

# Seed type and origin-dependent germination patterns in *Danthonia californica*, a cleistogamous species commonly used in grassland restoration

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## Abstract

*Danthonia californica* is a native perennial bunchgrass commonly used in the restoration of prairie ecosystems in the western United States. Plants of this species simultaneously produce both chasmogamous (potentially outcrossed) and cleistogamous (obligately self-fertilized) seeds. Restoration practitioners almost exclusively use chasmogamous seeds for outplanting, which are predicted to perform better in novel environments due to their greater genetic diversity. Meanwhile, cleistogamous seeds may exhibit greater local adaptation to the conditions in which the maternal plant exists. We performed a common garden experiment at two sites in the Willamette Valley, Oregon to assess the influence of seed type and source population (eight populations) on germination and found no evidence of local adaptation for either seed type. Cleistogamous seeds outperformed chasmogamous seeds regardless of whether seeds were sourced directly from the common gardens (local seeds), or other populations (nonlocal seeds). Furthermore, average seed weight had a strong positive effect on germination success, despite the fact that chasmogamous seeds had significantly greater mass than cleistogamous seeds. At one common garden we observed that seeds of both types sourced from north of our planting site performed significantly better than local or southern-sourced seeds. We also found a significant seed type and distance-dependent interaction, with cleistogamous germination peaking approximately 125km from the garden, which may be explained by differences in the pathogen content of cleistogamous and chasmogamous seeds. These results suggest that cleistogamous seeds should be considered for greater use in *D. californica* restoration.

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*Danthonia californica* is a native perennial bunchgrass commonly used in the restoration of prairie ecosystems in the western United States. Plants of this species simultaneously produce both chasmogamous (potentially outcrossed) and cleistogamous (obligately self-fertilized) seeds. Restoration practitioners almost exclusively use chasmogamous seeds for outplanting, which are predicted to perform better in novel environments due to their greater genetic diversity. Meanwhile, cleistogamous seeds may exhibit greater local adaptation to the conditions in which the maternal plant exists. We performed a common garden experiment at two sites in the Willamette Valley, Oregon to assess the influence of seed type and source population (eight populations) on germination and found no evidence of local adaptation for either seed type. Cleistogamous seeds outperformed chasmogamous seeds regardless of whether seeds were sourced directly from the common gardens (local seeds), or other populations (nonlocal seeds). Furthermore, average seed weight had a strong positive effect on germination success, despite the fact that chasmogamous seeds had significantly greater mass than cleistogamous seeds. At one common garden we observed that seeds of both types sourced from north of our planting site performed significantly better than local or southern-sourced seeds. We also found a significant seed type and distance-dependent interaction, with cleistogamous germination peaking approximately 125km from the garden, which may be explained by differences in the pathogen content of cleistogamous and chasmogamous seeds. These results suggest that cleistogamous seeds should be considered for greater use in *D. californica* restoration.

## Keywords

*common garden, local adaptation, climate warming, nonlocal*

## Introduction

Seed provenance is an important consideration for restoration practitioners seeking to re-seed grassland ecosystems (Bischoff et al. 2006, Vander Mijnsbrugge et al. 2010, Bischoff et al. 2010, Breed et al. 2018). Seemingly minor differences in the fitness of seeds sourced from different populations can have profound effects on the establishment of focal plant populations at an ecosystem scale (Middleton et al. 2010, Seifert & Fischer 2010). In 2020, the United Nations declared 2021-2030 the “Decade on Ecosystem Restoration” (UNEP and FAO, 2020). Grasslands have high potential for restoration under this declaration, but careful planning is needed to ensure long term success (Dudley et al. 2020). To achieve ambitious global restoration targets for grassland ecosystems, research on the relationship between seed provenance and plant fitness is urgently needed (Breed et al. 2018).

Restoration practitioners must consider the degree of local adaptation - the superior fitness of local genotypes - for plant species used in their projects. Populations under intense selective pressure are more likely to show local adaptation, providing them with a distinct “home” advantage over nonlocal populations at a given location (Joshi et al. 2001, Breed et al. 2018). Although intuitive from an evolutionary perspective, local adaptation is certainly not universal (Bischoff et al. 2006, Leimu & Fischer 2008, DeMarche et al. 2019). Ecologists frequently use reciprocal transplant and common garden experiments to measure the degree to which local adaptation exists in plant populations (Hereford 2010). Approximately 70% of reciprocal transplant studies show local adaptation (Leimu & Fischer 2008, Hereford 2009), which likely depends upon three variables (Hereford 2009): the difference in selection pressure between local and nonlocal genotypes (Schluter & Grant 1984), the amount of gene flow between populations (Garcia-Ramos & Kirkpatrick 1997, Lenormand 2002, Kawecki & Ebert 2004), and the genetic structure of each population (Linhart & Grant 1996).

Differences in selection pressure between populations are likely linked to differences in site environmental characteristics, which is often closely related to geographic distance (Leimu & Fischer 2008, Hereford 2009). Theory predicts that as environmental and geographic distance increase between populations, so too should the magnitude of local adaptation (Garcia-Ramos & Kirkpatrick 1997, Joshi et al. 2001). The underlying logic is simple; genotypes proven to perform well in a site should continue to do so in the future, while genotypes sourced from elsewhere may not, especially as the differentiation between sites increases. The degree

of local adaptation thus varies among populations and can be difficult to predict (Leimu & Fischer 2008, Gaillard et al. 2019). With germination being the critical first step in plant establishment, understanding how seeds germinate near and far from their maternal plants can help elucidate the degree of local adaptation in plant populations.

Another consideration for choosing seed sources for restoration is how to best maintain genetic diversity (McKay et al. 2005). Although most plant species produce a single type of seed, many exhibit seed heteromorphism – the production of multiple seed types. Nearly 700 angiosperm species exhibit cleistogamy, a breeding system that includes permanently closed, obligately self-pollinated flowers (Culley & Klooster 2007). The majority of these species are classified as dimorphically cleistogamous, producing seeds from both cleistogamous and chasmogamous (more typical, externally pollinated) flowers (Culley & Klooster 2007, Baskin & Baskin 2017). As such, cleistogamous seeds are likely to have less genetic diversity than their potentially outcrossed chasmogamous counterparts and could be more prone to inbreeding depression (Culley & Klooster 2007). Cleistogamous seeds also typically disperse much shorter distances than chasmogamous seeds (Schoen & Loyd 1984, Culley & Klooster 2007, Auld & de Casas 2013, Baskin & Baskin 2017), and average seed weight can differ substantially between the two types (Waller 1982). There are, however, several evolutionary advantages to cleistogamy, including insurance in the absence of external pollination, the reduced energy cost of production, and the retention of locally adapted gene complexes (Schoen & Loyd 1984, Culley & Klooster 2007, Baskin & Baskin 2017). Indeed, a review of field and lab studies comparing the germination of cleistogamous and chasmogamous seeds found that a higher proportion of cleistogamous seeds germinated in two-thirds of cases (Baskin & Baskin 2017). The inherent differences in genetic diversity and dispersal between these two seed types suggest that chasmogamous seeds might be better suited for success in novel environments, while cleistogamous seeds may perform better in the immediate vicinity of their maternal plant (Schoen & Loyd 1984, Culley & Klooster 2007).

To date, researchers have mostly recommended the use of locally-sourced seeds for restoration (Bischoff et al. 2010, Vander Mijnsbrugge et al. 2010, Bucharova et al. 2017), despite approximately 30% of plant populations surveyed not showing local adaptation (Hereford 2009). In these cases, stringent seed sourcing restrictions likely inhibit the genetic diversity of the restored population, which may have negative effects on the population’s ability to respond to changing environmental conditions (Broadhurst et al. 2008, Miller et al. 2011). There is growing support for the use of nonlocal seeds sourced from populations that may be better adapted to future climatic conditions, as the use of climate-adapted genotypes could facilitate the maintenance of ecosystem services and critical habitat structure (Broadhurst et al. 2008, Bischoff et al. 2010, Kreyling et al. 2011, Ramalho et al. 2017). Climate-motivated translocation of seeds is controversial, however, as it relies on a series of assumptions that are difficult to test. These assumptions include that the seeds are sufficiently adapted to their local climate, that this climate adequately matches the future climate of the restoration site, that the nonlocal seeds will germinate and establish in a restored site under current conditions (Kreyling et al. 2011), and that climate is the most important driver of performance (DeMarche et al. 2019). While considering the long-term effects of introducing novel genotypes, the germination of nonlocal seeds in a novel environment needs further study to ensure such an approach is feasible in the first place (Bucharova et al. 2017, Breed et al. 2018).

*Danthonia californica*, a perennial bunchgrass native to western North America, is commonly used in the restoration of prairie ecosystems in the Pacific Northwest, USA (Buisson et al. 2006, Hayes & Holl 2011, Stanley et al. 2011, Pfeifer-Meister et al. 2012). Individuals produce both chasmogamous and cleistogamous seeds (Appendix A; A,B), the latter of which are enclosed within the stem. Cleistogamous seeds are difficult to remove manually, potentially contributing to their infrequent use in *D. californica* restoration (Hayes & Holl 2011). Although mating system generally does not influence the degree of local adaptation across species (Hereford 2010), many studies have shown different fitness and local adaptation patterns for conspecific seeds produced via different mating systems (Schmitt & Gamble 1990, Lovell et al. 2014, Rushworth et al. 2020). However, the applied aspects of mating-system dependent seed selection for restoration are relatively rare in the literature (Coulter 1914, Charlesworth 2007, Rushworth et al. 2020). *Danthonia californica* thus provides an excellent opportunity to study the impacts of sourcing distance and mating system on local adaptation

in an ecosystem restoration context.

Here, we devised a common garden experiment using both chasmogamous and cleistogamous seeds collected from eight natural populations of *D. californica* across a latitudinal gradient in western Oregon and Washington, USA (Figure 1A). Our design allowed us to ask whether the effects of seed source origin (local vs. nonlocal) on germination are dependent on seed type, and whether there are other factors about seed source origin, such as the distance or direction (north or south) from the common garden, latitude, or average seed weight, that help explain germination patterns across source populations. Additionally, we experimented with seed processing techniques to facilitate cleistogamous seed preparation and decrease processing time for heteromorphic seed planting. This is necessary because cleistogamous seeds remain in the stem and are difficult to remove and separate.

We hypothesized the following: **H1a:** At each common garden, we predicted that both cleistogamous and chasmogamous seeds originating from that site (local seeds) would outperform seeds originating from other source populations (nonlocal seeds), regardless of whether the nonlocal seeds originated to the south or north of the common garden. **H1b:** However, we expected that the degree of local adaptation would depend on seed type. If inbreeding depression compromises local adaptation, then we would expect local chasmogamous seeds to outperform local cleistogamous seeds. Alternatively, if gene flow limits local adaptation, then we would expect local cleistogamous seeds to outperform local chasmogamous seeds. **H2:** Furthermore, we expected germination to decrease with increasing distance between source population and common garden (both geographic and environmental distance - the similarity in environmental conditions such as temperature, precipitation, etc.), considering that the magnitude of local adaptation between common garden and source sites should increase as distance does. **H3:** Finally, we predicted that nonlocal seed germination would decrease with increasing latitude, as seeds sourced from southern populations would outperform seeds sourced from northern populations due to recent climate warming. Demographic studies of natural *D. californica* populations, including most of the populations studied here, revealed that population growth rate decreases with increasing latitude and that locally, the population growth rate decreases under warmer and drier conditions (DeMarche et al. 2021). Thus, it follows that the higher-performing nonlocal seeds at the two common gardens should be those adapted to warmer and drier conditions (i.e., more southern populations).

## Materials and Methods

### *Experimental Design*

We selected two natural *D. californica* populations located outside of Eugene, Oregon as common garden sites for our experiment. The first common garden, Hazel Dell (hereafter HD; N44.01979, W123.21823, 157 masl), is a seasonal wet prairie at the southern end of the Willamette Valley (Appendix A; C). The second common garden, Horse Rock Ridge (hereafter HR; N44.29877, W122.87984, 570 masl), is an exposed ridgeline in the Coburg Hills (Appendix A; D), which are foothills of the Cascade Mountains. While these two sites are geographically close relative to the entire latitudinal range from which we sourced seeds (Fig. 1A), they represent very different ecological extremes at approximately the same latitude: HD being a mesic, deep soil, low elevation site (Appendix A; C), and HR being a steep slope with dry, shallow soil, and higher elevation site (Appendix A; D).

