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ABSTRACT Cheatgrass (*Bromus tectorum*) is an invasive species in the arid and semi-arid west of the USA, and is weedy in disturbed prairie landscapes. Perennial Russian wildrye (*Psathyrostachys juncea*) limits population growth of cheatgrass, but the mechanism is unclear. I conducted glasshouse and greenhouse experiments to test if intra- and inter-specific competitive interactions of seeds and seedlings of cheatgrass and Russian wildrye were different across a geographic soil gradient with different cultivation legacies in eastern Montana, USA. Seed-seed interactions occurred in both species. Cheatgrass and Russian wildrye inhibited one another's emergence in one edaphic condition in one experiment. Cheatgrass growth was less inhibited by Russian wildrye than by intraspecific neighbors. It appeared that cheatgrass was more sensitive to environmental conditions such as edaphic conditions and intraspecific competition than Russian wildrye. Understanding how environmental conditions prevent cheatgrass emergence is a key aspect of controlling cheatgrass invasion.

KEY WORDS cheatgrass, competition, germination, Russian wildrye, seed coat, soil

Since the 1930s, cheatgrass (*Bromus tectorum*) has invaded the arid western United States, changing the fire regime in this part of the continent and converting the Great Basin ecosystem from a carbon sink to a carbon source (Bradley et al. 2006). Annual weeds also are problematic in the northern Great Plains, particularly in disturbed areas (Eiswerth et al. 2009). Many experiments to determine factors that limit cheatgrass populations, such as herbicide control and competitive effects from perennial grass species, have been performed (Klomp and Hull 1972, Whitson and Koch 1998, Beckstead and Augsperger 2004, Mazzola et al. 2008, Blank 2010). Competition from perennial grasses may be important in limiting expansion of cheatgrass populations (Thacker et al. 2009). However, the effects of soil on competitive interactions that control cheatgrass are complex and need further study (Mazzola et al. 2008, Blank 2010, Emam et al. 2014).

Russian wildrye (*Psathryrostachys juncea*) is planted as a pasture grass throughout the intermountain west and northern Great Plains of the USA. Competition from Russian wildrye has been shown to reduce cheatgrass cover (Whitson and Koch 1998) as well as the cover of other invasive species (Ferrell et al. 1998), while other sown perennial grasses such as Siberian wheatgrass (*Agropyron fragile*) and crested wheatgrass (*A. cristatum*) do not compete well against cheatgrass in the western USA (Klomp and Hull 1972, Mazzola et al. 2008). Russian wildrye alters soil nutrient conditions by decreasing soil organic carbon and increasing soil pH, sodium, and sodium absorption ratios (Smoliak and Dormaar 1985, Dormaar et al. 1995), while cheatgrass either increases or decreases available nitrogen post-invasion depending on the ecological context (Rimer and Evans 2006, Stark and Norton 2015). High nitrogen levels increase cheatgrass competitive ability (Rimer and Evans 2006, Adair et al. 2008,

Rowe et al. 2008, Emam et al. 2014), however, some North American native soil microbial communities are able to sequester nitrogen away from this species, thus reducing its competitive advantage (Rowe et al. 2008).

Legacies of land use can affect plant community composition long after landscapes are returned to non-cultivated status (Jones et al. 2005, Morris et al. 2011). Legacies affecting plant community composition may be due to the signature of the disturbance of plowing (Dormaar et al. 1995, Davenport et al. 2014), propagule limitation in a landscape dominated by agricultural activities (e.g., Bekker et al. 1997), or changes in nutrients or microbial communities from cultivated plants (Smoliak and Dormaar 1985). Many soils of northern Great Plains of the USA have soils low in organic matter due to the farming practices of the region (USDA NRCS 2006).

Although other work has shown competitive dominance of Russian wildrye over cheatgrass (Mazzola et al. 2008, Whitson and Koch 2008), these studies have not determined which life history stage is responsible for the outcome of this interaction and whether this interaction may be edaphically-dependent. Edaphic conditions not only refer to soil nutrient and texture status but also the legacy effects mentioned above. Using a combination of glasshouse and greenhouse experiments, I tested three hypotheses: 1) Russian wildrye excludes cheatgrass pre-emergence, 2) Russian wildrye competitively excludes cheatgrass by resource pre-emption, and 3) strength of direct and apparent competitive effect depends on edaphic conditions.

