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244 Halogeton (*Halogeton glomeratus* (M. Bieb.) C.A. Mey. [Chenopodiaceae]) along a roadside among energy infrastructure in southwest Wyoming.

# Competitive interactions between an exotic annual, *Halogeton glomeratus*, and 10 North American native species

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## ABSTRACT

Invasive plant species diminish ecosystem integrity and limit restoration success when they compete with reintroduced native species. The invasive annual forb halogeton (*Halogeton glomeratus* (M. Bieb.) C.A. Mey. [Chenopodiaceae]) is increasing in abundance on disturbed lands and energy extraction sites in the Intermountain West. Successful seedlings in the presence of halogeton in the past relied on competitive nonnative forage species. Because disturbance increases nutrient availability in otherwise stressful environments, we hypothesized that annual native species may be more competitive at the seedling stage than are perennial natives. We hypothesized that annuals would increase aboveground growth in the presence of the exotic while perennials would increase allocation to root growth. We documented growth and survival of halogeton in the presence of 10 species native to the western North American basin shrublands and in monocultures. *Sporobolus cryptandrus* (Torr.) A. Gray (Poaceae), *Gaillardia aristata* Pursh (Asteraceae), and *Helianthus annuus* L. (Asteraceae) reduced survival of halogeton (< 30%). *Sporobolus* and *Gaillardia* had greater biomass while *Helianthus* grew taller in the presence of halogeton than when grown with conspecifics. Halogeton aboveground growth was less when grown with *H. annuus* and *Cleome serrulata* Pursh (Capparaceae) (2 annual forbs). Annuals that demonstrated rapid biomass production also limited survival of halogeton. In general, perennials did not differ in aboveground tissue allocation in competition with halogeton. We suggest reclamation seedling establishment may be improved by including native annuals with the potential for rapid aboveground growth on arid land restoration sites where halogeton seedbanks persist.

Prasser NP, Hild AL. 2016. Competitive interactions between an exotic annual, *Halogeton glomeratus*, and 10 North American native species. *Native Plants Journal* 17(3):244–254.

## KEY WORDS

*Artemisia*, *Cleome*, *Elymus*, *Gaillardia*, *Grindelia*, *Helianthus*, *Machaeranthera*, *Poa*, *Sporobolus*, revegetation, greenhouse, seedlings, Chenopodiaceae, Poaceae, Asteraceae, Capparaceae

## NOMENCLATURE

USDA NRCS (2015)

Photos by Nick P Prasser



Invasive species limit restoration success on disturbed arid lands in North America (Allen 1995) and diminish ecosystem function (Dukes and Mooney 2004; Pejchar and Mooney 2009). In southwestern Wyoming, human disturbances are positively correlated with the abundance of invasive plant species (Manier and others 2014). Projected impacts of energy development may influence as much as 24% of North American shrublands and have especially great impacts in Wyoming ( $\leq 42\%$  of Wyoming shrublands; Pocerwicz and others 2011). Wyoming shrublands provide habitat for wildlife species of concern such as greater sage-grouse (*Centrocercus urophasianus* [Phasianidae]) and pygmy rabbit (*Brachylagus idahoensis* [Leporidae]). Disturbances that increase short-term nutrient availability allow invasion of exotic annual species within otherwise nutrient-poor environments. Annuals and ruderal species can make quick use of increased resource avail-

ability immediately after disturbance. As sites age, perennial species that can sequester nutrients and invest in rooting structures to explore and capture resources within greater soil volume should gain an advantage. Because economic constraints usually allow for just one reseeding, we typically seed perennials at times when resource availability is high and favors ruderal establishment. As a consequence, restoration efforts must address this dichotomy in timing of resource constraints by selecting native species that most effectively capture early nutrients but also tolerate limited nutrient availability characteristic of arid land ecosystems in the long term.

Halogeton (*Halogeton glomeratus* (M. Bieb.) C.A. Mey. [Chenopodiaceae]) is increasingly common in disturbed Wyoming sagebrush and desert shrublands (Goodrich and Zobel 2011). The exotic annual forb decreases plant community diversity (Kitchen and Jorgensen 2001) and alters soil chemistry (Duda and others 2003). Native to southeastern Russia and northwestern China, halogeton was first recorded in North America near Wells, Nevada, in 1934 (USDA NRCS 2015). Halogeton stands alter soil chemistry (increase soil electrical conductivity), change nutrient availability (increase nitrogen, phosphorus, and potassium), and cause shifts in functional microbiologic soil diversity (Duda and others 2003). Halogeton is not known to benefit from mycorrhizal relationships and is well suited to disturbed soils lacking arbuscular mycorrhizal fungi (Allen and Allen 1988). Harper and others (1996) suggested that halogeton limits establishment of native seedlings by increasing pathogenic soil microbe loads. In the western US, halogeton historically caused extensive livestock losses, particularly in sheep because it contains toxic oxalates (Cronin 1965). Halogeton is now present in rangelands within 13 western US states and is designated a noxious weed in several (USDA NRCS 2015).