In June and July 2018, we collected approximately 50,000 cleistogamous and chasmogamous seeds (approximately 25,000 each) from natural *D. californica* populations at our two common garden sites and six other sites in the greater Klamath Mountain - Willamette Valley - Puget Lowland ecoregions (Fig. 1A). Both seed types were collected from each maternal plant; both occur on the same reproductive stems. We collected 5-10 reproductive stems from each of 11-21 large maternal plants (median = 15) at each population.

### *Seed Preparation*

Stems were stored in a cool, dry environment for no more than 90 days before we manually separated seeds by type. Chasmogamous seeds were shaken from inflorescences and manually extracted with forceps when necessary. We tested three approaches to separating cleistogamous seeds. Most were manually extracted from

stems by carefully slicing the stems so as not to damage seeds before removing them either individually or as a group when possible. However, we also soaked a random subset of stems containing both cleistogamous and chasmogamous seeds in room temperature tap water to facilitate cleistogamous seed extraction and sorting with a light table, hereafter referred to as soaked seeds. We compared these to an additional randomized subset of cleistogamous seeds that were still enclosed within the stem but separated into individual seed units, further facilitating seed processing, hereafter referred to as sheathed seeds. Once we extracted all seeds, we randomly weighed a subset of non-soaked or sheathed chasmogamous and cleistogamous seeds (~20 each) from each maternal plant to calculate average seed weights by maternal plant.

### *Common Garden Experiment*

We planted seeds at HD on September 29th, 2018, and HR on September 30th, 2018. In areas with mature *D. californica* individuals already present, we aligned 15-m transects with 1-m<sup>2</sup> quadrats alternating every other side of the transect (Appendix A; C,D), avoiding areas where large rocks were present. Each 1-m<sup>2</sup> quadrat was divided into 100 planting cells of 1-cm<sup>2</sup> each (Fig. 1B). If a cell was suitable for planting (i.e., with adequate soil and large adult plants absent), we installed 5.5-cm diameter, 1.25-cm deep PVC rings into the soil to define the planting area (Appendix A; C,D). We left approximately 10% of suitable cells undisturbed after ring installation as controls to allow for the detection of background *D. californica* germination from the natural population (Fig. 1B). In each of the remaining cells, we planted 25 seeds of a given type and maternal plant in a predetermined randomized order, thereby randomizing planting location.

### *Seedling Census*

We censused germination at HD on April 12th, 2019 and at HR on April 17<sup>th</sup>, 2019. We counted *D. californica* seedlings in all rings, including unplanted control cells to measure background germination. Seedlings and rings were manually removed from sites in June 2019 to avoid genetic contamination of natural populations.

### *Statistical Analyses*

We used R version 4.0.2 for all analyses and visualization (R Core Team 2021), using the package ‘lme4’ to fit mixed effect models (Bates et al. 2015), the ‘Anova’ function from the ‘car’ package (Fox & Weisberg 2019) using type III sum of squares to test for significant terms, the package ‘sjPlot’ (Lüdtke 2021) to calculate marginal and conditional R<sup>2</sup> values based on Nakagawa et al. (2017), and the package ‘emmeans’ (Lenth 2020) to calculate model estimated marginal means and conduct post-hoc tests for significant differences between categorical variables with more than two levels. To accommodate the type III sum of squares, we set contrasts = c(“contr.sum”, “contr.poly”). We used the ‘ggplot2’ package for data visualization (Wickham 2016).

We first tested for background germination by modeling the number of seedlings in each cell as a Poisson distribution, fitting the interaction of common garden (HD, HR) and cell type (planted, control) as fixed effects and quadrat as a random effect. To correct for the fact that many cells contained zero seedlings, we included an observation level random effect to account for overdispersion (Browne et al. 2005, Harrison 2015).

We also performed an initial coarse test of our seed processing techniques (soaked and sheathed) to see whether either technique affected germination rates (across the two gardens). We fit binomial logistic regressions separately for chasmogamous and cleistogamous seeds, with soaked as a fixed effect for chasmogamous and both soaked and sheathed as fixed effects for cleistogamous. Both models included random effects for quadrat, maternal plant nested within source population, and an observation level random effect for overdispersion.

To address our hypotheses, we fit a series of binomial logistic regressions separately for each common garden. Each model included average maternal seed weight as well as soaked and sheathed treatments as covariates, but we dropped the soaked and sheathed treatments when not significant (most often the case) to reduce model complexity. For random effects, we included quadrat, maternal plant nested within source population, and observation level random effects for overdispersion.

For hypotheses 1a-b regarding local adaptation, we fit a categorical model with the interaction of seed origin (local, nonlocal to the south of the garden, and nonlocal to the north of the garden) and seed type (chasmogamous, cleistogamous) as fixed effects. We also ran models separately for each pairwise combination of nonlocal source population and common garden, with the interaction of seed origin (local, nonlocal) and seed type as fixed effects. We then ran separate regression models for hypotheses 2 and 3 to explore the possible mechanisms that could explain the presence or absence of seed origin effects. These models addressed the geographic and environmental distances (separately) between source populations and common gardens and the latitudes of the source populations. Each of these models included interactions with seed type (cleistogamous, chasmogamous) and the geographic distance model also included a quadratic distance term to allow for nonlinearity.

We calculated geographic distance between source populations and common garden sites using NOAA's Latitude and Longitude distance calculator (Williams n.d.). We calculated environmental distance using the Euclidean distance of a principal components analysis on a set of environmental variables collected from each source population site in the year of seed collection (2018). These variables included spring precipitation, temperature (min, mean, and max), dew point (mean), vapor pressure deficit (min and max), elevation, and plant density as described in Mackin et al. (2021). We performed a principal components analysis on this set of nine environmental variables and calculated the Euclidean distance of each source population from each common garden using the first two principal components. We also performed a simple linear regression between geographic and environmental distance to see whether the two were correlated.

Finally, we tested whether average maternal seed weight, a covariate in all the germination rate models, could be explained by seed type, source population, or source population latitude. We fit two linear mixed effects models: the first including the interaction of source population and seed type as fixed effects and maternal plant as a random effect, and the second taking the average weight across cleistogamous and chasmogamous seed types and fitting source population latitude as a fixed effect and source population as a random effect.

## Results

### *Background germination and seed processing techniques:*

Seedling counts were greater at HD than HR and were significantly greater in planted cells than unplanted control cells at both sites (Fig. 2; common garden x cell type:  $p$ -value = 0.006). However, while background germination was essentially negligible at HR (0.01 mean seedlings per unplanted control cell), there was a mean of 1.5 seedlings per control cell at HD (Fig. 2). Neither of our seed processing techniques intended to facilitate seed extraction (soaked and sheathed) caused planted seeds to germinate at a different rate than untreated seeds ( $p$  0.12; Appendix B). Thus, we included all seed treatment subsets and untreated seeds together in further analyses.

### *Germination rate depends on seed origin, seed type, and seed weight:*

There was no evidence for local adaptation at HD or HR for either cleistogamous or chasmogamous seeds (Fig. 3A). However, germination did depend on seed origin: at HD, nonlocal seeds sourced to the north of the garden significantly outperformed both local (HD) and nonlocal seeds sourced to the south of the garden ( $P < 0.001$ ). At HR, nonlocal seeds sourced to the north significantly outperformed nonlocal seeds sourced to the south of the garden ( $P = 0.015$ ), but local (HR) seed performance was not significantly different from either nonlocal seed group. Models for each pairwise combination between nonlocal source populations and common garden revealed the specific differences in germination by source population (Appendix C).

At both gardens, cleistogamous seeds significantly outperformed chasmogamous seeds ( $P$  0.003; Fig. 3A), and seed weight was a significant positive predictor of germination ( $P < 0.001$ ; Fig. 3B; Appendix H, Table 1). Despite this, cleistogamous seeds were universally lighter weight than chasmogamous seeds across all source populations ( $P < 0.001$ ; Appendix D). There was no significant relationship between average seed weight and source population latitude ( $P = 0.559$ ; Appendix E).

### *Geographic distance and latitude, but not environmental distance, affect germination rate:*

There was a significant, nonlinear effect of geographic distance between source population and common garden at the HD garden, but this effect depended on seed type (distance<sup>2</sup> x seed type:  $P = 0.001$ ; Fig. 4; Appendix B). Chasmogamous seed germination decreased weakly as distance from garden increased, whereas cleistogamous seed germination was greatest when sourced somewhat close to ( $\sim 125$  km away) but not directly from the HD garden (Fig. 4). When modeled separately by seed type, however, the weak distance effect for chasmogamous seeds became nonsignificant (distance:  $P = 0.30$ ; distance<sup>2</sup>:  $P = 0.80$ ), whereas the effect remained significant for cleistogamous seeds (distance<sup>2</sup>:  $P = 0.002$ ). The overall trend appears to be similar at the HR garden, although there were no significant effects of distance or distance<sup>2</sup> at that garden (Fig. 4; Appendix H, Table 2).

The first two principal components explained 74.1% of the variation in the environmental data from source populations (Appendix F). However, there was no significant effect of environmental distance between source population and common garden on germination at either common garden (Fig. 5; Appendix H, Table 3). Furthermore, there was no significant correlation between geographic and environmental distances of source populations (Appendix G).

The effect of source population latitude on germination depended on seed type at HD ( $P = 0.023$ ) but was not significant at HR ( $P = 0.267$ ; Fig. 6; Appendix H, Table 4). Higher latitude exhibited a slight positive effect on germination for chasmogamous seeds but a negligible effect for cleistogamous seeds at HD (Fig. 6).

## Discussion

Research on the degree of local adaptation in plant communities is urgently needed to inform ecosystem restoration efforts (Bischoff et al. 2006, Vander Mijnsbrugge et al. 2010, Bischoff et al. 2010, Breed et al. 2018). Here, we devised a common garden experiment using both cleistogamous and chasmogamous seeds of *D. californica* and expected to see a local advantage for seeds of both types. However, we did not find any evidence for local seeds outperforming seeds sourced from other populations (nonlocal seeds) at either of our common garden sites. These results align with the findings of Hereford (2010) who, in a review of reciprocal transplant experiments, found that mating system does not generally influence local adaptation. Instead, we found that seeds of both types sourced from the north of our HD common garden performed significantly better than seeds sourced both locally and from more southern locations.

An absence of local adaptation could stem from intermediate levels of either inbreeding or gene flow, or a lack of strong divergent selective pressure on either of our common garden populations (Lenormand 2002, Hereford 2010). Another possibility for why we may not have seen local adaptation could be because our study looked exclusively at germination. Adaptation patterns may come from the accumulation of small fitness advantages over a plant's life history, which are not always consistent with those of the establishment stage (Rice & Knapp 2008, Jin et al. 2020).

### *Seed weight is an important predictor of germination success*

It is clear that seed weight is an important factor influencing the germination of both chasmogamous and cleistogamous seeds in our study. This is to be expected, as larger seed mass has long been linked to more energy investment and higher germination rates (Green & Hansen 1969, Hendrix 1984, but see Kitchen & Monsen 1984), although the tradeoff between seed size and dispersal ability, seed number, and susceptibility to predation all mitigate the overall fitness benefits of increased seed size (Gómez 2004, Gundel et al. 2012). Chasmogamous seeds of *D. californica* are heavier than cleistogamous seeds, but it was the cleistogamous seeds that generally outperformed chasmogamous seeds in our study. Our hypothesis that nonlocal chasmogamous seeds would outperform nonlocal cleistogamous seeds was primarily motivated by the genetic differences between seed types, although we would expect seed weight differences between seed types to reinforce this prediction. We were surprised to find the reverse phenomenon to be true across all three source groups in the HD common garden, with a significant seed type effect showing that non-local, obligately selfed, smaller cleistogamous seeds significantly outperformed non-local, potentially outcrossed, larger chasmogamous seeds.

### *Seed-type dependent geographic distance effect*

Even after controlling for seed mass, we saw a significant geographic distance effect on cleistogamous germination at the HD common garden. We found that cleistogamous germination peaked at approximately 125km from the HD garden, while chasmogamous germination declined slightly with increasing distance from the source population, although this effect was not significant. This corroborates our prior finding that non-local cleistogamous seeds germinate at a higher rate than non-local chasmogamous seeds at the HD garden, suggesting this pattern may be biologically significant. These results are surprising for the genetic and seed weight differences discussed previously, in addition to differences in the dispersal ability of the two seeds. In nature, cleistogamous seeds germinate almost exclusively within the length of a single stem of the maternal plant (Holsinger 2000), making them extremely unlikely colonizing mechanisms for *D. californica*. By contrast, chasmogamous seeds can disperse farther (Schmitt et al. 1985), making them better candidates to colonize novel environments (Culley & Klooster 2007, but see Masuda & Yahara 1992).

