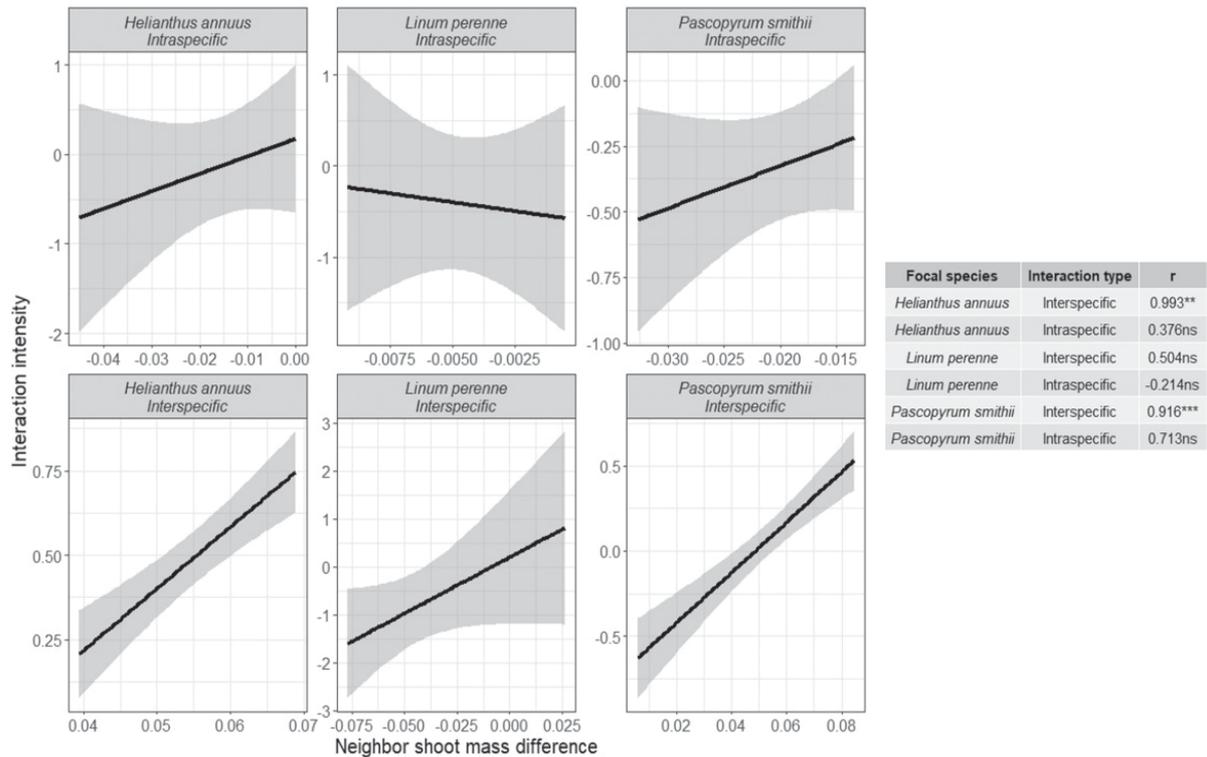


Fig. 2. The relationships between neighbor shoot mass differences and interaction intensity for three focal species and intraspecific and interspecific interactions. Fitted lines are the results of the best-fit linear model, and grey shading is the standard error values.

Table 2. The percent difference in shoot mass size for the focal plant when grown with conspecifics and with a heterospecific plant (Neighbor species). Positive percentage points indicate that conspecific interactions were more negative than heterospecific interactions and negative values denote more negative heterospecific interactions.

Focal species	Neighbor species	Interaction percent difference
<i>Helianthus annuus</i>	<i>Linum perenne</i>	59.6%
<i>Linum perenne</i>	<i>Helianthus annuus</i>	-62.97%
<i>Linum perenne</i>	<i>Pascopyrum smithii</i>	26.02%
<i>Pascopyrum smithii</i>	<i>Achillea millefolium</i>	65.39%
<i>Pascopyrum smithii</i>	<i>Linum perenne</i>	30.92%

## Results

Shoot mass differed by treatment with *P. smithii* being the largest of the focal species and *L. perenne* being the smallest overall (Fig. 1). *Helianthus annuus* had the lowest growth when grown alone, whereas *L. perenne* had greater growth when grown alone compared to its growth with neighbors. The best model explaining shoot mass ( $R^2 = 0.7$ ,  $F_{8,43} = 11.19$ ,  $p < 0.001$ ) included the additive terms of neighbor pair and nested in interaction type ( $p = 0.0001$ ) and treatment nested in interaction type ( $p < 0.001$ ).

Interaction intensity varied by focal species, and conspecific interactions were more negative than heterospecific interactions for four of the five interspecific pairings (Table 2). Focal plants with heterospecific plants were between 26.02% and 65.39% larger with a heterospecific plant than with a conspecific plant. *Linum perenne*, however, competed more intensely with the neighbor *H. annuus* and was 62.97%

smaller following interspecific competition than intraspecific competition. Lastly, interaction intensity varied significantly ( $p < 0.001$ ) with neighbor shoot difference and was moderated by interaction type ( $p = 0.006$ ) and focal species ( $p < 0.001$ ) ( $F_{4,45} = 16.9$ ,  $R^2 = 0.6$ ,  $p < 0.001$ ; Fig. 2). Overall, for all interspecific pairings, as shoot mass differences between neighbors increased, interactions became less negative. Intraspecific interactions for *H. annuus* and *P. smithii* exhibited the same directionality of the relationships, whereas for *L. perenne*, as shoot mass differences between conspecific neighbors increased, interactions became more negative (Fig. 2).

