**SEED SOURCE ENVIRONMENT PREDICTS DROUGHT RESPONSE IN *PLANTAGO PATAGONICA***

Running title:

***Variable precipitation at maternal source sites leads to higher mortality***

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**ZK and RMM conceived and designed the research, ZK collecte data and conducted analyses, ZK and RMM wrote and edited the manuscript.**

**Abstract**

The intensity, duration, and severity of drought is increasing across the American southwest and plant restoration efforts are often thwarted by drought induced effects. Careful selection of plant materials to match future environmental conditions could improve restoration success under climate change. Here we focus on *Plantago patagonica,* a priority aridlands restoration species in southwestern US. Using experimental drought in a greenhouse and common garden experiment, we quantified how seed-collection site environment impacted plant growth, performance, phenotypic plasticity, and evidence of local adaptation in 12 populations of *P. patagonica*. In the common garden, we found that plants sourced from wetter locations and those with more consistent precipitation regimes had lower mortality and higher SLA, a proxy for growth, under experimental drought. In the greenhouse, we found plants from hotter and drier environments had higher root:shoot ratios, while those from more variable precipitation regime had greater total biomass in response to drought. Populations sourced from warmer environments exhibited 7-fold greater plasticity in root:shoot ratio compared to those from cooler environments, and there was strong evidence for local adaptation in phenology, as populations sourced from sites nearer the common garden exhibited five times more flowering individuals than those sourced furthest from that garden. These results suggest plant performance of *Plantago patagonica* under drought conditions is strongly shaped by seed-collection site environment and may be a useful tool for improving restoration outcomes in a changing world.

***Keywords: Plantago patagonica, arid lands, drought, greenhouse, common garden, precipitation variability, temperature, seed-source environment, plasticity, local adaptation, plant traits***

**Implications for Practice**

* **Seed collection environment has strong effects on plant performance under drought conditions which can enhance restoration outcomes via increased survivorship and reproduction.**
* **Predictable rainfall regimes at collection sites yield high survivorship in both watered and drought conditions. Collections from such regimes may improve wild seed establishment, while the irrigation of cultivated annuals may enhance establishment and performance of restoration seed stock.**
* **Seed collection environment influences tissue allocation and plant strategy in the face of drought which can be leveraged to address restoration goals (e.g., weed or erosion control)**

**Introduction**

In southwestern drylands, restoration efforts are often thwarted by drought induced effects on plant germination, survival, and reproduction (Kildesheva et al. 2018; Shackelford et al. 2021; James et al. 2011). Under both moderate and high future emission scenarios, southwestern drought is predicted to become particularly severe (Cook et al. 2015, Woodhouse et al. 2010), and recent work has demonstrated that southwestern precipitation is already reduced and more variable (Zhang et al. 2021).  Seed sourcing is a critical step in a restoration, and ensuring successful germination, establishment, and reproduction of seeded populations under current and future conditions is of high importance. Current best-practices rely on locally adapted seed, or seed sourced from within a geographic or jurisdictionally bounded seed transfer zone (Bower et al. 2014, Erikson and Halford 2020), but recent research indicates that locally adapted seed may not offer resilience to future conditions (Havens 2015; Butterfield et al. 2017). As a result, there is a critical need to investigate how to best source plant materials to promote the success and persistence of restoration plants in the face of expected temperature and precipitation shifts.

