Preestablished Plant Influences on Antelope Bitterbrush (*Purshia tridentata* Pursh) Seedling Recruitment and Growth: Analysis of Species and Positional Effects

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Preestablished Plant Influences on Antelope Bitterbrush (*Purshia tridentata* Pursh) Seedling Recruitment and Growth: Analysis of Species and Positional Effects

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ABSTRACT: We evaluated the influence of preestablished plant species distance, direction, and identity on antelope bitterbrush (*Purshia tridentata* Pursh) seedling establishment and biomass production. Antelope bitterbrush seeds were planted 10- and 20-cm away from the base of three preestablished plant species. We monitored seedling establishment and growth during and after two growing seasons. Sowing antelope bitterbrush seeds 20-cm away from preestablished plant bases yielded 1.59 times greater seedling establishment than seeds sown 10-cm away, suggesting that established plants interfere with bitterbrush recruitment. Antelope bitterbrush seedling survival after 2 y of growth was greater than 96% for all treatments, suggesting that early growth phases were the primary bottlenecks to establishment. Antelope bitterbrush forage production decreased with proximity to preestablished plants. After 2 y of growth, antelope bitterbrush biomass was almost 3 times greater for plants grown without preestablished plant neighbors or with a preestablished grass (*Elymus elymoides* Raf.) than with preestablished forb species (*Dalea candida* Michx. ex Willd. or *Gaillardia aristata* Pursh). Inoculating preestablished plants with soil from native sites or arbuscular mycorrhizal fungi did not influence antelope bitterbrush establishment or growth. We suggest that plant trait complementarity and spatial relationships can be used to design seeding strategies to increase antelope bitterbrush establishment and forage production.

Index terms: competition, facilitation, forage, mule deer, soil inoculation, spatial relationships

INTRODUCTION

Antelope bitterbrush (*Purshia tridentata* Pursh) is a shrub species that occurs in the Intermountain West from British Columbia, Canada, to northern Mexico (Nord 1965; Giunta et al. 1978; Clements and Young 2002). It is one of the most important browse species for mule deer (*Odocoileus hemionus* Raf.) and other large ungulates in the western United States (Clements and Young 1997; Young and Clements 2002; Pierce et al. 2004). Many antelope bitterbrush stands are in decline (Young and Clements 2002). Altered fire regimes, overgrazing, invasive plant species, and competition from herbaceous perennial species are considered the primary causes of antelope bitterbrush stand decline (Guenther and Wambolt 1993; Young and Clements 2002). Concerns about wildlife habitat loss have stimulated interest in establishing antelope bitterbrush through seed or seedlings (Clements and Young 2002). There are several barriers to establishing shrub species in arid environments to meet restoration goals. Specific knowledge about the role of plant–plant and plant–microbe interactions could lead to improved techniques and outcomes for arid shrub species establishment.

Antelope bitterbrush seedlings and adults are sensitive to competition, especially competition from cheatgrass (*Bromus tectorum* L.) and other winter annual grasses (Holmgren 1956). Competition impedes seedling establishment (Holmgren 1956) and decreases forage production for wildlife (Sanderson et al. 1963). The perceived need to limit competition during antelope bitterbrush establishment presents a quandary for restoration practitioners and wildlife habitat managers. Establishment of competitive plant cover is the only long-term solution for invasive annual grass control (Booth et al. 2003; Chambers et al. 2007), but antelope bitterbrush alone is a poor competitor with winter annuals (Young and Clements 2002). Planting antelope bitterbrush into the herbaceous perennial communities required to fill niche space and suppress cheatgrass (McGlone et al. 2011) decreases antelope bitterbrush establishment and forage production (Sanderson et al. 1963). Seeding antelope bitterbrush without competition leaves sites susceptible to weed invasion (Clements and Young 2002).

Knowledge of interspecific plant interactions could provide insights into ways to increase shrub establishment and growth. Plant neighbor interactions range from facilitative to competitive and vary with growth stage (reviewed by Brooker et al. 2008). Inhibition, in its many forms, is the most studied plant interaction, but facilitation can also be important. Examples of facilitation include microclimate modification, changes in soil chemical and physical structure, alteration of microbial symbiont and pathogen communities, and influences on pollinators, seed dispersal agents, and plant defense guilds (Callaway 1995). Reports of facilitation are most

common in arid environments (Brooker et al. 2008). In the sagebrush steppe, for example, Reisner (2010) reported that Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*) facilitates bunchgrass establishment through microclimate modification. There is also precedent in the literature for interspecific facilitation of antelope bitterbrush. Hall et al. (1999) found that antelope bitterbrush seedling emergence and survival was greater in plots containing bluebunch wheatgrass (*Pseudoroegneria spicata* Pursh) than in bare-soil plots or plots containing crested wheatgrass (*Agropyron cristatum* L.) or cheatgrass. This study suggests that facilitative plant interactions could increase antelope bitterbrush establishment.

Plant competitive relationships are influenced by interactions with soil microbial communities (Klironomos 2002). Plants influence the growth of neighboring plants by changing soil communities. Inoculation of plants with specific arbuscular mycorrhizal fungi (AMF) species and whole soil inoculum collected from diverse plant communities could improve the establishment of species in degraded soils (Clements and Young 2000b; Verbruggen et al. 2013). The benefit of inoculum may spread to neighboring plants in degraded soils, as demonstrated by Middleton and Bever (2012).