STUDY AREA

At a north-south fence line in Bloomfield MT USA (533904E, 5232376N), cheatgrass was absent in the interspaces of Russian wildrye (RWR) on the west side of the

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fence, but present within the plant interspaces on the east side of the fence. Soils on both sides of this fence line are classified as Lonna silt loam with 2 to 4% slopes (USDA NRCS 2014). However, cultivation history and most recent biotic conditioning differs between the two pastures. The western hayfield consists mostly of Russian wildrye and a few crested wheatgrass plants that were sown in the early 1990s. The eastern Conservation Reserve Program lot was planted approximately 5 years later with a variety of perennial grass species native to the area as well as with crested wheatgrass and alfalfa. Although it was not seeded, Russian wildrye has colonized this pasture. It is likely that each field was fertilized at the time of planting. Neither field experienced livestock grazing since the time of seeding. To test the effect of edaphic conditions on seed-seed and plant-plant interactions, I collected soil from each field as well as from the boundary (three areas) and performed a glasshouse and a growth chamber experiment to determine the degree of influence of edaphic conditions on competitive dynamics under controlled conditions.

METHODS

I collected soil and seeds from three areas on 11 August 2009 along a fence line ecotone (300 m × 18 m). This ecotone spans a gradient of population densities for each of the study species. On the west side of the fence, Russian wildrye was planted in the early 1990s (HAYFIELD site); there were no cheatgrass plants (CHG) on this side of the fence. On the east side of the fence, a variety of native perennial bunchgrasses were planted prior to 2003 and a dense population of cheatgrass occurs in the interspaces (CONSERVATION site). Since 2003, the Russian wildrye population has expanded east across the fenceline into the cheatgrass population. The zone of expansion is the FENCE site. While this site has historically had high cheatgrass densities, in the years of the study there were few cheatgrass plants in Russian wildrye interspaces. I collected soil from each of the three sites (HAYFIELD, FENCE, and CONSERVATION). I collected seeds along a 100-m long transect in each of the three areas and collected four soil subsamples from perennial grass interspaces (each 0.5-m^2 and 10-cm deep) mixed within each transect for use in the glasshouse experiment. I sent one sample from each of the three bulked samples to Midwest Laboratories (Omaha, NE, USA) for nutrient analysis (Table 1). I stored soil and seeds at room temperature until the start of the experiment.

Glasshouse experiment

The experiment in the glasshouse was to test plant-plant interactions and their edaphic dependence on seedling emergence and growth in Russian wildrye and cheatgrass. I planted seeds in mid-December 2009 into square pots (9-cm

× 9-cm × 9-cm Dura pots; www.hummert.com). In each of the three edaphic conditions, I planted cheatgrass seeds either singly (123 seeds/m^2, eight replicates), at a density of four (494 seeds/m^2, five replicates), or a density of eight (988 seeds/m^2, five replicates) per pot. I planted Russian wildrye at a density of one (eight replicates), four (five replicates), eight (five replicates), or sixteen seeds (1,975 seeds/m^2, five replicates). Single-seed treatments had more replicates to reduce the variation I expected to see in this treatment because of the binary nature of emergence in single-seeded pots. Sown Russian wildrye seed densities were higher than cheatgrass due to lower seed germination rates of Russian wildrye observed in viability testing. Preliminary germination tests also showed that HAYFIELD-collected seeds were not viable, so only FENCE-collected Russian wildrye seeds were used in this experiment. To examine interspecific competition, I planted five replicates of mixes of cheatgrass and Russian wildrye (4 seeds of cheatgrass plus 8 seeds of Russian wildrye, total density 1,482 seeds/m^2) in each soil. Temperatures in the glasshouse averaged 11° C at night and 18° C during the day, with a 14-hr day length maintained by high-pressure sodium and metal halide lights. Plants were well-watered with reverse osmosis water. Emergence occurred within ten days of planting. After four months (mid-Apr), I collected all above-ground biomass of each plant, dried at 30° C for three days, and weighed to the nearest 0.01 milligram.

