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Intraspecific variation mediates density dependence in a genetically diverse plant species

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Abstract. Interactions between neighboring plants are critical for biodiversity maintenance in plant populations and communities. Intraspecific trait variation and genome duplication are common in plant species and can drive eco-evolutionary dynamics through genotype-mediated plant–plant interactions. However, few studies have examined how species-wide intraspecific variation may alter interactions between neighboring plants. We investigate how subspecies and ploidy variation in a genetically diverse species, big sagebrush (*Artemisia tridentata*), can alter the demographic outcomes of plant interactions. Using a replicated, long-term common garden experiment that represents range-wide diversity of *A. tridentata*, we ask how intraspecific variation, environment, and stand age mediate neighbor effects on plant growth and survival. Spatially explicit models revealed that ploidy variation and subspecies identity can mediate plant–plant interactions but that the effect size varied in time and across experimental sites. We found that demographic impacts of neighbor effects were strongest during early stages of stand development and in sites with greater growth rates. Within subspecies, tetraploid populations showed greater tolerance to neighbor crowding compared to their diploid variants. Our findings provide evidence that intraspecific variation related to genome size and subspecies identity impacts spatial demography in a genetically diverse plant species. Accounting for intraspecific variation in studies of conspecific density dependence will improve our understanding of how local populations will respond to novel genotypes and biotic interaction regimes. As introduction of novel genotypes into local populations becomes more common, quantifying demographic processes in genetically diverse populations will help predict long-term consequences of plant–plant interactions.

Key words: Artemisia tridentata*; common garden; intraspecific variation; negative density dependence; neighborhood models; plant–plant interactions; polyploidy; spatially explicit models; species coexistence; stress-gradient hypothesis.*

INTRODUCTION

Interactions between neighboring plants are a key driver of plant community structure and population dynamics (Wright et al. 2014). The relative strength of interactions between conspecific vs. heterospecific plant neighbors plays a critical role in maintaining coexistence between species (Chesson 2000, 2018). Within populations, negative density dependence is an important determinant of spatial and temporal dynamics (Law et al. 2003). Interactions between conspecific neighbors also underlie conservation and restoration outcomes, including tree species extinction after seed disperser loss (Caughlin et al. 2015), tree species density in forest plantations (Cordonnier et al. 2018), and plant reintroduction success in degraded sites where nurse plants facilitate establishment (Vogt et al. 2014). Many plant species exhibit intraspecific differences, such as local adaptation and genome size (Wood et al. 2009, Shryock et al. 2014), with potential consequences for genome-mediated neighbor interactions (Ehlers et al. 2016). While intraspecific variation within foundational species can have cascading effects on biotic interactions at the community level (Vellend and Geber 2005, Genung et al. 2012), understanding the role of species-wide variation in individual-level neighbor interactions remains a challenge.

Genetic variation, including local adaptations to abiotic conditions, is a source of intraspecific variability that can impact plant–plant interactions (Krannitzi and Caldwell 1995, Ehlers et al. 2016). The costs and benefits of local adaptations for spatial biotic interactions depend on environmental conditions, leading to context-

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dependent effects in the relative performance of plant genotypes and conspecific density dependence (e.g., Shao et al., 2018, Umaña et al., 2018). For example, Humphrey and Pyke (1998) investigated competitive interactions between two subspecies of the rhizomatous grass species, *Elymus lanceolatus*, that differ in growth strategies; they found that the competitive advantage of one subspecies over another was reversed when resource availability increased. To understand how abiotic factors mediate intraspecific density-dependence, we need to quantify outcomes of plant–plant interactions across environmental gradients (Hülsmann et al. 2020).

In addition to spatial variation in plant–plant interactions due to abiotic factors, the demographic impacts of plant–plant interactions are also likely to change over time. As stands develop, plants experience different levels of competition, due to changing neighbor density and size (Urza et al. 2019). Because small plants are at a competitive disadvantage relative to large plants, the effects of slight size differences during initial establishment tend to compound over time (Weiner and Damgaard 2006). Alternatively, plant–plant interactions may switch from facilitation to competition as nurse plants initially facilitate seedling establishment and then eventually compete with new recruits (Schupp 1995). Altogether, during establishment, there are concurrent changes in individual plant size and stand characteristics (Reisman-Berman 2007), that shape the development of plant–plant interactions. For example, self-thinning during the initial stages of stand development lowers population density and thereby decreases competition (Urza et al. 2019). Across the course of stand development and individual plant growth, the effects of intraspecific genetic variation are likely to vary. However, our understanding of how heritable traits mediate plant interactions across life stages is limited (Shefferson and Salguero-Gómez 2015, Whitham et al. 2020).