We examined the influence of three different preestablished native plant species on the establishment and vigor of antelope bitterbrush. We evaluated the influence of soil and AMF inoculants on antelope bitterbrush establishment and growth, and the importance of seed positional effects—the distance and direction of antelope bitterbrush in relation to preestablished plants. Our goal was to evaluate plant interactions to improve antelope bitterbrush establishment techniques. We hypothesized that (1) the identity of preestablished plant species, (2) the position of antelope bitterbrush seeds relative to established plants, and (3) the introduction of AMF and whole soil inoculum from native plant communities would influence antelope bitterbrush establishment and forage production.

METHODS

Study Site

This study took place on a private ranch in the Bitterroot Valley of western Montana, USA (46°40 42.11 N, 114°02 02.50 W). Historical climate data for the area (PRISM Climate Group 2012) recorded an average annual precipitation of approximately 35 cm and a mean annual temperature of 7 °C. Weather stations near our study site (https://www.mpgranch.com) recorded 18.7-cm precipitation in 2012 and 20.3-cm total precipitation in 2013. Annual temperature averaged 8.5 °C in 2012 and 8.2 °C in 2013.

Experimental Design

We used four different plant species in this experiment: an early season grass (squirreltail; *Elymus elymoides* Raf.), a perennial legume (white prairie clover; *Dalea candida* Michx. ex Willd), a perennial forb in the Aster family (blanketflower; *Gaillardia aristata* Pursh), and antelope bitterbrush. The forb and grass species were selected because of broad differences in functional traits. Squirreltail is one of the first species to become active after snowmelt in the spring (USDA NRCS 2016). It remains dormant much of the summer and becomes active again in the fall when moisture is sufficient. White prairie clover becomes active mid-spring, and flowers from mid- to late summer (USDA NRCS 2016). It grows 0.6 to 0.9-m tall and has fine-textured leaves. Blanketflower becomes active mid-spring and blooms late into the summer (USDA NRCS 2016). It has coarse leaves and grows to a height of 0.7 m. All seeds were obtained from a commercial source (Granite Seed, Lehi, Utah).

We started 200 individuals of each forb and grass species in a greenhouse. We filled 49- cm^3 pots (2.5 × 12 cm; Cone-tainers, Stuewe and Sons, Tangent, Oregon) with surface soils (0–8 cm) collected from the study site (see below) or from under each of two nearby undisturbed native plant community sites (described in Lekberg et al. 2013). Although we did not attempt to collect soils directly associated with an-

telope bitterbrush roots, both native plant community sites hosted mature antelope bitterbrush plants. Each soil had four AMF treatments: *Claroideoglomus etunicatum* culture MT108-8, *Claroideoglomus etunicatum* culture MT109-7, steam-treated inoculum as a no-AMF control, and no inoculation. Both inoculants were originally sourced from Montana grasslands and cultured by the International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi (INVAM; West Virginia University, Morgantown). Inoculants were added at the time of planting by placing approximately 1-cm^3 inoculum in a 1.5-cm depression, adding three seeds, then covering with field soil. Plants were in the greenhouse for 3 mo before transplanting them to our field site.

Our experimental site is a former agricultural field. The site was fallow for 2 y prior to our study. Soil on the site has sandy loam texture with a pH of 6.3. Weeds were controlled with a systemic herbicide (glyphosate) before planting and by pulling thereafter. To prevent damage to experimental plants by large animals, we installed a 2.5-m fence around the field. To prevent damage from small animals, we installed a 0.75-m fine mesh (0.635 cm) wire fence inside the large animal fence. We capped the small animal fence with metal flashing to prevent animals from climbing over the top. Small animals inside the exclosure were trapped before planting. To prevent small animal reestablishment, animal traps remained in the exclosure throughout the experiment.

We outplanted forbs and grasses in May 2011. Plant locations were randomized in 19 rows. We used a 1.25-m minimum separation distance between plants to decrease the potential for nontarget plant interactions. Plants were watered during the first growing season to facilitate establishment.

In fall 2011, we used a spatially stratified design to sow 48 antelope bitterbrush seeds around each of 400 established plants and in 112 control sites with no preestablished plant (Figure 1). We seeded on all sides of established plants to evaluate the importance of preestablished plant
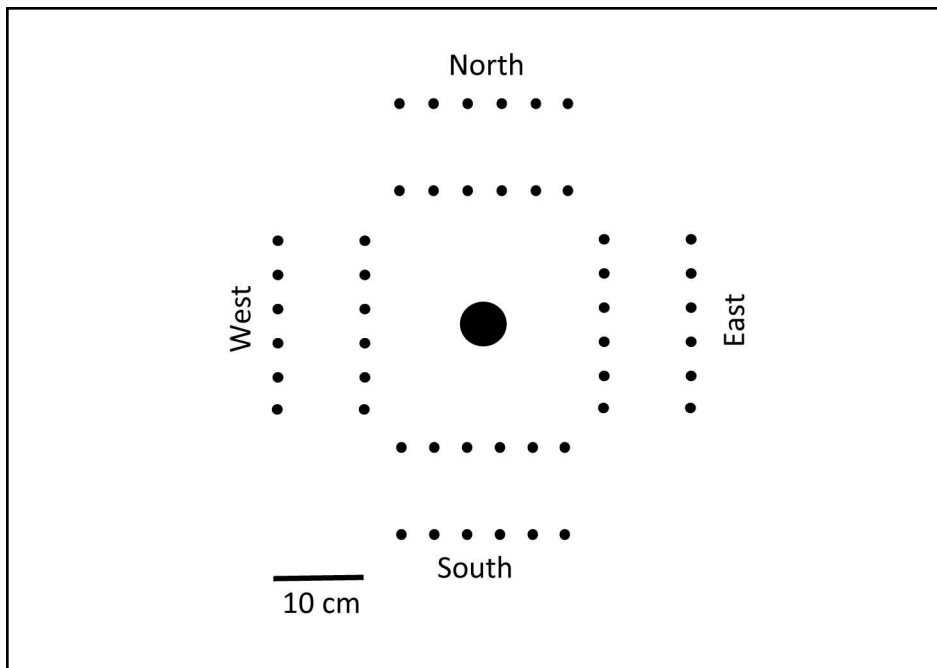
Figure 1. Plot design. The preestablished plant is indicated by the filled circle in the center. Antelope bitterbrush seed locations are depicted by small circles. The inner seed rows are 10 cm, and outer rows 20 cm, from the center of the preestablished plant.