In the Flaming Gorge National Recreation Area in southwestern Wyoming, conversion of native desert shrublands to halogeton monocultures follows disturbance (Goodrich and Zobel 2011). Although halogeton has been present in Wyoming since 1954 (Pemberton 1986), the species is increasingly prevalent on disturbed sites undergoing energy development (for example, well-pads and infrastructure corridors, pipelines, and roadways). Halogeton's wide geographic range and ease of establishment may be partially attributed to its ability to concurrently produce large quantities of dormant and nondormant seed. Dormant seed may remain viable in the seedbank for 10 y (Cronin 1965). Halogeton typically grows underground during the cool season and completes above-ground growth during the warm season, establishing in a variety of sites (Parker 1975; Stubbendieck and others 1986). Once established, halogeton's persistent seedbank and recolonization potential makes chemical control too costly on extensive arid and semi-arid lands in the western US. No biological control agents for halogeton are currently available.



Halogeton stand within salt-desert shrubland site near Green River, Wyoming, adjacent to a pipeline corridor.



Halogeton on heavy clay loam soils from shales near Green River, Wyoming.

Revegetation in areas containing halogeton has been accomplished using exotic perennial grasses that establish well (wheatgrasses [Poaceae]: crested [*Agropyron cristatum* (L.) Gaertn.], intermediate [*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey], tall [*Thinopyrum ponticum* (Podp.) Z.-W. Liu & R.-C. Wang]), and Russian wildrye (*Psathyrostachys juncea* (Fisch.) Nevski) (Cook 1965). Forage kochia (*Bassia prostrata* (L.) A.J. Scott [Chenopodiaceae]), introduced from central Eurasia, can dominate when seeded into dense halogeton infestations (Stevens and McArthur 1990), demonstrating that halogeton is not especially competitive. Although introduced forage species can effectively reduce halogeton, these exotic species are less desirable than native species for use in restoration seedings (Young and others 1972; Richards and others 1998; Roundy 1999). Some evidence suggests that native annuals can suppress exotic annuals on post-fire seedings (Herron 2010; Taylor and others 2014). Greenhouse experiments demonstrate success of annual sunflower (*Helianthus annuus* L. [Asteraceae]) and ragweed (*Ambrosia artemisiifolia* L. [Asteraceae]) in suppressing cheatgrass (*Bromus tectorum* L. [Poaceae]) and *Bromus japonicus* L. (Perry and others 2009). Robust native perennial post-wildfire seedings can suppress exotic invaders (Taylor and others 2014). To our knowledge, successful tactics to manage halogeton in restoration seedings using native species are unknown.

Resource availability strongly influences plant establishment, persistence, and competitive outcomes (Grime 1977). Soil disturbance that removes perennials favors ruderal species that quickly take advantage of greater resource availability. Consequently, we might suspect that annual natives' inclusion in reseeding mixes should be highly competitive with annual exotics on sites where disturbances have occurred causing increased nutrient availability. Native annuals, as plastic opportunists that compete well by way of rapid aboveground growth in nutrient-rich sites, should effectively limit exotic annuals. By contrast, perennial species, with slower growth rates but superior tolerance of limited nutrient availability, may be less competitive with exotic annuals (at least initially on nutrient-rich sites; Aerts 1999; Craine 2005). Perennials native to nutrient-poor sites are, instead, anticipated to grow slowly and to retain nutrients over longer periods (Aerts 1999), possibly allocating greater energy to extending roots rather than aboveground canopy growth. Over time, perennial species with their extensive rooting structures would eventually become more competitive on undisturbed, nutrient-poor sites. Here we examine 10 native species in competition with halogeton to test their root:shoot allocation patterns and survival in the presence of halogeton and in monoculture. We hypothesized that annual native species are more competitive than perennial native species when grown with halogeton during the seedling stage in nutrient-rich conditions.



MATERIALS AND METHODS

In spring 2013, we initiated a greenhouse experiment to test our hypothesis that annual species would demonstrate greater growth in the presence of halogeton whereas perennial species would not. We used combinations of halogeton with each of 10 species native to the Wyoming Basin (Table 1). The native species were selected to include 5 forbs (3 perennial, 2 annual), 4 perennial grasses (2 cool season, 2 warm season), and 1 shrub.