Contrary to prediction, the observed seed type and geographic distance effect cannot be explained by genetic differences between cleistogamous and chasmogamous seeds. Indeed, our observation that cleistogamous germination success is improved, while chasmogamous germination success decreases away from the source population fundamentally dissatisfies the conditions for dimorphic cleistogamy maintenance at the population level as outlined by Culley & Kooster (2007). Mating system evolution theory predicts that cleistogamous and chasmogamous seeds with different dispersal abilities can be jointly maintained if their dispersal abilities differ, as they do for *D. californica* (Schoen & Loyd 1984). The near and far dispersal model for the selection of cleistogamy predicts that resource allocation will first be spent on the production of cleistogamous seeds - a so-called *pessimistic* reproductive strategy - followed by chasmogamous seed production - an *optimistic* reproductive strategy (Zeide 1978, Schoen & Loyd). Our finding that cleistogamous seeds are generally more vigorous than their chasmogamous counterparts supports theory predicting that their investment should be prioritized and aligns with other studies that have found cleistogamous seeds to be generally superior (Dyksterhuis 1945, Cheplick & Quinn 1982, Schoen & Loyd 1984, Baskin & Baskin 2017). It is possible that our experimental design, which planted 25 seeds from the same maternal plant within close proximity, may have unintentionally favored cleistogamous germination as these seeds are more likely to be subjected to sibling competition than farther dispersing chasmogamous seeds (Schoen & Loyd 1984). This may partially explain our finding that cleistogamous seeds were more vigorous than chasmogamous seeds. Although density-dependent processes such as intraspecific competition could influence the expression of local adaptation, this is rarely addressed in local adaptation studies (Siepielski et al. 2016).

### *Environmental distance and latitude did not drive germination patterns*

Environmental distance between source population and common garden sites did not explain the observed seed-type and scale-dependent germination patterns. Although regional climate models do show that southern sites tend to be warmer and drier (PRISM Climate Group 2020), it is possible that the environmental covariates we used to estimate environmental distance were not meaningful, masking a potential environmental source effect on germination that can be difficult to detect (Hereford 2009). Other common garden studies have found that germination success is influenced by parental environment (Gallagher & Wagenius 2016). More source populations and environmental data could possibly reveal such a trend if one exists.

We expected to see higher germination of nonlocal seeds sourced from southern compared to northern sites due to recent warming patterns in the region (PRISM Climate Group 2020) but were surprised to find the reverse pattern in our study. A categorical comparison of locally sourced seeds to those sourced to the north and south of the HD common garden revealed that northern seeds performed significantly better than both local and southerly sourced seeds. This pattern was not as easily detected in a latitude-based germination model; as latitude increased, chasmogamous germination also increased slightly, while cleistogamous germination slightly decreased which produced a significant latitude by seed type interaction. It is likely that the highly reduced germination probability of cleistogamous seeds at only our most northerly site created this negative latitudinal trend for cleistogamous seeds. This suggests there may be a northern limit for seed sourcing success at Willamette Valley planting locations.

These results could be linked to our observation that seed weight slightly increased with latitude, although this trend is not significant. It is unlikely that the opposing effects of latitude on chasmogamous and cleistogamous seeds observed in our continuous latitude model are biologically meaningful. Perhaps sourcing from more sites would allow us to examine the impact of latitude on germination more accurately. Indeed, the latitudinal range for *D. californica* extends from British Columbia to southern California (Darris & Gonzalves n.d.). Of course, our study only measured the germination probability within one growing season, which makes the detection of climate-driven latitudinal fitness patterns unlikely (Gaillart et al. 2018, DeMarche et al. 2019). Other local adaptation studies have found significant latitudinal responses (van Boheemen et al. 2019, Zhang et al. 2019), although they may not necessarily be tied to climate (DeMarche et al. 2021).

#### *Northern seeds outperform southern seeds at HD common garden*

It is possible that seeds sourced from the south were of a generally inferior quality than northern seeds, which may be linked to greater climate-related environmental stresses at lower latitudes. Other studies have found that climate-based environmental stresses lead to decreased germination (Moreira de Oliveira et al. 2019, Yi et al. 2019, Ribeiro et al. 2021), which may help explain our finding that northern seeds outperform southern seeds at both common gardens.

Our prediction that southern seeds would outperform northern seeds also assumed that southern populations had adequately adapted to historically warmer conditions and that these conditions match recent climate warming. Given the rapid rate of climate change in the region and the high degree of habitat fragmentation throughout the Klamath Mountain and Willamette Valley ecoregions (Wilson 1998, Floberg et al. 2004), it is possible that southern populations may not yet be adequately adapted to their current climates. Because our study only lasted one growing season, we may have assessed germination during an abnormal winter that favored northern-sourced seed. Although a multi-year analysis of germination was outside the scope of this study, multi-year studies allow for a more thorough understanding of the mechanisms driving differential germination and establishment patterns (Rice & Knapp 2008, Pfeifer-Meister et al. 2012, Merges et al. 2020)

#### *Possibility for pathogen escape*

Using a subset of seeds collected and processed in the same manner and from the same source populations as our study, Mackin et al. (2021) found that epiphytic (seed surface) pathogen community diversity is significantly higher on chasmogamous than cleistogamous seeds of *D. californica*. Although they found higher in vitro germination with chasmogamous seeds, it is likely that the negative effects of antagonistic pathogens on seed germination are diminished in a laboratory setting (Mackin et al. 2021). Seed pathogens can be a significant barrier to in situ germination, although they are rarely accounted for in demography studies (Nelson 2017, Mackin et al. 2021). In general, outcrossed progeny have been shown to have higher infection scores when compared to self-fertilized progeny, suggesting that outcrossing can disrupt pathogen resistance (Busch et al. 2004, Koslow & Clay 2007). There are several theories to explain the maintenance of both cleistogamous and chasmogamous mating systems (Oakley et al. 2007), to which seed-type dependent pathogens could contribute.

It is important to note that not all seed-associated fungi are pathogenic. For example, some species of the *Danthonia* genus have a symbiotic relationship with the endophytic clavicipitaceous fungi *Atkinsonella hypoxylon* which improves host plant vigor (Clay 1984) and exclusively uses cleistogamous seeds for transmission (Clay 1994). The fungus also causes infected plants to abort chasmogamous inflorescences, further improving the adaptive potential for cleistogamous seeds (Clay 1984). However, Mackin et al. (2021) did not find any evidence of clavicipitaceous fungi inside any *D. californica* seeds sourced from the populations used in this study. However, they did find that cleistogamous seeds had fewer fungi negatively associated with germination than chasmogamous seeds, which may partially explain the observed higher germination rates of cleistogamous seeds in our common garden study.

Pathogen escape could explain the higher germination rates of cleistogamous seeds sourced from populations located an intermediate distance from the HD common garden. This fitness advantage quickly dissipated as distance between source and common garden increased, however, suggesting that some degree of local

adaptation may still play a role in germination. It appears that populations from farther away are still more maladapted to the common garden site, even if they do benefit from pathogen escape. Only the seeds from intermediately distanced populations likely stood to benefit from pathogen escape in our common garden experiment. Although most transplant experiments occur across much larger spatial scales (Joshi et al. 2001, Gaillard et al. 2018, van Boheemen et al. 2019, Zhang et al. 2019), nonlocal advantage at small scales could be common, especially if environmental heterogeneity is high (Hereford 2009).

### *Implications for restoration*

Restoration practitioners frequently use *D. californica* to reseed oak savanna and grassland ecosystems along the West Coast of the United States, although chasmogamous seeds have until now been used almost exclusively for this purpose (Maslovat 2002, Hayes & Holl, 2011, Lindh 2018). Our results from the HD common garden suggest that cleistogamous seeds are more vigorous than chasmogamous seeds, and that northerly-sourced seeds could germinate at a higher rate than both local and southerly-sourced seeds. We cannot, however, claim that higher germination probability will necessarily translate to greater fitness advantages over the plants' life history, or that this pattern is likely to be replicated across the Willamette Valley. Despite finding a significant seed type effect at both planting locations, more common garden site replication would be needed to suggest a regional phenomenon (but see Bischoff et al. 2006, Miller et al. 2011, Gallagher & Wagenius 2016). Future research at multiple planting sites and involving multiple life stages across several years is required to better address questions regarding seed translocation for restoration planting. Such a study should include multiple species of restoration importance in the Willamette Valley to investigate whether trends are consistent across species. This information would support ongoing efforts to create seed transfer zones of species used in the restoration of Willamette Valley ecosystems (Miller et al. 2011, Ramalho et al. 2017).

On a practical note, the methods we used to facilitate cleistogamous seed preparation substantially reduce the processing time for outplanting cleistogamous seeds. Our sheathed and soaked manipulations did not affect germination success for either cleistogamous or chasmogamous seeds, demonstrating that these methods can be used to make cleistogamous seed planting an accessible complement to chasmogamous planting. Although post-soaked individual cleistogamous seed extraction is a laborious process when done by hand, planting groups of cleistogamous seeds within their intact stems is much less labor-intensive. Our sheathed treatment demonstrates that planting cleistogamous seeds that are still enclosed within their stem can be an easy method to successfully germinate cleistogamous *D. californica* seeds at a scale necessary for ecosystem restoration. Restoration practitioners may benefit from incorporating cleistogamous seed planting as an insurance policy in the event of reduced chasmogamous germination in much the same way that the plants themselves do (Zeide 1978, Schoen & Loyd). This practice may be especially beneficial when local seed sourcing ability is limited.

Although the detailed pathogen census performed by Mackin et al. (2021) demonstrates the differences in cleistogamous and chasmogamous pathogen communities, we were unable to assess the impact pathogens had on in-situ germination and thus cannot be certain that pathogen escape explains the intermediate distance advantage in cleistogamous seeds at the HD common garden. Still, because pathogen pressure is likely a factor influencing in situ *D. californica* germination, and because pathogen communities vary between nearby sites, plug planting of larger individuals could also present an effective method of restoring *D. californica* populations, provided sterilized soil is used. Although this method is more time consuming and expensive than direct re-seeding (Gallagher & Wagenius 2016), accurately predicting the efficacy of re-seeding approaches may require an intimate understanding of epiphytic, endophytic and soil pathogen communities on both seed types, which was beyond the scope of this study. When seeding *D. californica* for restoration, practitioners should consider the pathogen communities of both source and planting sites, use cleistogamous seeds in addition to chasmogamous seeds, and consider sourcing cleistogamous seeds from more distant northerly populations than their chasmogamous counterparts.

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### Author Contributions

Conceptualization and methodology: all authors; formal analysis: P.B.R., M.L.D., W.F.M., S.H.J.; investigation: all authors; resources: B.A.R.; data curation: S.H.J.; writing—original draft preparation: S.H.J.; writing—review and editing: all authors; seed collection: all authors; seed preparation: S.H.J.; visualization: P.B.R.; project administration: W.F.M., B.A.R.; funding acquisition: B.A.R., W.F.M. All authors have read and agreed to the final version of the manuscript.

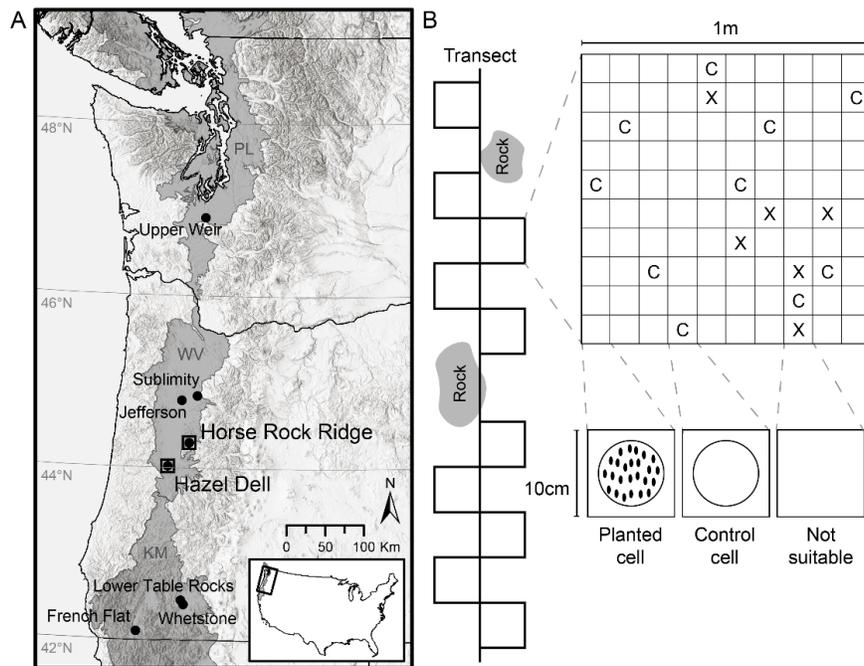
### Competing Interests Statement

The authors declare no competing interests.

