Inter- and Intraspecific Variation in Native Restoration Plants for Herbicide Tolerance

Holden J. Hergert, Brian A. Mealor and Andrew R. Kniss

ABSTRACT

Choosing appropriate plant materials for restoration projects can affect establishment and persistence of desirable species. In situations where herbicides are used to manage invasive weeds, plant materials able to tolerate herbicides at early growth stages could increase probability of successful restoration of vegetation. However, little is documented regarding relative herbicide tolerance of native species commonly used in restoration and information regarding intraspecific variation for such characteristics is missing. We conducted a greenhouse study in 2010 and repeated in 2011 to investigate seedling response of 17 desirable species (27 germplasm), Russian thistle, and downy brome to aminocyclopyrachlor, a relatively new herbicide with potential applications in reclamation and restoration. We applied aminocyclopyrachlor at six rates between 10 and 320 g ha^{-1} 30 days after planting. Grasses were in the three to five leaf stage and forbs and shrubs were less than five cm tall at the time of herbicide application. We used a log-logistic model to estimate dry weight reduction in response to aminocyclopyrachlor rate. Russian thistle biomass was reduced 95% at 120 g ha^{-1}. At that same aminocyclopyrachlor rate, grass biomass was reduced 0 to 48% and flax and sagebrush species were reduced ≥ 77%. We document variation among and within species for relative tolerance to this herbicide. If aminocyclopyrachlor were used in a restoration project for postemergence control of Russian thistle, most grasses in this experiment would experience negligible biomass reduction whereas the selected sagebrush and flax species were highly susceptible at this early growth stage even at low aminocyclopyrachlor rates.

Keywords: herbicide ecology, reclamation, revegetation, weed control

Undesirable plants may influence restoration projects in several ways. If they dominate the site, invasive plants may be the primary impetus for restoration (D'Antonio and Meyerson 2002). They may also colonize and impact sites where soil disturbance has occurred, but desirable, competitive plants have not yet established. In the case of drastic disturbance, such as natural resource extraction sites, annual weeds such as downy brome (*Bromus tectorum*) and Russian thistle (*Salsola tragus*) may compete with desired vegetation during establishment (Allen and Knight 1984). In extreme, but not unlikely, circumstances exotic weeds may prevent restoration success (Wilson et al. 2004). Active weed management is necessary to facilitate establishment of desirable species in such cases.

One approach to weed management in restoration is to use a selective herbicide to initially reduce weed density, and then seed competitive plants to establish a desirable plant community that may reduce the long-term probability of reinvasion and dominance by unwanted plants. Integrating herbicides and seeding of competitive desirable species has been effective for reducing Canada thistle (*Cirsium arvense*; Wilson and Kachman 1999), Russian knapweed (*Acroptilon repens*; Bottoms and Whitson 1998), downy brome (Whitson and Koch 1998) and other problematic weeds. In many of these cases, the desirable species best able to establish and compete with the invasive plants were non-native plants such as crested wheatgrass (*Agropyron cristatum*) or Russian wildrye (*Psathyroctachys juncea*).

While many of the most successful competitors with weeds have been relatively desirable introduced species, the use of locally-adapted native plants has become an increasingly important subject in restoration ecology (Lesica and Allendorf 1999, Jones 2013). On both public and private lands, managers and policy makers have recognized the importance of using locally-adapted native plants for restoration, and it is now common for regulations at both state and federal levels to strongly emphasize the use of native species (USDI-BLM 2008, USDA-USFS 2012).

When supplemental seeding is required to achieve desired species composition it is important that potential negative effects of herbicides on non-target, seeded species be kept

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to a minimum. Seeding species or varieties that display a higher relative tolerance to herbicides may provide an effective method for minimizing herbicide damage. Several studies have emphasized the need to evaluate potential negative effects of herbicides on desirable species (Baker et al. 2009, Morris et al. 2009, Sbatella et al. 2011), but little information is available on the relative herbicide tolerance of different genetic sources of native species often used in restoration.