Experimental Design and Treatments

We installed a modified replacement-series experiment to assess competitive interaction between halogeton and native species. We had 2 treatment types: conspecific competition (4 individuals in monoculture per pot) and intraspecific competition (2 halogeton individuals and 2 native competitors). The 2 competition treatments for the 10 native species and halogeton resulted in 21 treatments per block (11 intraspecific monocultures and 10 interspecific species combination treatments); all treatments were replicated in 5 experimental blocks, totaling 105 pots in the experiment.

Seed of each species was germinated in environmental growth chambers during an 18-d period in a commercial ger-

mination soil mix. The growth chambers provided alternating 12 h of light (20 °C [68 °F]) and dark (10 °C [50 °F]).

In June 2013, emerged seedlings were transplanted into competition treatment pots (a 15 cm diameter × 15 cm [6 in] tall cylindrical pot) within a greenhouse located in Laramie, Wyoming (41.3167 N, 105.5833 W). Each pot was filled with field soil from a disturbed site in the Laramie Basin (sandy clay loam, pH 7.8, EC 4.06 mS/cm, organic matter 1.63%, and macronutrients [ppm]: N, 10.1; P, 8.3; K, 255.4). Pots were surrounded by sand to buffer temperature changes in the greenhouse. Seedlings were irrigated with reverse osmosis water delivered through drip emitters controlled by an automated timer. Pots were irrigated with 60 ml (2.0 oz) twice daily for the first week to allow establishment of transplants and daily thereafter. Greenhouse temperatures were programmed to provide 20 °C (68 °F) daytime (7 am–7 pm) then 10 °C (50 °F) at night (7 pm–7 am). Natural sunlight was supplemented by artificial greenhouse lighting to augment ambient light variation within the greenhouse (250 watt high-pressure sodium and 250 watt metal halide lamps for 12 h per day). Air temperature was recorded daily at 10 am and 3 pm; the extreme high was 40 °C (104 °F) and the low was 18 °C (64 °F) over the entire study period.

TABLE 1

*Halogeton in competition with 10 native species were seeded in the greenhouse study.*

Family	Species <sup>z</sup>	Common name	Growth form, life span <sup>y</sup>	Seed source, Year
Asteraceae	<i>Helianthus annuus</i> L.	Annual sunflower	Forb, annual	Western Native Seed Company, 2013
Capparaceae	<i>Cleome serrulata</i> Pursh	Rocky Mountain beeplant	Forb, annual	Western Native Seed Company, 2013
Asteraceae	<i>Gaillardia aristata</i> Pursh	Blanket flower	Forb, perennial	Pawnee Buttes Seed Company, 2012
Asteraceae	<i>Grindelia squarrosa</i> (Pursh) Dunal	Curly cup gumweed	Forb, perennial	Wild collected Albany County, WY, 2012
Asteraceae	<i>Machaeranthera canescens</i> (Pursh) A. Gray	Hoary tansyaster	Forb, perennial	Aberdeen, ID PMC, 2012
Poaceae	<i>Sporobolus airoides</i> (Torr.) Torr.	Alkali sacaton	Grass, perennial	Pawnee Buttes Seed Company, 2009
Poaceae	<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	Sand dropseed	Grass, perennial	Western Native Seed Company, 2013
Poaceae	<i>Elymus trachycaulus</i> (Link) Gould ex Shinners	Slender wheatgrass	Grass, perennial	Meeker, CO PMC, 2007
Poaceae	<i>Poa secunda</i> J. Presl	Sandberg's bluegrass	Grass, perennial	Wind River Seed Company, 2001
Asteraceae	<i>Artemisia frigida</i> Willd.	Fringed sage	Sub-shrub, perennial	Western Native Seed Company, 2013
Chenopodiaceae	<i>Halogeton glomeratus</i> (M. Bieb.) C.A. Mey.	Halogeton	Forb, annual	Wild collected Carbon County, WY, 2012

<sup>z</sup> All species are native to the Wyoming Basin except *Halogeton glomeratus*.

<sup>y</sup> Delineations from online USDA plants database (<http://plants.usda.gov>).