While perennial species are often the focus of dryland restoration research because they are typically dominant, matrix-forming species and of high importance as feed for livestock, annual species contribute disproportionately to arid ecosystem biodiversity and function (Rolhauser and Pucheta 2015, Fry et al. 2013). Annual species may help facilitate perennial establishment by competing with and reducing the prevalence of invasive annuals (Prasser and Hild 2015). For example, native forbs with high germination rates better competed with cheatgrass (*Bromus tectorum*), which suggests native annuals may be particularly useful in restoration of highly invaded areas (Barak et al. 2015). Weather anomalies, an increasingly common phenomenon under climate change, can shift the balance of native, exotic, annual and perennial plants in restoration settings across seasons and over the landscape (Copeland et al. 2019; Young et al. 2015). Copeland et al. (2019) found that higher temperature and wetter precipitation anomalies in arid ecosystems influenced the relative cover and richness of non-native annuals and native perennials, where higher temperature anomalies increased non-native annual and native perennial cover in the cool season, and higher temperatures in the warm season decreased exotic annual and both native and exotic perennial cover. Because weather anomalies are increasing (Li et al. 2023; Trenberth et al. 2003; Trömel and Schönwiese 2006), and can alter community dynamics and plant dominance, identifying native seed sources that can successfully persist in response to fluctuating precipitation and temperature will improve restoration outcomes and generate resilient species assemblages. Because annual species contribute disproportionately to biodiversity and ecosystem function, identifying populations of annuals that are likely to persist in in response to weather anomalies is critically important for restoring climate-resilient arid lands.

Beyond weather anomalies, prevailing precipitation and temperature regimes are key drivers of plant community composition in arid ecosystems (Cleland et al. 2013; Butterfield et al. 2016; Berdugo et al. 2020) and these regimes are persistently and directionally shifting towards hotter and more arid conditions (Li et al. 2023). Plant community composition in arid grasslands and shrublands the Colorado Plateau is shifting towards shrub dominance (Munson et al. 2011; Winkler et al. 2019) in response to elevated temperatures and decreased precipitation, as shrubs exhibit highly effective drought-resistance strategies (e.g., deep rooting systems). In contrast, annual forbs in arid systems are highly sensitive to interannual variation in precipitation (Wilcox et al. 2020); with annual forb abundance and diversity declining dry years (Munson et al. 2011). This is because temperature and precipitation effect fitness in arid -adapted annuals by enhancing trade-offs between water use and growth (Gremer et al. 2012). For example, Kimball et al. (2010) found that desert annuals with high water use efficiency (WUE) have increased in the Sonoran Desert over the last few decades, while those with lower WUE have decreased.

Irrespective of directional climate change, high interannual variability in precipitation is a hallmark of the arid southwest (Tulley-Cordova et al. 2018; Georgescu et al. 2021). However, in recent decades this variation has become more extreme (Zhang et al. 2021) and restoration efforts that rely on establishment of native plants from seed have often failed following extreme weather events or periods of unexpected aridity (Shackelford et al. 2021). Because precipitation regimes can affect germination, growth (March-Salas et al. 2019 and 2021) and reproduction (Kimball et al. 2011), selecting plant materials based on maternal precipitation regime may improve chances of successful establishment and growth when restoring in an unpredictable and fluctuating environment. For example, populations from more variable environments (e.g., less predictable precipitation patterns and amounts, greater fluctuation in temperature) have been shown to display higher rates of plasticity and diversified bet-hedging ([Yin et al. 2019](https://doi.org/10.1111/ele.13373)) that may make them more resilient to unpredictable future conditions. High phenotypic plasticity is a driver of intraspecific variation that may help plants rapidly adapt to climate change (Nicotra et al. 2010,) but environmental variability or stress can alter the expression of phenotypic plasticity (Wright, Ames, and Mitchell 2016). For example, plasticity in plant height was minimized in *Prosopis pallida* populations sourced from harsh climatic conditions (Salazar et al. 2019), and plasticity in SLA was higher on less stressful north-facing slopes than in more-stressful south-facing slopes in *Fragraria vesca* (De-Kort et al. 2021). Although plasticity can help plants cope with environmental stress, it can also lead to maladaptation if environmental signals are mismatched or causes phenotypic expression that reduces fitness (Ashander, Chevin, and Baskett 2016). In a restoration context, avoiding maladaptation is critical to maintain both local and non-local populations into the future (Hufford and Mazer 2003). Because prevailing abiotic conditions can play a strong role in shaping phenotypic plasticity, understanding how environmental stress (e.g., temperature) and variability (e.g., precipitation regimes) at seed collection sites influence the expression of phenotypic plasticity in response to drought will lead to more resilient plant materials and more successful restoration outcomes in the face of climate change.