The herbicide resistance literature is replete with examples of intra-specific variation in susceptibility to herbicide injury. While herbicide-resistant weeds are a significant challenge facing agriculture today, the development of herbicide-resistant crops has provided farmers with an additional opportunity to efficiently reduce yield losses from weed competition. Although many herbicide-resistant crops were developed through biotechnology, some were identified and selected via traditional plant breeding methods (i.e. Clearfield® crops). Intraspecific variation for competitive ability against invasive weeds may provide an opportunity to identify competitive native plant materials for use in restoration (Mealor and Hild 2006, Lesica and Atthowe 2007, Mealor and Hild 2007, Leger 2008, Leger and Espeland 2010), but intraspecific variation for herbicide tolerance in native restoration species has not yet been investigated.

This study evaluates the susceptibility of 17 species often used for restoration in the western United States, comprised of 27 unique germplasm sources, to the broadleaf selective herbicide aminocyclopyrachlor. Restoration practitioners often consider genetic origin of seed sources and their suitability to site conditions, but little is known regarding variability among, and within, native plant seed sources in their response to herbicide application. More specifically, our objectives were to assess variation in seedling susceptibility to herbicide damage at different taxonomic levels: among functional groups, among genera, among species and within species of commonly-used native plant materials.

Methods

We conducted a greenhouse study to investigate seedling response of 17 desirable species (comprised of 27 unique germplasm sources) and two exotic weeds to aminocyclopyrachlor, a relatively new synthetic auxin herbicide registered by the EPA in 2010. The study was conducted in 2010 and repeated in 2011 at the Laramie Research and Extension Center, WY. The Upper Colorado and Bridger Plant Materials Centers provided us with all seed for the experiments except Russian thistle and downy brome. We collected seed for these two species near Lingle, WY from one naturally-occurring stand of each weedy species. We planted 27 different germplasm sources of 17 desirable species and two invasive weeds in 164 mL cone-shaped pots filled with a 3:2 volume volume^{-1} mixture of peat moss and sand on October 13, 2010 and again on March 21, 2011 (Table 1). We thinned plants to one plant per pot before herbicide application and watered each pot daily. No fertilizer was applied during the experiment.

The experiment was set in a randomized complete block design with seven replicates. We applied aminocyclopyrachlor 30 days after planting at rates of 10, 20, 40, 80, 160, and 320 g ha^{-1}. Nontreated controls were also included. All herbicide treatments included a 0.25% volume volume^{-1} rate of non-ionic surfactant (NIS). Grasses were at the three- to five-leaf growth stage and forbs and shrubs were less than five cm in height at the time of herbicide application. We applied herbicide in a spray chamber delivering 187 L ha^{-1} of total volume at 276 kPa. We harvested all plants 30 days after herbicide treatment, and washed and separated roots from aboveground biomass. Plant biomass was dried at 60°C for 48 hours and weighed to the nearest milligram.

Aboveground and belowground biomass data were combined into total biomass for analysis. First, a mixed-effects ANOVA was conducted on all grass species using total dry weight as the response variable. Aminocyclopyrachlor rate was considered a linear fixed effect. Random effects included grass species and germplasm within grass species. A second mixed model was then fit where germplasm was removed from the model. The full and restricted models were compared using a likelihood ratio test, where a significant ($p \leq 0.05$) test would suggest the full model was more appropriate, whereas a non-significant result would indicate the simplified model is more appropriate. This allowed us to determine whether germplasm within species explained enough variability in dry weight to warrant inclusion in further analysis. Nonlinear regression was then used to quantify the dose-response relationship (Seefeldt et al. 1995). A five-parameter log-logistic model similar to that proposed by Seefeldt et al. (1995) was used to estimate biomass production in response to aminocyclopyrachlor rate (Equation 1).

$$y = c + \frac{d - c}{(1 + \exp(b(\log(x) - \log(e))))^{f}} \qquad [1]$$

In Equation 1, y is the dry weight in g; x is aminocyclopyrachlor rate in g ha^{-1}; c is the lower limit, or estimated dry weight at very high doses; d is the upper limit, or estimated dry weight at the zero dose; b and e are shape parameters; and f is a parameter related to the asymmetry of the curve. For f equal to 1, the curve is symmetrical around the inflection point. Data from 2010 and 2011 studies were initially analyzed separately and were then combined where appropriate (no interaction effects). All statistical analyses were performed using R statistical software, with the add-on packages 'lme4' for mixed-effects models, and 'drc' for nonlinear regression (Ritz and Streibig 2005, R Development Core Team 2008, Bates et al. 2014).