## Monitoring

Beginning 1 wk following establishment (June 2013) and every 2 wk until October 2013 (14 wk), we documented growth of all seedlings (height, leaf number, and mortality of all species). Mortality was declared when all aboveground tissue had senesced. When mortality occurred, we harvested plants at soil surface to obtain aboveground biomass. We harvested surviving species' above and belowground biomass when mortality of 3 individuals in monoculture pots or 2 conspecifics in a competition treatment (for example, both halogeton individuals in competition with a native species) occurred. Above and belowground biomass was harvested at 14 wk for surviving individuals. Roots were separated from individual seedling root crowns by hand washing away soil while roots were suspended on a 0.5 mm (0.02 in) sieve. We did not characterize roots by diameter or length. When intertwined portions of roots became disconnected from the seedling root crown, the root samples were excluded from analyses. We recorded plant surface area (leaf and stem) by scanning all aboveground tissue with a

LiCor 3100 leaf area meter (recorded to 0.01 cm<sup>2</sup> [0.004 in<sup>2</sup>]). Biomass samples were then dried at 160 °C (320 °F) for 48 h and weighed (0.001 g [0.00004 oz]).

## Analyses

Leaf number and height of individuals were averaged within pots for each monitoring period and were subjected to a repeated measures (split plot in time) analysis of variance (ANOVA) for a randomized complete block design (RCB) (Table 2; SAS Institute 2012). We tested the sphericity assumption and in no case did violation of sphericity affect our significance outcomes. Because halogeton mortality was high by wk 14, halogeton leaf number and height data were analyzed until only wk 12. In our repeated measures analysis, treatment by time interactions never varied by treatment (in one case treatment by time interaction was caused by changes within treatments, plant growth over time), one native species height depended on competition treatment irrespective of time, and in general time was significant because plants grew. So we focused

TABLE 2

Seedling growth of 10 native species with and without the annual exotic *Halogeton glomeratus* in a greenhouse experiment.

Native species	Leaf number		Height cm (in)		Tiller number		Leaf length cm (in)		Root:shoot		Canopy area cm <sup>2</sup> (in <sup>2</sup> )		Specific area <sup>z</sup> cm <sup>2</sup> /g	
	+Hagl	Mono	+Hagl	Mono	+Hagl	Mono	+Hagl	Mono	+Hagl	Mono	+Hagl	Mono	+Hagl	Mono
<i>Cleome serrulata</i>	6.4	5.5	9.5 (3.7)	9.2 (3.6)	NA	NA	NA	NA	0.3	0.4	6.6 (1)	4.6 (0.7)	47.8	39.7
<i>Helianthus annuus</i>	7.3	6.1	<b>16.9b</b> <b>(6.7)</b>	<b>12.5a</b> <b>(4.9)</b>	NA	NA	NA	NA	0.2	0.3	20.5 (3.2)	13.3 (2)	53.2	49.1
<i>Grindelia squarrosa</i>	5.4	4.4	2.2 (0.9)	2 (0.8)	NA	NA	NA	NA	3.6	3.9	4.0 (0.6)	3.5 (0.5)	103.2	107.7
<i>Gaillardia aristata</i>	3.6	3.7	3 (1.2)	2.3 (0.9)	NA	NA	NA	NA	<b>2.6b</b>	<b>4.0a</b>	<b>9.4b</b> <b>(1.5)</b>	<b>5.4a</b> <b>(0.8)</b>	172.9	165.9
<i>Machaeranthera canescens</i>	7.1	7.2	1.1	1.3 (0.4)	NA (0.5)	NA	NA	NA	1.2	2.2	1.6	2.1 (0.2)	73.1 (0.3)	59.7
<i>Sporobolus airoides</i>	6.4	6.3	4.8 (1.9)	5.7 (2.2)	1.9	2.1	3.9 (1.5)	4.5 (1.8)	<b>4.5b</b>	<b>1.0a</b>	1.0 (0.2)	1.3 (0.2)	23.3	30.6
<i>Sporobolus cryptandrus</i>	5.2	5.1	8.8 (3.5)	6.7 (2.6)	1.8	1.6	6.8 (2.7)	5.1 (2)	0.9	0.8	3.2 (0.5)	2.6 (0.4)	43.6	50.5
<i>Poa secunda</i>	5.9	5.8	1.7 (0.7)	1.6 (0.6)	1.4	1.4	1.8 (0.7)	1.7 (0.7)	3.9	2.7	0.6 (0.09)	1.0 (0.2)	44.4	56.4
<i>Elymus trachycaulus</i>	3.4	3.4	13.4 (5.3)	15.1 (5.9)	1	1.1	11.6 (4.6)	12.4 (4.9)	1.3	1.0	3.6 (0.6)	3.7 (0.6)	84.9	65.8
<i>Artemisia frigida</i>	19.4	23.7	1.1 (0.4)	0.9 (0.3)	NA	NA	NA	NA	2.0	1.5	1.9 (0.3)	2.1 (0.3)	66.5	46.8

Notes: Native seedlings were grown for 14 wk in monoculture (mono) or with halogeton neighbors (+ Hagl) at a constant density of 4 individuals (4 natives in monoculture or 2 halogeton with 2 natives) in pot 15 cm tall by 15 cm diameter. Values for root:shoot ratios, canopy area, and aboveground specific area are means for individuals harvested at study conclusion. Leaf number, height, tiller number, and leaf length are 14-wk means of individuals. Within each species and growth trait (for example, *Cleome serrulata*, an annual forb), letters compare competition treatments (grown in monoculture versus grown with halogeton). Mean values in bold differ ( $P < 0.05$ , LSD).