The coexistence of non-local with local plant genotypes in natural populations is becoming increasingly common due to factors such as climate-induced shifts in range boundaries, plant invasion, and large-scale restoration projects that require geographic seed transfer (Schlaepfer et al. 2010, Havens et al. 2015, Germino et al. 2018). Big sagebrush, *Artemisia tridentata* Nutt., represents an ideal study species to quantify the impact of intraspecific variation on plant–plant interactions under novel competitive regimes. This perennial shrub is locally adapted to a wide range of soil and climatic conditions across western North America and exhibits high genetic diversity (Richardson et al. 2012). A combination of morphological and ecological differences has led to recognizing three widespread subspecies (Shultz 2009). Additionally, *A. tridentata* is characterized by high frequencies of polyploidy (henceforth cytotypes) with multiple evolutionary origins (Richardson et al. 2012). Accounting for local adaptation in genetically diverse *A. tridentata* populations is an increasingly important component of regional conservation planning and has direct application to the restoration of the imperiled sagebrush steppe (Chaney et al. 2017).

We quantified how plant–plant interactions impact the growth and survival of individuals that represent a range-wide intraspecific diversity of *A. tridentata*. Our study included data from plots in a common garden experiment, and entailed repeated censuses on >1,300 individual plants, representing 55 seed source locations, three subspecies, and two ploidy levels. Because experimental plots were distributed at a regional scale spanning a wide range of environmental conditions and monitored for eight years, we were able to quantify how spatial and temporal variation impacts plant–plant interactions. Using these experimental data, we parameterized spatially explicit models for growth and survival to test the following four hypotheses. (1) A trade-off between competition tolerance and maximum growth rate is fundamental to plant life history (Chapin et al. 1993). We hypothesized such a trade-off at the intraspecific level within *A. tridentata* and predicted that subspecies with higher growth rates would be more susceptible to conspecific neighbor crowding. (2) Polyploid populations can have a wider range of environmental stress tolerance (Moghe and Shiu 2014), and we predicted that *A. tridentata* tetraploids would have higher neighbor tolerance compared to diploids. (3) Environmental gradients can alter the strength of plant–plant interactions, with generally weaker competition in stressful environments (Bertness and Callaway 1994). We predicted that the crowding effect would vary among the three experimental sites that encompass range-wide variation in abiotic conditions. (4) During stand development in our common garden, we expected plants to interact more as they become larger (Weiner and Damgaard 2006). Thus, we hypothesized that intraspecific competition would intensify over time.

Material and Methods

Study site

Our study includes three experimental common gardens established in 2010. The three locations represent an environmental gradient of precipitation (mean annual precipitation 297–610 mm) and temperature (mean annual temperature 6°–11°C) characteristic of the Great Basin region (Appendix S1: Table S1). The gardens were established between April and June 2010, when 468–470 seedlings were randomly outplanted in each garden. Survival and growth were monitored for the first two years after establishment for all three common gardens, and monitoring was resumed five years later in the Orchard and Majors Flat gardens, but not in the Ephraim common garden, which underwent land development (Appendix S1: Table S2). Crown volume was measured during the stages of early stand development in Orchard (419 plants), Majors Flat (448), and Ephraim (434); and late stand development during 2018 in Orchard (255 plants) and Majors Flat (368 plants). The survival data set includes the period between 2012 and 2018 in Orchard (421), and Majors Flat (448 plants).

We transformed measurements of height and width into a crown volume using a standard equation for spheroid volume. We calculated plant growth for each census interval as a difference in crown volume from time t to $t + 1$. To facilitate the comparison between growth across sites and years, we rescaled the growth rates as the change in volume per month. Although there were slight discrepancies in calendar dates of data collection, *A. tridentata* is a species that has vegetative growth mainly during the spring and summer (Evans et al. 1991). This period of active growth was captured in all sites and years of growth monitoring. For survival, we analyzed a long-term interval for Orchard (five) and Majors Flat (six years). The length of this interval ensured that we had enough mortality events for statistical analysis while excluding the initial two years after planting when mortality due to density-independent factors is more likely.

All three common gardens include combinations of three widespread subspecies and two ploidy levels (subspecies : cytotype) : *A. t. tridentata:2*x, *A. t. tridentata*:4x, *A. t. vaseyana*:2x, *A. t. vaseyana*:4x, and *A. t. wyomingensis*:4x. The seeds were sourced from 55 different populations across the arid west (Chaney et al. 2017). The subspecies differ considerably in their habitat preferences, stress tolerance, and life-history traits. In general, *A. t. wyomingensis* and *A. t. tridentata* occupy lower elevation, warm-dry environments of the region, while *A. t. vaseyana* is typically found in cold-mesic higher elevations. Furthermore, *A. t. tridentata* is characteristic of drainages and often achieves large stature, while *A. t. wyomingensis* tends to be smaller and is often found in shallow-soil plains (Kolb and Sperry 1999).

Plants within each garden were organized in a grid with 1 and 1.5 m spacing on two axes, respectively. To analyze spatial interactions between the individuals, we calculated a distance matrix, i.e., pairwise distances between all plants in each common garden. Based on empirical and experimental evidence on lateral root zone in big sagebrush (Sturges 1977, Zaiats et al. 2020), we expected no direct effect from neighbors beyond a 4-m distance, and, therefore, considered plant neighbors in a radius of <4 m from target plants.