Table 1. Model parameters and estimated dry weight reduction from 120 g ha^{-1} aminocyclopyrachlor applied 30 days after planting in a greenhouse study for 29 different plant materials; 2010 and 2011 data combined.

			Parameter estimates					Dry weight reduction from 120 g ha^{-1} aminocyclopyrachlor	
Common name	**Species**	**Germplasm**	**b**	**c**	**d**	**e**	**f**	**Estimate**	**95% CI**
crested wheatgrass	*Agropyron cristatum*	Common	25	0.13	0.19	43	0.04	20	1–39
bottlebrush squirreltail	*Elymus elymoides*	9019219	4.7	0	0.22	14	0.28	25	13–36
bottlebrush squirreltail	*Elymus elymoides*	BLM CO	11	0	0.22	23	0.28	40	29–51
bottlebrush squirreltail	*Elymus elymoides*	Baggs	7.6	0.02	0.22	25	0.28	25	14–36
slender wheatgrass	*Elymus trachcyaulus*	Common	54	0.16	0.29	21	0.02	35	27–43
slender wheatgrass	*Elymus trachycaulus*	'Pryor'	82	0.18	0.29	86	290	36	26–46
Junegrass	*Koeleria macrantha*	Common	1.7	0	0.12	19800	554	11	–5–26
basin wildrye	*Leymus cinereus*	'Trailhead'	5.7	0.05	0.27	90	0.12	15	–2–31
basin wildrye	*Leymus cinereus*	Common	8.1	0.05	0.22	84	0.12	22	–1–45
salina wildrye	*Leymus salinus*	Common	0.41	0	0.17	17.4×10^5	15	25	19–31
western wheatgrass	*Pascopyrum smithii*	'Rosana'	0.56	0.04	0.31	310	1.6	45	39–52
western wheatgrass	*Pascopyrum smithii*	BLM CO	1.2	0.04	0.18	0.7	0.83	47	31–63
western wheatgrass	*Pascopyrum smithii*	'Arriba'	17	0.04	0.2	42	0.05	44	25–64
big bluegrass	*Poa ampla*	'Sherman'	1.6	0	0.14	0.83	0.31	28	–5–61
Sandberg bluegrass	*Poa secunda*	'High plains'	2.4	0.03	0.15	2.4	0.035	23	13–33
Sandberg bluegrass	*Poa secunda*	BLM CO	1.7	0.03	0.15	18	0.035	9	–1–18
Sandberg bluegrass	*Poa secunda*	County road 73	1	0.03	0.15	47	0.035	4	–8–15
muttongrass	*Poa fendleriana*	Common	0.062	0	0.17	139	2.9	14	6–21
Russian wildrye	*Psathyrostachys juncea*	'Bozoisky'	6.6	0	0.14	88	0.05	10	–16–36
bluebunch wheatgrass	*Pseudoroegneria spicata*	'Anatone'	1.1	0	0.18	279	0.95	26	14–39
bluebunch wheatgrass	*Pseudoroegneria spicata*	'Piceance'	0.82	0	0.18	120	0.95	48	36–60
bluebunch wheatgrass	*Pseudoroegneria spicata*	BLM CO	1.3	0	0.18	325	0.95	20	8–32
fringed sage	*Artemisia frigida*	Common	3.3	0.004	0.13	6.3	0.96	97	91–103
Wyoming big sagebrush	*Artemisia tridentata*	Common	1.2	0.004	0.08	8.5	0.96	91	83–99
silver sagebrush	*Artemisia cana*	'Cedar springs'	1.2	0.004	0.08	32	0.96	77	64–90
prairie flax	*Linum lewisii*	'Maple grove'	12	0.003	0.033	8.8	0.68	92	85–99
blue flax	*Linum perenne*	Common	1.7	0.003	0.024	5.1	0.68	87	79–95
downy brome	*Bromus tectorum*	Common	14	0	0.31	57	0.012	12	0–23
Russian thistle	*Salsola tragus*	Common	1.6	0.018	0.17	43	1.6	na	na