<sup>z</sup> Specific area is for all aboveground tissue.

our attention on final growth data sets (root:shoot ratios, aboveground canopy area, specific aboveground area, belowground, aboveground, and total biomass). Final growth of halogeton in intraspecific competition pots with each native species and in monoculture (11 total treatments) was tested using an RCB one-way analysis of variance (ANOVA). We calculated halogeton aboveground biomass in intraspecific compe-

tition treatments (10 treatments) relative to the entire pot (% of all aboveground biomass) and used a one-way RCB ANOVA to test significance; mean separation was performed with Fisher's least significant difference. Each native species' final growth with and without halogeton (2 treatments for each native species) was analyzed using a 2 group *t*-test. To satisfy assumptions of homogenous variances in ANOVA tests we used

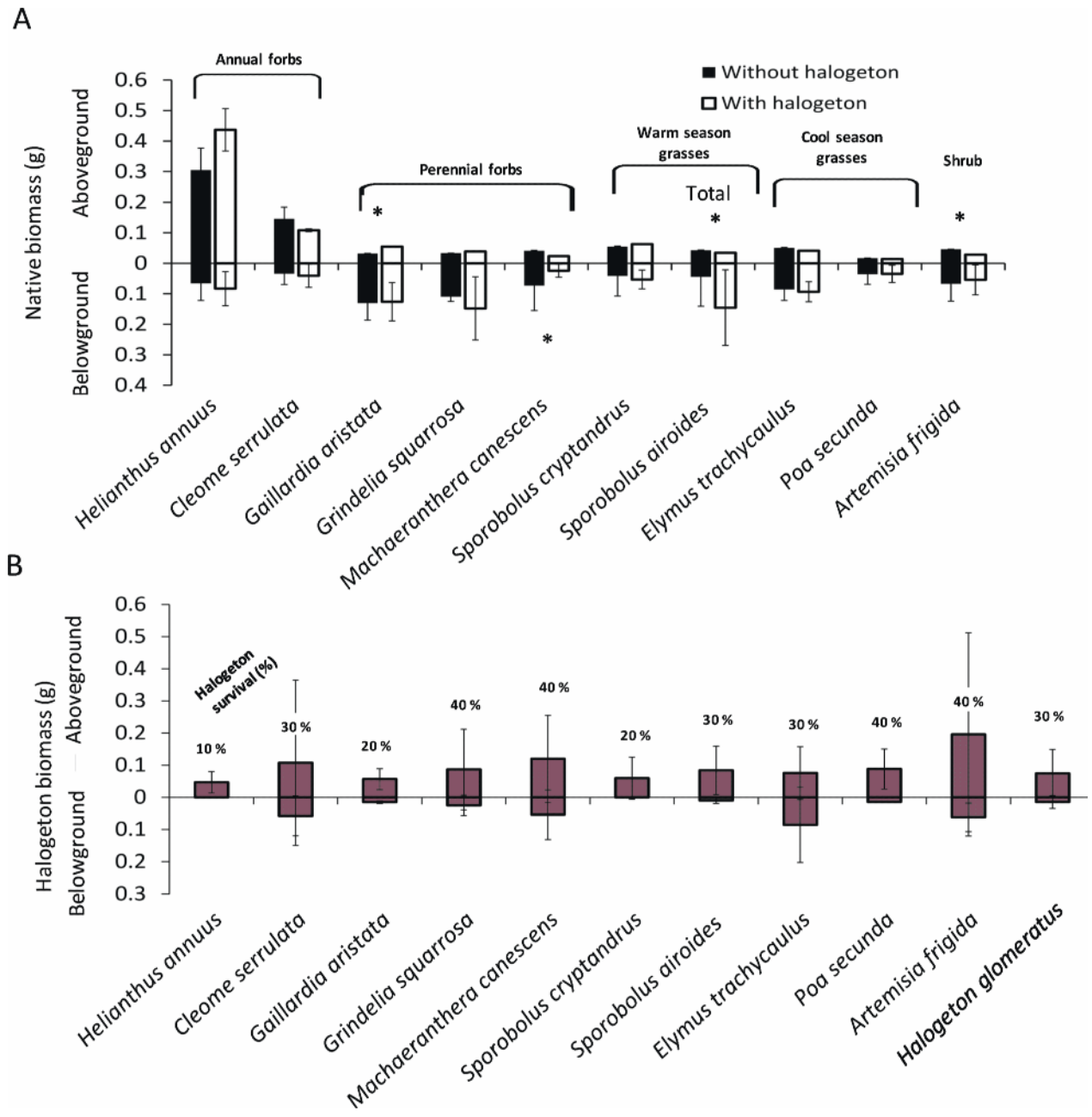


Figure 1. Native species biomass (A) when grown with and without *Halogeton glomeratus* after 14 wk and halogeton biomass and survival (B) when grown with each of 10 native competitors and in monoculture after 14 wk in the same greenhouse experiment. Halogeton seedlings were grown with each native species and all species were grown separately in monoculture, at a density of 4 individuals for all treatments. Biomass is an average across seedlings presented as the biomass of an individual seedling. Comparisons between competition treatments are indicated in belowground biomass (lower case letters), aboveground biomass (uppercase letters), and total biomass production (asterisk, alpha 0.05 in all comparisons). Error bars are one standard deviation of the mean. Missing columns for halogeton belowground biomass with *H. annuus* and *S. cryptandrus* are attributable to root loss during soil washing or mortality of halogeton seedlings.

weighted values, and for *t*-tests we used a square root transformation or the Satterthwaite approximation. We used an alpha of 0.05 in all significance tests.

RESULTS