Data analysis

The goal of our statistical model was to quantify how conspecific neighboring plants impact *A. tridentata*'s growth and survival across three common gardens and two stand development stages spanning eight years. The crowding effect represents the per capita impact of local neighbors on each target plant (Canham and Uriarte 2006, Chu and Adler 2015). We tested if the effect of conspecific crowding differed for each *A. tridentata* subspecies : cytotype target group. We allowed the crowding effect to range from negative to positive values, potentially representing both competition and facilitation effects on the growth and survival of intraspecific taxonomic groups. We fit hierarchical Bayesian models for each site, year, and vital rate, resulting in a total of seven models. We decided to fit separate models, rather than pooling all data together in a single model, based on our expectation that growth and survival are likely to vary widely between sites and years. For all models, we included random effects of intraspecific groups, enabling shared variance between subspecies : cytotype levels (Gelman and Hill 2006).

We modeled target plant growth as a function of subspecies : cytotype levels, target plant size, and a crowding term as an aggregate measure of neighborhood characteristics. Crowding was modeled as a sum of neighbors' crown size weighted by their distance from the target plant, accounting for neighbor intraspecific taxonomic group (Fig. 1):

$$\phi_{i,s} = \sum_{j=1,\, j\neq i}^{n-1} c_{[s]} \mathrm{Size}_{j,s} e^{-bD_j^2} \tag{1}$$

where Φ is a cumulative crowding experienced by plant i belonging to subspecies : cytotype group s, Size is the crown volume of neighbor j, b is the scaling factor that determines the rate of decline in effect with distance, D, from neighbor j to target plant i. Parameter $c_{[s]}$ estimates the contribution of each subspecies : cytotype group to the crowding term as a normally distributed random effect. Similar spatial models have been successfully applied to model competition between neighbors of a closely related sagebrush species (Adler et al. 2010, 2018*a*).

We used inverse modeling to estimate the strength and spatial scale of per capita crowding impact (Adler et al. 2010, Chu and Adler 2015; Barber et al., *unpublished manuscript*). We modeled growth as a normally distributed random variable using the following structure:

$$g_{s,t} \sim \mathrm{Normal}\left(\mu_{i,s,t}, \sigma^2\right) \tag{2}$$

$$\mu_{i,s,t} = \alpha_{[s]} + \beta_{[s]}\mathrm{Size}_{i,t-1} + \gamma_{[s]}\phi_{i,t-1} \tag{3}$$

where g_t is growth at time t, $\alpha_{[s]}$ is the average growth rate of subspecies : cytotype group s, Size_i is the crown volume of the target plant at $t - 1$, and $\gamma_{[s]}$ determines the neighborhood effect on a target plant i. All three unknown parameters were modeled as random effects by subspecies : cytotype group identity $[s]$. The survival models had a similar structure and predictors, but were modeled using a Bernoulli distribution

$$s_{s,t} \sim \mathrm{Bernoulli}(\theta_{i,s,t}) \tag{4}$$

$$\mathrm{logit}(\theta_{i,s,t}) = \alpha_{[s]} + \beta_{[s]}\mathrm{Size}_{i,t-1} + \gamma_{[s]}\phi_{i,t-1}. \tag{5}$$

The hierarchical model structure enabled us to fit models that relate to our four hypotheses. To test