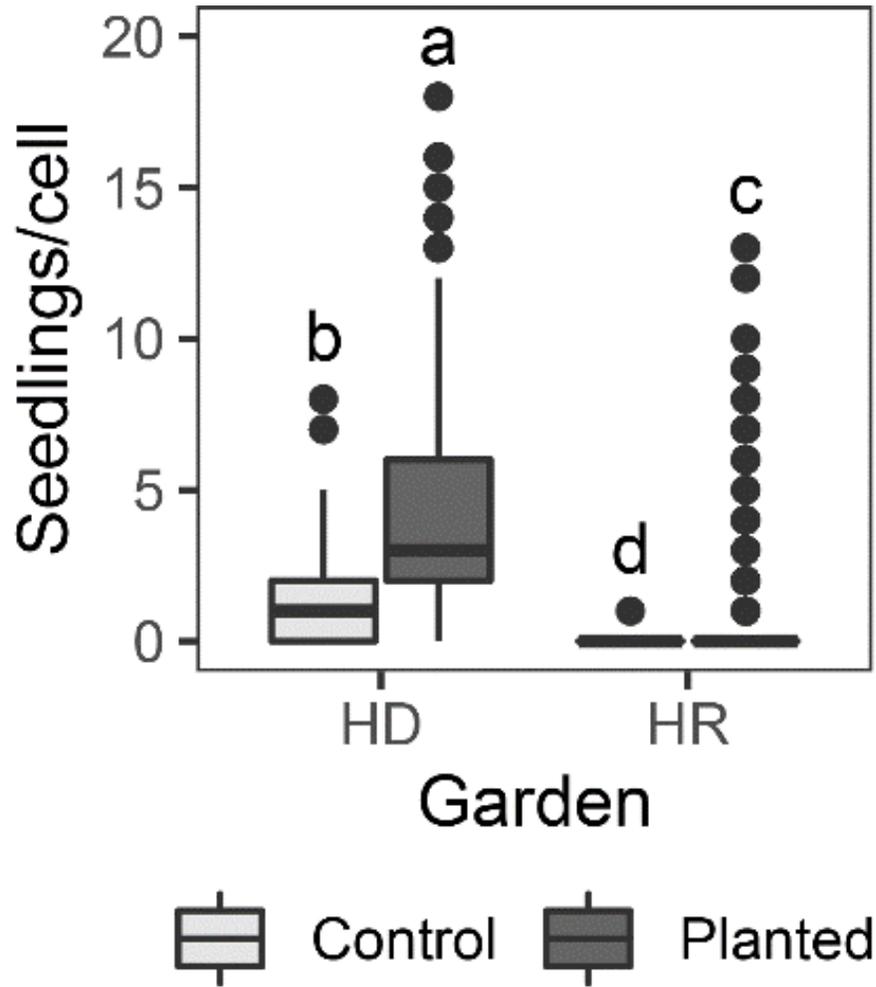
### Data Accessibility Statement

Upon acceptance, all data and script files used in this study will be made available to the public via Dryad.

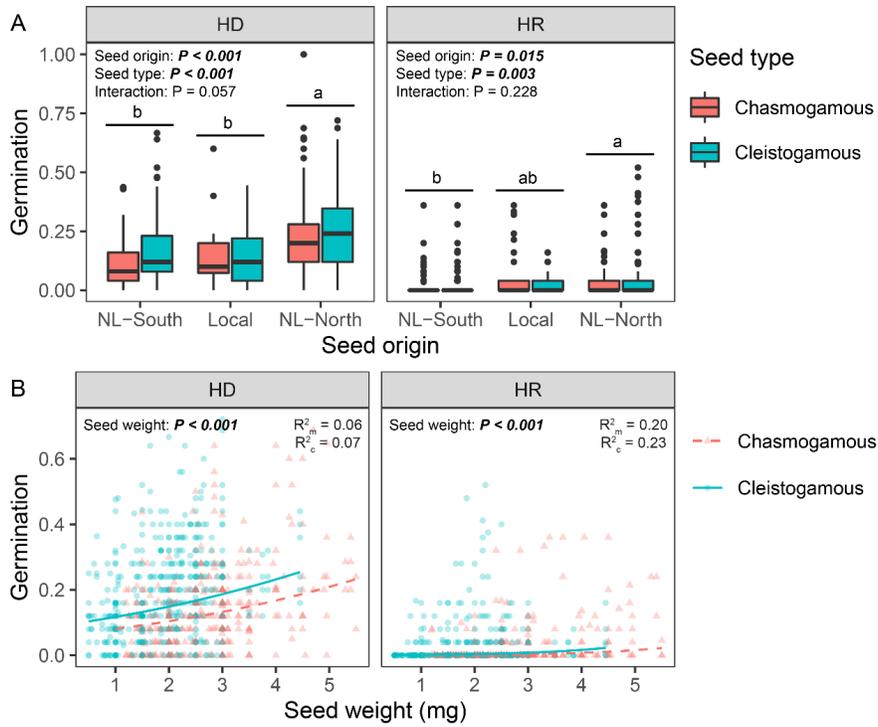
### Figures



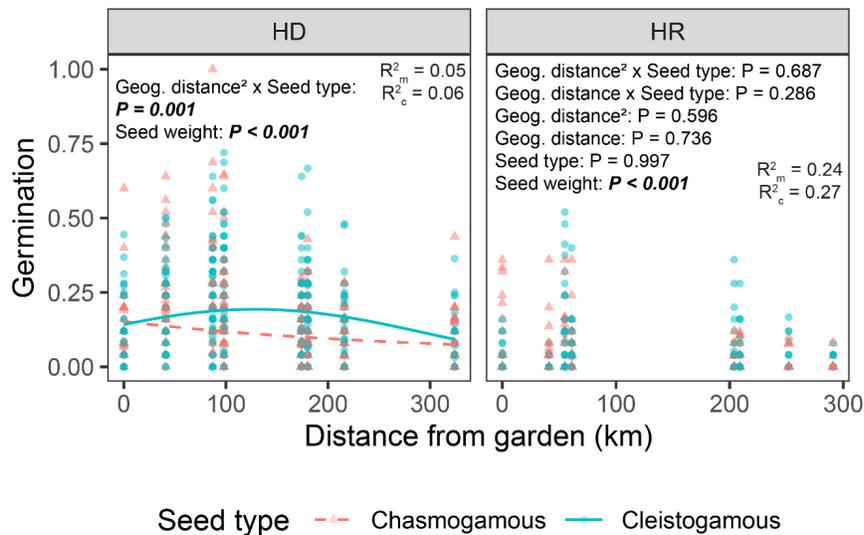
**Figure 1.** *Experimental design* . (A) Seed source locations (circles) and common garden (squares) of *D. californica* population locations within the Klamath Mountain (KM), Willamette Valley (WV) and Puget Lowland (PL) ecoregions. (B) Planting design showing alternating square meter grids along transects within natural *D. californica* populations at common garden sites. Each square meter grid was composed of 100 cells that were either planted, left as a control for background germination (C), or deemed not suitable for planting (X). See Appendix H Table 5 for site location and environmental data and Appendix A for site photographs.



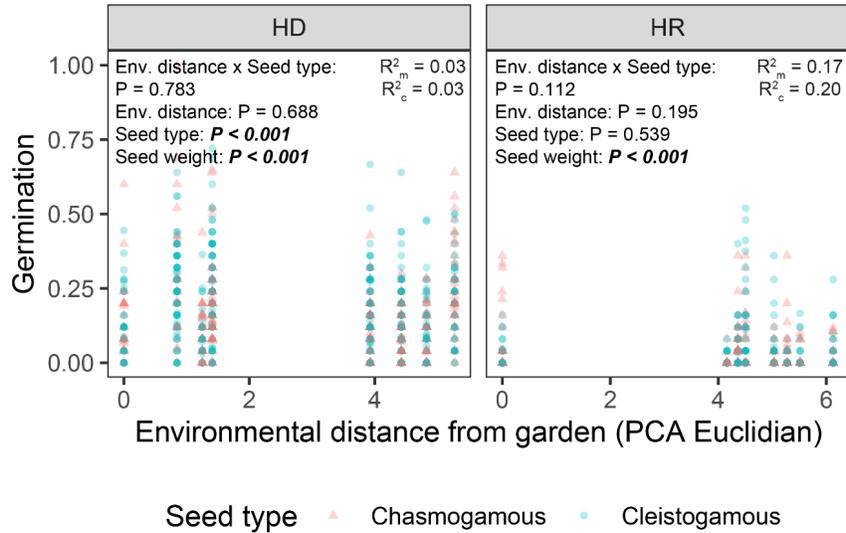
**Figure 2.** Background germination levels at the two common garden sites (HD = Hazel Dell; HR = Horse Rock Ridge). Both control and planted cells had significantly higher germination at HD than HR. Background germination at HD averaged 1.5 seedlings per cell and was negligible (~0.01 seedlings per cell) at HR. Planted cells averaged 3.9 and 0.6 seedlings per cell at HD and HR, respectively. Letters denote statistically significant differences between groups (p-value <0.05).



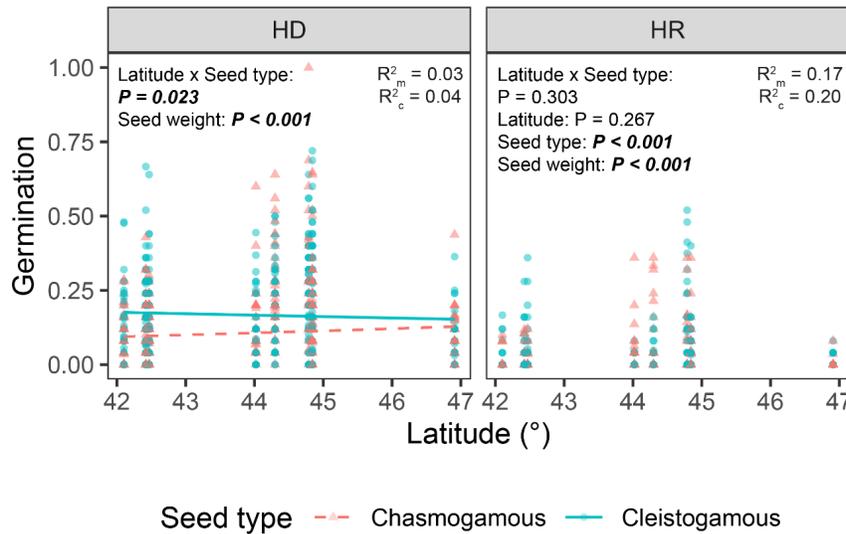
**Figure 3.** (A) Seed origin and seed type affect germination at both common garden sites (HD = Hazel Dell; HR = Horse Rock Ridge; NL = nonlocal). Nonlocal northern seeds outperform both local and southern seeds at the HD common garden, while nonlocal northern seeds outperform nonlocal southern seeds at HR. Letters indicate significant differences among seed origins, separately for each garden. At both gardens, cleistogamous seeds significantly outperformed chasmogamous seeds. (B) Seed weight is also a significant positive predictor of germination rates at both gardens. Predicted lines are averaged across seed origins. See Appendix H Table 1 for complete model results.



**Figure 4.** Geographic distance effects vary by seed type in the Hazel Dell (HD) garden but are not significant at Horse Rock Ridge (HR). Chasmogamous seed germination decreases weakly as source distance from HD increases. Cleistogamous seeds show the highest probability of germination when sourced between 100 and 200 km from HD. See Appendix H Table 2 for complete model results.



**Figure 5.** Environmental distance between source population and common garden has no effect on germination rates at either common garden (HD = Hazel Dell; HR = Horse Rock Ridge). Environmental distance was calculated using the first two principal components of a principal components analysis (PCA) (Figure S4). See Appendix H Table 3 for complete model results.



**Figure 6.** Source population latitude effects vary by seed type in the Hazel Dell (HD) common garden but are not significant at Horse Rock Ridge (HR). Latitude exhibits a slight positive effect on germination for

chasmogamous seeds but a negligible negative effect for cleistogamous seeds at HD. See Appendix H Table 4 for complete model results.