## Discussion

I found evidence that the study species varied in shoot biomass in response to interaction treatments imposed. Importantly, the intensity of interactions varied given the differ-

ences in shoot biomasses between neighbors and conspecific interactions were more negative than heterospecific interactions for four of the five interspecific pairings. These findings point to some variability in species response to neighbor size differences and emerging evidence that variability in whether the focal species competed more intensely with conspecific or heterospecific neighbors and variation in the magnitude of the relationship. These findings require further examination in long-term scenarios, but they suggest that variability may have consequences for the selection of germplasm for both agricultural and restoration needs.

The shoot mass of the focal plants following the interaction treatments varied by species and in response to neighbor identity and whether interactions were intraspecific or interspecific. *Linum perenne* was smallest overall and its growth was suppressed most by competition with *H. annuus*. This is corroborated by the 62.97% shoot mass reduction when *L. perenne* grew with *H. annuus* compared to with conspecifics. Some evidence suggests that plants from the same functional group may compete more intensely than with other functional groups due to greater similarities in resource needs (FARGIONE and TILMAN, 2005). This may explain the relationship of interacting forbs *L. perenne* with *H. annuus* and the more positive interactions with *P. smithii* of a differing functional group (C3 grass (READ and MORGAN, 1996)). This does not explain responses of *H. annuus* with *L. perenne* which was positive and more pairings with other species within and outside of the forb functional group will help elucidate the responses of *L. perenne*.

Suppression from forb species for *L. perenne* suggest that pairing these populations of *L. perenne* with *H. annuus* in restoration scenarios may lead to poor aboveground productivity for *L. perenne* that may negatively influence its long-term persistence. The response of *L. perenne* may also be confounded by its introduced status. While aspects of the biology of introduced species make them attractive for meeting restoration goals (e.g., benefits of providing shelter and forage for animals (SCHLAEPFER et al., 2011)), they have some negative consequences such as outcompeting native species, that are a downside to their use in restorations (SCHLAEPFER et al., 2011). While *L. perenne* is non-native and not invasive, its performance contradicts expectations posited by the evolution of increased competitive ability hypothesis that release from herbivores may allow for the evolution of competitive success through re-allocation of resources (e.g., EICA; CALLAWAY and RIDENOUR, 2004). Though FELKER-QUINN et al. (2013) found weak evidence for this hypothesis among invasive species. Conspecific interactions were more negative than heterospecific interactions for four of the five interspecific pairings in which *H. annuus* with *L. perenne* and *P. smithii* with *A. millefolium* had the greatest aboveground biomass response with heterospecifics in this study and corroborates the generality that intraspecific neighbors compete more intensely than interspecific neighbors (ADLER et al., 2018). These outcomes also add to evidence that species vary in whether they compete more intensely with intraspecific relative to interspecific neighbors (CRUZ et al., 2020; LI et al., 2020), and the magnitude of benefit towards aboveground productivity varied between 26.02% and 65.39% greater growth with a heterospecific plant. Whether and how much a population of a species has improved growth with a heterospecific plants represents an important avenue for evaluating plants used for mixtures in both agricultural and restoration contexts. Future work should evaluate whether plant pairings that were productive in controlled settings is maintained in field

settings for the long-term.

I also show influences of shoot mass differences on interspecific interactions and that as shoot mass differences increased between neighboring plants, the interactions became less negative and following predictions of the trait distance hypothesis (KRAFT et al., 2014). The outcome was similar for intraspecific interactions, but for *L. perenne*, as shoot mass differences between conspecific neighbors increased, interactions became slightly more negative, indicating a hierarchical relationship in which smaller plants experience greater competition and suppression from larger plants (*trait hierarchy hypothesis* (KRAFT et al., 2014)). The relationships between interaction intensity and neighbor mass differences exhibited greater variability for conspecific than heterospecific pairings. This suggests the maintenance of shoot size variation among intraspecific neighbors, but also indicates shoot mass difference variability suppression, or convergence, due to interspecific neighbors.

Shoot size has been shown to respond to competitive interactions and predicts competitive ability (KEDDY et al., 2002), however, contrary to our findings, ABBOTT and STACHOWICZ (2016) identified root mass differences, and not shoot mass differences drove the competitive exclusion and patterns of coexistence in eelgrass genotypes. Their findings highlight that plant roots can drive plant-plant interactions more strongly than shoots (FOXX and FORT, 2019; KIAER et al., 2013), likely due to contesting finite resources in a finite space that varies in profitability for the plant with depth (e.g., phosphate and water availability (CASPER and JACKSON, 1997)). I was not able to assess the roots, but because these plants are from arid environments and the importance of roots and their traits have been long established (FOWLER, 1986; SCHENK and JACKSON, 2002), work to explicitly compare root mass differences in these species will help to elucidating patterns of size difference on interactions for aridland and drought tolerant species. Future work should also assess the impacts of traits as they influence interactions and plant species coexistence (HERBEN et al., 2020; KRAFT et al., 2014). Lastly, an additional study limitation is of low sample size in some treatments and treatment representation due to low germination response and seedling mortality. Whether mortality held deterministic patterns in relation to interaction treatments was outside of the capacities of this work, though could indicate intense competition (HORTAL et al., 2017). Furthermore, including more interacting species will help to identify other potential cases in which inter- and intraspecific interactions contradict expectations.

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