



RESEARCH ARTICLE

Functional Ecology



Intraspecific variation in surface water uptake in a perennial desert shrub

Andrii Zaiats¹ | Brynne E. Lazarus² | Matthew J. Germino² | Marcelo D. Serpe¹ | Bryce A. Richardson³ | Sven Buerki¹ | T. Trevor Caughlin¹

¹Department of Biological Sciences, Boise State University, Boise, ID, USA

²U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Boise, ID, USA

³USDA Forest Service, Rocky Mountain Research Station, Moscow, ID, USA

Correspondence

Andrii Zaiats

Email: andriizaiats@boisestate.edu

Funding information

USDA Forest Service; Rocky Mountain Research Station; Great Basin Native Plant Project; US Bureau of Land Management; Boise State University; Dan Montgomery Graduate Student Award; NSF Idaho EPSCoR Program, Grant/Award Number: OIA-1757324; US Geological Survey; National Science Foundation, Grant/Award Number: 1415297

Handling Editor: Laura Yahdjian**Abstract**

1. Despite broad recognition that water is a major limiting factor in arid ecosystems, we lack an empirical understanding of how this resource is shared and distributed among neighbouring plants. Intraspecific variability can further contribute to this variation via divergent life-history traits, including root architecture. We investigated these questions in the shrub *Artemisia tridentata* and hypothesized that the ability to access and utilize surface water varies among subspecies and cytotypes.
2. We used an isotope tracer to quantify below-ground zone of influence in *A. tridentata*, and tested whether spatial neighbourhood characteristics can alter plant water uptake. We introduced deuterium-enriched water to the soil in plant interspaces in a common garden experiment and measured deuterium composition of plant stems. We then applied spatially explicit models to test for differential water uptake by *A. tridentata*, including intermingled populations of three subspecies and two ploidy levels.
3. The results suggest that lateral root functioning in *A. tridentata* is associated with intraspecific identity and ploidy level. Subspecies adapted to habitats with deep soils generally had a smaller horizontal reach, and polyploid cytotypes were associated with greater water uptake compared to their diploid variants. We also found that plant crown volume was a weak predictor of water uptake, and that neighbourhood crowding had no discernable effect on water uptake.
4. Intraspecific variation in lateral root functioning can lead to differential patterns of resource acquisition, an essential process in arid ecosystems in the contexts of changing climate and seasonal patterns of precipitation. Altogether, we found that lateral root development and activity are more strongly related to genetic variability within *A. tridentata* than to plant size. Our study highlights how intraspecific variation in life strategies is linked to mechanisms of resource acquisition.

KEYWORDS

Artemisia tridentata (big sagebrush), below-ground interactions, deuterium tracer, intraspecific variation, lateral roots, resource competition, surface water uptake

1 | INTRODUCTION

The spatial organization of roots in plant communities impacts multiple processes, from individual plant fitness to ecosystem function. Patterns of below-ground resource acquisition and interactions between neighbouring plants could be one mechanism leading to biodiversity-maintaining niche differences (Chesson, 2018; Kulmatiski & Beard, 2013; O'Keefe, Nippert, & McCulloh, 2019). Furthermore, below-ground processes are subject to global ecological changes, including increasing rates of biological invasions, altered disturbance regimes and climate change (Chapin III et al., 2000; Germino, Chambers, & Brown, 2016; Havens et al., 2015). In arid environments, these changes are likely to have particularly strong impacts on below-ground ecological processes as altered precipitation regimes impact the partitioning of scarce resources (Chesson et al., 2004; Fowler, 1986). Fine-scale variation in life-history strategies can affect the dynamics of resource acquisition, which is a key to predicting the effects of climate change on plant populations (Shriver, 2017). Intraspecific adaptive variation in root architecture is one source of diversification in life-history traits that could contribute to resource partitioning and biodiversity maintenance. However, conflicting evidence and a paucity of experimental studies on spatial structure and functioning of plant roots limit our understanding of how intraspecific variation affects below-ground processes and mechanisms of resource acquisition (Münzbergová, 2007).

Below-ground resource competition and root interactions are likely to play a major role in species and community dynamics of arid ecosystems (Chesson et al., 2004). Altered disturbance regimes across the western United States threaten natural communities, where intraspecific variation and local adaptations of the keystone shrub, *Artemisia tridentata* 'big sagebrush', are critical for the success of restoration efforts and conservation strategies (Germino, Moser, & Sands, 2018; Richardson & Chaney, 2018). Management decisions aimed at restoring imperiled sagebrush can have implications for big sagebrush recovery and distribution on the regional scale (Requena-Mullor, Maguire, Shinneman, & Caughlin, 2019). On the scale of individual plants, there is evidence for strong plant-plant interactions between congeneric sagebrush plants and heterospecific neighbours, with implications for long-term species coexistence (Adler, Ellner, & Levine, 2010). Despite a consensus that water availability is an important covariate in plant performance, explicitly linking water limitation to neighbour competition is difficult (e.g. DiCristina & Germino, 2006; Loik, Breshears, Lauenroth, & Belnap, 2004). However, competition for water could drive observed patterns of negative density dependence for shrub species in arid ecosystems as competition for light is rare in these systems due to generally sparse canopy cover (Adler et al., 2010; Miriti, Wright, & Howe, 2001; Schenk & Mahall, 2002).

Big sagebrush is a long-lived perennial that requires extensive monitoring to understand its demographic variation (Germino, Moser, et al., 2018; Shriver et al., 2019). The acquisition of soil resources (e.g. water) is likely to be a key process that underlies longer-term demography of plant populations in arid areas (Chesson

et al., 2004). On the other hand, short-term measurements of water and nutrient uptake (Grossiord et al., 2014) can provide a semi-mechanistic basis to understand long-term competitive processes and demographic variation (Schwinning & Weiner, 1998; Weigelt & Jolliffe, 2003). Predicting the strength of below-ground interactions in sagebrush ecosystems is complicated by significant intraspecific variation in the dominant shrub species of these ecosystems *A. tridentata*. This intraspecific variation relates to local adaptation across *A. tridentata*'s wide geographical distribution as well as high genetic diversity within big sagebrush populations (Chaney, Richardson, & Germino, 2017). The mechanisms that maintain high intraspecific diversity within big sagebrush populations are not well understood. For stable coexistence of species-level diversity, ecological theory proposes that intraspecific competition must be stronger than the interspecific competition (Adler et al., 2010; Chesson, 2018). Additionally, niche segregation may contribute to maintaining intraspecific diversity, but its role is less clear (Hart, Schreiber, & Levine, 2016; Uriarte & Menge, 2018). Along with long-term consequences for eco-evolutionary dynamics, variation in ecophysiological characteristics between genetically different sagebrush populations has practical importance for restoring big sagebrush to degraded areas. An increasing body of evidence suggests that choosing sagebrush seeds from locally adapted populations is critical to establishment success (Germino, Moser, et al., 2018). Local adaptations may be partly the result of root characteristics that affect the acquisition of nutrients and water, but the extent to which different big sagebrush populations vary in root traits remains largely unknown.