## Literature Cited

- Auld, J. R., & Rubio de Casas, R. (2013). The correlated evolution of dispersal and mating-system traits. *Evolutionary Biology*, 40(2), 185–193. <https://doi.org/10.1007/s11692-012-9202-7>
- Bartolome, J. W., Fehmi, J. S., Jackson, R. D., & Allen-Diaz, B. (2004). Response of a native perennial grass stand to disturbance in California’s Coast Range grassland. *Restoration Ecology*, 12(2), 279–289. <https://doi.org/10.1111/j.1061-2971.2004.00355.x>
- Baskin, J. M., & Baskin, C. C. (2017). Seed germination in cleistogamous species: Theoretical considerations and a literature survey of experimental results. *Seed Science Research*, 27(2), 84–98. <https://doi.org/10.1017/S0960258517000058>
- Bischoff, A., Vonlanthen, B., Steinger, T., & Müller-Schärer, H. (2006). Seed provenance matters — effects on germination of four plant species used for ecological restoration. *Basic and Applied Ecology*, 7(4), 347–359. <https://doi.org/10.1016/j.baae.2005.07.009>
- Breed, M. F., Harrison, P. A., Bischoff, A., Durruty, P., Gellie, N. J. C., Gonzales, E. K., Havens, K., Karmann, M., Kilkenny, F. F., Krauss, S. L., Lowe, A. J., Marques, P., Nevill, P. G., Vitt, P. L., & Bucharova, A. (2018). Priority actions to improve provenance decision-making. *BioScience*, 68(7), 510–516. <https://doi.org/10.1093/biosci/biy050>
- Broadhurst, L. M., Lowe, A., Coates, D. J., Cunningham, S. A., McDonald, M., Vesk, P. A., & Yates, C. (2008). Seed supply for broadscale restoration: Maximizing evolutionary potential. *Evolutionary Applications*, 1(4), 587–597. <https://doi.org/10.1111/j.1752-4571.2008.00045.x>
- Browne, W. J., Subramanian, S. V., Jones, K., & Goldstein, H. (2005). Variance partitioning in multilevel logistic models that exhibit overdispersion. *Journal of the Royal Statistical Society: Series A (Statistics in Society)*, 168(3), 599–613. <https://doi.org/10.1111/j.1467-985X.2004.00365.x>
- Buisson, E., Holl, K. D., Anderson, S., Corcket, E., Hayes, G. F., Torre, F., Peteers, A., & Dutoit, T. (2006). Effect of seed source, topsoil removal, and plant neighbor removal on restoring California coastal prairies. *Restoration Ecology*, 14(4), 569–577. <https://doi.org/10.1111/j.1526-100X.2006.00168.x>
- Charlesworth, D. (2007). Plant sex chromosome evolution. *Current Biology*, 17(8), 405–420. <https://doi.org/10.1016/j.cub.2007.02.045>
- Cheplick, G. P. & Quinn, J. A. (1982). *Amphicarpum purshii* and the “Pessimistic Strategy” in Amphicarpic Annuals with Subterranean Fruit. *Oecologia*, 52(3), 327–332. <https://doi.org/10.1007/BF00367955>
- Clay, K. (1994). Hereditary symbiosis in the grass genus *Danthonia*. *The New Phytologist*, 126(2), 223–231.
- Coulter. (1914). The evolution of sex in plants. University of Chicago Press.
- Darris, Dale C., and Peter Gonzalves (n.d.). California oatgrass *Danthonia californica* plant fact sheet. United States Department of Agriculture, Natural Resources Conservation Service.
- DeMarche, M. L., Doak, D. F., & Morris, W. F. (2019). Incorporating local adaptation into forecasts of species’ distribution and abundance under climate change. *Global Change Biology*, 25(3), 775–793. <https://doi.org/10.1111/gcb.14562>
- DeMarche M.L., Bailes, G., Hendricks, L. B., Pfeifer-Meister, L., Reed, P. B., Bridgham, S. D., Johnson, B. R., Shriver, R., Waddle, E., Wroton, H., Doak, D. F., Roy, B. A., & Morris, W. F. (2021). Latitudinal gradients in population growth do not reflect demographic responses to climate. *Ecological Applications*, 31(2), e2242–n/a. <https://doi.org/10.1002/eap.2242>
- Dudley, Eufemia, L., Fleckenstein, M., Periago, M. E., Petersen, I., & Timmers, J. F. (2020). Grasslands and savannahs in the UN Decade on Ecosystem Restoration. *Restoration Ecology*, 28(6), 1313–1317. <https://doi.org/10.1111/rec.13272>
- Dyksterhuis, E. J. (1945). Axillary Cleistogenes in *Stipa Leucotricha* and their Role in Nature. *Ecology (Durham)*, 26(2), 195–199. <https://doi.org/10.2307/1930824>
- Floberg J, Goering M, Wilhere G, and 16 others. (2004). Willamette Valley–Puget Trough–Georgia Basin ecoregional assessment, Volume one: Report. Prepared by The Nature Conservancy with support from the Nature Conservancy of Canada, Washington Department of Fish and Wildlife, Washington Department of Natural Resources (Natural Heritage and Nearshore Habitat programs), Oregon State Natural Heritage Information Center and the British Columbia Conservation Data Centre.
- Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.
- Gallagher, M. K., & Wagenius, S. (2016). Seed source impacts germination and early establishment of dominant grasses in prairie restorations. *Journal of Applied Ecology*, 53(1), 251–263. <https://doi.org/10.1111/1365-2664.12564>
- Galliard, M., Bello, N., Knapp, M., Poland, J., St Amand, P., Baer, S., Maricle, B., Smith,

A. B., & Johnson, L. (2019). Local adaptation, genetic divergence, and experimental selection in a foundation grass across the US Great Plains' climate gradient. *Global Change Biology*, 25(3), 850–868.<https://doi.org/10.1111/gcb.14534>

Garcia-Ramos, & Kirkpatrick, M. (1997). Genetic Models of Adaptation and Gene Flow in Peripheral Populations. *Evolution*, 51(1), 21–28.<https://doi.org/10.1111/j.1558-5646.1997.tb02384.x>

Gomez, J. M. (2004). Bigger is not always better: Conflicting selective pressures on seed size in *Quercus ilex*. *Evolution*, 58(1), 71–80.<https://doi.org/10.1111/j.0014-3820.2004.tb01574.x>

Green, N. E., & Hansen, R. M. (1969). Relationship of seed weight to germination of six grasses. *Journal of Range Management*, 22(2), 133.<https://doi.org/10.2307/3896199>

Gundel, P. E., Garibaldi, L. A., Martinez-Ghersa, M. A., & Ghersa, C. M. (2012). Trade-off between seed number and weight: Influence of a grass–endophyte symbiosis. *Basic and Applied Ecology*, 13(1), 32–39.<https://doi.org/10.1016/j.baae.2011.10.008>

Harrison. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ (San Francisco, CA)*, 2, e616–e616.<https://doi.org/10.7717/peerj.616>

Harrison. (2015). A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. *PeerJ (San Francisco, CA)*, 3, e1114–e1114.<https://doi.org/10.7717/peerj.1114>

Hayes, G. F., & Holl, K. D. (2011). Manipulating disturbance regimes and seeding to restore mesic Mediterranean grasslands. *Applied Vegetation Science*, 14(3), 304–315.<https://doi.org/10.1111/j.1654-109X.2011.01127.x>

Hendrix, S. D. (1984). Variation in seed weight and its effects on germination in *Pastinaca sativa* L. (Umbelliferae). *American Journal of Botany*, 71(6), 795–802.<https://doi.org/10.1002/j.1537-2197.1984.tb14144.x>

Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *The American Naturalist*, 173(5), 579–588.<https://doi.org/10.1086/597611>

Hereford, J. (2010). Does selfing or outcrossing promote local adaptation? *American Journal of Botany*, 97(2), 298–302.<https://doi.org/10.3732/ajb.0900224>

Holsinger, K. E. (2000). Reproductive systems and evolution in vascular plants. *Proceedings of the National Academy of Sciences*, 97(13), 7037–7042.<https://doi.org/10.1073/pnas.97.13.7037>

Jin, H., Yuan, Y., Gao, F., Oduor, A. M. O., & Li, J. (2020). The invasive plant *Solidago canadensis* exhibits partial local adaptation to low salinity at germination but not at later life-history stages. *American Journal of Botany*, 107(4), 599–606.<https://doi.org/10.1002/ajb2.1456>

Joshi, J., Schmid, B., Caldeira, M. C., Dimitrakopoulos, P. G., Good, J., Harris, R., Hector, A., Huss-Danell, K., Jumpponen, A., Minns, A., Mulder, C. P. H., Pereira, J. S., Prinz, A., Scherer-Lorenzen, M., Siamantziouras, A.-S. D., Terry, A. C., Troumbis, A. Y., & Lawton, J. H. (2001). Local adaptation enhances performance of common plant species. *Ecology Letters*, 4(6), 536–544.<https://doi.org/10.1046/j.1461-0248.2001.00262.x>

Kamalov, Elnagar, A., & Leung, H. H. (2021). Ensemble Learning with Resampling for Imbalanced Data. In *Intelligent Computing Theories and Application* (pp. 564–578). Springer International Publishing. [https://doi.org/10.1007/978-3-030-84529-2\\_48](https://doi.org/10.1007/978-3-030-84529-2_48)

Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, 7(12), 1225–1241.<https://doi.org/10.1111/j.1461-0248.2004.00684.x>

Kitchen, S. G., & Monsen, S. B. (1994). Germination rate and emergence success in Bluebunch Wheatgrass. *Journal of Range Management*, 47(2), 145.<https://doi.org/10.2307/4002823>

Koslow, J. M., & Clay, K. (2007). The mixed mating system of *Impatiens capensis* and infection by a foliar rust pathogen: Patterns of resistance and fitness consequences. *Evolution*, 61(11), 2643–2654.<https://doi.org/10.1111/j.1558-5646.2007.00224.x>

Leavelle, T. N. (1998). “We will make it our own place”: Agriculture and adaptation at the Grand Ronde Reservation, 1856–1887. *American Indian Quarterly*, 22(4), 433–456.<https://doi.org/10.2307/1184835>

Leimu, R., & Fischer, M. (2008). A meta-analysis of local adaptation in plants. *PloS One*, 3(12), e4010–e4010.<https://doi.org/10.1371/journal.pone.0004010>

Lenoir, & Svenning, J.-C. (2015). Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography (Copenhagen)*, 38(1), 15–28.<https://doi.org/10.1111/ecog.00967>

Lenormand, T. (2002). Gene flow and the limits to natural selection. *Trends in Ecology & Evolution*, 17(4), 183–189.[https://doi.org/10.1016/S0169-5347\(02\)02497-7](https://doi.org/10.1016/S0169-5347(02)02497-7)

Lenth, R. (2020). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.0. <https://CRAN.R-project.org/package=emmeans>

Lindh, B. C. (2018). Tipping the native-exotic balance: succession in restored upland prairies in Oregon’s Willamette Valley. *Ecological Restoration*, 36(1), 28–40.<https://doi.org/10.3368/er.36.1.28>

Linhart, Y. B. and M. C. Grant. (1996). Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27: 237–277. Lovell,

J. T., Grogan, K., Sharbel, T. F., & McKay, J. K. (2014). Mating system and environmental variation drive patterns of adaptation in *Boechera spatifolia* (Brassicaceae). *Molecular Ecology*, 23(18), 4486–4497. <https://doi.org/10.1111/mec.12879>

Ludecke D (2021). *sjPlot: Data Visualization for Statistics in Social Science*. R package version 2.8.10, <https://CRAN.R-project.org/package=sjPlot>.

Mackin, H. C., Shek, K. L., Thornton, T. E., Evens, K. C., Hallett, L. M., McGuire, K. L., Peterson, M. L., & Roy, B. A. (2021). The ‘black box’ of plant demography: How do seed type, climate and seed fungal communities affect grass seed germination? *The New Phytologist*, 231(6), 2319–2332. <https://doi.org/10.1111/nph.17532>

Maslovat, C. Y. T. (2002). Germination ecology of native grass species, *Danthonia californica* and *Elymus glaucus*, in Garry oak ecosystems and the implications for restoration [Master of Science Thesis, University of Victoria]. Proquest Information and Learning (Order No. MQ68181).