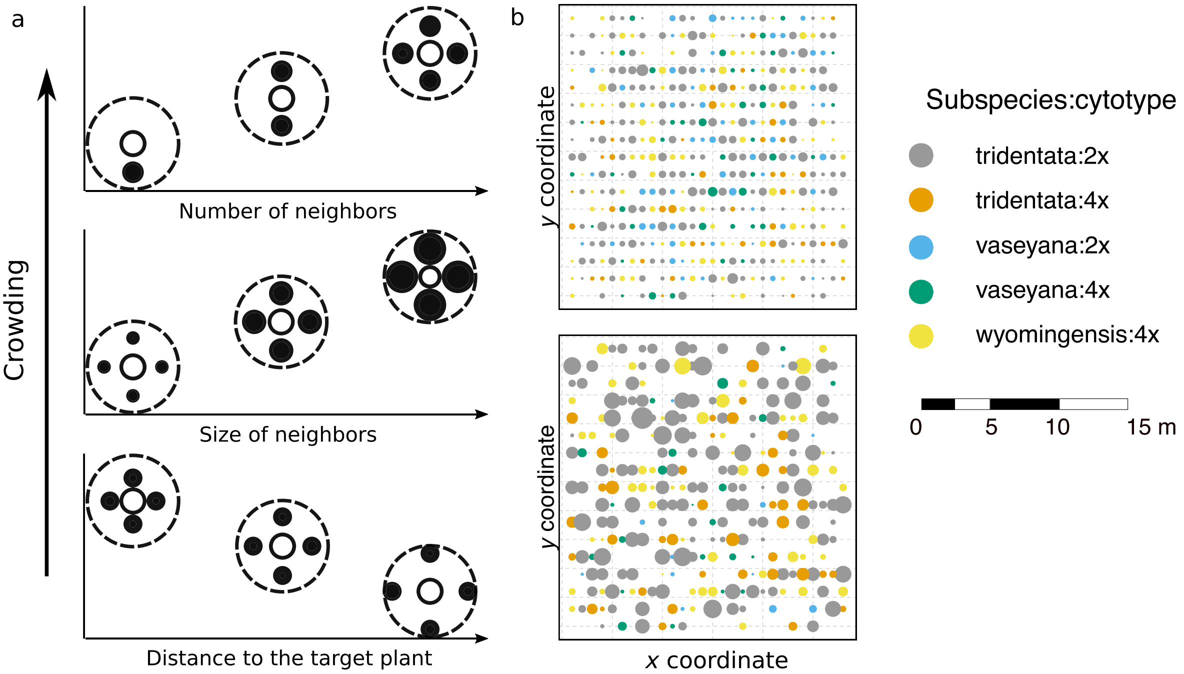

FIG. 1. A conceptual diagram of expected neighborhood dynamics (a) showing how neighborhood characteristics (filled circles) can impact a target plant (empty circles). (b) The observed spatial patterns in Orchard common garden 2011 (top) and 2018 (bottom) census intervals, where the relative size of circles indicates differences in crown volume.

hypotheses one and two, the relationship between crowding effect, growth rate, and ploidy level, we analyzed how the crowding parameter (γ) varied between cytotype groups and subspecies. We anticipated a trade-off between higher growth rate and crowding tolerance among target subspecies and cytotypes. To test the third hypothesis, that favorable environmental conditions intensify negative plant–plant interactions, we compared the estimated crowding effect (γ) between sites that varied widely in environmental conditions. To test the fourth hypothesis, that competition between plants intensifies during stand development, we compared neighborhood effects between the early and late stages of stand development. We expected that the crowding effect in the early stage would be weaker compared to the later stage. In all models we included the size of target plants as a covariate (Eqs. 3, 5) to account for growth differences in target plants with respect to the changing plant size over the course of the experiment (Merow et al. 2014).

We fit hierarchical Bayesian models using the Hamiltonian Monte Carlo algorithm from rstan package in R version 3.6.3 (R Core Team 2020, Stan Development Team 2020). To evaluate model convergence, we visually assessed the behavior and mixing of chains and checked that *R*-hat values were below a threshold of 1.1 (Gelman and Rubin 1992). We chose weakly informed, normally distributed priors centered at zero, with a variance that captured biologically meaningful effect sizes. All predictors were standardized by centering around the mean and dividing by two standard deviations (Gelman and Hill 2006). We evaluated the absolute model fit of our spatial models using R^2 and mean absolute error (MAE) for our continuous response variable (growth), and log-loss for our binary response variable (survival). In addition, we evaluated the relative fit of spatial models with plant–plant interactions and non-spatial models without plant–plant interactions (i.e., without the neighborhood term, $\gamma_{([s])}\phi$ in Eqs. 1, 3, and 5), using the LOO Information Criterion (Vehtari et al. 2017). Because our modeling goals were inferential, focused on testing hypotheses related to the strength of plant–plant interactions, we report effect sizes from the spatial models.

RESULTS

The three sites and two censuses varied greatly in growth, survival, and crowding effects (Fig. 2, Appendix S1: Fig. S3, Table S3). In 2011, the growth rate was higher in the Majors Flat and Ephraim common gardens, compared to the Orchard common garden. The growth rate decreased over time in Majors Flat and increased over time in Orchard (Appendix S1: Fig. S7). Between the subspecies, *A. t. tridentata* had a higher growth rate than the other groups in two of the three sites (Fig. 2). For Orchard 2018, and Majors Flat 2018