In general, all species increased leaf number (significant effect of time  $P < 0.05$ , all species, data not shown), most increased in height, and all had greater biomass by the end of the study, as would be anticipated. Five species demonstrated differential growth in the presence of halogeton. Annual sunflower seedlings grew taller ( $P = 0.0035$ ) when grown with halogeton (mean height, 16.6 cm [6.5 in]) than without halogeton (12.5 cm [4.9 in]; Table 2) when averaged across all weeks. Blanket flower grown with halogeton was taller (3.0 cm [1.2 in]) and had greater aboveground biomass at the end of the study than did blanket flower in monoculture ( $P = 0.0126$ , Figure 1A). Blanket flower root:shoot ratios were smaller when grown with halogeton than when grown in monoculture ( $P = 0.0308$ ; Table 2) and its aboveground canopy was greater in wk 14 when grown with halogeton (9.4 cm<sup>2</sup> [1.5 in<sup>2</sup>]) than in monoculture (5.4 cm<sup>2</sup> [0.84 in<sup>2</sup>]; Table 2). By contrast, hoary tansyaster had greater root mass when grown in monoculture than when grown with halogeton ( $P = 0.0342$ ; Figure 1A). The aboveground weight of the shrub fringed sage was less when grown with halogeton than when grown in monoculture ( $P = 0.0378$ ; Figure 1A).

Although the perennial grasses grew over time, in no grass species did height or leaf number differ between competition treatments irrespective of week ( $P > 0.05$  in all cases). Alkali sacaton seedling root:shoot ratios were higher ( $P < 0.0001$ ; Table 2) and total plant biomass was greater ( $P = 0.0108$ ; Figure 1A) when grown with halogeton than those of seedlings in monoculture.

Halogeton

Halogeton height and leaf number (Table 3) and below-ground biomass (Figure 1B) did not differ ( $P > 0.05$ , all cases) in competition with any native species in any week. Halogeton aboveground biomass (% of all aboveground biomass within a pot) depended on competitor ( $P = 0.0001$ ) and ranged from 11% when grown with annual sunflower to 84% when grown with Sandberg’s bluegrass (Figure 2). Halogeton total biomass, root:shoot ratios, and aboveground surface area (leaf and stem) were comparable between competition treatments ( $P > 0.05$ ; Table 3).

Mortality of All Species

Native species mortality remained low throughout the study period. In competition with halogeton, one fringed sage and one Rocky Mountain beepplant individual died by wk 14. Under conspecific competition, one individual of Rocky Mountain beepplant, blanket flower, Sandberg’s bluegrass, and sand dropseed died by wk 14. Halogeton survival

TABLE 3

Halogeton glomeratus (annual exotic) seedling growth with 10 native species and in monoculture in a greenhouse experiment.