This study measures the impacts of seed-source (hereafter referred to as “home”) mean annual temperature (MAT) and precipitation (MAP), and mean annual precipitation variability (CV) on plant performance, phenotypic plasticity and local adatpation of *Plantago patagonica* under experimental drought conditions. Using a common garden and greenhouse approach, we experimentally imposed drought on 12 populations sourced from sites with a wide range of MAT(8.8—15.2°C) and MAP (167—394mm) and that differed in the variability of rainfall amounts over a 30-year period. We monitored ~1800 individuals in a greenhouse and common garden over the course of one growing season. We asked the following questions: (1) Do populations from hotter, drier, or more variable home rainfall environments differ in performance (survivorship, SLA, and flowering) in response to drought? (2) Are there population level differences in biomass allocation patterns (i.e., root:shoot ratio, R:S) in response to drought? (3) do populations sourced from hotter, drier, or more variable environments display greater phenotypic plasticity? And (4), do populations show evidence of local adaptation? We hypothesized that response to drought would vary by population. Specifically, we predict that plants sourced from hotter, drier, or more variable home sites would have lower mortality, higher flowering, higher SLA (a proxy for relative growth rate; Cornelissen et al. 2003) , and allocate more biomass to roots than those sourced from more cooler, wetter, or more predictable precipitation home sites. We predicted populations adapted to variable rainfall would show higher plasticity in traits in response to drought and we expect that geographic proximity will not predict success of populations at the common garden.

**Methods**

***Species and Population Selection***

We chose *Plantago patagonica* (wooly plantain) as our study species based on its life history, ease of propagation, broad home range, and high wild collected seed availability. *Plantago patagonica* is a small statured, self-pollinating annual forb native to North and South America. Within the southwestern US, *P. patagonica* is common and widespread, and lives as both a winter and spring annual depending on the prevailing climate. *Plantago patagonica* was identified as a priority restoration species by the Bureau of Land Management’s Colorado Plateau Native Plant Program due to its high likelihood for establishment in large scale projects ([Wood et al. 2015](https://doi.org/10.3375/043.035.0117)), high germination probability (Gremer and Venable 2014), the ability to form a seed bank (Haight et al. 2019), and its potential role in promoting perennial establishment (Barak et al. 2015).

We chose 12 populations of *P. patagonica* (Map 1)from a pool of 81 potential source locations based on the following criteria: first, we classified populations from northern regions (Utah and Colorado) and southern regions (New Mexico and Arizona) of the southwest. This sorted populations by dominant precipitation patterns within the region ([Schwinning et al. 2008](https://www.ecologyandsociety.org/vol13/iss2/art28/)). Coarsely, southern populations receive monsoonal rainfall, and northern states do not experience a monsoonal precipitation pattern. Second, we stratified each region into three temperature categories based on 30-year mean annual temperature (MAT): high (12-18ºC), medium (11-12ºC), and low (8-11ºC). Lastly, using 30-year mean annual precipitation (MAP) and standard deviation of MAP for each site, we calculated the coefficient of variation (CV) and classified rainfall variability for each source into high (29.5-45%) and low (23-29.4%) variability. To create a balanced design that captured prevailing precipitation patterns and temperature ranges from both the southern and northern regions of the southwest, we chose six populations from high and low cv levels in each temperature category (high, mid, low) which resulted in 12 total populations (Table 1). We obtained all home environmental characteristics using Oregon State University’s PRISM data explorer for individual locations (PRISM Climate Group).

***Propagation and Planting***

We completed one greenhouse experiment and one common garden experiment to measure the effects of drought on differently sourced populations of *Plantago patagonica*. In order to ensure sufficient sample size and replication, all individuals for both experiments were germinated in the greenhouse. Seeds were lightly scarified with 150-grit sandpaper, soaked roe 12 hours in tap water, and planted into 2-inch diameter “cone-tainers” (Stuewe & Sons, Tangent Ore.) We sowed 300-600 seeds per population in a soilless potting mix consisting of equal parts sphagnum moss, perlite, and vermiculite. The Greenhouse was maintained at 12° C under 12 hours of daylight and 12 hours of darkness ([Pendleton and Pendleton 2013](http://npj.uwpress.org/content/15/1/17)). We planted three to five seeds in each cone-tainer, and watered all individuals daily to saturation for the first 14 days to ensure germination. No fertilizer was applied over the course of the experiment. We thinned to a single individual on day 14 of the experiment. Plants for the common garden experiment were moved to a hoop house on day 14 for hardening and planted at garden on day 30. We transplanted individuals in the greenhouse experiment in 4-in cone-tainers on day 21 to provide ample space for root growth. For both experiments, we randomly assigned plants to a drought treatment 30 days after sowing.