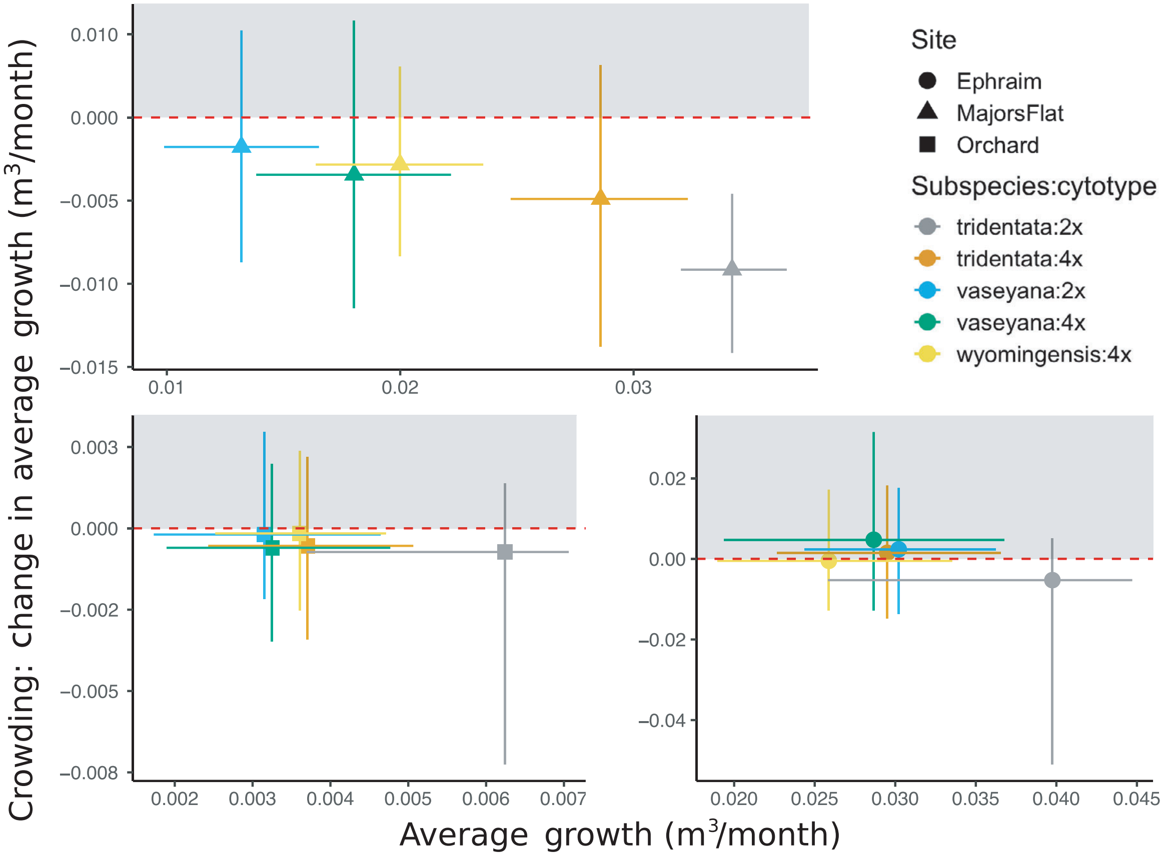

FIG. 2. Posterior samples representing the relationship between the average growth and crowding effect in three *Artemisia tridentata* common gardens during the 2011 census interval. The *y*-axis represents the change in average growth for the plants of average size when the crowding pressure is increased by two standard deviations. The symbols show median estimates and the error bars indicate 95% credibility intervals. Positive *y* values suggest the growth was enhanced by neighbors (facilitation), while negative values suggest reduced growth (competition).

models, the differences in the average growth rate among subspecies : cytotype groups were minimal with overlapping posterior distributions.

Similar to growth, survival was also highest in Majors Flat with an average of 80%, compared to 56% in Orchard. The median probability of survival in Orchard was lowest for *A. t. vaseyana*:2x at 22%, and highest for *A. t. tridentata*:4x at 88% (Appendix S1: Fig. S1). In Majors Flat, the estimates of survival for different subspecies : cytotype groups showed a similar pattern but the baseline survival at this site was higher.

Hypothesis 1 and 2: Intraspecific variation and ploidy level alters plant–plant interactions

We found that *A. t. tridentata*, the subspecies with the highest growth rate, experienced stronger crowding impact on growth compared to slower-growing subspecies, a consistent pattern across all locations (Fig. 2). The sensitivity of this subspecies to crowding was partly mediated by ploidy level, where the probability of negative crowding effect on *A. t. tridentata*:2x was >95% compared to 93.5% for *A. t. tridentata*:4x at Majors Flat site (Fig. 3). In contrast to our finding that target plant tolerance to neighbors (γ in Eqs. 3 and 5) varied depending on taxonomic identity, we did not find support for differences in impacts of neighbors on target plants across *A. tridentata* taxonomic groups (*c* in Eq. 1). This result suggests that the neighborhood suppression effects were comparable across neighbor identities.

Hypothesis 3: Environmental conditions mediate the strength of plant–plant interactions

Neighborhood effects were more pronounced for growth in Majors Flat and Ephraim, the sites with higher average growth rates, but the effect size varied among the target taxonomic groups (Appendix S1: Table S4). Conversely, the site with slowest average growth (Orchard common garden) had the smallest estimates of crowding effect. We did not find evidence for differential crowding effect on survival of the