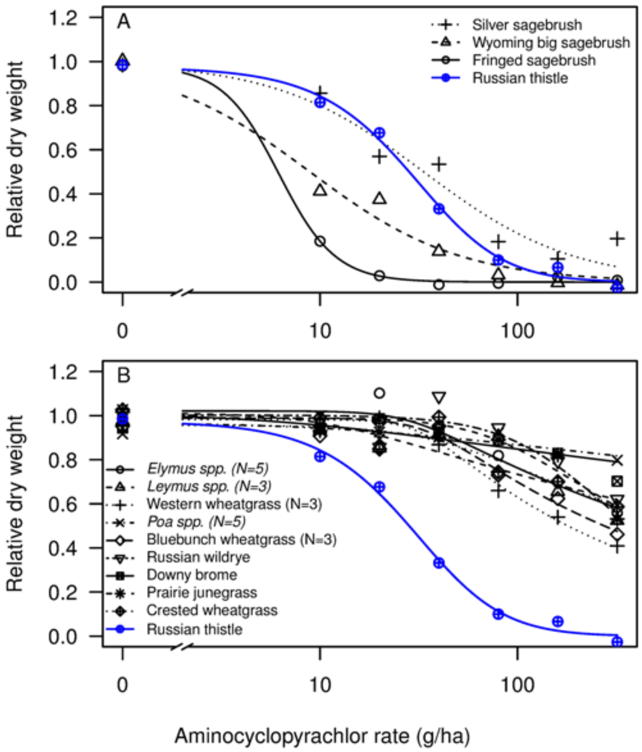

Figure 1. Dry weight (proportion of nontreated estimate) of A) forb and shrub genera and B) grass genera plotted with Russian thistle as a reference in response to aminocyclopyrachlor applied 30 days after planting in a greenhouse study. Curves generated from 2010 and 2011 data fit to Equation 1; model parameters can be found in Table 1.

For plotting, the y-axis was re-scaled to proportion of the dry weight estimate for the zero dose (*d* parameter) to make comparisons between germplasm more intuitive.

From the model, we estimated the rate of aminocyclopyrachlor that would cause a 95% reduction in dry weight (ED_{95}) of Russian thistle (one of our weed standards) to create a standardized means of comparison. This Russian thistle ED_{95} is an estimate of the aminocyclopyrachlor rate required to achieve acceptable weed control. The predicted response of each of the remaining species to the Russian thistle ED_{95} rate could then be derived from each model (as % dry weight reduction). This gives an estimated response of the desirable species at a rate that is likely to provide good weed control. We used Russian thistle as a standard of comparison because it is commonly found on disturbed sites, and has been previously shown to be susceptible to aminocyclopyrachlor (Kniss & Lyon 2011). Russian thistle is also a common exotic ruderal that can be found throughout the Intermountain West and the predicted response of desirable species to a rate that would control Russian thistle has direct implications for restoration or reclamation projects.

Results

We observed variation for tolerance to aminocyclopyrachlor at the functional group, genus, species, and intraspecific levels. When models with and without a random effect of germplasm within species were compared using