***Greenhouse Experiment***

We used a greenhouse approach to quantify biomass allocation, SLA, survivorship, and reproduction in a tightly controlled environment. Each population was represented by 88 individuals (total n=1056), of which half were randomly assigned to the drought treatment (n=44). Watering amounts for the control treatment were equal to the 30-year mean spring (March-June) rainfall amounts for the wettest seed source location in our study (60mm/week). For the drought treatment, we used 50% of the 30-year mean spring rainfall amount for the driest location in our study (15mm/week) ensuring all populations experienced drought stress. Watering occurred 3 times per week at 5mm (drought) and 20mm (control) per watering using a syringe. Drought treatments began on day 30 and ended on day 65 (April 4th - May 10th, 2021).

We measured plant height at 7, 14, and 21 days after planting and every 2 weeks thereafter. Mortality and presence of reproductive structures was measured weekly throughout the experiment. On day 65, we collected one mature, healthy leaf per individual to measure specific leaf area (SLA) then destructively measured aboveground, belowground, and total plant biomass and to calculate biomass allocation between roots and shoots (root to shoot ratio; r:s). The mass of the removed leaf was added back to the total above-ground biomass for each individual for analysis.

***Common Garden Experiment***

## The common garden is located at the Petchesky Conservation Center on New Mexico Land Conservancy owned land southwest of Santa Fe, New Mexico USA (35.612602, -106.004360). The 262-acre conservation area is dominated by grasslands and pinyon-juniper woodlands, which is representative of typical *P. patagonica* habitat in the Southwest. The common garden has a 30-year mean annual precipitation of 331 mm and ranges annually in temperature from -0.30 ºC to 22 ºC. The garden has little slope and there are no systematic differences in soil moisture across the garden. The garden is fenced to prevent disturbance from wildlife or humans.

To quantify the effects seed-source rainfall variability, temperature, and precipitation on drought response in *P. patagonica,* we compared supplemental watering (“watered”) to ambient precipitation conditions at the garden (“drought”). Watering and drought treatments were implemented from early May to late June 2021, during the spring growing season of *P. patagonica* at this elevation. The watered plots received a supplemental watering equivalent to ~200% of the 30-year average for the experimental period (May-June 2021). We considered the ambient condition in Santa Fe, NM as drought due to the recurring and persistent southwestern megadrought that has dominated the region for the last 22 years (Williams et al. 2022; NOAA 2021), however our study year was an average year, with the garden receiving 48mm of rainfall over the study period, ~100% of normal.

Our common garden design consisted of 30 1 m2 sampling plots within two treatment blocks: watered and drought (15 sampling plots per treatment). Blocks were separated by a 3-meter buffer to eliminate the influence of the supplemental watering on the drought block. Each sampling plot consisted of 36 individuals with three representatives of each of the 12 populations randomly assigned a position in each plot; individuals of all populations were represented in all plots. We spaced individuals ~ 16 cm apart to minimize competition. Individuals were transplanted from the hoop house into the garden 30 days after germination. Immediately after transplanting, all plants received daily supplemental watering to saturation for one week to enhance establishment. We planted between 55-120 individuals per population in the common garden with 28-60 individuals per population and treatment (n= 1080). We measured the height of each individual prior to transplanting and assessed transplant mortality before initiating our treatment one week after transplant. Once treatment began, we monitored mortality and presence of reproductive structures once per month. On day 75, we harvested 5 mature leaves per individual to quantify SLA.