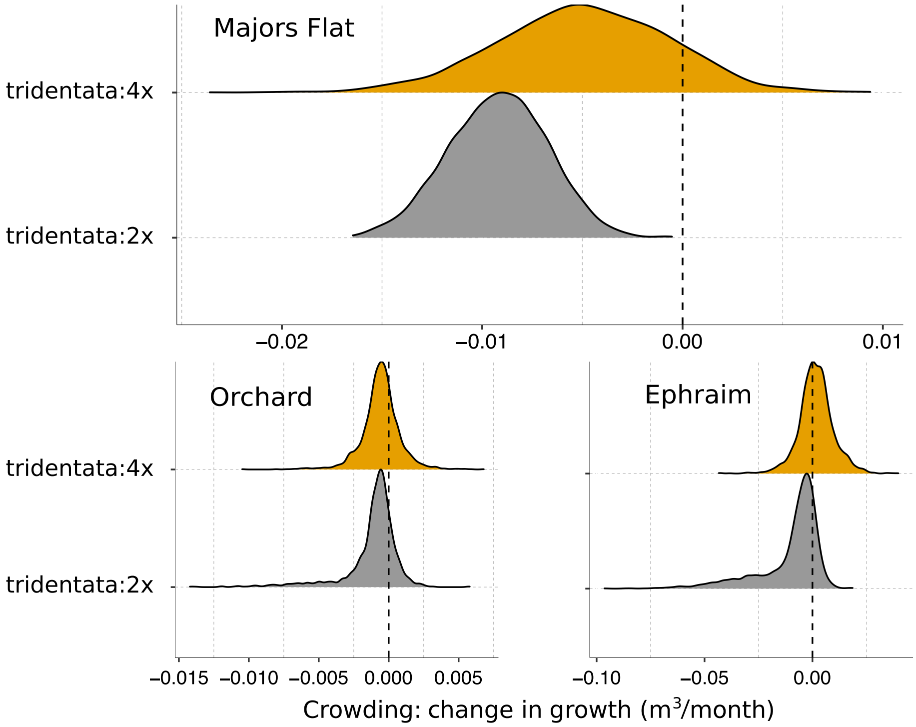

FIG. 3. Density plots showing differences in crowding effect between diploid and tetraploid cytotypes of *A. t. tridentata* during the 2011 census interval. The *x*-axis indicates the change in average growth when the crowding increases by two standard deviations.

subspecies : cytotype groups in any of the gardens, but there was a community-level facilitative effect in Majors Flat (Fig. 4). In this garden, the site with the higher average growth rate, the crowding effect was positive with indiscernible differences between subspecies : cytotypes, in contrast to the dryer site in Orchard common garden, where the crowding effect for all groups was indiscernible from zero.

Hypothesis 4: Stand development age intensifies plant–plant interactions

We hypothesized that neighbor interaction would be weak earlier in stand development because the distance between plants (1–1.5 m spacing) was much greater than plant size (0.18–0.31 m crown radii in 2011). Our results did not support this hypothesis. Instead, we found a stronger neighbor effect during earlier stand development, at least for the two sites characterized by higher growth rates (Fig. 2). In Orchard, on the other hand, the crowding at the early stage was indiscernible, but became stronger over time coinciding with an increase in growth rates at the late stage for this site. By the late stage in Orchard, the probability of a negative crowding effect on growth increased, while in Majors Flat the negative impacts observed in 2011 were no longer evident in 2018 (Fig. 2, Appendix S1: Fig. S3).

The scaling parameter associated with the rate of decline in neighbor effect (*b* in Eq. 1) varied but overall was similar across time and space (Appendix S1: Fig. S4). We modeled this parameter as a fixed effect that indicates the spatial extent at which neighbors affect the target plant. The estimated values for this parameter suggest that the effect of neighbors becomes negligible beyond a distance of three meters from the target plant (Fig. 5).

Model performance metrics were similar when comparing spatial and non-spatial models. For Majors Flat 2011, accounting for crowding effect improved model fit. For other sites and years, the predictive capacity was comparable to those without the spatial term (Appendix S2: Tables S1, S2). Across all sites and years, the range of R^2 and MAE in growth models was 3–60% and 0.009–0.0567 m^3/month, respectively.

DISCUSSION

We found evidence that the outcome of conspecific interactions between big sagebrush plants depends on subspecies and ploidy. Long-term monitoring of a replicated common garden experiment enabled us to quantify how stand development and environmental conditions alter the outcomes of interactions between genetically distinct plant populations. The effect of neighboring