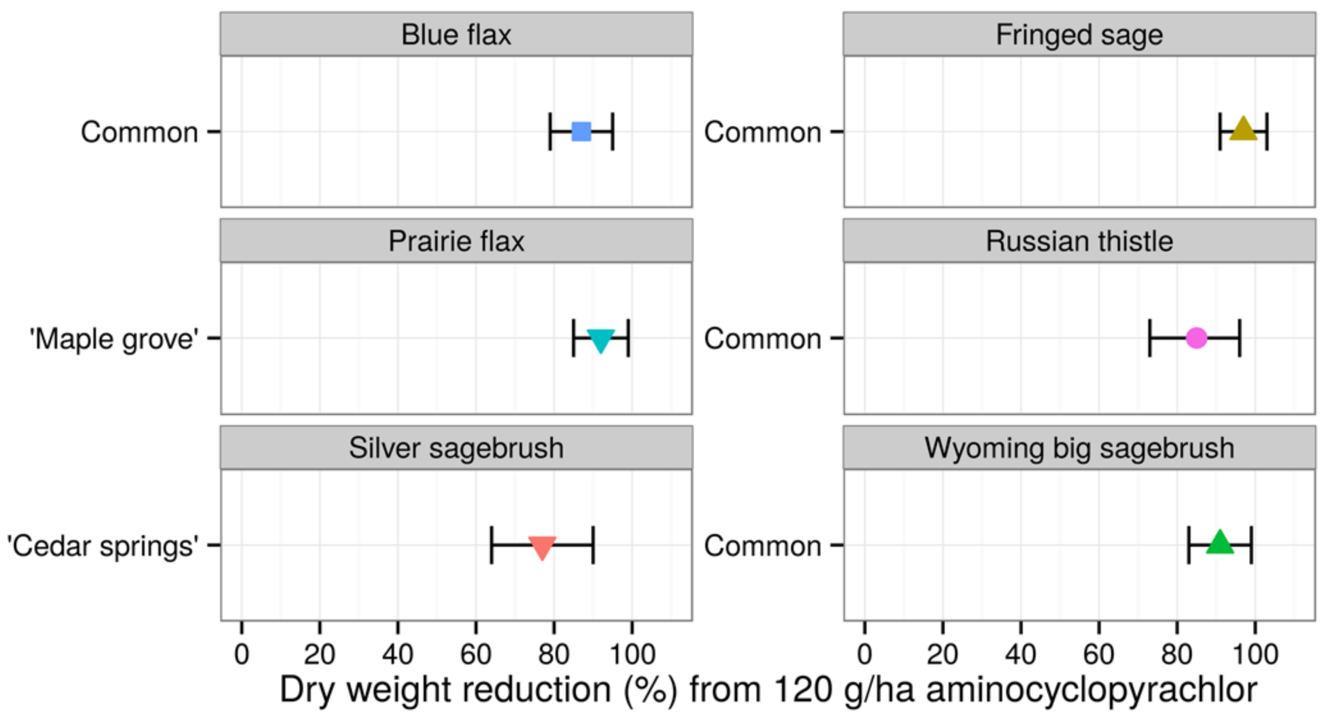

Figure 2. Dry weight reduction (± 1 SE) of six forb and shrub species from 120 g ha^{-1} aminocyclopyrachlor applied 30 days after planting in a greenhouse study. Symbols denote nativity, breeding history and desirability of plant materials: ▲ = native; ▼ = native improved cultivar; ■ = introduced desirable; ● = introduced weed.