There was a seed bank in the FENCE and CONSERVATION pots; more cheatgrass plants germinated than the number of cheatgrass seeds sown in 48 of the 82 pots of these soil collections in this experiment. One HAYFIELD pot had more cheatgrass emerged than was sown. To limit the potential for extremely abundant cheatgrass seed banks to influence my results, I eliminated pots with greater than eight cheatgrass plants from all summaries and analyses (8 pots). There were three pots of CONSERVATION where singly-sown Russian wildrye produced more than one Russian wildrye plant. These three pots were removed from the emergence summary but included in the competition analyses. I calculated average number of emerged plants per species per treatment (Table 2). To test for experimental effects on emergence, I only analysed pots of HAYFIELD where there was negligible evidence of a seed bank. I evaluated the effects of sowing treatment on square root-transformed percent emergence of Russian wildrye and of cheatgrass using a multiple regression least square means method in JMP 10.0.2 (SAS Institute, Cary, NC, USA). I determined differences among treatments for emergence with Tukey's HSD.

Because of the presence of a seed bank and variable germination, I chose to represent the inter- and intra-specific competitive environment during seedling growth by a continuous predictor variable (number of plants/pot of each species). I used an index of relative competitive intensity as the dependent variable to examine how the number and type of plant neighbors affect individual plant growth. Relative

Table 1. Measured characteristics of HAYFIELD, FENCE and CONSERVATION edaphic conditions.

Edaphic conditions	HAYFIELD	FENCE	CONSERVATION
Organic Matter (ppm)	2.2	2.9	2.9
Weak Bray P (ppm)	4	33	41
Strong Bray P (ppm)	24	103	124
Bicarbonate P (ppm)	6	34	36
Potassium (ppm)	320	496	590
Magnesium (ppm)	367	485	451
Calcium (ppm)	2,841	2,226	1,401
Sodium (ppm)	7	8	10
pH	8.1	7.8	6.9
CEC (meq/1000g)	181	165	123
Nitrate-N (ppm)	2	2	13

Table 2. Average number of Russian wildrye (RWR) and cheatgrass (CHG) plants per pot in the glasshouse experiment by edaphic condition and sowing treatment. Numbers in parentheses are one standard deviation.

Treatment	HAYFIELD		FENCE		CONSERVATION	
	RWR	CHG	RWR	CHG	RWR	CHG
Single species RWR						
1 seed	0.5 (0.5)	0.0	0.5 (0.5)	0.6 (1.2)	0.6 (0.6)	6.4 (1.5)
4 seeds	1.4 (1.9)	0.0	1.6 (1.1)	1.4 (3.1)	1.4 (0.6)	5.2 (0.8)
8 seeds	3.6 (2.3)	0.2 (0.4)	4.4 (1.7)	0.8 (0.5)	2.6 (1.7)	4.6 (3.4)
16 seeds	4.4 (1.8)	0.0	7.0 (2.2)	1.2 (0.8)	4.6 (2.5)	4.6 (2.3)
Single species CHG						
1 seed	0.3 (0.5)	0.4 (0.5)	0.13 (0.4)	0.63 (0.5)	0.0	3.0 (3.7)
4 seeds	0.4 (0.6)	4.0 (0)	0.6 (0.9)	4.2 (1.1)	0.2 (0.5)	5.0 (2.8)
Mixed species	0.0	0.0	2.6 (1.1)	4.6 (0.9)	3.0 (1.6)	13.2 (2.4)

competitive intensity (RCI) is calculated by using the average biomass of the species grown singly in pots as a constant (μs). For each pot with more than one plant in it, the average per plant biomass (μc) is subtracted from the constant (μs), and divided by the constant (μs). $\mathrm{RCI} = \dfrac{\mu s - \mu c}{\mu s}$ (Goldberg et al. 1999). Thus, when plants grown with neighbors are larger than plants grown alone this index is a negative number (facilitation). The largest value of this index is 1 (complete competitive suppression). I calculated the constant (μs) and RCI for each species, using only biomass for Russian wildrye in the RCI_{RWR} calculation and only using biomass for cheatgrass in the RCI_{CHG} calculation. Using a multiple regression least square means method model in JMP 10.0.2, I examined the effects of the number of emerged cheatgrass plants, the number of emerged Russian wildrye plants, edaphic condition, and all two-way interactions on arcsine-transformed RCI_{RWR} and RCI_{CHG}. The RCI index calculates the competitive effect, and the statistical model asks if competitor identity, competitor density, edaphic condition and their interaction contribute significantly to the competitive effect. Shapiro-Wilk W values of transformed RCI were > 0.69, which indicates the data were close to normal distribution. Because I performed this analysis to examine interactions among growing plants (not seed-seed or plant-seed interactions), only pots with emerged plants were included in this analysis. The exclusion of pots with no emerged plants and the exclusion of pots with more than eight cheatgrass plants resulted in per site sample sizes of RCI_{RWR} on CONSERVATION = 21, HAYFIELD = 16, and FENCE = 24 and RCI_{CHG} on CONSERVATION = 27, HAYFIELD = 8, and FENCE = 20.