species–facilitated differences in sunlight and wind interception on antelope bitterbrush recruitment. After plant mortalities, preestablished plant numbers included 130 squirreltail, 95 white prairie clover, and 175 blanketflower individuals. A single seed was placed in a 1.25-cm depression at each point (Figure 1) and covered with field soil.

We measured preestablished plant height and width each summer after maximum yearly growth. Antelope bitterbrush height was measured in spring, summer, and fall beginning in the summer of 2012 and ending in the spring of 2014. After observing army cutworm (*Euxoa auxillaris* Grote) damage to preestablished forb species in the spring of 2014, we harvested, air-dried, and weighed antelope bitterbrush aboveground biomass.

Statistical Analyses

Binary logistic regression analyses were used to examine the influence of established plant identity, direction from established plant, and distance from established plant on antelope bitterbrush establishment in

summer 2012. Seedling distance and direction from each plant served as predictor variables. For this analysis, we consider antelope bitterbrush plants that were visible and alive in summer 2012 to be established.

Two-way general linear models were used to evaluate the influence of antelope bitterbrush seed placement direction and distance from each preestablished plant species on antelope bitterbrush biomass. The average biomass of antelope bitterbrush plants growing in each distance and direction on each plot served as the response variable. Direction and distance from preestablished plants served as explanatory variables.

To evaluate the importance of antelope bitterbrush plant distance from all preestablished plant species, we averaged antelope bitterbrush biomass data for plants growing at 10 cm and at 20 cm away from each plot center. We analyzed the data using a two-way general linear model with antelope bitterbrush biomass as the response variable and distance and preestablished plant identity as explanatory variables.

We evaluated preestablished plant influenc-

es on antelope bitterbrush height at each measurement time using one-way general linear models. Antelope bitterbrush height on each plot was averaged before analysis. Preestablished plant identity was used as the explanatory variable.

One-way general linear models were used to evaluate the influence of established plant identity on antelope bitterbrush growth seasonality. The percent of total antelope bitterbrush growth on each sample date was used as the response variable and preestablished plant identity as the explanatory variable.

Differences in preestablished plant height and width in 2012 and 2013 were evaluated using one-way general linear models. Preestablished plant species identity was used as the predictor variable.

Antelope bitterbrush biomass data was log-transformed before analysis to meet assumptions of normality. General linear models were calculated using the General Linear Models module of SPSS (ver. 20). Tukey's HSD post hoc analyses were conducted to evaluate pairwise differences. Binary logistic regressions were calculated using the Generalized Linear Models module of SPSS (ver. 20).

RESULTS

Antelope Bitterbrush Establishment and Survivorship

Sown antelope bitterbrush seeding establishment measured in summer 2012 ranged from 2.70% for seeds planted around prairie clover, to 3.20% for seeds planted around blanketflower (Table 1). The average seedling establishment was 2.94% across all plots. Differences between preestablished plant treatments were not significant ($\chi^2 = 5.99$; df = 3; $P = 0.112$).

Antelope bitterbrush growing without preestablished plants had the lowest plant mortality (0.63%) in 2014 (Table 1). The highest antelope bitterbrush mortality (5.60%) occurred in plants grown with blanketflower (Table 1). Antelope bitterbrush mortality between summer 2012

Table 1. Bitterbrush seeds planted, seedling emergence in summer 2012, and plants surviving at the end of the experiment in 2014.

Established plant species	Antelope bitterbrush				
	Seeds planted	Emerged 2012	Percent emerged	Survived 2014	Percent mortality
No plant	5376	159	2.96%	158	0.63%
Squirreltail	6240	182	2.92%	172	5.49%
Prairie clover	4560	123	2.70%	117	4.87%
Blanketflower	8400	268	3.20%	253	5.60%

and spring 2014 averaged 4.15% for all treatments.

Antelope bitterbrush establishment was greater for seeds sown 20 cm from preestablished plants than 10 cm (Figure 2 and Table 2). Direction from preestablished plant and direction*distance interactions were not significant for any treatment (Table 2). Seed location had no influence on antelope bitterbrush establishment in the no–established plant plots (Figure 2 and Table 2).