***Statistical Analysis***

We used a combination of linear regression and linear mixed-effects models to assess the effects of home environmental characteristics on both demographic and response traits in populations experiencing drought. All analyses were completed using R 4.1.4 (R Core Team 2022). We included treatment, population, and their interaction as fixed effects in our first order linear regression models to measure whether traits responded to treatment effects by population. Cumulative survivorship, cumulative number of individuals flowering, specific leaf area (SLA), total biomass and R:S were analyzed using linear mixed-effects models using the R-package lmerTest (Kunetzova 2022). In the common garden model, population was nested within plot as a random effect. In the greenhouse model, population was included as a random effect to account for expected variation between populations. We selected the most parsimonious model through an iterative selection process using AIC values (Aho et al. 2014).

To answer our first (Do populations from hotter, drier, or more variable home rainfall environments differ in performance in response to drought?) and second (Are there population level differences in biomass allocation patterns (i.e., R:S) in response to drought?) research questions, we used the model structure:

Trait ~ Home Spring Precipitation + Home Spring Temperature + Home Annual Rainfall Variability + Treatment + Home Spring Precipitation x Treatment + Home Spring Temperature x Treatment + Home inter-Annual Rainfall Variability x Treatment + random

Home spring precipitation, temperature and home rainfall variability were calculated for each population using 30-year means for April, May, June from 1989 - 2019.

To test whether plasticity was impacted by home climate characteristics, we calculated plasticity (trait mean at watered/control – trait mean at ambient/drought) for each population and trait and for each treatment (Valladares, Sanchez-Gomez, and Zavala 2016). To address our 3rd research question (Do populations sourced from more stressful or variable environments display greater phenotypic plasticity in drought-response traits?) our model structure was:

Plasticity ~ Home Spring Precipitation + Home Spring Temperature + Home Annual Rainfall Variability

To test whether local adaptation played a role in population success at the common garden (Question 4), we used linear regression models to assess survivorship, flowering, SLA, and r:s as a function of treatment and geographic proximity to the garden.

Trait ~ Treatment + Geographic Distance

**Results**

***Performance, biomass, and growth response to drought***

At the common garden, drought significantly decreased survival and SLA but had no effect on flowering. Our first order models demonstrated that significant differences exist between both populations and treatments for survivorship and SLA, but only between populations for flowering (Table 1). For all traits analyzed we found no significant interactions between treatment and home environment. In our mixed-effects models, there were no significant interactions between environmental characteristics and treatment (Table 2). At the common garden, rainfall variability (CV) was the only a significant predictor of survival (Table 2, Figure 2). In both drought and non-drought conditions, populations from high rainfall variability locations had lower survival rates than populations from low rainfall variability areas (Table 2). Flowering had a significant, but weak positive relationship with spring annual temperature and spring annual precipitation. Populations sourced from cooler, drier environments flowered less where populations sourced from warmer, wetter environments flowered more in both treatments. In the drought treatment, wetter spring precipitation source populations had on average 9% higher SLA values than populations sourced from drier environments (Table 2 and Figure 2 summarize results).

In the greenhouse, drought significantly increased R:S, decreased total biomass, but had no effect on SLA (Table 2, Figure 2), survivorship or flowering. In our greenhouse drought experiment, only 3 plants died, and 50 plants flowered out of 1,000 individuals. While some populations did not flower at all, there were no significant differences in flowering by population (Table 2). In our first order model, the effect of treatment on R:S and total biomass depended on population as indicated by a significant population x treatment interaction (Table 1). Based on our mixed models, all populations allocated more resources to shoot production when experiencing control conditions, but under the drought treatment, populations from hotter environments allocated 97% more to roots compared to populations from cooler temperature environments. All populations had reduced total biomass under drought conditions, but there was a significant population by treatment interaction. Under the drought treatment, populations from high rainfall variability environments had 18% more total biomass than populations from low rainfall variability environments. Populations from hotter environments had on average 8.5% lower SLA than populations from cooler environments. Additionally, populations from more variable rainfall environments had on average 2.7% higher SLA than populations from predictable environments (Table 2 and Figure 2 summarize results).