	Leaf number	Height cm (in)	Root:shoot	Canopy area (cm <sup>2</sup> [in <sup>2</sup> ])	Specific area (cm <sup>2</sup> /g)
<i>Cleome serrulata</i>	23.5	2.0 (0.8)	0.1 <sup>z</sup>	10.5 (1.6)	21.7
<i>Helianthus annuus</i>	16.1	1.7 (0.7)	NA <sup>y</sup>	1.8 <sup>z</sup> (0.3)	22.3 <sup>z</sup>
<i>Grindelia squarrosa</i>	23.1	2.1 (0.8)	0.9	2.9 (0.5)	21.4
<i>Gaillardia aristata</i>	19.6	2.3 (0.9)	0.2	1.6 (0.3)	22.7
<i>Machaeranthera canescens</i>	26.3	2.7 (1)	0.5	4.4 (0.7)	67.8
<i>Sporobolus airoides</i>	25.4	4.0 (1.6)	0.1	1.7 (0.3)	15.2
<i>Sporobolus cryptandrus</i>	19.4	2.1 (0.8)	NA <sup>y</sup>	1.6 <sup>z</sup> (0.3)	33.5 <sup>z</sup>
<i>Poa secunda</i>	25.3	2.8 (1.1)	0.1	3.2 (0.5)	21.9
<i>Elymus trachycaulus</i>	23.8	2.5 (1)	0.2 <sup>z</sup>	2.9 (0.5)	25.5
<i>Artemisia frigida</i>	23.7	3.2 (1.3)	0.1	11.5 (1.8)	23.7
<i>Halogeton glomeratus</i>	23.4	2.2 (0.9)	0.2	2.7 (0.4)	28.4

Notes: Halogeton seedlings were grown for 14 wk at a constant density of 4 individuals in each pot (15 cm tall by 15 cm diameter) in all treatments (4 halogeton in monoculture and 2 halogeton with 2 natives). Values for root:shoot ratios, canopy area, and aboveground specific area are means harvested at study conclusion. Leaf number and height are 14-wk means. Halogeton growth did not differ between competition treatments with any native species ( $P > 0.05$ , all cases).

<sup>z</sup> Not a mean single value.

<sup>y</sup> Data lost to mortality and loss of fine root samples during root washing.