Antelope Bitterbrush Growth

Soil origin and AMF inoculation did not significantly influence antelope bitterbrush biomass ($F = 1.17_{(5, 2252)}$; $P = 0.311$; data not shown). Established plant species identity influenced antelope bitterbrush total biomass. Antelope bitterbrush plants grown with prairie clover or blanketflower were smaller than plants grown with squirreltail or without a preestablished plant (Figure 3). Antelope bitterbrush biomass was similar for plants grown with squirreltail or without a preestablished plant (Figure 3).

Antelope bitterbrush grown 10 cm from preestablished plant bases had lower final biomass than antelope bitterbrush grown 20 cm away (Figure 3 and Table 3). Direction from preestablished plants did not significantly influence antelope bitterbrush biomass (Table 3). Interactions between distance and direction were not significant for any treatment (Table 3).

Antelope bitterbrush height was greater for the no–established plant and preestablished squirreltail treatments than for plants grown with preestablished white prairie clover or blanketflower at all measurement times after summer 2012 (Figure 4). Preestablished plant identity changed the timing of antelope bitterbrush height gains (Figure 5). In the fall of 2012 and 2013, percent of total antelope bitterbrush height gains were greater for no–preestablished plant and squirreltail than when grown with either forb species. In contrast, antelope bitterbrush plants grown with either forb species exhibited greater percent of total height gain in summer 2012 and spring 2013 (Figure 5).

Preestablished Plant Growth

Blanketflower height was greater than white prairie clover in 2012 but not in 2013 (Figure 6a). Height of both forbs was greater than squirreltail in 2012 and 2013. Blanketflower width was greater than white prairie clover and squirreltail in 2012 (Figure 6b). In 2013, white prairie clover width was greater than blanketflower and squirreltail, while blanketflower width was greater than squirreltail in 2013.
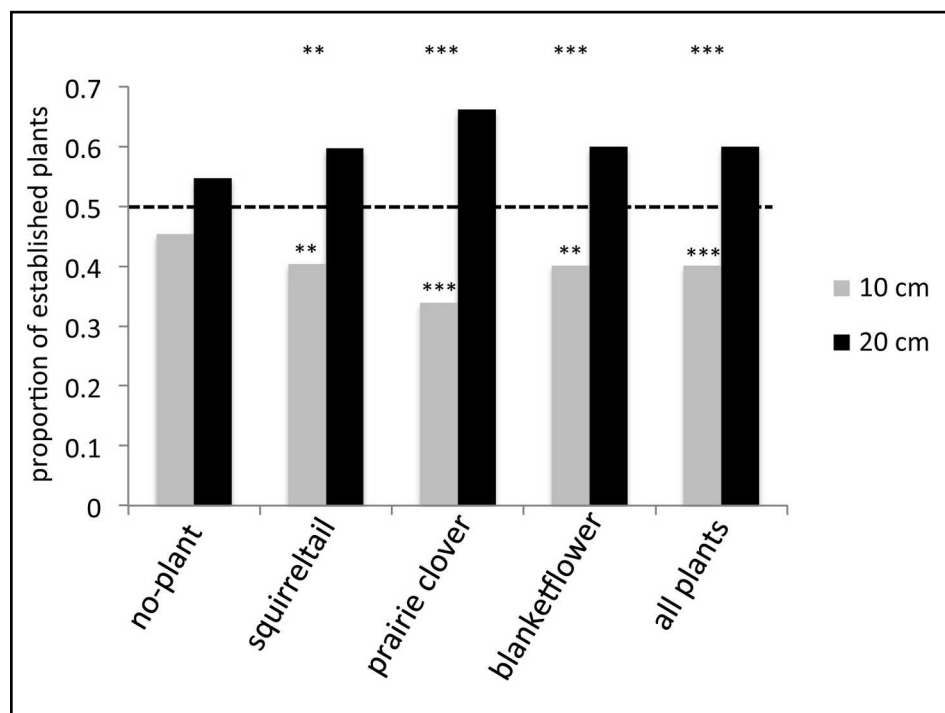

Figure 2. The relative proportion of bitterbrush plants within plant treatments that established at 10- and 20-cm distances from plot centers. The dashed line indicates equal establishment. The symbols at the top indicate significant differences within treatment as determined by binary logistic regression. Symbols directly above each bar indicate significant differences in establishment compared with the no–established plant treatment; ** and * indicate significance at $P < 0.01$ and $P < 0.001$, respectively.**

Table 2. Relationships between seed position and bitterbrush plant establishment. Significant relationships are depicted in bold.