When competitor density was significant in the initial RCI model, I ran a follow-up model, including pots only with more than one competitor of the significant species and constraining the predictor variable to the same data range for each soil type when the interaction was significant. For the RCI_{CHG} model, intraspecific density did not vary in HAYFIELD pots (density always equal to 4), so this edaphic condition was removed from the follow up model.

Growth chamber experiment

Emergence measured in the glasshouse experiment combines experimental effects of the life history stages of germination and emergence. I used the growth chamber experiment to examine germination dynamics alone. I tested germination of cheatgrass with and without Russian wildrye on filter paper and in each edaphic condition in petri plates in July 2012. Seeds used for this experiment were from original 2009 collections that had been stored at room temperature, while the soil was freshly- collected from the site in July 2012. As in the previous experiment, I took four soil samples from perennial grass interspaces on 100 m transects in each site type and bulked within transects. These samples were smaller than for the previous experiment: each was taken with an 11-cm tall conical bulb planter (base and top diam. 6 and 7.5 cm, respectively). Each petri plate was lined with filter paper then sown. Cheatgrass was sown with one of three treatments: 4 or 8 seeds (single species); or 4 seeds of cheatgrass plus 8 seeds of Russian wildrye (mixed-species). Russian wildrye was sown with one of four treatments: 4, 8, or 16 seeds (single species); or 4 seeds of cheatgrass plus 8 seeds of Russian wildrye (mixed-species). For non-filter paper emergence media, I placed 0.5 cm of each edaphic condition (HAYFIELD, FENCE, and CONSERVATION) on top of the seeds. I sieved soil to remove the seed bank prior to deposition in the petri plate. The replication level of this experiment was five. Prior to initiating the experiment, I watered soil in the petri dishes and loosely wrapped each dish with Parafilm (Beemis Flexible Packaging, Neema WI, USA). Seeds were germinated for two weeks in a dark environmental chamber with 14 hr at 17.2° C and 10 hr at 8.9° C. The soil in the petri plates was still damp at the end of the two weeks. I classified a seed as emerged if cotyledons were visible. At the end of the experiment, I excavated unemerged cheatgrass seeds to determine if germination (radicle protrusion through the seed coat) occurred.

I tested differences among emergence media and sowing treatment using a multiple regression least square means method model in JMP 10.0.2 on square root transformed germination percentages. I performed Tukey's HSD to further explore significant effects. I used a chi-squared test to determine if germinated, but not emerged cheatgrass seeds (or, "failed germination" as in Chambers and MacMahon 1994) were distributed differently across the treatments.

RESULTS

Glasshouse experiment

Treatment effects on seedling emergence test apparent competition: plants are too small to directly compete for resources. The effect of sowing treatment on emergence was tested only in the HAYFIELD soil because of the presence of cheatgrass seed banks in the other two edaphic conditions. There was no significant effect of seeding treatment on Russian wildrye ($F_{4, 27} = 2.18$, $P = 0.10$), but the presence of Russian wildrye seeds inhibited cheatgrass emergence in HAYFIELD pots, with no cheatgrass emerging in the mix sowing ($F_{2, 17} = 10.28$, $P < 0.001$), and 100% of sown cheatgrass emerging in the cheatgrass-only high-density sowing (Table 2).

I used RCI to examine direct resource competition among plants. RCI_{CHG} was affected by the interaction of intraspecific density and edaphic condition ($F_{2, 54} = 29.57$, $P < 0.001$). The follow up model indicates that RCI_{CHG} increases with increasing intraspecific density and this relationship differs between FENCE and CONSERVATION edaphic conditions ($F_{1, 43} = 22.68$, $P < 0.001$, Fig. 1A). RCI_{CHG} was marginally affected by Russian wildrye densities ($F_{1, 54} = 3.87$, $P = 0.06$, Fig. 1B), in FENCE and CONSERVATION pots (cheatgrass did not emerge in the mix treatment in HAYFIELD pots). RCI_{RWR} was affected by both intraspecific and interspecific densities when all pots were included in the analysis ($F = 35.28_{1, 60}$ $P < 0.001$; $F = 15.82_{1, 60}$ $P < 0.001$, respectively). The follow up model analysing pots where only multiples of the significant competitor were present indicated that increasing cheatgrass densities did not affect RCI_{RWR} ($F_{1, 89} = 0.03$, $P = 0.87$), but that increasing intraspecific densities reduced Russian wildrye growth ($F_{1, 43} = 22.68$, $P < 0.001$, Fig. 2).