High variability within *A. tridentata* also includes frequent and widespread polyploidy (Richardson, Page, Bajgain, Sanderson, & Udall, 2012). As a genomic trait that can alter plant fitness, polyploidy is a key component of intraspecific variation in plant populations (Černá & Münzbergová, 2013). For at least some taxa, studies suggest higher drought tolerance in polyploids than diploids populations (e.g. Li, Berlyn, & Ashton, 1996; Van Laere et al., 2011; but see Münzbergová, 2007). The basis for these differences is not clear but may include differences in water use efficiency, root to shoot ratio and root architecture (Leger, 2008; Maherali, Walden, & Husband, 2009; Schwinning & Kelly, 2013). Furthermore, differences in drought tolerance may lead to spatially segregated populations that occupy distinct hydrological niches (Araya et al., 2011; Xiong, Wang, Mao, & Koczan, 2006). For diploid and tetraploid genotypes of big sagebrush (hereafter cytotypes), understanding plant characteristics and interactions that affect the acquisition and use of water would contribute to explaining the evolution and coexistence of genetically diverse populations.

Over its range, *A. tridentata* occupies habitats with distinct characteristics, including differences in soil profile depth. These differences underlie intraspecific patterns of big sagebrush distribution and are associated with morphological and physiological traits related to plant water and nutrient use (Kolb & Sperry, 1999; Shultz, 2009). Local adaptations, including adaptations to soil profile depth, are likely to be mediated by different patterns of root development and functioning. For example, the ability of *A. tridentata*

to utilize water resources from deep and shallow soils may lead to varying water acquisition patterns among the subspecies (Donovan & Ehleringer, 1994; Kolb & Sperry, 1999). Also, the ability to retain functional lateral roots through the dry season may be important for the maintenance of plant water status and photosynthesis, which ultimately can enhance seed production (Evans, Black, & Link, 1991; Leffler, Ivans, Ryel, & Caldwell, 2004; Loik, 2007). Thus, differences in the density and spread of functionally active lateral roots in shallow soils are likely to be important for plant growth and reproduction, and reflect adaptations to particular soil profiles and precipitation patterns. In arid environments, such information may be essential for the understanding of mechanisms that determine negative interactions between neighbouring individuals (Goldberg, 1990). Investigating below-ground resource partitioning, however, is difficult due to the high plasticity and variability of root systems and the logistical complexity of measuring them.

We examined intraspecific variation in lateral water uptake using an isotope tracer experiment in an *A. tridentata* common garden. We applied spatially explicit models to characterize below-ground zone of influence as a relative capacity of a plant to alter surrounding soil environment (*sensu* Casper, Schenk, & Jackson, 2003); and to quantify how the size of neighbouring individuals affects tracer uptake by a target plant (*i.e.* crowding effect). To investigate the knowledge gap in mechanistic understanding of density-dependence in arid ecosystems (Adler et al., 2010; DiCristina & Germino, 2006), we hypothesized that resource accessibility and uptake may be related to above-ground crown size if there is a positive relationship between above- and below-ground biomass (Cleary, Pendall, & Ewers, 2008). In addition, we investigated whether intraspecific variability at the subspecies and ploidy level is related to differences in tracer uptake. Specific questions that we asked in this study include the following: (i) Do subspecies identity and ploidy level have an effect on the uptake of water from shallow soils? (ii) What is the horizontal extent of lateral roots in shallow soils? (iii) Does the size of neighbouring individuals affect water uptake by a target plant?

2 | MATERIALS AND METHODS

2.1 | Study system

Measurements were made in a 8-year-old plantation of big sagebrush at NRCS Orchard Range Site in south-eastern Idaho, USA (43°19'19"N, 115°59'49"W). The common garden represents range-wide intraspecific variability of big sagebrush, including three commonly recognized subspecies and two cytotypes sourced from 55 populations across the western United States. The climate at the experimental site has a Koeppen classification of BSk, cold semiarid steppe (Peel, Finlayson, & McMahon, 2007), with an average annual precipitation of 294 mm (Soil Climate Analysis Network: Orchard Range Site, <https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=674>). Relative to the *A. tridentata* range, the site is characterized by warm temperatures and low precipitation regimes, and is generally

representative of *A. t. wyomingensis* and *A. t. tridentata* habitats. The common garden was established in April 2010 with 468 individuals outplanted randomly in a grid with 1 by 1.5 m spacing intervals. A more detailed description of the experimental plot, including the associated climate covariates, is outlined in Chaney et al. (2017). Due to mortality, a total of 244 individuals of three subspecies were present at the time of our experiment of which 173 were included in the experiment. The crown size of the plants was measured 1 month before the experiment and converted to a crown volume using a standard ellipsoid volume equation.

2.2 | Plant water balance

Considering the variability of big sagebrush root activity in shallow soil horizons in response to sparse summer precipitation, we chose to conduct the tracer addition experiment at the beginning of 1–3 June 2018. This consideration was based on the possibility that shallow roots may fall into physiological dormancy during the dry period of the year (Germino & Reinhardt, 2014). We selected a rainless period for the experiment to avoid a precipitation event interfering with the deuterium label concentration. We obtained a monthly record of soil moisture measurements preceding the experiment from an adjacent weather station (Soil Climate Analysis Network: Orchard Range Site). The moisture probes (HydraProbe Analog [2.5 Volt], Stevens Water Monitoring Systems Inc.) at 0.05, 0.2 and 0.5 m depths are located close to the common garden, in the same soil type, and are representative of the long-term soil moisture content preceding the deuterium addition. To evaluate the overall water status of the plants during the experiment, we randomly selected four individuals for each of the five subspecies:cytotype groups ($n = 20$) and measured pre-dawn and mid-day water potentials of foliated shoots on the day of the experiment using a Scholander pressure chamber (Model 1000, PMS Instrument Co).

2.3 | Deuterium labelling

We split the common garden into 14 spatially separated subplots. Each subplot corresponded to one deuterium oxide injection and a buffer distance that included the subject plants. The replication of experimental treatments was aimed to minimize the potential mismatches associated with localized isotope additions and the presence of roots in that location (Kulmatiski, Adler, Stark, & Tredennick, 2017). Considering that lateral roots of *A. tridentata* rarely exceed 1.5 m from the base of plants (Reynolds & Fraley, 1989; Sturges, 1977), we defined the dimensions of subplots to be 6 by 6 m with the injection point in the centre of the square area. Given the documented lateral root length, we assumed that plants were unlikely to uptake isotope tracer from the neighbouring subplots relative to uptake from the injection point within the same subplot. We introduced a deuterium oxide solution in the centre of each subplot, so the injection location was equidistant to

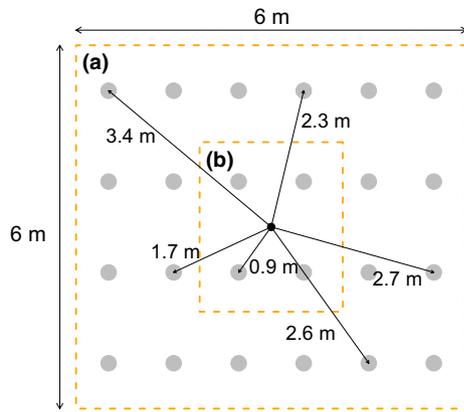


FIGURE 1 A diagram of experimental subplots in Orchard common garden used to test root lateral extent (a) and crowding effect (b). The centroid of the subplot is a location where deuterium-enriched water was introduced, the grey points show the grid of plants, and the arrows indicate the distance of each plant to the subplot centroid

the four nearest plants (Figure 1a). Each subplot would have had 24 plants in the original planting, but due to mortality, there were between 8 and 17 plants per subplot. The proximity of individual plants to the source location in the centroid was at six distance increments (0.9, 1.7, 2.3, 2.6, 2.7 and 3.4 m) with this experimental design. Therefore, in our total sample size ($n = 173$), there were 21–38 plants in each distance increment and 4–92 plants in each subspecies:cytotype group (Figure S3).