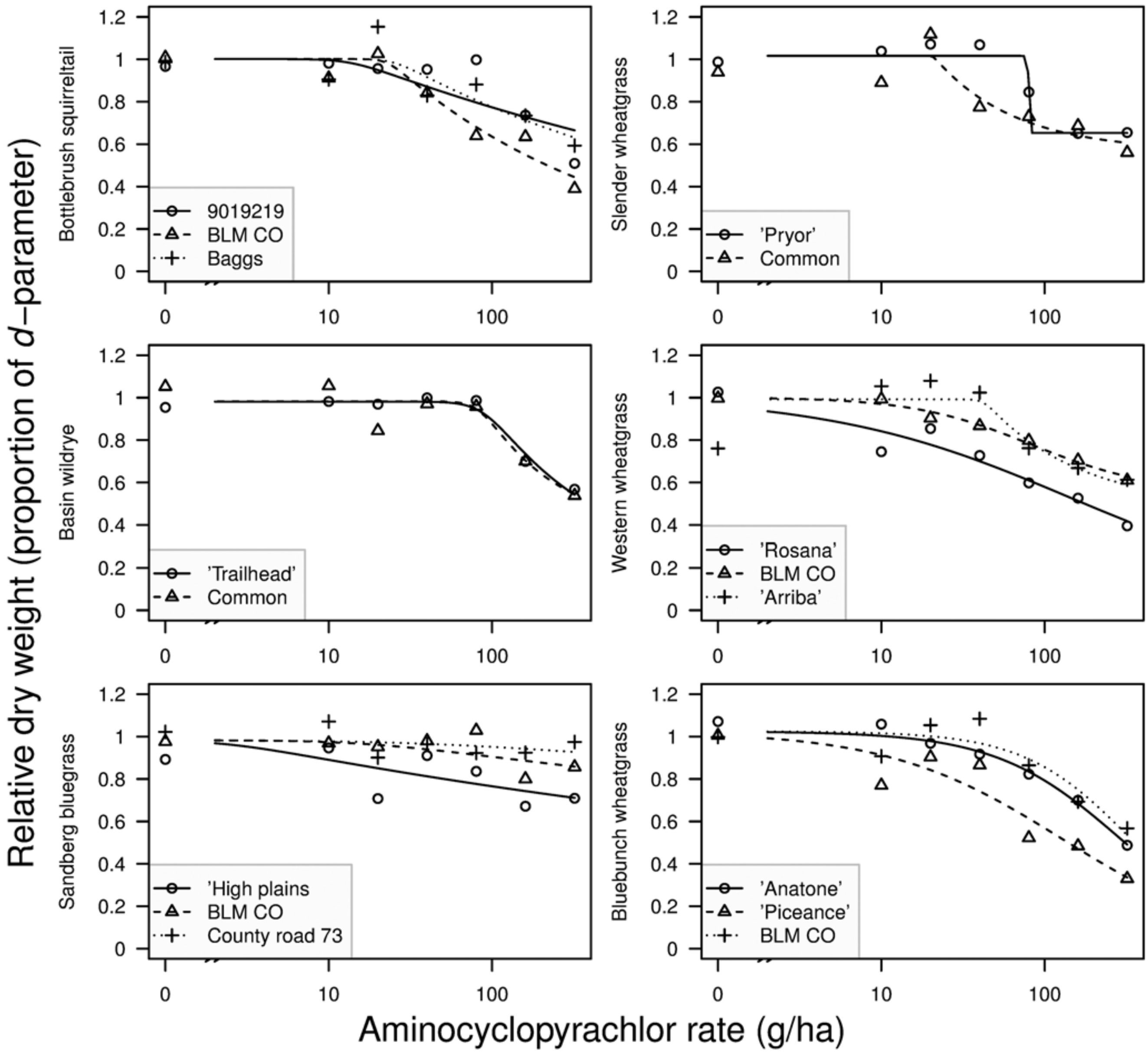

Figure 3. Dry weight (proportion of nontreated estimate) of separate germplasm of six grass species in response to aminocyclopyrachlor applied 30 days after planting in a greenhouse study. Curves generated from 2010 and 2011 data fit to Equation 1; model parameters can be found in Table 1.

a likelihood ratio test, the reduced model (without germplasm) resulted in a significant lack-of-fit (p = 0.0001). This result indicated that germplasm within grass species contributed significantly to explaining dry weight response to aminocyclopyrachlor; therefore, subsequent analyses included the effect of germplasm source within species.

Aminocyclopyrachlor reduced growth of all germplasm tested (Table 1). As expected, broadleaf species were more susceptible to aminocyclopyrachlor compared to grasses (Figure 1). Russian thistle biomass production was reduced 95% by aminocyclopyrachlor when applied at 120 g ha^{-1}. Of the three sagebrush species, silver sagebrush was the most tolerant to aminocyclopyrachlor (Figure 1A); but at the 120 g ha^{-1} rate, dry weight was reduced by > 75% for all three species (Figure 2). Both flax species (*Linum spp*) were similarly susceptible to aminocyclopyrachlor.

All grass genera were more tolerant to aminocyclopyrachlor compared to Russian thistle, but subtle differences existed among genera (Figure 1B). *Poa spp.* and *Bromus tectorum* exhibited the greatest level of tolerance among grass species.