Growth chamber experiment

Emergence results exhibited in the glasshouse could be due to either germination or emergence dynamics. The growth chamber experiment specifically examines the germination response to seeding treatment and germination medium (the three edaphic conditions plus filter paper). In the petri plate germination test, both Russian wildrye and cheatgrass were affected by germination medium ($F_{3, 79} = 7.67$, $P < 0.001$; $F_{3, 59} = 7.00$, $P < 0.001$, respectively). Cheatgrass germination did not differ among the three sowing treatments or the interaction between treatment and medium ($P > 0.5$). Russian wildrye did not differ among the four sowing treatments or the interaction between treatment and medium ($P > 0.5$). Filter paper supported the greatest germination for both species. Russian wildrye exhibited nearly twice the germination on filter paper compared to other media, and cheatgrass demonstrating almost complete germination (Table 3). There were 2 germinated, unemerged seeds in the CONSERVA-
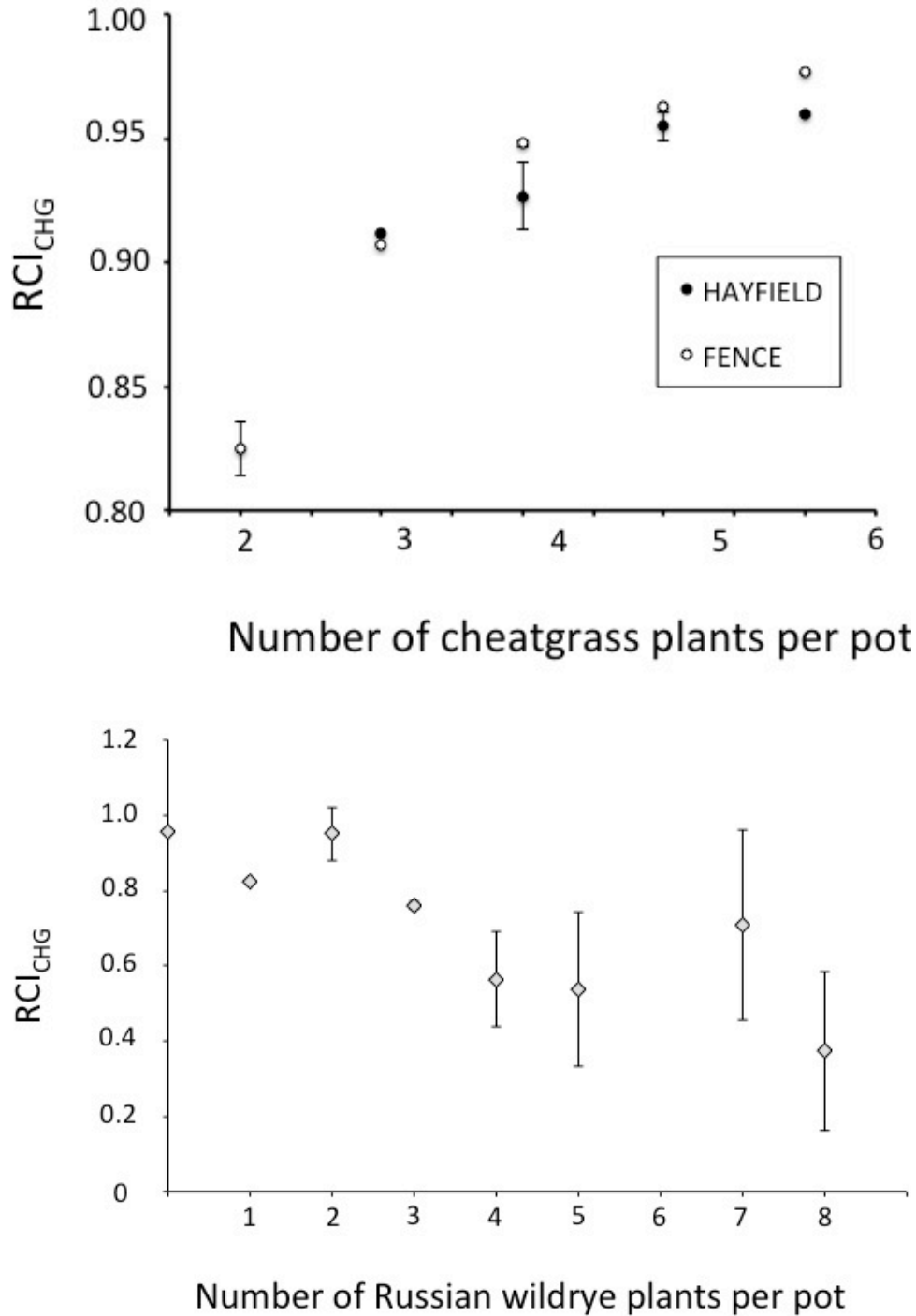