We prepared the labelling solution by mixing $^2\text{H}_2\text{O}$ concentrate (99.8%, Cambridge Isotope Laboratories, Inc.) and tap water ($\delta^2\text{H} \sim -123\text{‰}$), which resulted in a solution of $\delta^2\text{H} \sim -15,950\text{‰}$, a concentration assumed to be adequate for label detection based on preliminary tests. Background $\delta^2\text{H}$ in soils was $-106.8\text{‰} \pm 9.8$ ($M \pm 1$ SD). We introduced 1 L of the solution to the soil, starting at a depth of 5 cm below the surface (beneath litter and annual weed roots that were removed prior to labelling). We poured the solution into 0.11 m radius plastic cylinders to prevent run-off and thereby force downward infiltration. Following label application, the volume of soil that became saturated under each injection location was estimated to be $\sim 0.008 \text{ m}^3$, assuming a cylindrical plume to a depth of 0.2 m. We empirically obtained these estimates from preliminary tests on similar soils adjacent to the common garden, in which we were able to excavate around the injection point to visually assess how injections would disperse in the soil. Injections took place in the morning, and measurements of plant water status and $\delta^2\text{H}$ were made ~ 30 hr later in the afternoon of the following day. This sampling time was estimated based on previous ^2H tracer experiments (e.g. Kulmatiski & Beard, 2013) and was also tested in preliminary additions next to the experimental site. Based on the reported estimates of sap flow velocity in *A. tridentata* (Gifford, 1968), we expected a peak in deuterium composition in individuals closest to the source location (i.e. 0.9 m) approximately 30 hr after the injection. We verified these estimates during our preliminary trial on four plants outside the common garden (Figure S4). After 30 hr, we obtained a measure of label

uptake that was maximum for the closest plants and decreased for more distant individuals due to longer travel time. Overall, this measure reflects the relative potential of a plant to alter the environment, as well as the probability of resource uptake (Casper et al., 2003).

For xylem sampling, we collected branches with visible secondary growth that were typically 10 cm long (shorter from smaller plants), and about 0.6 cm in diameter. We removed the bark immediately after cutting the branch, wrapped the sample with parafilm and placed it in an airtight glass vial, which was stored at 3°C until analysis (Grossiord et al., 2014; Lazarus & Germino, 2017). We used a Picarro Induction Module (IM) coupled to a CRDS isotopic analyzer (L2120-i, Picarro Inc.) to analyse the isotopic composition of water vapour extracted directly from xylem sections by induction heating, following Lazarus, Germino, and Vander Veen (2016). We derived and analysed 3–8 xylem sections per stem sample and averaged the final 2–3 readings to avoid memory bias from previous samples (Cui, Tian, Gerlein-Safdi, & Qu, 2017), resulting in one isotope measurement for each plant. Samples were weighed immediately after analysis and again after oven drying for 24 hr at 65°C to verify that all water had been removed during the analysis (data not shown). Lazarus et al. (2016) showed that no spectral interference from organic compounds occurred for big sagebrush stems analysed by this method. Isotope ratios were standardized to the VSMOW/SLAP scale using isotopic water standards (Los Gatos Research) introduced on dried-then-labelled sagebrush stem sections (Lazarus et al., 2016).

2.4 | Data analysis

We calculated the difference between the post-treatment and pre-treatment $\delta^2\text{H}$ values, where the pre-treatment values represent natural ^2H abundance in plant stems. We used this calculated difference as a response variable in the statistical models representing the amount of labelled water taken up by each plant. We discarded one outlier reading that was 13 standard deviations above the average difference between pre- and post-treatments. Data are available online in Dryad Data Repository <https://doi.org/10.5061/dryad.pk0p2ngjm> (Zaiats et al., 2020).

The objective of our statistical models was to determine the effects of intraspecific variation and size-based crowding on the deuterium uptake rates. To answer questions (i) and (ii), we used the identity, size and distance of plants from the label injection locations as predictors of deuterium uptake to quantify below-ground zone of influence. We modelled the response using a modified negative exponential function with two parameters, the intercept and the change in deuterium content with distance (Equation 1):

$$\text{Deuterium uptake} = \alpha e^{-D^2\beta}, \quad (1)$$

where D is its distance from the centroid of the subplot, α is the intercept and β is the decline in deuterium content with distance.

Both α and β parameters were modelled as random effects with five categories corresponding to the five subspecies:cytotype combinations. Random effects acknowledge the similarity between

subspecies by estimating a shared variance parameter for all subspecies while allowing the coefficients to vary between groups (Gelman & Hill, 2007). In our case, modelling these parameters enabled us to address questions (i) and (ii) by quantifying variability in spatial reach of deuterium uptake by roots among cytotypes and subspecies.

To answer question (iii), the effect of neighbours on uptake of the label, we subset the observations to include only the nearest neighbours of the deuterium source location (Figure 1b). We excluded more distant plants because the effect on resource acquisition imposed by distant individuals is likely to be negligible, compared to advantages to plants that are nearest the source. Because of the smaller sample size, we modelled the response of three subspecies without differentiating between ploidy levels. Our crowding model included the base (average) deuterium uptake by a target plant, and a ratio of the cumulative crown volume of the neighbours to the crown volume of the target plant, reflecting the relative above-ground physical space occupied by the neighbours compared to that of the target plant. We modelled the parameters as random or fixed effects corresponding to the three subspecies of *A. tridentata* (Equation 2):

$$\text{Deuterium uptake} = \alpha_{0,i,[s]} + \alpha_{1,i} \left[\frac{1}{S_i} \sum_{j=1, j \neq i}^n S_j \right], \quad (2)$$

where α_0 is the average deuterium uptake with subspecies as a random effect, n is the number of plants nearest to the source and α_1 is a neighbour effect on the target plant uptake rate modelled as a fixed effect with no pooling of variance.

We fit Hierarchical Bayesian models in R using Hamiltonian Monte Carlo algorithm from the RSTAN package (Monnahan, Thorson, & Branch, 2017; R Core Team, 2018; Stan Development Team, 2018). The non-spatial predictors were standardized by centring them around the mean and dividing by two standard deviations (Gelman & Hill, 2007). We used non-informative priors for all parameters in the model. For model selection, we used in-sample widely applicable information

criterion (WAIC) scores and calculated mean absolute error (MAE) as a measure of model fit (Vehtari, Gelman, & Gabry, 2017).