Masuda, & Yahara, T. (1992). Dispersal of chasmogamous and cleistogamous seeds in *Viola honoensis* W. Backer et H. Boiss. *The Botanical Magazine Tokyo*, 105(2), 323–326. <https://doi.org/10.1007/BF02489424>

Merges, Albrecht, J., Bohning-Gaese, K., Schleuning, M., & Neuschulz, E. L. (2020). Environmental context determines the limiting demographic processes for plant recruitment across a species’ elevational range. *Scientific Reports*, 10(1), 10855–10855. <https://doi.org/10.1038/s41598-020-67602-5>

Middleton, E. L., Bever, J. D., & Schultz, P. A. (2010). The effect of restoration methods on the quality of the restoration and resistance to invasion by exotics. *Restoration Ecology*, 18(2), 181–187. <https://doi.org/10.1111/j.1526-100X.2008.00501.x>

Miller, S. A., Bartow, A., Gisler, M., Ward, K., Young, A. S., & Kaye, T. N. (2011). Can an ecoregion serve as a seed transfer zone? Evidence from a common garden study with five native species. *Restoration Ecology*, 19(201), 268–276. <https://doi.org/10.1111/j.1526-100X.2010.00702.x>

Moreira de Oliveira, Santos da Silva, F. F., Araujo, M. do N., Campos da Costa, D. C., Vieira Gomes, S. E., Matias, J. R., Angelotti, F., Pelacani Cruz, C. R., Seal, C. E., & Dantas, B. F. (2019). Environmental stress, future climate, and germination of *Myracrodruon urundeuva* seeds. *Journal of Seed Science*, 41(1), 32–43. <https://doi.org/10.1590/2317-1545v41n1191945>

Nakagawa S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R<sup>2</sup> and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, 14(134). <https://doi.org/10.1098/rsif.2017.0213>

Nelson, E. B. (2018). The seed microbiome: Origins, interactions, and impacts. *Plant and Soil*, 422(1–2), 7–34. <https://doi.org/10.1007/s11104-017-3289-7>

Oakley, C. G., Moriuchi, K. S., & Winn, A. A. (2007). The maintenance of outcrossing in predominantly selfing species: Ideas and evidence from cleistogamous species. *Annual Review of Ecology, Evolution, and Systematics*, 38, 437–457.

Pfeifer-Meister, L., Roy, B. A., Johnson, B. R., Krueger, J., & Bridgham, S. D. (2012). Dominance of native grasses leads to community convergence in wetland restoration. *Plant Ecology*, 213(4), 637–647. <https://doi.org/10.1007/s11258-012-0028-2>

PRISM Climate Group (2018). <https://prism.oregonstate.edu/>

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Ramalho, C. E., Byrne, M., & Yates, C. J. (2017). A climate-oriented approach to support decision-making for seed provenance in ecological restoration. *Frontiers in Ecology and Evolution*, 5. <https://doi.org/10.3389/fevo.2017.00095>

Ribeiro, Barbosa, E. R. M., & Borghetti, F. (2021). How regional climate and seed traits interact in shaping stress-tolerance of savanna seeds? *Seed Science Research*, 31(4), 300–310. <https://doi.org/10.1017/S0960258521000234>

Rice, K. J., & Knapp, E. E. (2008). Effects of competition and life history stage on the expression of local adaptation in two native bunchgrasses. *Restoration Ecology*, 16(1), 12–23. <https://doi.org/10.1111/j.1526-100X.2007.00257.x>

Rushworth, C. A., Brandvain, Y., & Mitchell-Olds, T. (2020). Identifying the fitness consequences of sex in complex natural environments. *Evolution Letters*, 4(6), 516–529. <https://doi.org/10.1002/evl3.194>

Schmitt, J., & Gamble, S. E. (1990). The effect of distance from the parental site on offspring performance and inbreeding depression in *Impatiens capensis*: A test of the local adaptation hypothesis. *Evolution*, 44(8), 2022–2030. <https://doi.org/10.1111/j.1558-5646.1990.tb04308.x>

Schmitt, J., Ehrhardt, D., & Swartz, D. (1985). Differential Dispersal of Self-Fertilized and Outcrossed Progeny in Jewelweed (*Impatiens capensis*). *The American Naturalist*, 126(4), 570–575.

Schoen, D. J., & Lloyd, D. G. (1984). The selection of cleistogamy and heteromorphic diaspores. *Biological Journal of the Linnean Society*, 23(4), 303–322. <https://doi.org/10.1111/j.1095-8312.1984.tb00147.x>

Schluter, D. and P. R. Grant. (1984). Ecological correlates of morphological evolution in a Darwin’s finch, *Geospiza difficilis*. *Evolution* 38: 856–869.

Seifert, B., & Fischer, M. (2010). Experimental establishment of a declining

dry-grassland flagship species in relation to seed origin and target environment. *Biological Conservation*, 143(5), 1202–1211. <https://doi.org/10.1016/j.biocon.2010.02.028>

Siepielski, A. M., A. Nemirov, M. Cattivera, & A. Nickerson. (2016). "Experimental Evidence for an Eco-Evolutionary Coupling between Local Adaptation and Intraspecific Competition." *The American Naturalist* 187: 447–456.

Stanley, A. G., Dunwiddie, P. W., & Kaye, T. N. (2011). Restoring invaded Pacific Northwest prairies: Management recommendations from a region-wide experiment. *Northwest Science*, 85(2), 233–246. <https://doi.org/10.3955/046.085.0212>

UNEP and FAO (2020). The UN Decade on Ecosystem Restoration 2021-2030. The United Nations Environmental Program Fact Sheet, June 2020.

van Boheemen, L. A., Atwater, D. Z., & Hodgins, K. A. (2019). Rapid and repeated local adaptation to climate in an invasive plant. *New Phytologist*, 222(1), 614–627. <https://doi.org/10.1111/nph.15564>

Waller D. M. (1982). Factors Influencing Seed Weight in *Impatiens capensis* (Balsaminaceae). *American Journal of Botany*, 69(9), 1470–1475. <https://doi.org/10.1002/j.1537-2197.1982.tb13395.x>

Wang, Y., Xu, W., Yuan, W., Chen, X., Zhang, B., Fan, L., He, B., Hu, Z., Liu, S., Liu, W., & Piao, S. (2021). Higher plant photosynthetic capability in autumn responding to low atmospheric vapor pressure deficit. *The Innovation*, 2(4), 100163. <https://doi.org/10.1016/j.xinn.2021.100163>

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4. <https://ggplot2.tidyverse.org>.

Williams, E. (n.d.). "Latitude/Longitude Distance Calculator." National Oceanic and Atmospheric Administration. Retrieved from <https://www.nhc.noaa.gov/gccalc.shtml>.

Wilson MV. (1998). Wetland prairie. In: Part I the US Fish and Wildlife Service Willamette Basin Recovery Plan. Portland (OR): US Fish and Wildlife Service. Order No. 13420-6-0287 (2). 23 p.

Yi, Wang, Z., Baskin, C. C., Baskin, J. M., Ye, R., Sun, H., Zhang, Y., Ye, X., Liu, G., Yang, X., & Huang, Z. (2019). Seed germination responses to seasonal temperature and drought stress are species-specific but not related to seed size in a desert steppe: Implications for effect of climate change on community structure. *Ecology and Evolution*, 9(4), 2149–2159. <https://doi.org/10.1002/ece3.4909>

Zeide, B. (1978). Reproductive Behavior of Plants in Time. *The American Naturalist*, 112(985), 636–639. <https://doi.org/10.1086/283305>

Zhang, M., Suren, H., & Holliday, J. A. (2019). Phenotypic and genomic local adaptation across latitude and altitude in *Populus trichocarpa*. *Genome Biology and Evolution*, 11(8), 2256–2272. <https://doi.org/10.1093/gbe/evz151>

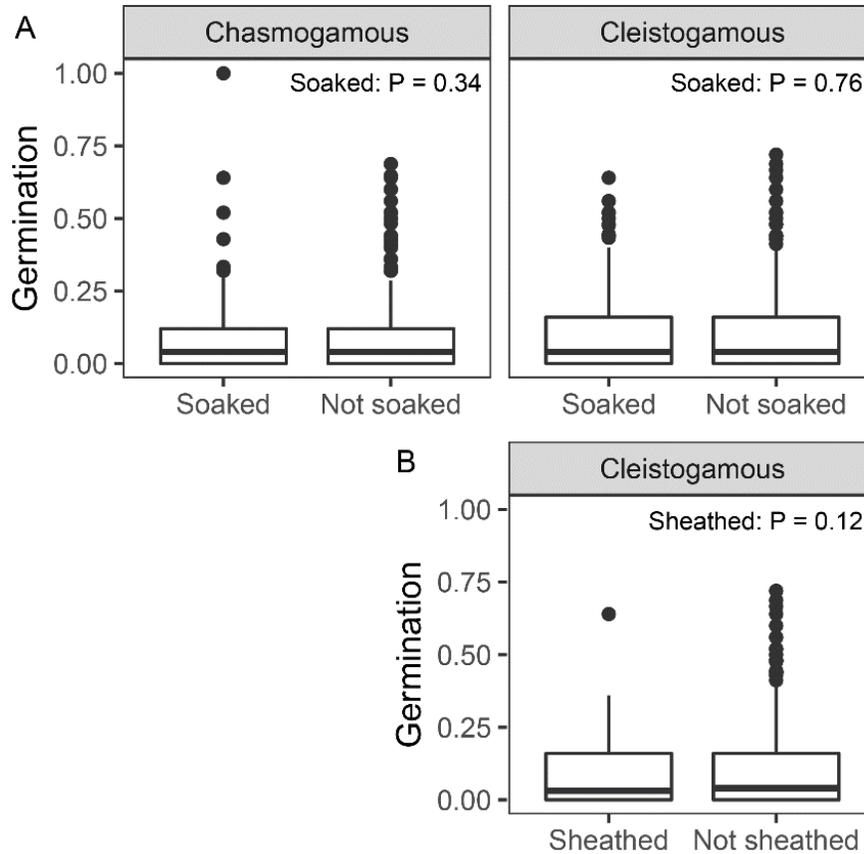
## Appendix A

*Danthonia californica* experiment. A) chasmogamous spikelets; B) cleistogamous spikelets (at arrow); C) garden at Hazel Dell; D) garden at Horse Rock Ridge. Photos by B. A. Roy.



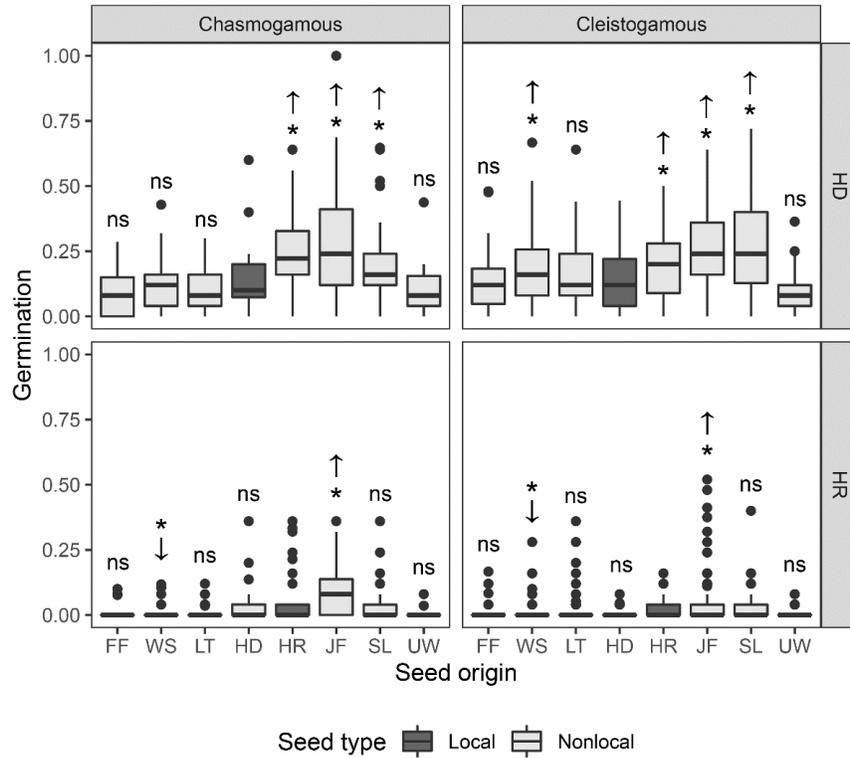
## Appendix B

Neither soaked (A) nor sheathed (B) seed treatments affect germination of chasmogamous or cleistogamous seeds. The sheathed treatment is unique to cleistogamous seeds since sheathed refers to being enclosed within the stems.