Figure 1. Plant density is associated with relative competitive intensity (RCI) for cheatgrass. Bars equal to one standard error. Note differences in y-axes. (A) Edaphic conditions alter relationship of competitive intensity to per capita intraspecific competition ($P < 0.05$). As the number of cheatgrass plants per pot increases, intraspecific competitive effect (RCI_{CHG}) increases. In CONSERVATION pots, transformed $RCI_{CHG} = 1.021 + 0.046 \times$ # cheatgrass plants per pot ($P = 0.0003$, $R^2 = 0.56$). Per capita competitive intensity is greater in FENCE pots: transformed $RCI_{CHG} = 0.837 + 0.094 \times$ # cheatgrass plants per pot ($P < 0.001$, $R^2 = 0.89$). (B) As the number of Russian wildrye plants per pot increases, interspecific competitive effect (RCI_{CHG}) decreases: transformed $RCI_{CHG} = 1.197 - 0.066 \times$ # Russian wildrye plants per pot ($P < 0.001$, $R^2 = 0.14$).
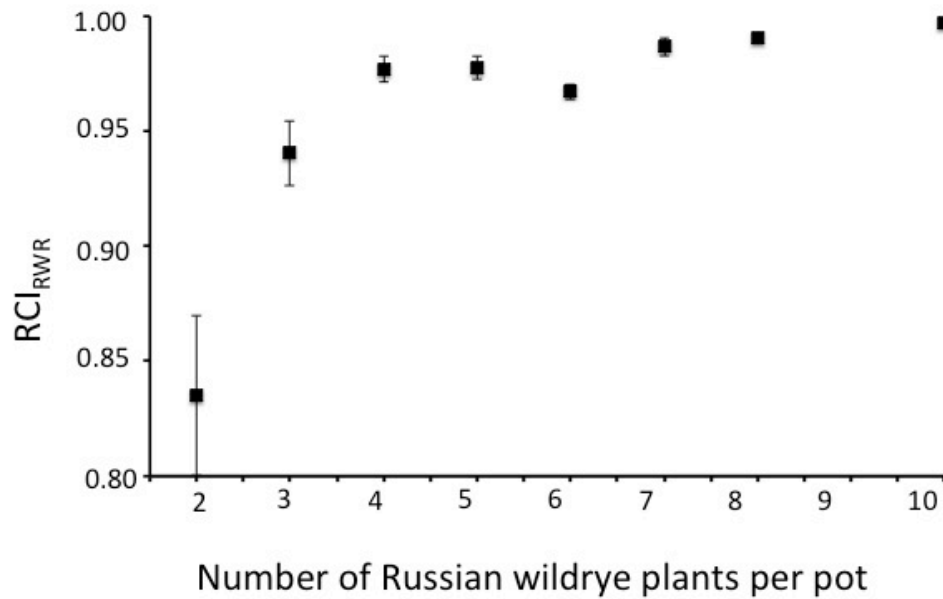
Figure 2. Intraspecific density is associated with a increase relative competitive intensity (RCI) for Russian wildrye. Bars equal to one standard error. As the number of Russian wildrye plants per pot increases, intraspecific competitive effect (RCI_{RWR}) increases. Transformed RCI_{RWR} = 1.006 + 0.062 × # Russian wildrye plants per pot ($P < 0.001$, $R^2 = 0.35$).