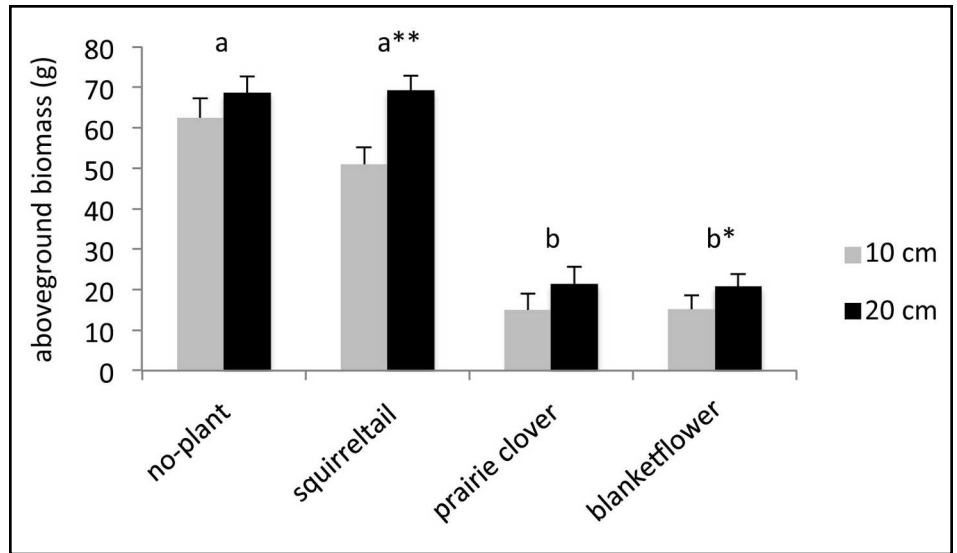|	No plant		Squirreltail		Prairie clover		Blanketflower		All plants	
	χ^2 (df)	P	χ^2 (df)	P	χ^2 (df)	P	χ^2 (df)	P	χ^2 (df)	P
Direction	2.01 (3, 532)	0.58	2.50 (3, 741)	0.48	0.68 (3, 504)	0.89	2.10 (3, 999)	0.55	1.79 (3, 2253)	0.62
Distance	2.27 (1, 535)	0.13	8.70 (1, 744)	**<0.01**	14.41 (1, 507)	**<0.01**	13.38 (1, 1002)	**<0.01**	34.05 (1, 2256)	**<0.01**
Direction * distance	1.65 (3, 529)	0.65	0.26 (3, 738)	0.97	5.70 (3, 501)	0.13	4.01 (3, 996)	0.26	1.25 (3, 2250)	0.74

Figure 3. Aboveground biomass of bitterbrush plants that established 10 and 20 cm from plot centers. Different letters above bars for preestablished plant treatments indicate significant differences ($P <$ 0.05) in bitterbrush biomass between preestablished plant treatments as determined using a two-way general linear model; * and ** indicate significant ($P < 0.05$ and $P < 0.01$, respectively) within-treatment differences in bitterbrush biomass for plants growing 10 and 20 cm away from plot centers. Error bars indicate standard error.

DISCUSSION

Wildlife habitat managers seed antelope bitterbrush to provide forage and cover for large and small animals, but antelope bitterbrush survival and forage production after seeding is often low (Clements and Young 2000a). Satisfactory establishment requires that the competitive environment in seeded areas is conducive to seedling establishment and growth.

Our results indicate that the proximity of antelope bitterbrush seeds to preestablished plants influences antelope bitterbrush establishment. Antelope bitterbrush seeds were 1.59 times more likely to establish if located 20 cm from the base of an established plant (352 seedlings established) than if located 10 cm away (221 seedlings established). This result suggests that competitive effects at 10-cm distance outweighed potential modification of seedbed conditions by established plants that may have facilitated antelope bitterbrush emergence. Antelope bitterbrush establishment was similar for seeds sown 20 cm from established plants and for seeds sown in the no–established plant control, suggesting that seeds can be positioned around established plants in ways that max-

imize antelope bitterbrush establishment. Seeding antelope bitterbrush into plant interspaces or artificially opening niches in dense herbaceous plant communities, for example, may increase antelope bitterbrush establishment.

Similar to herbaceous arid grassland species (James et al. 2011), we found that early growth stages were the primary bottleneck for establishment. Competition did not strongly influence antelope bitterbrush survival after initial spring establishment and antelope bitterbrush survival rates were high regardless of established plant species.

In addition to effects on antelope bitterbrush establishment, distance from preestablished plants influenced antelope bitterbrush forage production. Antelope bitterbrush biomass production decreased with proximity to preestablished plants, suggesting that alternating seed drill rows with herbaceous species to increase the distance between seeded species, as recommended by Monsen and Shaw (1983), may be a way to increase antelope bitterbrush forage production. However, intraspecific competition can also be important. Clements and Young (2002) found that dense antelope bitterbrush emergence

Table 3. Relationships between seed position and bitterbrush biomass. Significant relationships are depicted in bold.

	No plant		Squirreltail		Prairie clover		Blanketflower		All plants	
	F (df)	P	F (df)	P	F (df)	P	F (df)	P	F (df)	P
Direction	0.50 (3, 78)	0.9	1.36 (3, 103)	0.26	0.48 (3, 69)	0.7	0.63 (3, 158)	0.59	1.42 (3, 395)	0.24
Distance	1.44 (1, 78)	0.24	6.72 (1, 103)	**0.01**	2.41 (1, 69)	0.12	5.42 (1, 158)	**0.02**	17.61 (3, 395)	**<0.01**
Direction * distance	0.54 (3, 78)	0.43	0.13 (3, 103)	0.94	0.11 (3, 69)	0.95	0.94 (3, 158)	0.42	0.14 (3, 395)	0.94

and establishment resulted in high intra-specific competition that affected growth and flowering.

Antelope bitterbrush size differences between preestablished plant species treatments were apparent early in the experiment. Antelope bitterbrush neighboring the large forbs, white prairie clover or blanketflower, had only one-third the total growth of antelope bitterbrush plants neighboring our smallest established plant species, squirreltail. Antelope bitterbrush neighboring squirreltail had total growth similar to the no–established plant treatment. Antelope bitterbrush size differences were greatest the second growing season when size differences between squirreltail and white prairie clover or blanketflower treatments were the most pronounced.