***Home Environment Influence on Phenotypic Plasticity***

We found only r:s-plasticity and spring annual temperature were significantly correlated. Overall, r:s-plasticity was 7x higher in populations sourced from hotter environments compared to those sourced from cooler environments (p-value = 0.02, F(1,10) = 6.45; Figure 3).

***Local Adaptation in population performance***

Survival and flowering were used to measure local adaptation of populations at the common garden. There was no significant indication that survival of a population depended on geographic distance from the garden (p-value = 0.072) but the number of flowering individuals in each population had a significant but weak relationship with geographic distance from the garden, indicating local adaptation for flowering (p-value < 0.001, R2m = 0.03, R2c = 0.16). Populations sourced closest to the common garden in both drought and watered treatments, had approximately 5 times more flowering individuals than populations sourced farthest from the garden (Figure 4).

**Discussion**

We used 12 populations of *Plantago patagonica*, sourced from both variable and predictable rainfall environments across a temperature and precipitation gradient to understand how home environment influences performance, plasticity, and the extent of local adaptation. Our results illustrate that seed collection environmental characteristics influence plant performance and impact plasticity of biomass allocation in response to experimentally imposed drought. Additionally, there was little evidence of local adaptation as measured by geographic transfer distance from the garden, although one phenological characteristic, the number of individuals flowering, was negatively correlated with distance between home-site and the common garden. These results, taken together, indicate that home environmental conditions of collected seeds can influence drought response and susceptibility of restoration relevant plants. Our findings indicate that, when faced with strong abiotic filters like drought, key home environment variables, rather than local provenance or geographic transfer distance, will influence drought response in juvenile and adult plants, which has important implications for restoration practice.

The ability for a plant to survive in a new environment is a key step in restoration. We had generally high survivorship (> 50% in drought; > 80% in watered) in all populations when they were transplanted into the common garden. Although this technique was implemented to ensure the ability to test our hypotheses, our success in establishing young plants indicates that plugging juvenile plants during a rainy period may yield high establishment of desired species.

***Influence of Home Environment on Plant Performance***

Plant populations from hot, dry, and predictable rainfall environments may be more resilient to current and future drought conditions when compared to plant populations from cool, wet, and unpredictable environments. While we expected populations from hot, dry, and unpredictable rainfall environments to have higher survival rates under drought at the common garden, we found that only predictability of rainfall was related to survivorship. Regardless of treatment, populations from predictable rainfall environments (low CV in MAP) had higher survival in both the drought and ambient treatments (Figure 2, upper left panel). Prior research on environmentally induced parental seed provisioning in plants has suggested that these effects are most likely when conditions experienced by parental plants are autocorrelated with those experienced by offspring (Galloway and Etterson 2007), and little evidence exists about the prevalence or benefits of parental provisioning in highly temporally variable ecosystems like arid lands (Metz et al. 2015). Our findings support this line of thinking, as seed sourced from less variable home sites had higher survivorship across both treatments in our common garden study, suggesting that these seeds were well provisioned for growth compared to those from more variable sites. Prior work in an arid annual has demonstrated that parental provisioning of seeds was triggered by levels of plant-plant competition following precipitation, rather than by precipitation amounts themselves (Metz et al. 2015). In our study region, annual plant cover and abundance is highly correlated with seasonal precipitation (Munson et al. 2011), which may be correlated with competition in more predictable home sites. Further research on the role of abiotic and biotic drivers of seed provisioning are certainly needed, but the improved survivorship of plants from predictable, presumably more competition-heavy locales, might suggest that row cultivation of arid annals with irrigation for restoration projects may improve outcomes.