3 | RESULTS

Measurements of ambient soil moisture revealed that moisture content was relatively high and stable during the month preceding the experiment (Figure S1). The leaf water potentials indicated that plant water status was variable but within the range tolerated by *A. tridentata* (Kolb & Sperry, 1999). There was a significant difference between the pre-dawn and mid-day water potentials ($F_{1,38} = 281.3, p < .001$), but no differences among groups during the mid-day measurements ($F_{4,15} = 2.051, p = .139$; Figure 2). These results suggest

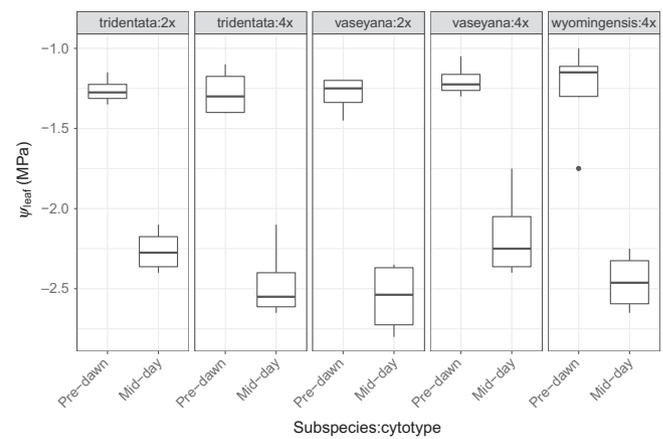


FIGURE 2 Box and whisker plots showing the median, lower and upper quartiles for *Artemisia tridentata* plant water status at the Orchard common garden during the deuterium tracer experiment. The values are shown for pre-dawn and mid-day leaf water potential measurements for five different subspecies:cytotype groups of big sagebrush (2x is diploid, 4x is tetraploid)

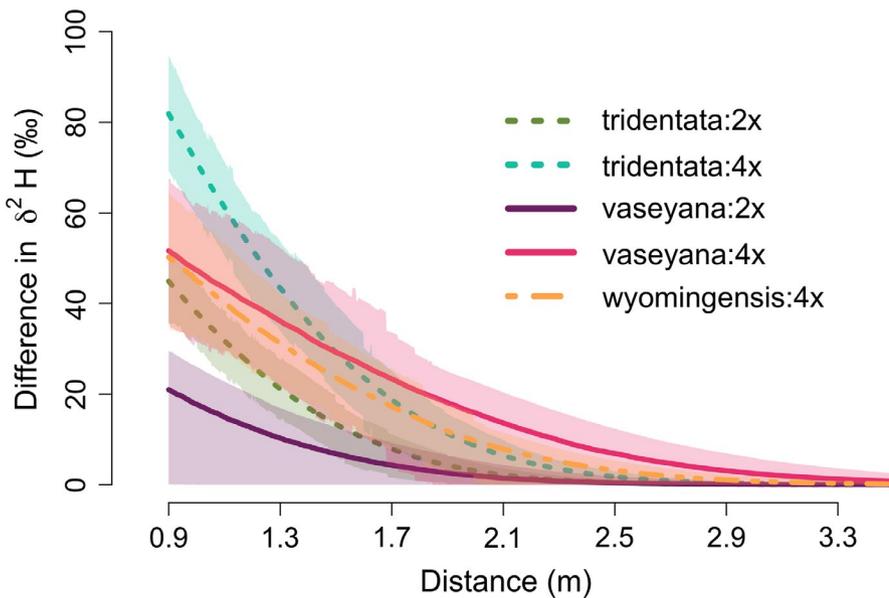


FIGURE 3 *Artemisia tridentata* uptake of deuterium ($^2\text{H}_2\text{O}$) enriched water as a function of distance between the source location and plants. The label was introduced into plant interspaces in Orchard common garden in Spring 2018. The vertical axis indicates the difference in $\delta^2\text{H}$ in plant stems between the post- and pre-treatment. Different colours indicate subspecies and cytotype of big sagebrush (2x is diploid, 4x is tetraploid), and the shaded areas represent one SD around the posterior mean

that the observed subspecies:cytotype differences in label uptake can be attributed to differences in below-ground zone of influence and not to differences in plant water status.

Our final model for below-ground zone of influence was a nonlinear response function with an asymptote at zero. Among the linear and non-linear models that we tested, we found that a modified negative exponential regression had the best fit and highest predictive power (Table S1). Our model revealed that the probability of plants taking up deuterated water declined steeply within the radius of 2 m around the target plant. Our first hypothesis was partially supported by label uptake differences among subspecies:cytotype groups. All dissimilarities, however, became negligible beyond the 2-m radius where deuterium uptake was estimated to be minimal for all subspecies. In the range of 0.9–1.5 m from the source, we found noticeable differences in deuterium absorption between subspecies:cytotype categories (Figure 3). Notably, *A. t. vaseyana*:2x was associated with lower water uptake compared to other groups, even though its leaf water potential was similar. Additionally, tetraploids tended to have higher isotope uptake compared to diploids within subspecies *A. t. tridentata* and *A. t. vaseyana* in magnitude and lateral extent, respectively (Figures 3 and 4).

We did not find a discernible effect of crowding on deuterium uptake. Moreover, we excluded the size of the target plant as a separate predictor from the model because its effect was not detectable, and it did not improve the overall model fit. The estimated median of deuterium uptake under the average crowding pressure (i.e. intercept) was highest for subspecies *A. t. tridentata*, but the credibility intervals for all groups highly overlapped (Figure 5). We did not find strong evidence that neighbours had an effect on deuterium uptake by a target plant. The median response to crowding of *A. t. vaseyana* and *A. t. wyomingensis* was very close to zero. While the median

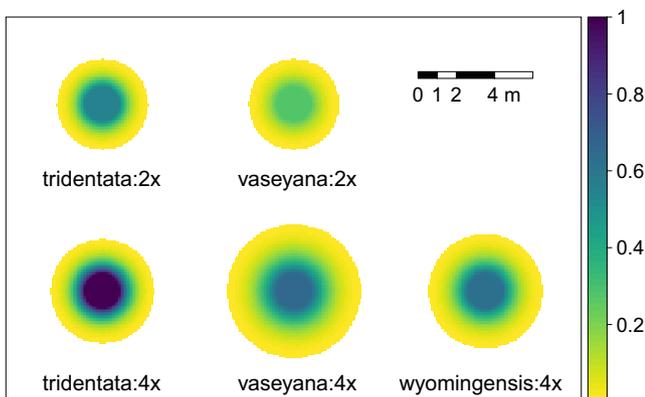


FIGURE 4 Predicted below-ground zone of influence of *Artemisia tridentata* subspecies:cytotype groups in Orchard common garden. The figure shows deuterium content where colour intensity corresponds to quantile-scaled values of water uptake from shallow, 5–25 cm, soil horizon. The scale shows the quantiles >0.01 as mean posterior predictions for each subspecies:cytotype group (2x is diploid, 4x is tetraploid). Projections <0.9 m (circle centres) are interpolated based on the predicted values at this distance, as these areas were outside the model range