Interactions between established plant root distribution, phenology, and size may explain our results. Antelope bitterbrush develops a long taproot that reaches up to 5.4 m (McConnell 1961), but has few shallow roots (McConnell 1961; Baker and Torrey 1979; but see Loik 2007). White prairie clover is reported to have a coarse, non-fibrous root system with a strong woody taproot that is 1.7–2.0 m deep (Weaver 1954). Blanketflower has a taproot supported by several large laterals arising near the soil surface (Coupland and Johnson 1965). The main root branches of blanketflower penetrate to depths of at least 1.3–1.7 m (Coupland and Johnson 1965). Squirreltail has a fibrous root system that extends to a depth of ≥1 m (Reynolds and Fraley 1989). Our results suggest that plant neighbors having shallow root systems are less competitive with antelope bitterbrush after antelope bitterbrush is established and will make better candidates for antelope bitterbrush companion species in restoration projects.

Squirreltail is one of the first species to initiate growth in the spring (Jones 1998), well before white prairie clover and blanketflower (pers. obs.). Early-season growth of squirreltail may have created a temporal niche overlap that influenced antelope bitterbrush establishment. After antelope bitterbrush develops a deep root system, niche overlap with squirreltail would be expected to be less than with white prairie clover or blanketflower.

Our results indicate that the competitive balance shifted differently over the growing season depending on preestablished plant identity and phenology. Antelope bitterbrush is an evergreen species and can remain active the entire growing season, with pulses of growth in response to rain (Loik 2007). Antelope bitterbrush plants grown with early-growing squirreltail, or without an established neighbor, exhibited greater height gains in the fall compared with plants grown next to either forb. Conversely, antelope bitterbrush grown with either later-growing forb grew higher in the first summer and in the spring. Although we did not measure antelope bitterbrush width, we suspect that differences in preestablished plant aboveground morphology contributed to differences in height gains. Plants grown next to large neighbors may allocate more resources to height than width to capture light (Grime 1966; Schwinning and Wiener 1998). No plants grew better than the no–established plant treatment, indicating that competitive rather than facilitative interactions explain the variation between treatments.

Although analysis of microbial communities is beyond the scope of this study, there are a number of potential explanations for why inoculants did not alter antelope bitterbrush performance (reviewed by Verbruggen et al. 2013). We expected that former agricultural management on our experimental plots selected for decreased abundance and diversity of beneficial microbial taxa (Schnoor et al. 2011), but substantive data is not available. Inoculation into an abundant, diverse AMF community may be less likely to increase plant performance (Lekberg and Koide 2005; Wagg et al. 2011). Inoculants, either from AMF cultures or native soils, may not have included fungal and bacterial species beneficial to antelope bitterbrush. The AMF symbiosis is highly variable, dependent upon the identity of the AMF and host species involved, and dependent on local conditions (Johnson et al. 1997). Inoculants may be less well adapted to conditions in our former agricultural field than local communities and were excluded from the
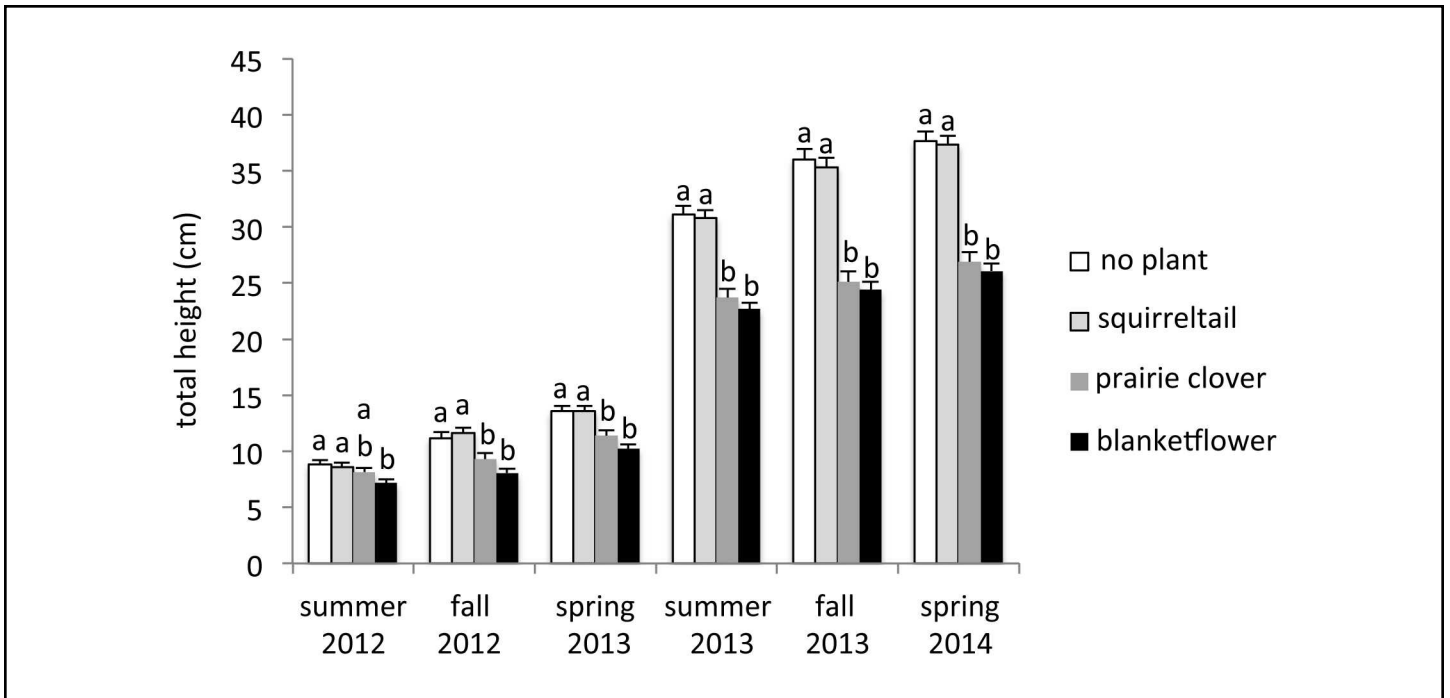
Figure 4. Antelope bitterbrush height recorded at each sample time for all treatments. Different letters above bars at each sample time indicate significant height differences (*P* < 0.05) at each sample time. Error bars indicate standard error.