Response differences were observed among species when there were multiple species evaluated within a genus (Table 1, Figures 3 and 4). Of the six species with multiple germplasm, three had noticeable intraspecific differences among germplasm sources (Figure 3). Two germplasm of slender wheatgrass had similar growth reduction from 120 g ha^{-1} (Figure 4). Sandberg bluegrass germplasm was relatively

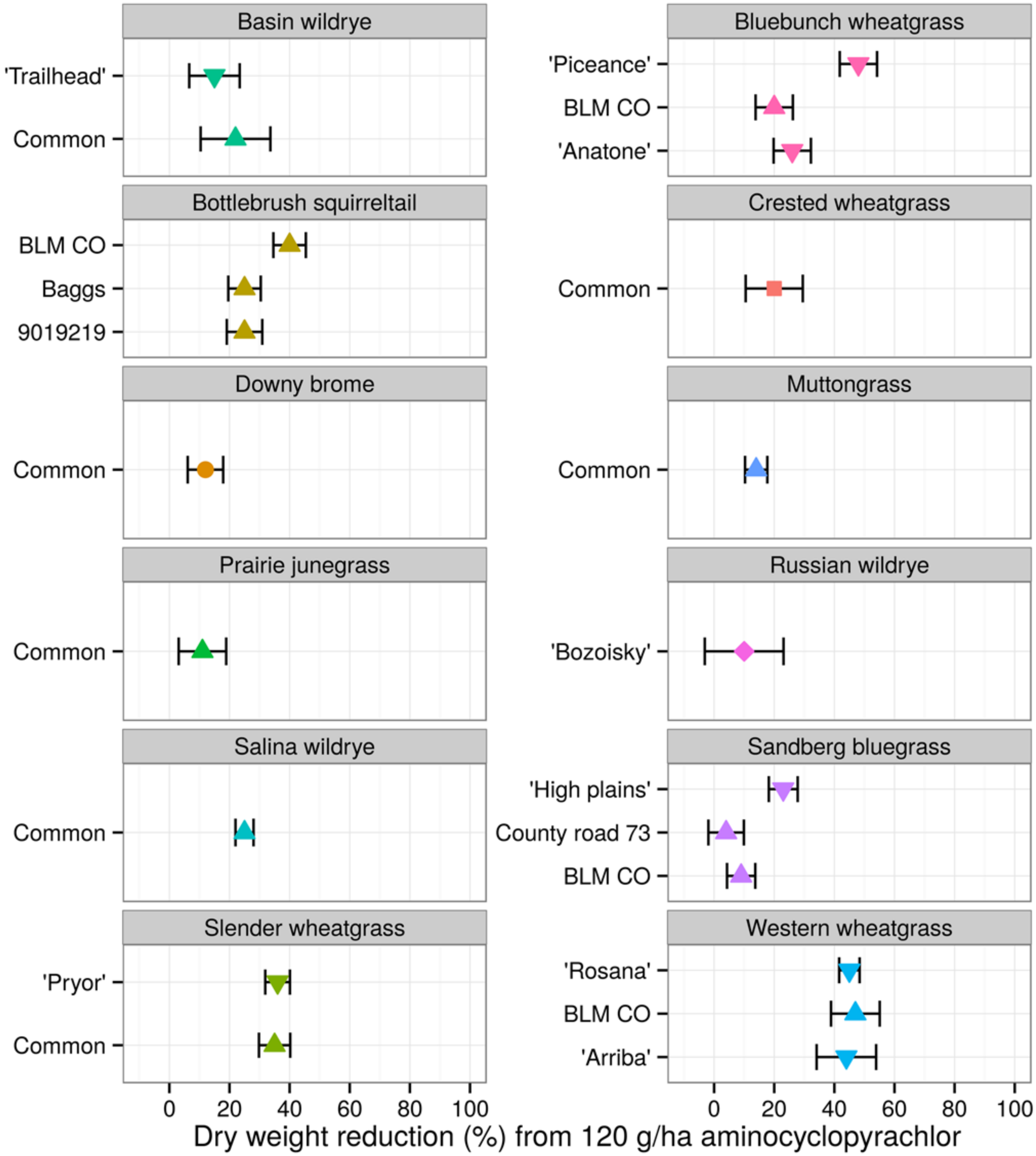

Figure 4. Dry weight reduction (± 1 SE) of 12 grass species comprised of multiple germplasm from 120 g ha^{-1} aminocyclopyrachlor applied 30 days after planting in a greenhouse study. Symbols denote nativity, breeding history and desirability of plant materials: ▲ = native; ▼ = native improved cultivar; ■ = introduced desirable; ♦ = introduced improved cultivar; ● = introduced weed.

tolerant of aminocyclopyrachlor as a species, but 'High Plains' sources were affected more than the others (Figure 4). A similar trend was observed for bottlebrush squirreltail and bluebunch wheatgrass, which also had significant intraspecific variation with respect to their response to 120 g ha^{-1} aminocyclopyrachlor rate (Figure 4).