Table 3. Mean percent germination of Russian wildrye (RWR) and cheatgrass (CHG) by emergence medium and sowing treatment in the growth chamber. Numbers in parentheses are one standard deviation. Data superscripted different symbols indicate significant differences within species among germination media (Tukey's HSD, $P < 0.05$). Blank cells represent no data.

Treatment	HAYFIELD		FENCE		CONSERVATION		Filter Paper	
	RWR	CHG	RWR	CHG	RWR	CHG	RWR	CHG
Single species								
4 seeds	20 (21)	85 (14)	40 (38)	63 (18)	25 (25)	95 (11)	55 (37)	95 (11)
8 seeds	13 (18)	83 (27)	28 (28)	85 (27)	18 (17)	90 (6)	40 (14)	100 (0)
16 seeds	9 (3)		11 (8)		8 (3)		35 (14)	
Mixed species	12 (15)	75 (0)	29 (19)	75 (18)	13 (22)	90 (14)	58 (29)	100 (0)
Average	13 (14) [*]	81 (14) [¶,+]	25 (23) [*,§]	74 (21) [¶]	16 (17) [*]	92 (10) [+,γ]	47 (23) [§]	98 (6) [γ]

TION, 5 in FENCE, and 9 in HAYFIELD emergence media. The distribution of germinated, unemerged seeds was not significantly different among edaphic conditions (χ^2_3 = 11.09, P = 0.27).

DISCUSSION

These experiments show that Russian wildrye has a greater potential to limit cheatgrass pre-emergence than through competitive dynamics expressed during early plant growth. Cheatgrass is not suppressed by Russian wildrye presence once cheatgrass has emerged. In addition to commonly-

found interspecific competitive suppression of cheatgrass (Perry et al. 2009, Thacker et al. 2009), other studies have shown interspecific facilitation of cheatgrass where the presence of intraspecific neighbors increases cheatgrass biomass (Adair et al. 2008), although this relationship can depend on the genotype of the neighbor (Rowe and Leger 2011). The direct competitive effect of Russian wildrye on cheatgrass was small compared to intraspecific competition. Per capita effects of Russian wildrye on cheatgrass got smaller the more Russian wildrye plants were present in a pot. Although cheatgrass emergence was too low in HAYFIELD pots to examine intraspecific competition in this edaphic condition, per capita

intraspecific growth interference occurred in the other two conditions. In the glasshouse experiment, cheatgrass emergence in the soil collected from the HAYFIELD area was reduced to zero by the presence of Russian wildrye seeds, and Russian wildrye also did not emerge in this treatment under this edaphic condition. Cheatgrass germination was also low in HAYFIELD petri plates. Although not statistically significant, the highest number of failed germinations (germinated but unemerged seeds) was in HAYFIELD plates. This evidence, taken together, suggests that edaphic conditions in association with Russian wildrye presence may play a role in moderating cheatgrass abundance at very early life history stages.

In contrast to cheatgrass, Russian wildrye seems to be quite stable in emergence and competitive dynamics. Edaphic conditions alone did not influence Russian wildrye competitive response, germination, or emergence. Parallel with cheatgrass, Russian wildrye did not emerge in the mixed sowing of HAYFIELD pots in the glasshouse. The significance of cheatgrass presence in the preliminary competition model but not in the follow up model indicates that the presence of cheatgrass reduced Russian wildrye growth, but there were no per capita effects of cheatgrass on Russian wildrye. Russian wildrye exhibited reduced growth when there were more intraspecific competitors. However, intraspecific competition in Russian wildrye appears to be less influential in the biology of Russian wildrye than the influence of intraspecific competition on cheatgrass: less of the variance in Russian wildrye size is explained by intraspecific competition than the variance explained in cheatgrass size.