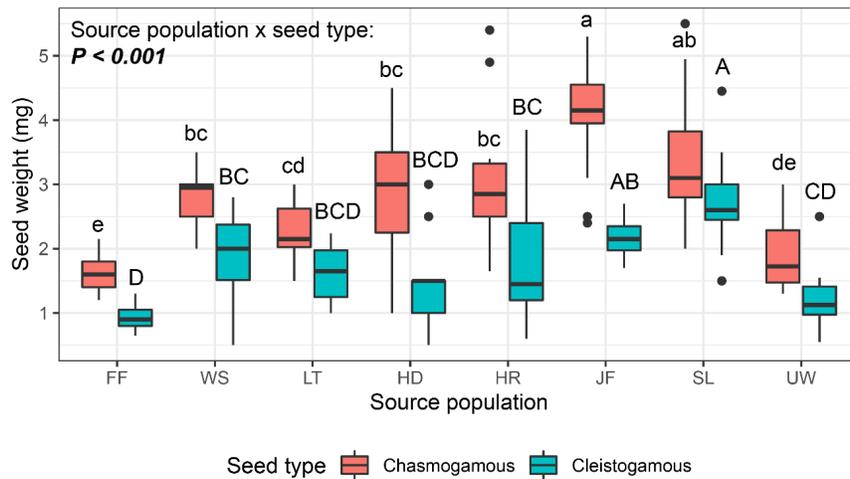
## Appendix C

Germination at the two gardens as a function of source population and seed type (from pairwise models). Each model included the interaction of seed origin and seed type. Asterisks denote a significant difference ( $P < 0.05$ ) between seeds from that source population and seeds sourced locally from the garden, separately by seed type. Arrows (up/down) signify whether that source population had significantly greater or lesser germination relative to the local seeds. ‘ns’ = not significant ( $P > 0.05$ ). Source populations are organized from left to right by increasing latitude. FF = French Flat, WS = Whetstone, LT = Lower Table Rocks, HD = Hazel Dell, HR = Horse Rock Ridge, JF = Jefferson, SL = Sublimity, UW = Upper Weir.



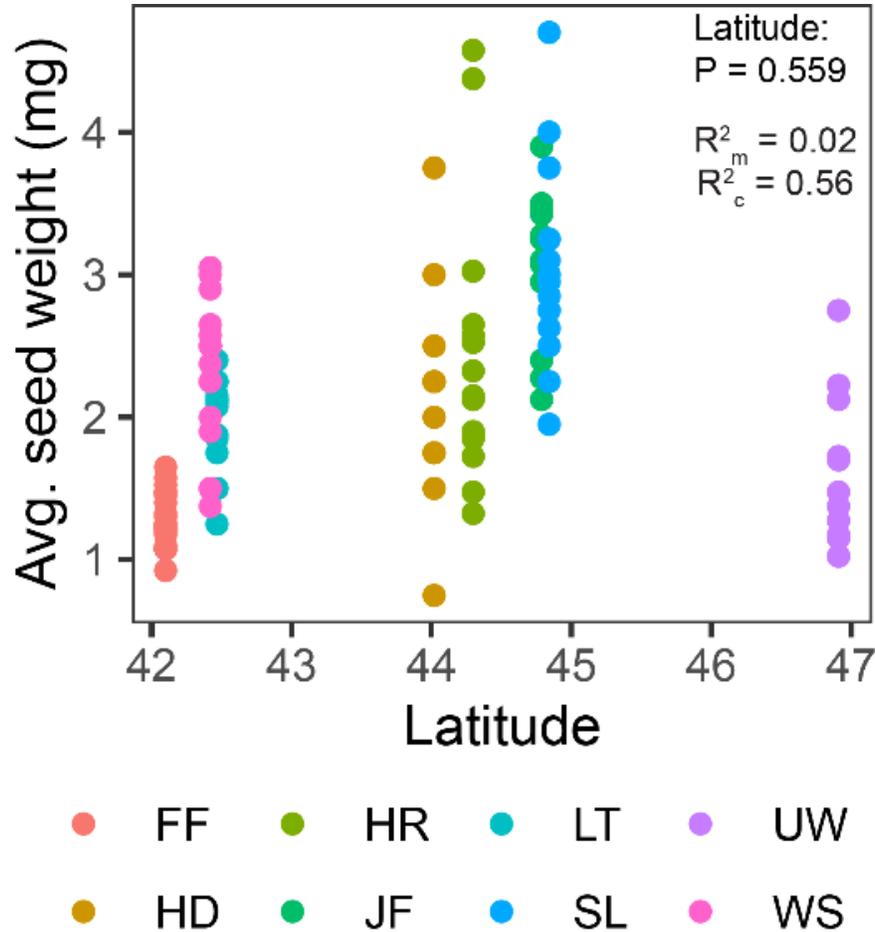
## Appendix D

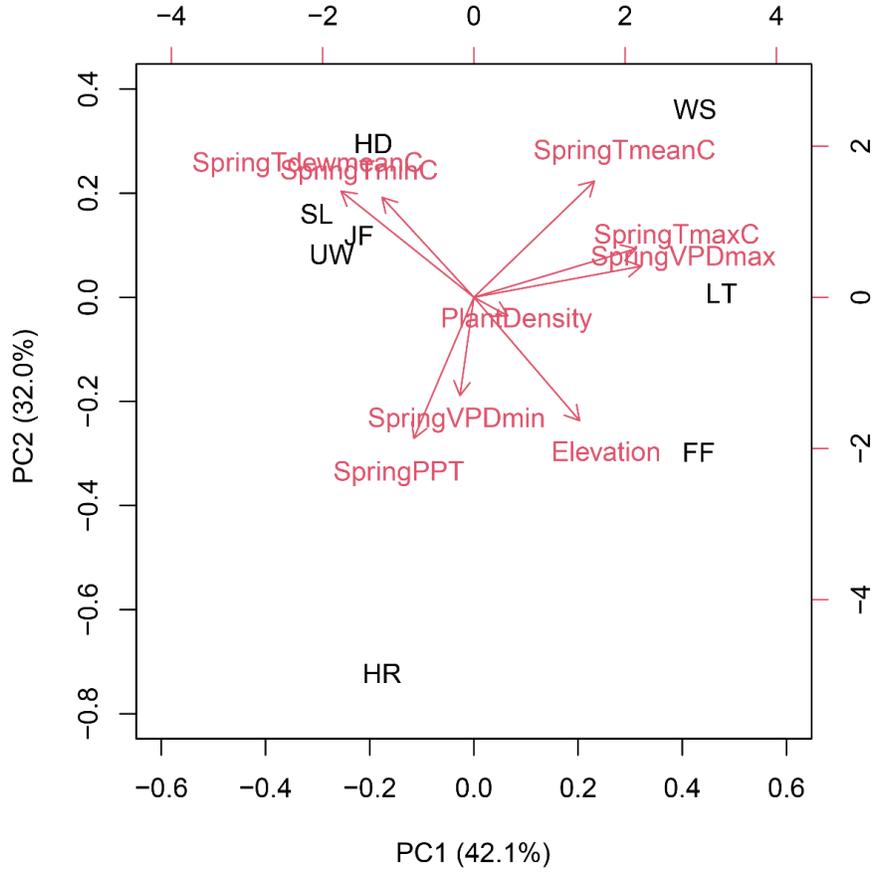
Maternal plant seed weight depends on seed type and source population. Cleistogamous seeds are universally lighter weight than chasmogamous seeds across all source populations ( $P < 0.05$ ), but the differences in source population depends on seed type ( $P < 0.001$ ). Letters indicate significant differences among source populations separately for each seed type. Source populations are organized from left to right by increasing latitude. FF = French Flat, WS = Whetstone, LT = Lower Table Rocks, HD = Hazel Dell, HR = Horse Rock Ridge, JF = Jefferson, SL = Sublimity, UW = Upper Weir.



### Appendix E

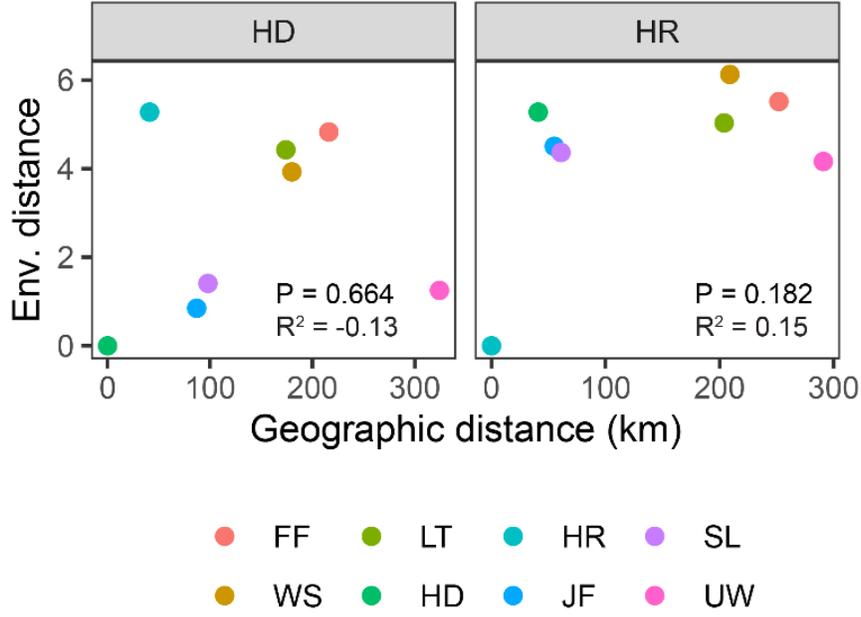
Average maternal plant seed weight (averaging cleistogamous and chasmogamous together) is not related to source population latitude. FF = French Flat, HD = Hazel Dell, HR = Horse Rock, JF = Jefferson, LT = Lower Table Rocks, SL = Sublimity, UW = Upper Weir, WS = Whetstone.





## Appendix G

There is no significant relationship between environmental distance and geographic distance at either common garden (HD = Hazel Dell; HR = Horse Rock Ridge).



## Appendix H

### Tables

**Table 1.** Binomial logistic mixed effect model results for the categorical analysis of seed origin x seed type on germination rates at the two common gardens (Hazel Dell and Horse Rock Ridge). Coefficient estimates are expressed as log-odds values, using contrasts = c("contr.sum", "contr.poly") to compare each group against the grand mean, where the intercept is the grand mean and others are deviations from that. For random effects:  $\sigma^2$  = residual variance of logistic regression model;  $\tau_{00}$  = between-subject variance partitioned to each random effect in the model; ICC = intraclass correlation coefficient; N = number of levels to each random effect. OLRE = observation level random effect. Marginal  $R^2$  provides the variance explained by the fixed effect(s) only while Conditional  $R^2$  provides the variance explained by both the fixed and random effects, as calculated in Nakagawa et al. (2017).

Categorical seed origin analysis	Hazel Dell			Horse Rock		
	Log-Odds	CI	p	Log-Odds	CI	p
(Intercept)	-2.54	-2.80 – -2.27	<0.001	-7.65	-8.79 – -6.51	<0.001
seedorigin NorS1	-0.25	-0.43 – -0.07	0.008	0.2	-0.28 – 0.67	0.421
seedorigin NorS2	0.39	0.27 – 0.52	<0.001	0.29	-0.07 – 0.65	0.112
seedtype1	-0.2	-0.30 – -0.10	<0.001	-0.42	-0.71 – -0.14	0.003
seed weight mg	0.28	0.18 – 0.37	<0.001	0.72	0.44 – 1.01	<0.001
seedorigin NorS1 : seedtype1	0.13	-0.03 – 0.29	0.119	0.32	-0.08 – 0.72	0.119
seedorigin NorS2 : seedtype1	0	-0.11 – 0.10	0.964	-0.08	-0.37 – 0.22	0.601
sheathed1				0.69	-0.04 – 1.41	0.063
<b>Random Effects</b>						
$\sigma^2$	3.29			3.29		
$\tau_{00}$	0.42 <sub>OLRE</sub>			2.82 <sub>OLRE</sub>		
	0.03 <sub>mother</sub>			0.43 <sub>mother</sub>		
	0.03 <sub>quadrat</sub>			0.18 <sub>quadrat</sub>		
ICC	0.01			0.04		
N	11 <sub>quadrat</sub>			12 <sub>quadrat</sub>		
	122 <sub>mother</sub>			122 <sub>mother</sub>		
	808 <sub>OLRE</sub>			793 <sub>OLRE</sub>		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.064 / 0.069			0.200 / 0.233		
AIC	3739.522			1430.241		

**Table 2.** Binomial logistic mixed effect model results for the analysis of geographic distance between source population and common garden x seed type on germination rates at the two common gardens (Hazel Dell and Horse Rock Ridge). Coefficient estimates are expressed as log-odds values, using contrasts = c(“contr.sum”, “contr.poly”) to compare each group against the grand mean, where the intercept is the grand mean and others are deviations from that. For random effects:  $\sigma^2$  = residual variance of logistic regression model;  $\tau_{00}$  = between-subject variance partitioned to each random effect in the model; ICC = intraclass correlation coefficient; N = number of levels to each random effect. OLRE = observation level random effect. Marginal R<sup>2</sup> provides the variance explained by the fixed effect(s) only while Conditional R<sup>2</sup> provides the variance explained by both the fixed and random effects, as calculated in Nakagawa et al. (2017).