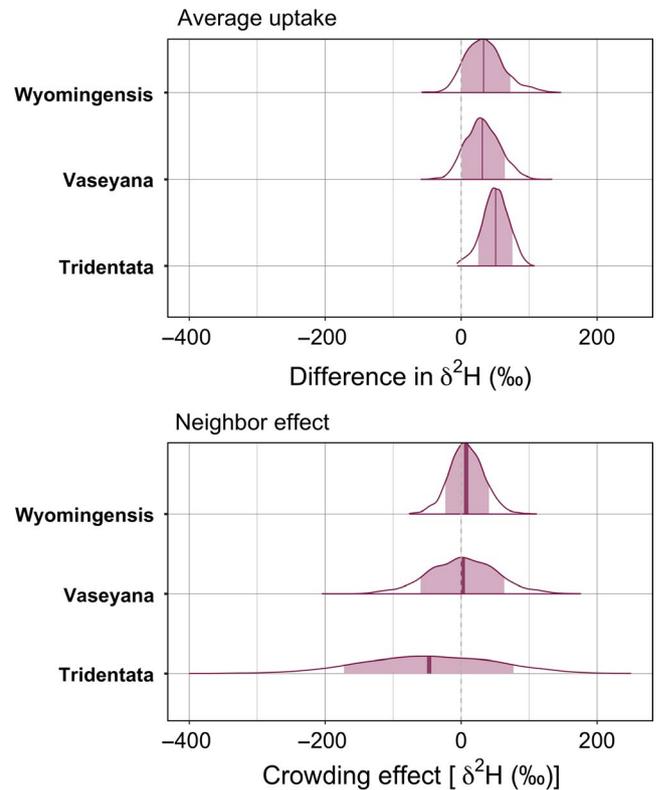


FIGURE 5 Posterior distribution of average deuterium uptake by a target plant located 0.9 m from the isotope source under average crowding (upper panel), and expected crowding effect on the label uptake under 2 SD increase in crowding ratio (lower panel), where zero indicates no effect. Categories correspond to three subspecies of *Artemisia tridentata* (*tridentata*, *vaseyana* and *wyomingensis*) without differentiation of cytotypes

response to crowding for *A. t. tridentata* was slightly negative, this effect had high uncertainty, including 95% credibility intervals that overlapped zero.

4 | DISCUSSION

Intraspecific variability in below-ground plant architecture and spatial interactions is a key knowledge gap in the current ecological literature. Here, we quantified below-ground zone of influence for *A. tridentata* in a common garden setting and experimentally tested whether plant neighbourhood size asymmetry could underlie potentially unequal partitioning of water resources. Our experiment using a deuterium tracer constitutes one of the few attempts to test ecophysiological mechanisms of water uptake among intraspecific variants in a common garden setting. We found that taxonomic variants of *A. tridentata* can have differential water uptake from shallow soil horizons, suggesting intraspecific variability in structural and functional root architecture. Contrary to our expectations, we did not find that above-ground crown volume was a strong predictor of below-ground zone of influence. Similarly, the cumulative crown volume of plant neighbours was not a strong predictor of water uptake. Instead, our results showed that the differences in water

uptake from shallow soils in *A. tridentata* were more related to the subspecies identity and ploidy level of target plants. These differences may have implications for subspecies' ecological responses to global changes, including changing precipitation patterns (Knapp et al., 2008; Schwinning & Kelly, 2013).

The observed variation in functional lateral roots and below-ground zone of influence generally agrees with the physiological constraints on water availability for *A. tridentata*, which can take up water from shallow and deep soil horizons (Germino & Reinhardt, 2014; Ryel, Leffler, Ivans, Peek, & Caldwell, 2010). Within this general pattern, the results of our study revealed that for both subspecies, tetraploids had higher water uptake from shallow soil layers than their diploid variants. These differences suggest that within subspecies, tetraploids develop more shallow roots than diploids, giving the former more access to nutrient-rich surface layers (Araya et al., 2011). Diploid variants of both subspecies showed a relatively narrow zone of influence, suggesting stronger development in the vertical dimension (i.e. deeper roots, Figure 4). Differences associated with ploidy variation were consistent for both subspecies, *A. t. tridentata* and *A. t. vaseyana*. We hypothesize that such differences may be mechanistically linked to drought tolerance and root developmental plasticity under environmental stress (Xiong et al., 2006). For example, under drought conditions, plant response may include an elongation of vertical and inhibition of lateral roots to sustain an access to deep soil moisture (De Smet, Zhang, Inzé, & Beeckman, 2006). In the context of our study, big sagebrush has dimorphic roots where root plasticity in response to environmental conditions may be key in driving adaptive variation in root architecture. Polyploidy in many plant species generally can lead to higher drought tolerance (Greer, Still, Cullinan, Brooks, & Meinzer, 2018; Ramsey, 2011), which in *A. tridentata* may allow tetraploid plants to develop and maintain more lateral roots compared to more drought-sensitive diploids.

The results for diploid *A. t. tridentata* and *A. t. vaseyana* suggest that they have a less developed lateral root system than tetraploids; however, the survival between the two diploid groups in the common garden varies (Chaney et al., 2017). Although our data indicate no differences in plant water status during the experiment, the environmental conditions at the experimental site are more favourable for *A. t. tridentata:2x* compared to *A. t. vaseyana:2x*, which overall had lower survival. A generally low performance of diploid *A. t. vaseyana*, including potential lateral root growth inhibition, could be related to repeated drought effects on the maladapted populations over the course of the experiment. This trend highlights a potential mismatch between abiotic conditions at the experimental site and the typical climatic niche characteristic of mountain big sagebrush (*A. t. vaseyana*).

The development and activity of lateral roots is highly relevant to *A. tridentata* performance under seasonal precipitation patterns in the Great Basin. We found that between plants with different ploidy levels, the largest differences in water uptake by lateral roots occurred within close proximity to a plant (<1.5 m; Figure 3). Specifically, tetraploids showed higher water uptake, suggesting more roots in the horizontal plane. Greater lateral water uptake

could enhance fall seed production when soils are dry but sporadic rain events occasionally wet surface soils (DePuit & Caldwell, 1973; Evans & Black, 1993; Goldberg & Novoplansky, 1997); however, the tetraploids tend to have less seed production than diploids in *A. tridentata*. For example, *A. t. tridentata:2x* was observed to be more consistent in seed production over the years compared to more variable *A. t. wyomingensis:4x*, which could be related to differences in lateral root architecture (B.A. Richardson, unpubl. data). Based on our results, this trait can be related to the ploidy level that persisted across subspecies, as both *A. t. vaseyana* and *A. t. tridentata* tetraploids had higher average water uptake than their diploid variants (Figures 3 and 4). Nutrient availability in shallow soils can be another consideration related to lateral root functioning and plant performance. Higher decomposition rates in shallow soils in combination with sporadic rain events during the dry season of the year could represent a mechanism of additional supply of dissolved nutrients available for the plants with more developed lateral roots (Leffler et al., 2004; Richards & Caldwell, 1987).

Deuterium tracer experiments provide an opportunity to experimentally test spatial and temporal patterns of below-ground processes, including neighbour interactions. The coexistence of genetically different populations of big sagebrush in natural settings is not uncommon and may increase in the future. Factors contributing to population mixing may include both natural (e.g. varied soil depth and type, frequent polyploidy and hybridization) as well as anthropogenic drivers, including large-scale disturbances and the following revegetation efforts (Germino, Barnard, et al., 2018). In our study, we aimed to understand how individuals of *A. tridentata* respond to a local water resource pulse in an arid environment, and how the resource was spatially distributed among neighbouring individuals. In congruence with the finding from an excavating study of *Larrea tridentata* (Brisson & Reynolds, 1994), we did not find strong evidence that the size of a target plant and neighbours influenced patterns in resource acquisition. This finding, however, could be an artefact of (a) inadequate sample size for the neighbourhood model, mainly for the subspecies that had high mortality prior to our study resulting in relatively low sample size for these subspecies (e.g. *A. t. vaseyana:2x*), or (b) common garden experimental design. For example, if plants are outplanted at the same time, we would expect that their root systems develop unobstructed until their roots interface with those of the neighbours. This pattern could potentially result in a relatively proportional occupancy of the shallow soil space within a subplot (Figure 1b), which would minimize asymmetric resource partitioning and could underlie the weak effect of above-ground neighbour size in our models.