Discussion

Most grasses used in this study were relatively tolerant to aminocyclopyrachlor in their early stages of growth (three to five leaf stage). These results were expected since aminocyclopyrachlor is a broadleaf-selective herbicide. It is interesting to note that among the genera that displayed the highest tolerance to aminocyclopyrachlor were *Agropyron, Bromus,* and *Psathyrostachys* because the species representing these genera are all introduced to North America. Downy brome displayed one of the highest levels of tolerance to aminocyclopyrachlor in this study.

We observed no consistent pattern of herbicide tolerance related to whether a plant material was a released cultivar or otherwise. In some species, named varieties had greater tolerance to aminocyclopyrachlor (i.e. 'Anatone' bluebunch wheatgrass) whereas other varieties were more susceptible to growth reduction than common or source-identified germplasm (i.e. 'Piceance' bluebunch wheatgrass and 'High plains' Sandberg bluegrass). Native seed producers likely do not intentionally select for herbicide-tolerant native plant genetics, and this may be reflected in the lack of tolerance in recognized cultivars. Our experimental design did not specifically address potential maternal effects (Roach and Wulff 1987), so explicitly assigning observed intraspecific differences to genetic differentiation is not warranted. However, our results strongly suggest that variation for tolerance to aminocyclopyrachlor exists within native plants and further research could help clarify the mechanisms driving these differences.

If this herbicide were used to control a common broadleaf annual weed such as Russian thistle, grass injury would be minimal with an early post-emergent timing based on our greenhouse results. The results of this greenhouse study should be interpreted with some caution because increased environmental stress expected under field conditions in arid and semiarid environments may not elicit the same magnitude of response at the same herbicide rates used in this study. However, recent research suggests a relatively close relationship between native forb response to herbicides under greenhouse and field conditions (Mikkelson and Lym 2013).

According to our observations, aminocyclopyrachlor will substantially injure sagebrush and flax species used in this experiment at rates used to control an annual broadleaf weed such as Russian thistle. However, plants in this experiment were in a highly susceptible state (less than five cm in height). Timing of herbicide application and seeding of desirable species can influence establishment success, and the response is often species- and situation-specific (see Sbatella et al. 2011, Kyser et al. 2013). We did not investigate how restoration plant materials at different stages of growth responded to aminocyclopyrachlor, but such information is needed to make effective recommendations for managers seeking to use this herbicide in restoration projects.

If aminocyclopyrachlor were used in a reclamation situation, careful attention to the desirable forb component would be necessary. Use of other, more tolerant, species might be required. Aminocyclopyrachlor can remain active in the soil for multiple years and its breakdown is likely influenced by environmental conditions such as soil characteristics and precipitation (EPA 2010, Conklin and Lym 2013). Delayed planting of forbs to avoid the soil residual activity of this herbicide or delaying herbicide application until plants become more mature may be alternatives, but more research is needed on this topic. These results indicate that at aminocyclopyrachlor rates needed to successfully control broadleaf annual species, most of the grasses used in this experiment would be fairly tolerant, but relative tolerance may vary depending on the genus, species, and germplasm used.

Although this study is only a first look at such variation among different taxonomic levels of native species, it underscores the importance of selecting appropriate plant materials for the environmental pressures they may face during the establishment phase. For years, plant breeders have selected for desirable characteristics in multiple species. Our results indicate that a potentially beneficial direction for groups working to develop native plant materials for restoration may also consider is selecting for characteristics, such as herbicide tolerance, that may increase our ability to manage weed infestations in wildland restoration settings.

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