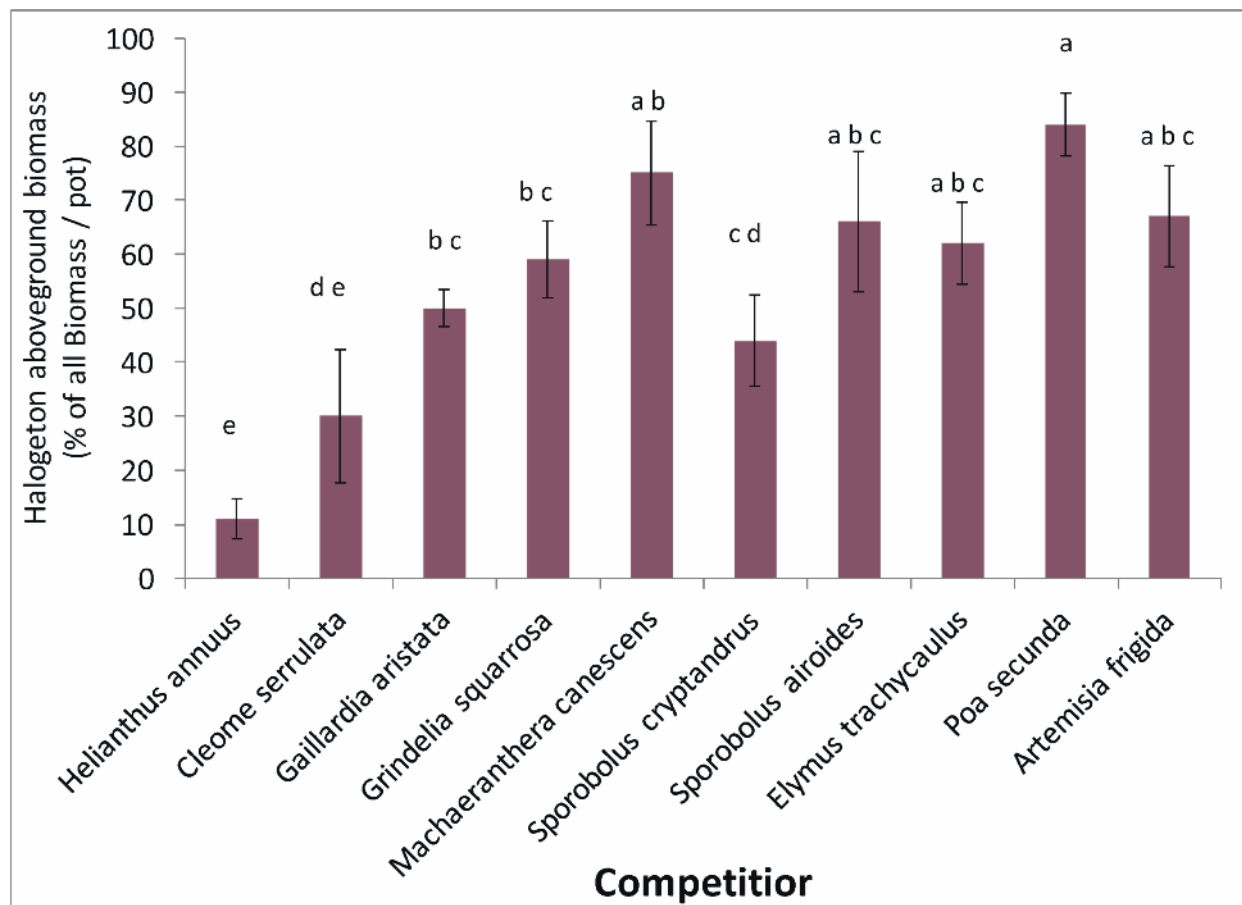


Figure 2. Aboveground biomass of halogeton seedlings (as a percentage of pot total aboveground biomass) when grown in monoculture or with one of the 10 native competitor seedlings for 14 wk in a greenhouse. Halogeton biomass means with the same letters do not differ among competitor species treatments ( $P > 0.05$ , LSD). Error bars are one standard deviation of the mean.

was 30% with conspecifics by wk 14 (Figure 1B). Halogeton survival fell below 30% when grown with annual sunflower, sand dropseed, and blanket flower competitors. Halogeton grown with Rocky Mountain beeplant, alkali sacaton, and slender wheatgrass had comparable survival to halogeton grown with conspecifics. The native species curly cup gumweed, Hoary tansyaster, and Sandberg's bluegrass allowed 40% survival of halogeton (Figure 1B).

## DISCUSSION

In semi-arid settings under low nutrient availability, long-term persistence of seedlings requires successful establishment and slow canopy growth rates (Aerts 1999). Aerts (1999) suggested that seedlings that tolerate stressors of unpredictable arid environments should exhibit plasticity in their investments in root growth, which should contribute to successful long-term competitive ability. High relative growth rates aboveground may be a more successful strategy for initial site capture when resources are readily available (Aerts 1999; Craine 2005) and the influence of neighbor competition is low.

Our hypothesis that annuals as initial competitors would grow larger aboveground in response to available resources was only partially supported in our results (annual sunflower grew taller in competition with halogeton). As anticipated, annual forbs' belowground mass did not differ between treatments, but Rocky Mountain beeplant did not increase aboveground growth in the presence of halogeton. We also expected annuals to effect greater mortality of halogeton than perennials, and presence of annual species resulted in mortality of halogeton comparable to or greater than conspecific competitors.

Our proposal that perennial seedlings engaging a long-term strategy for nutrient-poor sites would increase belowground investment was only partially supported. In general, perennials did not differ in aboveground tissue allocation in competition with halogeton, although blanket flower did have a larger canopy in the presence of the exotic—opposite our predictions. A perennial grass increased root growth in the presence of halogeton, although a perennial forb decreased its roots in competition with the exotic. Of 8 perennial species, only 2 (sand dropseed and blanket flower) reduced halogeton survival below that of conspecific neighbors.

The study period and conditions likely influenced the response of perennials in this study. Although we did not examine competition among our native species, reclamation seedlings often place species into separate portions of the seedbed (drill rows or broadcast). We are confident that perennial growth results would be drastically different if examined over longer time frames and in cooler conditions. The cool-season perennials (for example, Sandberg's bluegrass) would be expected to accumulate biomass slowly and to develop more completely given more ideal temperatures and greater time. Companion field studies would greatly inform the results we present here. For example, in a field study in northern Utah, halogeton declined within 3 y in the presence of robust native grasses and in the presence of the annual exotic cheatgrass in the absence of perennial competitors (Taylor and others 2014).

We conclude that the ability to garner biomass quickly as seedlings can be a successful competitive strategy for some annual natives when resources are available immediately post-disturbance but is not uniform across plant growth form. Reclamation settings often provide nutrient availability in otherwise stressful environments. Perennial native species were not as compellingly competitive in the short term as were annual forbs. Reclamation seed mixes that contain species with mixed growth strategies may offer competitive natives that employ perennial slow growth strategies and annuals employing fast aboveground growth to optimize reclamation potential.

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