Parallel interpretation of the glasshouse and growth chamber results are not only hampered by the presence of a seed bank in the edaphic conditions used for the glasshouse experiment, but also by differences in soil storage and seed storage that occurred in between the two experiments. Soils used in the glasshouse experiment were stored at room temperature for 4 months, while soils used in the growth chamber experiment were freshly-collected. Storage can alter both nutrient and microbial conditions in soils (Zornoza et al. 2009, Mian et al. 2011). However, these changes are often minimal in soils from arid environments (Zornoza et al. 2009), such as in eastern Montana. In addition, *in situ* soil nutrient levels and microbial communities can change among years (Fernandes et al. 2002, Bottomley et al. 2006), which could have caused differences among collections made in 2009 and those made in 2012. Seeds used in the glasshouse experiment were recently-collected, while seeds used in the growth chamber experiment had been stored at room temperature for three years. Seed storage generally reduces both dormancy (Allen and Meyer 2002) and seed viability (Allen 1957), and I observed that RWR germination percentages did appear to be lower in the growth chamber experiment. It is possible that differences in soil collection timing and storage as well as seed age explain differences in Russian wildrye

and cheatgrass emergence in HAYFIELD edaphic conditions between the two experiments. While freshly-collected HAYFIELD soil reduced cheatgrass germination, the combination of stored HAYFIELD soil with fresh Russian wildrye seed inhibited cheatgrass emergence. It is also important to note that freshly-collected Russian wildrye seed did not emerge in the HAYFIELD soil collection when cheatgrass was also sown, although both Russian wildrye and cheatgrass emerged in this soil collection when planted monospecifically.

While the lack of multiple samples make the potential for inference from soil nutrient availability to plant growth extremely limited, we can see that the HAYFIELD and FENCE edaphic conditions appear to have much lower nitrogen compared to CONSERVATION. In the long term, Russian wildrye has been shown to reduce organic material and raise pH and sodium in soils (Smoliak and Dormaar 1985, Dormaar et al. 1995). Therefore, I expected that HAYFIELD would be distinct from the other two conditions. Although organic matter appeared a little lower, and pH a little higher, sodium actually appeared lower in the HAYFIELD collection than CONSERVATION and FENCE. The low levels of nitrogen in FENCE could have reduced competitive intensity in that edaphic condition, similar to the results of Emam et al. (2014). There are indications that cheatgrass growth is nitrogen limited in other studies (Rimer and Evans 2006, Adair et al. 2008, Rowe et al. 2008). The effects of nitrogen limitation on cheatgrass emergence are unknown: none of these works cited above have specifically examined early life history stages such as emergence dynamics.

Because both Russian wildrye and cheatgrass emerged in the HAYFIELD edaphic condition in monospecifically-planted pots in the glasshouse experiment, and because mixed-sown pots supported emergence of both species in the pots, I conclude that seed-seed interactions modified by edaphic conditions are likely responsible for the lack of emergence of both species in the mixed-sown HAYFIELD pots. Seed-seed interactions found in other studies have largely been examined in *ex situ* conditions using neutral germination media (Dyer et al. 2000). However, Laterra and Bazzalo (1999) found that the strength of seed-seed interactions increased in pasteurized soil compared to filter paper. Although those results indicate that physical and chemical soil characteristics can increase allelopathic effects, the function of allelopathic chemicals can also be modified by soil microbial communities (Kobayashi 2004). The mechanism of the exclusion of Russian wildrye and cheatgrass emergence in HAYFIELD edaphic conditions observed in the glasshouse experiment is unknown. However, these experiments do show that edaphic conditions can determine the outcome of seed-seed interactions as well as plant-plant interactions for Russian wildrye and cheatgrass in controlled environments.

Competition from desirable species is critical for inexpensive, long-term invasive species control (Whitson and Koch 1998, Waldron et al. 2005), although herbicide use is also an

important component (Blank and Young 2004, Weidenhamer and Callaway 2010). When cheatgrass biomass is reduced by competition, smaller, competitively suppressed cheatgrass is still capable of producing seed (Pierson and Mack 1990). Others have suggested that effective integrated management of cheatgrass invasion should exploit factors that cause extreme variation in emergence and survival (Mack and Pyke 1984, Pierson and Mack 1990). Biocontrol soil biota for cheatgrass that targets germinating seed is under development (Kennedy et al. 1991, Meyer et al. 2007), however, pathogens that prevent cheatgrass emergence can depend on edaphic context for efficacy (Finch et al. 2013), therefore we need to understand the specific contribution of soils to this form of cheatgrass control.

MANAGEMENT IMPLICATIONS

This study shows that cheatgrass is limited by intraspecific competition and that increasing the density of one desirable species does not result in additive interspecific competitive suppression of cheatgrass. However, interspecific seed-seed interactions mitigated by edaphic conditions can reduce cheatgrass emergence to zero. This study suggests that focusing on conditions that prevent emergence may be the most effective management strategy for this invasive species.

ACKNOWLEDGMENTS

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