community. Clements and Young (2000a) found that inoculation of container stock with soils collected from under antelope bitterbrush stands increased survivorship after transplanting. Although these authors did not examine soil microorganisms or root nodulation, lack of beneficial soil organisms, specifically *Frankia* species, were thought to inhibit uninoculated plants. We inoculated preestablished plants, whereas these authors directly inoculated antelope bitterbrush seedlings. Here, inoculants may not have thrived in association with preestablished plants or spread to antelope bitterbrush.
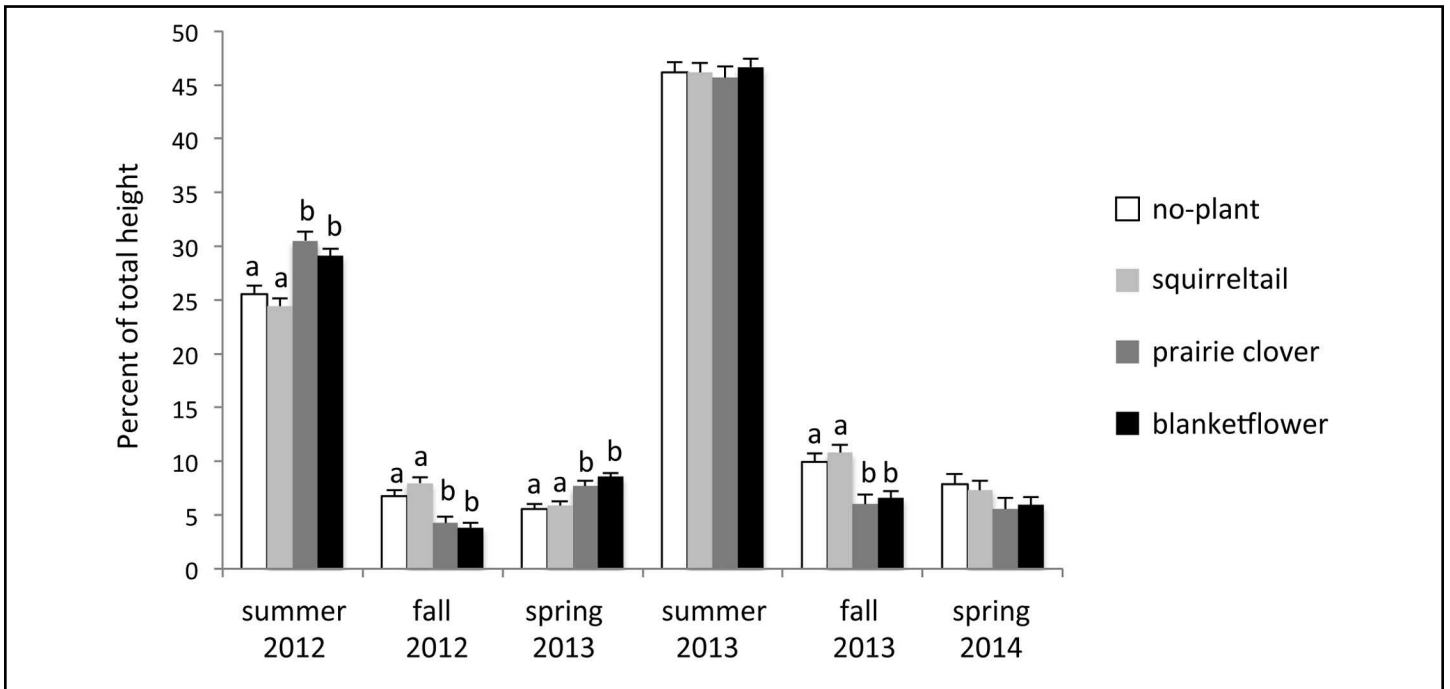

Figure 5. Antelope bitterbrush percent of total height at each measurement time. Different letters above bars indicate significant within-measurement time differences (*P* < 0.05). Error bars indicate standard error.

Developing weed-resistant plant communities that provide desired ecosystem services is a goal of restoration ecology (Pokorny et al. 2005). Squirreltail, Sandberg bluegrass (*Poa secunda* J. Presl.), and other shallow-rooted, early-season grasses have received recent attention as potential competitors with invasive winter annual grasses (Jones 1998; Jones et al. 2010; McGlone et al. 2011; Phillips and Leger 2015). Established perennial grasses suppress invaders of western grasslands (Whitson and Koch 1998; DiTomaso 2000; Chambers et al. 2007), but the influence of different perennial grasses on the establishment and growth of antelope bitterbrush varies. In a field study, Monsen and Shaw (1983) found that Idaho fescue (*Festuca idahoensis* Elmer) cover had a negative relationship, and squirreltail a positive relationship, with antelope bitterbrush cover. We suggest that antelope bitterbrush can be sown with a species that is competitive with salient invaders of western grasslands without decreased forage production. Future work should examine antelope bitterbrush establishment and forage production in mixed communities in the context of restoration seedings on multiple sites.