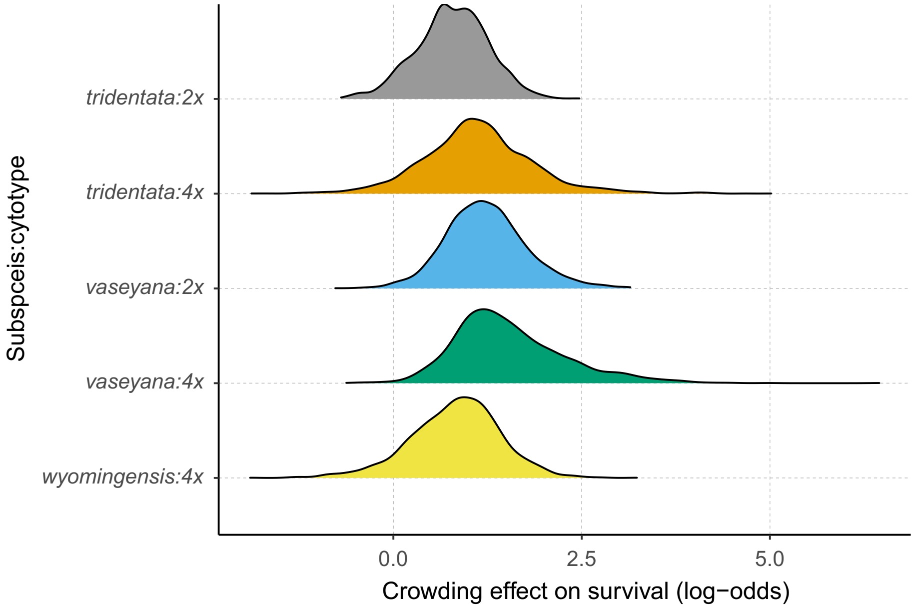

FIG. 4. The effect of crowding on the probability of survival of the different subspecies and cytotypes of *Artemisia tridentata* in the Majors Flat common garden. The effect sizes are based on a census interval between 2012 and 2018, and the values represent the change from the average survival when crowding is increased by two standard deviations.

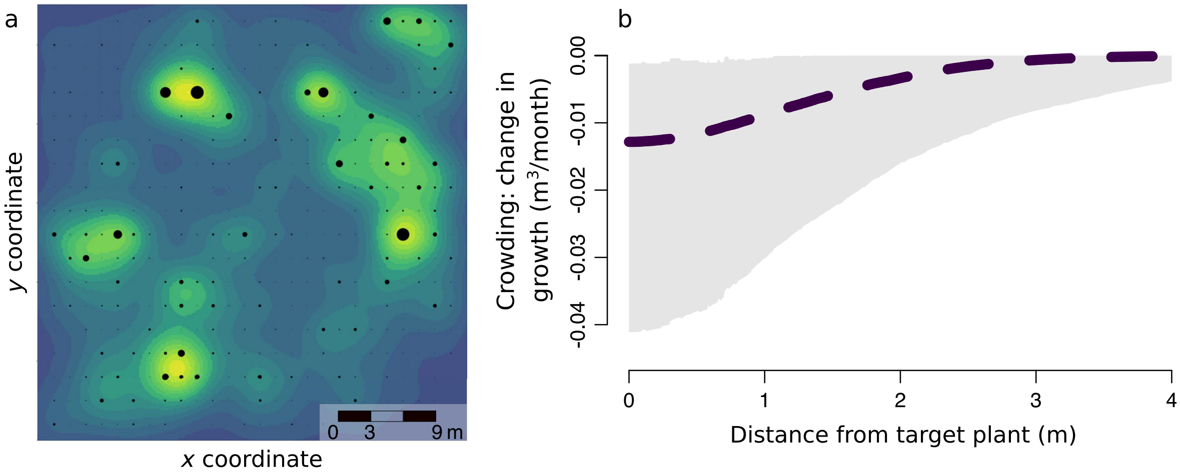

FIG. 5. The spatial pattern of plant–plant interactions in *Artemisia tridentata* common garden. (a) The pattern of competition an average size *A. t. tridentata*:2x individual would experience across the common garden. Lighter colors indicate higher predicted neighborhood effect and existing plants are displayed as black dots, with the size of each dot corresponding to relative crown size. (b) The spatial effect that generates the competitive surface in the common garden, which represents pairwise crowding between an individual plant and a single neighbor.

plants on growth and survival was more evident in sites with higher average growth rates, albeit with differences between target subspecies : cytotype groups. Along with environmental differences across sites, crowding effects on growth were also dependent on stand development, with generally negative effects during early stages of stand development. Altogether, our study demonstrates the dynamic nature of neighbor interactions mediated by differences in intrinsic growth and genome size, site characteristics, and temporal changes in stand development.

Across three common gardens and contrasting stand development stages, a consistent result of our research was that the subspecies : cytotype level with highest growth rates (*A. t. tridentata*:2x) was also most strongly affected by neighborhood crowding (Fig. 2). The per capita response of a plant to neighbors could combine an array of stress-tolerance traits, including a trade-off between growth and stress tolerance, as well as its competitive ability (Goldberg and Fleetwood 1987, Chapin et al. 1993, Wang et al. 2010). Our results show that the relationship between neighbor tolerance and intrinsic growth can persist across broad environmental gradients and range-wide intraspecific variation in *A. t. tridentata*. Further, plant–plant interactions can contribute to maintain species richness in sagebrush ecosystems (Adler et al. 2010, 2018*b*). Here, we demonstrate that within-species differences may play a role in coexistence mechanisms among genetically diverse populations of big sagebrush, a species of high genetic and ecological diversity (Richardson et al. 2012, Lazarus et al. 2019).