Subspecies that invest more into their lateral roots would have higher root density within their lateral zone of influence but may not necessarily have a competitive advantage detectable from the presented time snapshot of a temporal process such as resource acquisition (Kulmatiski et al., 2017). One mechanism that can potentially explain this pattern is root suberization in response to local nutrient or water deficiency, where suberized cell walls could pose a barrier and reduce water transport despite a high root density

(Barberon et al., 2016). Additionally, isotope experiments with localized isotope injections are also sensitive to variation in root density in a given specific location. An experiment in a natural system, including larger sample size and repeated sampling following the treatment, could disentangle this uncertainty. Furthermore, a replicated experiment along a climatic gradient that captures seasonal phenology may have a stronger causal power to evaluate the effect of the abiotic regime on root formation and functioning in *A. tridentata*. On the other hand, our results indicate that the partitioning of a localized water pulse may be dependent upon the density of functionally active roots in the resource island. The results also suggest that the roots of neighbouring *A. tridentata* individuals in the common garden may have a high degree of overlap, which was previously documented for *A. t. vaseyana* in natural settings (Krannitzi & Caldwell, 1995).

5 | CONCLUSIONS

Our experiment illustrates how a deuterium tracer can be used to evaluate a species' below-ground zone of influence and local interactions such as short-term resource competition. The results complement the existing knowledge of below-ground root architecture in *A. tridentata* obtained from excavating studies by evaluating below-ground zone of influence based on the physiological activity of a target plant (Reynolds & Fraley, 1989; Sturges, 1977). Moreover, our results indicate some intraspecific differences that may be related to the tendency of the different subspecies and cytotypes to occupy sites with either deep or shallow soils or to be more adept at utilizing water from seasonal rainfall events. In the context of global changes, including shifts in precipitation patterns (Knapp et al., 2008), understanding plant root architecture and resource partitioning patterns in arid environments could improve management practices and conservation decision-making. Intraspecific variation in root functioning is an essential consideration for ecological restoration and conservation of arid scrublands.

ACKNOWLEDGEMENTS

We thank Keith Reinhardt and two anonymous reviewers for their helpful suggestions to improve the manuscript. We also thank Cristina Barber, Juan Miguel Requena-Mullor, Cara Applestein, Merry Davidson, Bill Davidson, Anand Roopsind, Chris Wilson for their helpful comments and feedback during this project; and US Geological Survey Forest and Rangeland Ecosystem Science Center for providing experimental materials, equipment and lab support. Installation and maintenance of the common garden were funded by the USDA Forest Service, Rocky Mountain Research Station, Great Basin Native Plant Project and the US Bureau of Land Management. We acknowledge Jen Forbey for her intellectual and organizational support. This publication was made possible by Boise State University, Dan Montgomery Graduate Student Award, the NSF Idaho EPSCoR Program under award number OIA-1757324, and by the US Geological Survey. T.T.C. and A.Z. acknowledge support from the National Science Foundation

under grant #1415297 in the SBE programme. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government.

AUTHORS' CONTRIBUTIONS

B.A.R. designed the common garden; M.J.G., B.E.L., T.T.C. and A.Z. conceived the ideas, designed the tracer experiment and methodology; B.E.L. and A.Z. extracted and analysed isotope samples; A.Z. and T.T.C. collected field data, performed modelling work and data analysis; A.Z. wrote the first draft of the manuscript. All authors contributed critically to data interpretation and manuscript revisions and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad Data Repository <https://doi.org/10.5061/dryad.pkOp2ngjm> (Zaiats et al., 2020). Modelling scripts: uploaded as online supporting information.

ORCID

Andrii Zaiats  <https://orcid.org/0000-0001-8978-4152>

Brynne E. Lazarus  <https://orcid.org/0000-0002-6352-486X>

Matthew J. Germino  <https://orcid.org/0000-0001-6326-7579>

Bryce A. Richardson  <https://orcid.org/0000-0001-9521-4367>

T. Trevor Caughlin  <https://orcid.org/0000-0001-6752-2055>

REFERENCES

- Adler, P. B., Ellner, S. P., & Levine, J. M. (2010). Coexistence of perennial plants: An embarrassment of niches. *Ecology Letters*, 13(8), 1019–1029. <https://doi.org/10.1111/j.1461-0248.2010.01496.x>
- Araya, Y. N., Silvertown, J., Gowing, D. J., McConway, K. J., Linder, H. P., & Midgley, G. (2011). A fundamental, eco-hydrological basis for niche segregation in plant communities. *New Phytologist*, 189(1), 253–258. <https://doi.org/10.1111/j.1469-8137.2010.03475.x>
- Barberon, M., Vermeer, J. E. M., De Bellis, D., Wang, P., Naseer, S., Andersen, T. G., ... Geldner, N. (2016). Adaptation of root function by nutrient-induced plasticity of endodermal differentiation. *Cell*, 164(3), 447–459. <https://doi.org/10.1016/j.cell.2015.12.021>
- Brisson, J., & Reynolds, J. F. (1994). The effect of neighbors on root distribution in a creosotebush (*Larrea tridentata*) population. *Ecology*, 75(6), 1693–1702. <https://doi.org/10.2307/1939629>
- Casper, B. B., Schenk, H. J., & Jackson, R. B. (2003). Defining a plant's belowground zone of influence. *Ecology*, 84(9), 2313–2321. <https://doi.org/10.1890/02-0287>
- Černá, L., & Münzbergová, Z. (2013). Comparative population dynamics of two closely related species differing in ploidy level. *PLoS ONE*, 8(10), e75563. <https://doi.org/10.1371/journal.pone.0075563>
- Chaney, L., Richardson, B. A., & Germino, M. J. (2017). Climate drives adaptive genetic responses associated with survival in big sagebrush (*Artemisia tridentata*). *Evolutionary Applications*, 10(4), 313–322. <https://doi.org/10.1111/eva.12440>
- Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., ... Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405(6783), 234–242. <https://doi.org/10.1038/35012241>
- Chesson, P. (2018). Updates on mechanisms of maintenance of species diversity. *Journal of Ecology*, 106(5), 1773–1794. <https://doi.org/10.1111/1365-2745.13035>
- Chesson, P., Gebauer, R. L. E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M. S. K., ... Weltzin, J. F. (2004). Resource pulses, species

- interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141(2), 236–253. <https://doi.org/10.1007/s00442-004-1551-1>
- Cleary, M. B., Pendall, E., & Ewers, B. E. (2008). Testing sagebrush allometric relationships across three fire chronosequences in Wyoming, USA. *Journal of Arid Environments*, 72(4), 285–301. <https://doi.org/10.1016/j.jaridenv.2007.07.013>
- Cui, J., Tian, L., Gerlein-Safdi, C., & Qu, D. (2017). The influence of memory, sample size effects, and filter paper material on online laser-based plant and soil water isotope measurements. *Rapid Communications in Mass Spectrometry*, 31(6), 509–522. <https://doi.org/10.1002/rcm.7824>
- De Smet, I., Zhang, H., Inzé, D., & Beeckman, T. (2006). A novel role for abscisic acid emerges from underground. *Trends in Plant Science*, 11(9), 434–439. <https://doi.org/10.1016/j.tplants.2006.07.003>
- DePuit, E. J., & Caldwell, M. M. (1973). Seasonal pattern of net photosynthesis of *Artemisia tridentata*. *American Journal of Botany*, 60(5), 426–435. <https://doi.org/10.2307/2441499>
- DiCristina, K., & Germino, M. (2006). Correlation of neighborhood relationships, carbon assimilation, and water status of sagebrush seedlings establishing after fire. *Western North American Naturalist*, 66(4), 441–449. [https://doi.org/10.3398/1527-0904\(2006\)66\[441:CONRCA\]2.0.CO;2](https://doi.org/10.3398/1527-0904(2006)66[441:CONRCA]2.0.CO;2)
- Donovan, L. A., & Ehleringer, J. R. (1994). Water stress and use of summer precipitation in a Great Basin shrub community. *Functional Ecology*, 8(3), 289–297. <https://doi.org/10.2307/2389821>
- Evans, R. D., & Black, R. A. (1993). Growth, photosynthesis, and resource investment for vegetative and reproductive modules of *Artemisia tridentata*. *Ecology*, 74(5), 1516–1528. <https://doi.org/10.2307/1940079>
- Evans, R. D., Black, R. A., & Link, S. O. (1991). Reproductive growth during drought in *Artemisia tridentata* Nutt. *Functional Ecology*, 5(5), 676–683. <https://doi.org/10.2307/2389488>
- Fowler, N. (1986). The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, 17(1), 89–110. <https://doi.org/10.1146/annurev.es.17.110186.000513>
- Gelman, A., & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. Cambridge, UK: Cambridge University Press.
- Germino, M. J., Barnard, D. M., Davidson, B. E., Arkle, R. S., Pilliod, D. S., Fisk, M. R., & Applestein, C. (2018). Thresholds and hotspots for shrub restoration following a heterogeneous megafire. *Landscape Ecology*, 33(7), 1177–1194. <https://doi.org/10.1007/s10980-018-0662-8>
- Germino, M. J., Chambers, J. C., & Brown, C. S. (2016). *Exotic brome-grasses in arid and semiarid ecosystems of the Western US: Causes, consequences, and management implications*. New York, NY: Springer.
- Germino, M. J., Moser, A. M., & Sands, A. R. (2018). Adaptive variation, including local adaptation, requires decades to become evident in common gardens. *Ecological Applications*, 29(2). <https://doi.org/10.1002/eap.1842>
- Germino, M. J., & Reinhardt, K. (2014). Desert shrub responses to experimental modification of precipitation seasonality and soil depth: Relationship to the two-layer hypothesis and ecohydrological niche. *Journal of Ecology*, 102(4), 989–997. <https://doi.org/10.1111/1365-2745.12266>
- Gifford, G. F. (1968). Apparent Sap Velocities in Big Sagebrush as related to nearby environment. *Journal of Range Management*, 21(4), 266–268. <https://doi.org/10.2307/3895830>
- Goldberg, D. E. (1990). 3-Components of resource competition in plant communities. In J. B. Grace & D. Tilman (Eds.), *Perspectives on plant competition* (pp. 27–49). <https://doi.org/10.1016/B978-0-12-294452-9.50007-2>
- Goldberg, D. E., & Novoplansky, A. (1997). On the relative importance of competition in unproductive environments. *Journal of Ecology*, 85(4), 409–418. <https://doi.org/10.2307/2960565>
- Greer, B. T., Still, C., Cullinan, G. L., Brooks, J. R., & Meinzer, F. C. (2018). Polyploidy influences plant–environment interactions in quaking aspen (*Populus tremuloides* Michx.). *Tree Physiology*, 38(4), 630–640. <https://doi.org/10.1093/treephys/tpx120>
- Grossiord, C., Gessler, A., Granier, A., Berger, S., Bréchet, C., Hentschel, R., ... Bonal, D. (2014). Impact of interspecific interactions on the soil water uptake depth in a young temperate mixed species plantation. *Journal of Hydrology*, 519, 3511–3519. <https://doi.org/10.1016/j.jhydrol.2014.11.011>
- Hart, S. P., Schreiber, S. J., & Levine, J. M. (2016). How variation between individuals affects species coexistence. *Ecology Letters*, 19(8), 825–838. <https://doi.org/10.1111/ele.12618>
- Havens, K., Vitt, P., Still, S., Kramer, A. T., Fant, J. B., & Schatz, K. (2015). Seed sourcing for restoration in an era of climate change. *Natural Areas Journal*, 35(1), 122–133. <https://doi.org/10.3375/043.035.0116>
- Knapp, A. K., Beier, C., Briske, D. D., Classen, A. T., Luo, Y., Reichstein, M., ... Weng, E. (2008). Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience*, 58(9), 811–821. <https://doi.org/10.1641/B580908>
- Kolb, K. J., & Sperry, J. S. (1999). Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). *Ecology*, 80(7), 2373–2384. <https://doi.org/10.2307/176917>
- Krannitzi, P. G., & Caldwell, M. M. (1995). Root growth responses of three Great Basin perennials to intra and interspecific contact with other roots. *Flora*, 190(2), 161–167. [https://doi.org/10.1016/S0367-2530\(17\)30647-3](https://doi.org/10.1016/S0367-2530(17)30647-3)
- Kulmatiski, A., Adler, P. B., Stark, J. M., & Tredennick, A. T. (2017). Water and nitrogen uptake are better associated with resource availability than root biomass. *Ecosphere*, 8(3), e01738. <https://doi.org/10.1002/ecs2.1738>
- Kulmatiski, A., & Beard, K. (2013). Root niche partitioning among grasses, saplings, and trees measured using a tracer technique. *Oecologia*, 171(1), 25–37. <https://doi.org/10.1007/s00442-012-2390-0>
- Lazarus, B. E., & Germino, M. J. (2017). Methodological considerations regarding online extraction of water from soils for stable isotope determination. *Rapid Communications in Mass Spectrometry*, 31(19), 1677–1680. <https://doi.org/10.1002/rcm.7948>
- Lazarus, B. E., Germino, M. J., & Vander Veen, J. L. (2016). Online induction heating for determination of isotope composition of woody stem water with laser spectrometry: A methods assessment. *Isotopes in Environmental and Health Studies*, 52(3), 309–325. <https://doi.org/10.1080/10256016.2016.1141205>
- Leffler, A. J., Ivans, C. Y., Ryel, R. J., & Caldwell, M. M. (2004). Gas exchange and growth responses of the desert shrubs *Artemisia tridentata* and *Chrysothamnus nauseosus* to shallow-vs. deep-soil water in a glasshouse experiment. *Environmental and Experimental Botany*, 51(1), 9–19. [https://doi.org/10.1016/S0098-8472\(03\)00041-8](https://doi.org/10.1016/S0098-8472(03)00041-8)
- Leger, E. A. (2008). The adaptive value of remnant native plants in invaded communities: An example from the Great Basin. *Ecological Applications*, 18(5), 1226–1235. <https://doi.org/10.1890/07-1598.1>
- Li, W.-L., Berlyn, G. P., & Ashton, P. M. S. (1996). Polyploids and their structural and physiological characteristics relative to water deficit in *Betula papyrifera* (Betulaceae). *American Journal of Botany*, 83(1), 15–20. <https://doi.org/10.1002/j.1537-2197.1996.tb13869.x>
- Loik, M. E. (2007). Sensitivity of water relations and photosynthesis to summer precipitation pulses for *Artemisia tridentata* and *Purshia tridentata*. *Plant Ecology*, 191(1), 95–108. <https://doi.org/10.1007/s11258-006-9217-1>
- Loik, M. E., Breshears, D. D., Lauenroth, W. K., & Belnap, J. (2004). A multi-scale perspective of water pulses in dryland ecosystems: Climatology and ecohydrology of the western USA. *Oecologia*, 141(2), 269–281. <https://doi.org/10.1007/s00442-004-1570-y>
- Maherali, H., Walden, A. E., & Husband, B. C. (2009). Genome duplication and the evolution of physiological responses to water