Geographic distance analysis	Hazel Dell			Horse Rock		
	Log-Odds	CI	p	Log-Odds	CI	p
(Intercept)	-2.39	-2.85 – -1.93	<0.001	-6.78	-8.10 – -5.47	<0.001
distance	0.13	-0.36 – 0.63	0.598	-0.2	-1.35 – 0.96	0.736
distance^2	-0.1	-0.25 – 0.05	0.179	-0.11	-0.54 – 0.31	0.596
seedtype1	0.04	-0.14 – 0.22	0.664	0	-0.49 – 0.50	0.997
seed weight mg	0.28	0.18 – 0.38	<0.001	0.58	0.27 – 0.89	<0.001
distance : seedtype1	-0.44	-0.68 – -0.21	<0.001	-0.53	-1.50 – 0.44	0.286
distance^2 : seedtype1	0.12	0.05 – 0.19	0.001	0.07	-0.28 – 0.42	0.687
sheathed1				0.65	-0.07 – 1.37	0.075
<b>Random Effects</b>						
$\sigma^2$	3.29			3.29		
$\tau_{00}$	0.41 <small>OLRE</small>			2.70 <small>OLRE</small>		
	0.03 <small>mothersource_pop</small>			0.45 <small>mothersource_pop</small>		
	0.03 <small>quadrat</small>			0.18 <small>quadrat</small>		
	0.03 <small>source_pop</small>			0.00 <small>source_pop</small>		
ICC	0.01			0.04		
N	11 <small>quadrat</small>			12 <small>quadrat</small>		
	122 <small>mother</small>			122 <small>mother</small>		
	8 <small>source_pop</small>			8 <small>source_pop</small>		
	808 <small>OLRE</small>			793 <small>OLRE</small>		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.048 / 0.055			0.235 / 0.265		
AIC	3746.82			1424.704		

**Table 3.** Binomial logistic mixed effect model results for the analysis of environmental distance between source population and common garden x seed type on germination rates at the two common gardens (Hazel Dell and Horse Rock Ridge). Coefficient estimates are expressed as log-odds values, using contrasts = c(“contr.sum”, “contr.poly”) to compare each group against the grand mean, where the intercept is the grand mean and others are deviations from that. For random effects:  $\sigma^2$  = residual variance of logistic regression model;  $\tau_{00}$  = between-subject variance partitioned to each random effect in the model; ICC = intraclass correlation coefficient; N = number of levels to each random effect. OLRE = observation level random effect. Marginal R<sup>2</sup> provides the variance explained by the fixed effect(s) only while Conditional R<sup>2</sup> provides the variance explained by both the fixed and random effects, as calculated in Nakagawa et al. (2017).

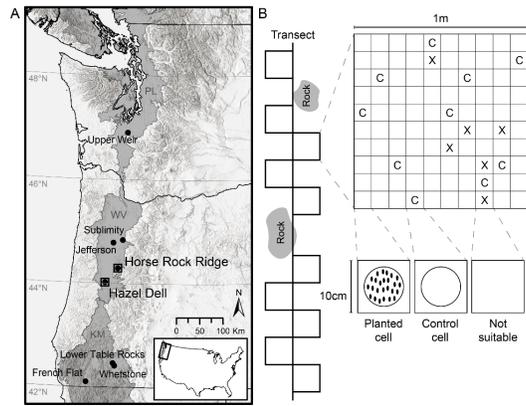
Environmental distance analysis	Hazel Dell			Horse Rock		
	Log-Odds	CI	p	Log-Odds	CI	p
(Intercept)	-2.66	-3.11 – -2.21	<0.001	-7.35	-8.81 – -5.89	<0.001
env dist	0.02	-0.08 – 0.12	0.688	-0.11	-0.28 – 0.06	0.195
seedtype1	-0.26	-0.40 – -0.12	<0.001	-0.17	-0.72 – 0.38	0.539
seed weight mg	0.32	0.22 – 0.43	<0.001	0.79	0.49 – 1.10	<0.001
env dist : seedtype1	0	-0.04 – 0.03	0.783	-0.09	-0.20 – 0.02	0.112
sheathed1				0.65	-0.06 – 1.36	0.073
<b>Random Effects</b>						
$\sigma^2$	3.29			3.29		
$\tau_{00}$	0.43 <sub>OLRE</sub>			2.53 <sub>OLRE</sub>		
	0.03 <sub>mother:source pop</sub>			0.44 <sub>mothersource pop</sub>		
	0.03 <sub>quadrat</sub>			0.30 <sub>quadrat</sub>		
	0.07 <sub>source pop</sub>			0.07 <sub>source pop</sub>		
ICC	0.01			0.04		
N	11 <sub>quadrat</sub>			12 <sub>quadrat</sub>		
	122 <sub>mother</sub>			122 <sub>mother</sub>		
	8 <sub>source pop</sub>			8 <sub>source pop</sub>		
	808 <sub>OLRE</sub>			793 <sub>OLRE</sub>		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.026 / 0.033			0.165 / 0.198		
AIC	3761.167			1433.234		

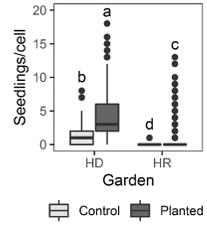
**Table 4.** Binomial logistic mixed effect model results for the analysis of latitude x seed type on germination rates at the two common gardens (Hazel Dell and Horse Rock Ridge). Coefficient estimates are expressed as log-odds values, using contrasts = c(“contr.sum”, “contr.poly”) to compare each group against the grand mean, where the intercept is the grand mean and others are deviations from that. For random effects:  $\sigma^2$  = residual variance of logistic regression model;  $\tau_{00}$  = between-subject variance partitioned to each random effect in the model; ICC = intraclass correlation coefficient; N = number of levels to each random effect. OLRE = observation level random effect. Marginal R<sup>2</sup> provides the variance explained by the fixed effect(s) only while Conditional R<sup>2</sup> provides the variance explained by both the fixed and random effects, as calculated in Nakagawa et al. (2017).

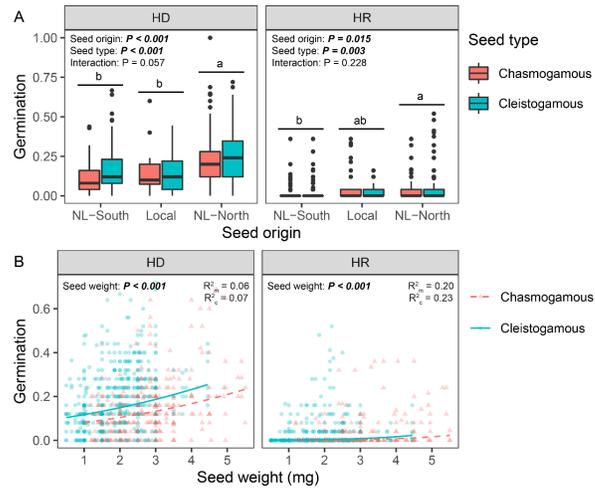
Latitude analysis	Hazel Dell			Horse Rock		
	Log-Odds	CI	p	Log-Odds	CI	p
(Intercept)	-2.58	-2.90 – -2.25	<b>&lt;0.001</b>	-7.89	-9.09 – -6.69	<b>&lt;0.001</b>
latitude	0.03	-0.17 – 0.22	0.791	0.18	-0.14 – 0.50	0.267
seedtype1	-0.27	-0.35 – -0.19	<b>&lt;0.001</b>	-0.58	-0.83 – -0.32	<b>&lt;0.001</b>
seed weight mg	0.31	0.21 – 0.41	<b>&lt;0.001</b>	0.8	0.50 – 1.11	<b>&lt;0.001</b>
latitude : seedtype1	0.08	0.01 – 0.14	<b>0.023</b>	0.11	-0.10 – 0.33	0.303
sheathed1				0.65	-0.07 – 1.37	0.075
<b>Random Effects</b>						
$\sigma^2$	3.29			3.29		
$\tau_{00}$	0.42 <sub>OLRE</sub>			2.57 <sub>OLRE</sub>		
	0.03 <sub>mother:source pop</sub>			0.46 <sub>mother:source pop</sub>		
	0.03 <sub>quadrat</sub>			0.29 <sub>quadrat</sub>		
	0.07 <sub>source pop</sub>			0.06 <sub>source pop</sub>		
ICC	0.01			0.04		
N	11 <sub>quadrat</sub>			12 <sub>quadrat</sub>		
	122 <sub>mother</sub>			122 <sub>mother</sub>		
	8 <sub>source pop</sub>			8 <sub>source pop</sub>		
	808 <sub>OLRE</sub>			793 <sub>OLRE</sub>		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.030 / 0.037			0.170 / 0.203		
AIC	3756.35			1435.087		

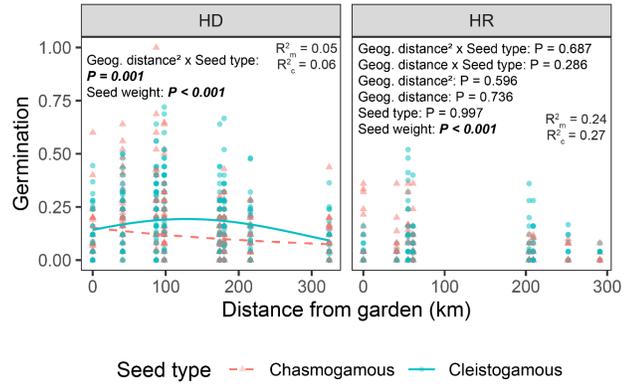
**Table 5.** Site and transect location data for *D. californica* sources and common gardens. Common garden sites highlighted in bold.

SITE	Region	Transect	GPS Start Lat	GPS start Long	GPS End Lat	GPS End Long	DistanceHR (km)	DistanceHD (km)	Latitude
Upper Weir	WAS		2 N 46.90931	W 122.70974	N 46.90932	W 122.70932	290.57	323.72	46.90908
Sublimity	COR		1 N 44.841218	W 122.767179	N 44.841263	W 122.76488	60.97	98.1	44.841218
Jefferson	COR		1 N 44.787292	W 123.018684	N 44.787167	W 123.017999	55.42	86.8	44.787292
<b>Horse Rock Ridge</b>	<b>COR</b>	<b>2</b>	<b>N 44.29877</b>	<b>W 122.87984</b>	<b>N 44.2988</b>	<b>W 122.87996</b>	<b>0</b>	<b>41.12</b>	<b>44.29804</b>
<b>Hazel Dell</b>	<b>COR</b>	<b>1</b>	<b>N 44.01979</b>	<b>W 123.21823</b>	<b>N 44.01955</b>	<b>W 123.21808</b>	<b>41.12</b>	<b>0</b>	<b>44.01979</b>
Lower Table Rocks	SOR		1 N 42.46811	W 122.94635	N 42.46787	W 122.94623	203.62	173.93	42.4681
Whetstone	SOR		2 N 42.41961	W 122.90685	N 42.41938	W 122.90685	208.95	179.7	42.4204
French Flat	SOR		1 N 42.10083	W 123.63493	N 42.10090	W 123.63479	251.93	216.04	42.1008









**Figure 4.** Geographic distance effects vary by seed type in the Hazel Dell (HD) garden but are not significant at Horse Rock Ridge (HR). Chasmogamous seed germination decreases weakly as source distance from HD increases. Cleistogamous seeds show the highest probability of germination when sourced between 100 and 200 km from HD. See Appendix H Table 2 for complete model results.