Annual plants must flower and produce viable seed in order to persist on the landscape. In the face of drought, arid-adapted annual plants can either tolerate drought, slowing growth until precipitation increases, or escape drought by rapidly flowering and senescing (Volare 2018). In our common garden we expected the number of individuals producing flowers to be influenced by home rainfall variability as we anticipated that more predictable regimes would yield plants exhibiting drought tolerance and thus flowering less in response to experimental drought. Instead, we found floweringdepended on home spring rainfall amount and temperature, with little impact of our drought treatment on flowering. These results suggest that maternal effects of flowering cues are stronger than environmental signals in shaping how many individuals flower and that flowering is generally higher in populations from hot and dry locations (drought escape; Sherrard and Maherali 2007; Kimball et al. 2017). While not statistically significant, populations from unpredictable rainfall environments had both fewer survivors and flowered less than populations from predictable rainfall environments indicating that populations from unpredictable environments overall performed poorly in drought conditions. While-initially counterintuitive in the context of improving drought resilience, sourcing seeds from locations that have consistent annual rainfall amounts and are from warm and dry sites, may improve annual survivorship and flowering under future drought conditions.

***Influence of Home Environment on Resource-use Strategy and Growth Rates***

We found the relative growth of populations in drought, as quantified by SLA (a proxy for relative growth rate, Cornelissen et al. 2003), differed between the common garden and the greenhouse. Overall, we found growth rate between both experiments to be similar (equal SLA), but populations grown in the common garden exhibited a narrower range of SLA values under experimental drought, while populations in the greenhouse showed a larger range in SLA for both the drought and watered treatment. It is likely that growth rate was constrained by many other factors at the common garden than were present in the greenhouse setting(e.g., lower soil moisture, cooler average temperatures, seasonal light availability, inconsistent water availability, herbivory). In addition, atmospheric drought (i.e., increased vapor pressure deficit) has recently been shown to have large impacts on plant stress and growth. Inducing atmospheric drought in a greenhouse setting is challenging, and it is likely that plants in the common garden experienced much higher VPD than those in a warm, humid greenhouse. Despite this, we found a significant population-level effect in the greenhouse and common garden on growth rate. Specifically, common garden populations from wetter environments had higher relative growth rates under drought, where greenhouse populations from cooler and unpredictable growing conditions had higher relative growth rates regardless of treatment. This finding aligns with other studies (Angert et al. 2007; Gremer et al. 2012) and has important implications for restoration. These populations may be particularly useful in seed mixes to establish native plant cover and out compete invasive annual grasses (Prasser and Hild, 2016), because their higher growth rate in all precipitation conditions may aid in rapid establishment and increased native plant cover. The discrepancy in treatment effects between the common garden and greenhouse studies also suggests that growth rate in *P. patagonica* is highly plastic in response to growing season conditions, and that mean differences in growth between populations is loosely influenced by home environment (Kuijiper and Hoyle, 2015).

Drought often causes plants to allocate more biomass to roots than shoots (Eziz et al. 2017), improving water uptake while decreasing transpiration losses (Garbowski et al. 2020), a strategy which can be leveraged to improve performance in future environments (Balazs et al. 2020). We expected higher R:S in droughted individuals from hotter, drier, or more unpredictable home sites. We found that home environmental characteristics predict tissue allocation strategy and total biomass production under drought conditions. Populations from hot or dry environments allocated more resources to roots under drought than populations from cool or wet rainfall environments. Our findings demonstrate that tissue allocation under drought varies considerably across a limited geographic range and within a single species, and that this variability is strongly shaped by home environment. Populations from predictable, dry, or hot areas demonstrate a larger shift in allocation to roots when experiencing drought (tolerance), whereas populations from unpredictable, dry, and hot environments demonstrate higher overall biomass and growth (escape). This suggests a legacy effect of home environment on a population’s drought response strategy that could have significant impacts on restoration goals and outcomes. For example, populations exhibiting drought escape may be less effective at out-competing weedy annuals like *Bromus tectorum* if they rapidly complete their lifecycle and senesce, while drought tolerating populations may both out-compete exotic annuals and provide microsites for perennial germination over a longer growing season.