We found evidence that tetraploid plants in *A. tridentata* tend to have higher neighbor tolerance than their diploid variants (Figs. 2, 3). These results support other studies (Schlaepfer et al. 2010, Hahn et al. 2012), suggesting that polyploids have a higher capacity to tolerate neighborhood crowding (but see Thompson et al. 2015). Newly arisen tetraploid recruits in diploid neighborhoods face genetic (Kramer et al. 2018), demographic, and ecological establishment constraints (Rodriguez 1996, Fowler and Levin 2016); thus, high tolerance to competition from neighboring plants may be critical for their establishment. Our results demonstrate greater neighborhood tolerance in tetraploid plants across a range-wide gradient of environmental conditions. Explicitly accounting for neighbor interactions in space will provide insights into the mechanisms that facilitate the establishment of polyploids in plant populations.

Among the three common gardens, the signal of plant–plant interactions was strongest in sites with higher growth rates. Based on the site differences in average growth rates, our growth models generally support the stress-gradient hypothesis: favorable environmental conditions intensify negative interactions (Bertness and Callaway 1994). In contrast to growth, the survival response to neighbor presence was weak to positive for all subspecies : cytotypes with indiscernible differences between groups. Despite the highly variable neighbor effect across two sites, the survival of long-lived species, such as *A. tridentata*, can have large consequences for population fitness and warrants further investigation in the context of demographically structured neighborhood dynamics (Dalgleish et al. 2011).

We found that the impact of plant–plant interactions on demography varied from initial planting to maturity. While we expected to find a stronger neighbor effect during the later stages of stand development, when plants were large, our results show the opposite. The negative crowding was strongest during the early development stage in the two sites with the highest growth rates. This result was also reflected in model fit, with best performance of spatial models in sites with highest growth rates. Slower growth in later years, associated with weaker plant–plant interactions in our study, could indicate that plants are reaching their maximum potential size (Evans et al. 1991). In the driest site, the onset of spatial interactions appeared delayed (Appendix S1: Table S4); further long-term monitoring of additional common garden sites will be necessary to test the generality of this result. In later stages of stand development, competitive interactions could also alter other demographic rates, such as seed production (Richardson et al. 2021). Overall, our finding that crowding effects occurred earlier in stand development reinforces the importance of establishment stages in plant populations for community dynamics.

The results from our common garden experiment contribute to our understanding of negative density dependence in plant populations, particularly in light of recent criticism of observational studies of density dependence (Adler et al. 2018*a*, Detto et al. 2019). Adler et al. (2018*a*) point out that a combination of both experimental and observational studies will be necessary to forecast demographic outcomes of density dependence in plant populations. A main difference between our common garden design and natural populations of *A. tridentata* is that our plants established with even spacing. This is in contrast to the clustered pattern of natural recruits with higher densities near seed sources in natural populations. Consequently, we might expect to find even stronger competitive effects in natural populations. Detto et al. (2019) have also questioned the strength of density dependence quantified from observational studies, pointing out that unaccounted variation in measurements of plant neighborhoods can bias results. Intraspecific variation in competition, driven by genetic differences between plants, is one potential source of unaccounted variation in plant neighborhoods that should be considered to strengthen studies of negative density dependence. Finally, both Detto et al. (2019) and Adler et al. (2018*a*) emphasize the importance of mechanistic studies to complement observational studies of competition in plant populations. In our arid study system, direct root-to-root interactions and competition for water is one obvious mechanism for suppressed growth in crowded neighborhoods (Krannitzi and Caldwell 1995). Nevertheless, a water isotope tracer experiment in one of our common garden sites did not support direct root competition in surface water uptake (Zaiats et al. 2020). In addition to observational studies that confirm our results, developing mechanistic hypotheses that can explain our findings will be an important next step.

Genetically mixed plant populations are increasingly common in natural ecosystems as human activity results in reintroductions, transplants, and invasions (Havens et al. 2015). While local seed sourcing is increasingly prioritized in long-term planning for resilient plant populations, in practice, restoration projects often mix plant material from genetically distant populations. In the Great Basin, sagebrush restoration projects often represent a mixture of genotypes and subspecies (Davidson et al. 2019). Considering demographic impacts of interactions between plants in restoration projects can improve plant performance and ultimately restoration outcomes (Ibáñez and Rodríguez 2020). Our work supports the idea that the genotype of source material can impact plant–plant interactions (Lorts and Lasky 2020), a result with implications for ecological restoration. This possibility could be considered when designing management interventions that match seed sources to local conditions. Additionally, instances where restoration interventions have led to co-occurrence of genetically distinct subpopulations represent potentially valuable case studies for understanding eco-evolutionary feedbacks (LaRue et al. 2017). In sum, studies that evaluate neighborhood interactions between introduced and local plant populations will provide new insights for both basic and applied ecology.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3502/suppinfo

OPEN RESEARCH

Modeling scripts are uploaded as Data S1 in the Supporting Information. Data (Zaiats et al. 2021) are available in the Dryad digital repository: https://doi.org/10.5061/dryad.kwh70rz3r.