Interspecific plant interactions ranging from negative to neutral influenced antelope bitterbrush establishment and growth. The influence of neighboring plants on antelope bitterbrush growth was species specific. This shows that consideration of plant trait compatibility will help development of strategies to establish antelope bitterbrush in restoration settings. Careful selection of antelope bitterbrush companion species could allow plant communities to be constructed that do not impede antelope bitterbrush growth. Planting antelope bitterbrush with small-statured, shallow-rooted perennial grass species may allow the construction plant communities with high forage production and resistance to weed invasion.

Our study identified that distance from, and the identity of, established neighboring plants is important to antelope bitterbrush growth and forage production. While we acknowledge that additional studies are needed to examine a broader range of companion species and their traits, our study
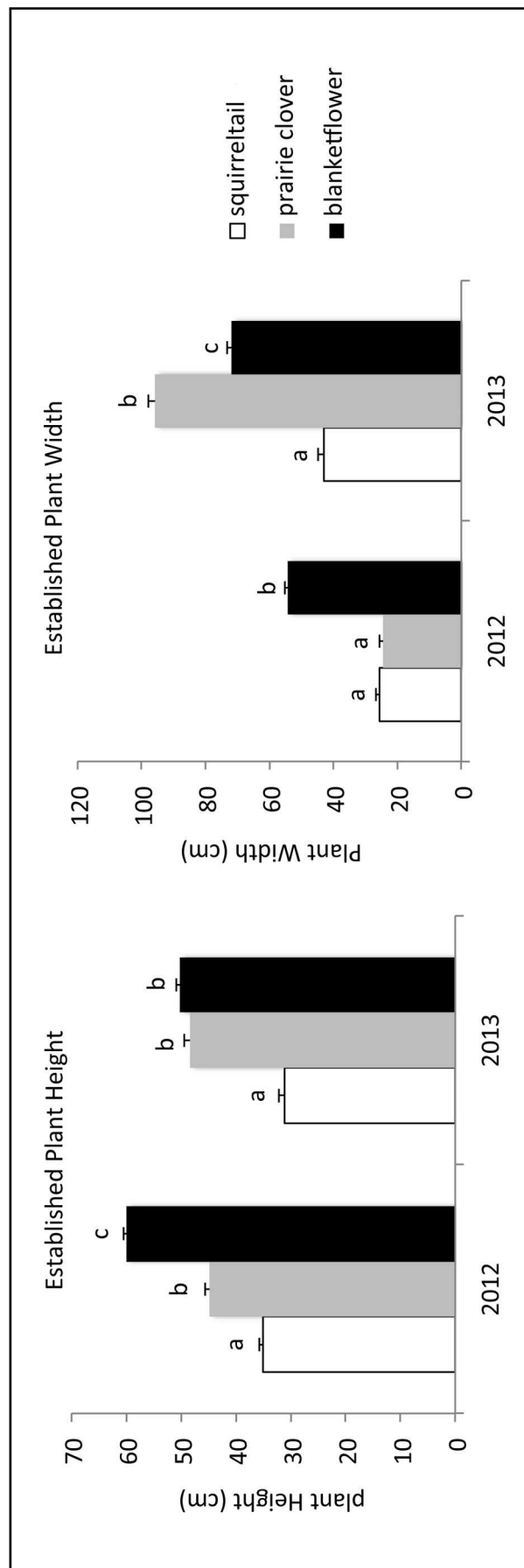

Figure 6. Preestablished plant height (a) and width (b) at maximum yearly growth in 2012 and 2013. Different letters above bars indicate significant within-year differences ($P < 0.05$). Error bars indicate standard error.

suggests that a trait-based strategy for constructing plant communities could increase antelope bitterbrush ecosystem services. Our study examined interactions between established plants and antelope bitterbrush seedlings. Future studies are needed that examine the influence of intraspecific and interspecific seed and seedling interactions on antelope bitterbrush establishment and growth. Seed caching may be the primary mechanism of antelope bitterbrush seedling establishment (West 1968; Vander Wall 1994) and some studies suggest that antelope bitterbrush benefits from intraspecific seed and seedling interactions. Ferguson and Basile (1967) and West (1968) found that antelope bitterbrush seedlings growing in clusters are more likely to establish than seedlings grown alone. Knowledge of intraspecific and interspecific seedling interactions could lead to improved antelope bitterbrush establishment strategies (Madsen et al. 2012).

ACKNOWLEDGMENTS

Daniel L. Mummey earned his BA in microbiology at Eastern Washington University, his MS in soil science at Washington State University, and his PhD in soil science and restoration ecology at the University of Wyoming. After graduating in 2004, he worked as an assistant research professor in the Department of Biological Sciences at the University of Montana, Missoula. Dan's research focuses on how soil structure, soil organisms, and plants determine plant community composition and ecosystem function. In Dan's current role at MPG Ranch, he develops and implements methods to establish healthy native plant communities in disturbed areas.

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