***Role of Home Environment on Phenotypic Plasticity***

Increased trait plasticity in drought is expected to support plant function and maintain persistence in stressful environments (Gianoli and Gonzalez-Tueber 2005, Ackerly et al. 2000). Previous work has demonstrated that, in environments with reliable environmental cues (i.e. consistent summer drought), low levels of plasticity have evolved to buffer against low levels of environmental variability (Reed et al. 2010, Kuijper and Hoyle, 2015; Heschel et al. 2004). In unpredictable environments, high levels of plasticity may evolve to aid survival by responding quickly to fluctuating and unreliable environments (Chevin and Hoffman, 2016). However, beneficial effects of plasticity induced by maternal home environment on offspring fitness is dependent on the autocorrelation between both generations’ environments (Kuijper and Hoyle, 2015); the maternal environment benefits the offspring generation only when strength of selection for a trait is strong (i.e. mortality). We found that home temperature was the only environmental characteristic to have a relationship with phenotypic plasticity, and only in one measured trait: R:S. Populations from hot environments showed a larger shift of biomass to roots than populations from cooler environments. Our finding supports the previous finding that drought response strategy varies across environmental gradients (Brouillette et al. 2014) and that plasticity in R:S was higher in plants from more arid regions (Carvajal et al. 2017, Lázaro-Nogal et al. 2015). The larger shift to root biomass found in populations from hot environments in our study suggests a greater capacity to efficiently forage for scarce water. Sourcing seeds from populations that demonstrate the ability to plastically respond to drought conditions will improve the success and resilience of restoration outcomes under future conditions.

***Role of Local Adaptation in Plant Performance***

It is commonly assumed, and many studies indicate, that when plants are locally adapted, they will perform better when planted in geographically close locations compared to plants that are sourced from more distant locations and that distantly sourced seed may introduce maladaptation to local populations. Seed-transfer zones rely explicitly on this spatial assumption (Bower 2014). However, local adaptation based on proximity may be less common in plants than assumed (Leimu and Fischer, 2008) and recent studies have found that rates of climate change are outstripping rates of local adaptation (Anderson and Adgymar 2020), which raises new challenges when sourcing plant materials for restoration. Our study demonstrates that local adaptation does not act equally across traits. Of the measured performance and growth metrics only the number of individuals flowering was negatively correlated with distance between collection site and the common garden. While of little importance for self-pollinating *P. patagonica* such shifts in phenology, if common, could have larger consequences for pollinator-dependent plants or restoration efforts aimed at enhancing pollinator habitat by introducing significant phenological mismatch (Bucharova XXX). Further examination of the assumptions underlying seed transfer zones and local seed collection are critically important as practitioners attempt to restore assemblages and functions in the face of climate change.

Overall, we conclude that seed collection site environment has strong impacts on plant performance under drought conditions. We found (a) populations from predictable environments have higher survivorship and collection site temperature and precipitation significantly influence growth-rate, reproduction, and drought strategy (b) home environment, specifically temperature, influences population-level drought responses in biomass allocation and plasticity, and (c) signals of local adaptation are weak for *P. patagonica*. In the future, restoration practitioners, seed-collectors, and seed-increase operations should carefully consider the role of seed-source environmental characteristics and variability when selecting and growing seeds. Our finding that predictable rainfall environments lead to higher plant survival, even under drought conditions, are especially promising for seed-increase operations, where irrigation may be used to improve seed production.

Table 1

Table 2



Fig. 1******

**Fig. 2**

**Figure 2.** Response variables and relationships with home environmental characteristics. Temperature and precipitation refer to seed-source environment spring values, rainfall variability is based on mean annual rainfall for each site. Common garden results are above dotted line and greenhouse are below. Insignificant effect of treatment is indicated by a grey trend line. Confidence intervals are indicated by dashed lines and correspond with drought treatment (yellow) and non-drought (blue). We used standard error to form confidence intervals.



**Fig 3.**



**Figure 4.** Relationship between R:S plasticity (mean difference in r:s for drought and control treatments) and seed-source spring temperature (C). Error bars illustrate SE +/- mean value of r:s plasticity for each population. Temperature gradient (low to high) is represented by the color gradient (blue to orange).

**Fig. 4**



**Figure 5.** The effect that distance from garden has on percent flowering. Confidence intervals are indicated by dashed lines for each treatment and are SE +/- mean of total flowering. \*\*\* indicate p < 0.001. R

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