- stress. *New Phytologist*, 184(3), 721–731. <https://doi.org/10.1111/j.1469-8137.2009.02997.x>
- Miriti, M. N., Wright, S. J., & Howe, H. F. (2001). The effects of neighbors on the demography of a dominant desert shrub (*Ambrosia dumosa*). *Ecological Monographs*, 71(4), 491–509. [https://doi.org/10.1890/0012-9615\(2001\)071\[0491:TEONOT\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2001)071[0491:TEONOT]2.0.CO;2)
- Monnahan, C. C., Thorson, J. T., & Branch, T. A. (2017). Faster estimation of Bayesian models in ecology using Hamiltonian Monte Carlo. *Methods in Ecology and Evolution*, 8(3), 339–348. <https://doi.org/10.1111/2041-210X.12681>
- Münzbergová, Z. (2007). No effect of ploidy level in plant response to competition in a common garden experiment. *Biological Journal of the Linnean Society*, 92(2), 211–219. <https://doi.org/10.1111/j.1095-8312.2007.00820.x>
- O'Keefe, K., Nippert, J. B., & McCulloh, K. A. (2019). Plant water uptake along a diversity gradient provides evidence for complementarity in hydrological niches. *Oikos*, 128(12), 1748–1760. <https://doi.org/10.1111/oik.06529>
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11(5), 1633–1644. <https://doi.org/10.5194/hess-11-1633-2007>
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ramsey, J. (2011). Polyploidy and ecological adaptation in wild yarrow. *Proceedings of the National Academy of Sciences of the United States of America*, 108(17), 7096–7101. <https://doi.org/10.1073/pnas.1016631108>
- Requena-Mullor, J. M., Maguire, K. C., Shinneman, D. J., & Caughlin, T. T. (2019). Integrating anthropogenic factors into regional-scale species distribution models – A novel application in the imperiled sagebrush biome. *Global Change Biology*, 25(11), 3844–3858. <https://doi.org/10.1111/gcb.14728>
- Reynolds, T. D., & Fraley, L. (1989). Root profiles of some native and exotic plant species in southeastern Idaho. *Environmental and Experimental Botany*, 29(2), 241–248. [https://doi.org/10.1016/0098-8472\(89\)90056-7](https://doi.org/10.1016/0098-8472(89)90056-7)
- Richards, J. H., & Caldwell, M. M. (1987). Hydraulic lift: Substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia*, 73(4), 486–489. <https://doi.org/10.1007/BF00379405>
- Richardson, B. A., & Chaney, L. (2018). Climate-based seed transfer of a widespread shrub: Population shifts, restoration strategies, and the trailing edge. *Ecological Applications*, 28(8), 2165–2174. <https://doi.org/10.1002/eap.1804>
- Richardson, B. A., Page, J. T., Bajgain, P., Sanderson, S. C., & Udall, J. A. (2012). Deep sequencing of amplicons reveals widespread intraspecific hybridization and multiple origins of polyploidy in big sagebrush (*Artemisia tridentata*; Asteraceae). *American Journal of Botany*, 99(12), 1962–1975. <https://doi.org/10.3732/ajb.1200373>
- Ryel, R. J., Leffler, A. J., Ivans, C., Peek, M. S., & Caldwell, M. M. (2010). Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone Journal*, 9(3), 548. <https://doi.org/10.2136/vzj2010.0022>
- Schenk, H. J., & Mahall, B. E. (2002). Positive and negative plant interactions contribute to a north-south-patterned association between two desert shrub species. *Oecologia*, 132(3), 402–410. <https://doi.org/10.1007/s00442-002-0990-9>
- Schwinning, S., & Kelly, C. K. (2013). Plant competition, temporal niches and implications for productivity and adaptability to climate change in water-limited environments. *Functional Ecology*, 27(4), 886–897. <https://doi.org/10.1111/1365-2435.12115>
- Schwinning, S., & Weiner, J. (1998). Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, 113(4), 447–455. <https://doi.org/10.1007/s004420050397>
- Shriver, R. K. (2017). Rainfall variability and fine-scale life history tradeoffs help drive niche partitioning in a desert annual plant community. *Ecology Letters*, 20(10), 1231–1241. <https://doi.org/10.1111/ele.12818>
- Shriver, R. K., Andrews, C. M., Arkle, R. S., Barnard, D. M., Duniway, M. C., Germino, M. J., ... Bradford, J. B. (2019). Transient population dynamics impede restoration and may promote ecosystem transformation after disturbance. *Ecology Letters*, 22(9), 1357–1366. <https://doi.org/10.1111/ele.13291>
- Shultz, L. M. (2009). Monograph of *Artemisia subgenus Tridentatae* (Asteraceae-Anthemideae). *Systematic Botany Monographs*, 89, 1–131.
- Stan Development Team. (2018). *RStan: The R Interface to Stan*. R package version 2.17.3.
- Sturges, D. L. (1977). Soil water withdrawal and root characteristics of big sagebrush. *American Midland Naturalist*, 98(2), 257. <https://doi.org/10.2307/2424978>
- Uriarte, M., & Menge, D. (2018). Variation between individuals fosters regional species coexistence. *Ecology Letters*, 21(10), 1496–1504. <https://doi.org/10.1111/ele.13130>
- Van Laere, K., França, S. C., Vansteenkiste, H., Van Huylenbroeck, J., Steppe, K., & Van Labeke, M.-C. (2011). Influence of ploidy level on morphology, growth and drought susceptibility in *Spathiphyllum wallisii*. *Acta Physiologiae Plantarum*, 33(4), 1149–1156. <https://doi.org/10.1007/s11738-010-0643-2>
- Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27(5), 1413–1432. <https://doi.org/10.1007/s11222-016-9696-4>
- Weigelt, A., & Jolliffe, P. (2003). Indices of plant competition. *Journal of Ecology*, 91(5), 707–720. <https://doi.org/10.1046/j.1365-2745.2003.00805.x>
- Xiong, L., Wang, R.-G., Mao, G., & Koczan, J. M. (2006). Identification of drought tolerance determinants by genetic analysis of root response to drought stress and abscisic acid. *Plant Physiology*, 142(3), 1065–1074. <https://doi.org/10.1104/pp.106.084632>
- Zaiats, A., Lazarus, B. E., Germino, M. J., Serpe, M. D., Richardson, B. A., Buerki, S., & Caughlin, T. T. (2020). Data from: Intraspecific variation in surface water uptake in a perennial desert shrub. *Dryad Data Repository*, <https://doi.org/10.5061/dryad.pk0p2ngjm>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Zaiats A, Lazarus BE, Germino MJ, et al. Intraspecific variation in surface water uptake in a perennial desert shrub. *Funct Ecol*. 2020;34:1170–1179. <https://doi.org/10.1111/1365-2435.13546>