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Simon A. Lei

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Interspecific Competition Between *Coleogyne ramosissima* Seedlings and *Bromus rubens*

Simon A. Lei

Department of Biology, Nevada State College, 1125 Nevada State Drive, Henderson, Nevada 89015

Abstract.—Interactive effects of red brome grass (*Bromus rubens*) density and time of establishment on the early survival and growth of blackbrush (*Coleogyne ramosissima*) seedlings were quantitatively investigated. Seeds of *Coleogyne* and *Bromus* were collected from Cold Creek of the Spring Mountains in southern Nevada. A series of pot trial experiments were conducted in a controlled environmental glasshouse. In mixed culture pots when *Coleogyne* seedlings planted four weeks later than *Bromus* at medium and high density levels, survival of *Coleogyne* seedlings (experimental populations) was greatly reduced compared to single *Coleogyne* seedlings that grew alone (control population). Significant interactions were detected between neighboring *Bromus* density and time of planting for shoot height, root/shoot ratio, leaf length, and shoot water potential of experimental *Coleogyne* populations. When *Bromus* density was examined independently, all measured growth parameters of experimental *Coleogyne* populations were significantly reduced compared to the control population. When time of planting was examined independently, shoot height, root/shoot ratio, shoot biomass, leaf length, and water potential of experimental *Coleogyne* populations were significantly reduced. Results of this study revealed that some *Coleogyne* mortalities occurred in the absence of interspecific competition, and that growth among surviving seedlings were significantly reduced under conditions of increased density of neighboring *Bromus* and early *Bromus* establishment.

Seed germination alone does not mean that a plant has become successfully established in a community. The seedling stage in plant life histories is the most vulnerable stage in development. During the developmental state, competition for space and resources does not occur between all plants in a population, but rather between the individual in question and the plants immediately surrounding the individual (Harper 1977; Antonovics and Levin 1980; Florentine and Fox 2003). Competition between plant species can be investigated directly by using pot trial experiments to minimize variation in all other factors that can independently and/or jointly affect survival and growth (Florentine and Fox 2003). Competition in plant communities implies that the supply of light, water, or nutrients to plants is diminished by the presence of neighbors and the proximity of plants to plants of either the same or different species (Harper 1977; Tilman 1982). The intensity of interspecific competition is highly dependent on the number of neighbors already present to capture the available space and resources (Florentine and Fox 2003). When plant density is high, individual plants can interfere with each other both aboveground and belowground (Mack and Harper 1977).

Interspecific competition occurs within shrublands between shrubs and grasses that differ in life history traits, including life cycles and growth patterns (Florentine and Fox 2003). In general, seedlings of woody species do not compete well with adjacent herbaceous species (Van Auken and Bush 1988). Grasses can use soil moisture and mineral nutrients faster than perennial shrubs (Jackson and Roy 1986). In mixed cultures of two species involving a woody and a herbaceous plant, the mean yield of woody species is heavily dependent on the relative density and percent cover of adjacent herbaceous species (Harper 1977; Florentine and Fox 2003).

Red brome grass (*Bromus rubens*) was introduced into the western United States during the mid-nineteenth century, but did not spread into the Mojave Desert until the early twentieth century (Hunter 1991). *Bromus* invaded springs, roadsides, and disturbed areas of the Mojave Desert during 1920's. It was not common, however, until after 1950 (Hunter 1991). *Bromus* is common in some locations around 4,000 to 5,000 feet in elevation at the Nevada Test Site (Hunter 1991). It is often a dominant herbaceous species found below 5,000 feet in *Coleogyne* and creosote bush-white bursage (*Larrea tridentata-Ambrosia dumosa*) shrublands of southern Nevada (Beatley 1966; Newman 1991). Competition for soil moisture from cheatgrass (*Bromus tectorum*), a closely related species to red brome grass, is a major cause in the reduction of *Coleogyne* seedling establishment at high and medium soil fertility levels under controlled laboratory conditions (Pendleton et al. 1999). Fertilization as a restoration technique may increase *Coleogyne* growth but, at the same time, can reduce survival and result in competitive exclusion of *Coleogyne* in the presence of *B. tectorum* (Pendleton et al. 1999).

Recruitment of *Coleogyne* is episodic in the Mojave Desert of southern Nevada. Growth activities in *Coleogyne* generally occur from March through mid-June when soil moisture is available in southern Utah (Bowns and West 1976) and southern Nevada (Lei and Walker 1997). Large numbers of *Bromus* also emerge around this period of time. By early to mid-June, *Bromus* have completed their entire life cycle, leaving abundant standing dead stems that persist for a year or two in the field (Hunter 1991; Newman 2001).

The survival and growth of newly emerged *Coleogyne* seedlings are variable in time and space under natural field conditions. If *Coleogyne* seeds germinate among dense carpets of *Bromus,* they may have a reduced chance of survival with a limited seedling growth due to competition effects compared to fewer, or no other, individuals of *Bromus* present. An understanding of the interspecific competition between *Coleogyne* and *Bromus* is critical to determine the cycle of seed germination, seedling establishment, and early mortality of *Coleogyne*. From casual observations, seedling densities and frequencies of *Coleogyne* are not high in natural fields. This phenomenon suggests that either *Coleogyne* seed production is very low, or that competition with other species for limited space and/or resources is high in southern Nevada.

This study investigated interspecific competition between *Coleogyne* seedlings and *Bromus* at different densities and times of planting under controlled environmental conditions using a series of pot trial experiments. Two hypotheses were made prior to data collection. First, the survival and growth of *Coleogyne* seedlings (experimental populations) were reduced with increasing *Bromus* density or early *Bromus* establishment (time of planting) relative to *Coleogyne* seedlings that grew alone (control population). Second, there were interactions between neighboring *Bromus* density and time of planting for many growth characteristics of *Coleogyne* seedlings.

Methods

Seed Collection Site

Seeds of *Coleogyne* and *Bromus* were collected at mid-elevations of a nearly monospecific *Coleogyne* shrubland in Cold Creek (36°25′N and 115°28′W; 1,250 to 1,405 m in elevation), located on the eastern slope of the Spring Mountains in southern Nevada. A total of 300 *Coleogyne* and 800 *Bromus* seeds, along with their corresponding field soils from the upper 10 cm, were collected in late July 2004. From casual observations, flattened, wrinkled, or empty (potentially inviable) seeds of both species were discarded in the field before transporting to a laboratory at Nevada State College (NSC).

Germination Experiments

After initial screenings, seeds were placed at room temperature (22°C) for storage. *Bromus* and *Coleogyne* seeds were placed in a cool chamber (dry chilled) at 4°C for two and six weeks without light, respectively, prior to the initiation of germination and pot trial experiments. Ungerminated seeds that were firm and turgid were recorded as potentially viable.

During the germination period, 20 seeds of the same species were placed between two layers of filter papers moistened with tap water inside a 10-cm diameter Petri dish. Stacks of Petri dishes were placed in transparent plastic bags in the cool chamber to decrease evaporative water loss, and water was added as necessary to maintain saturation of filter papers during incubation. *Coleogyne* seeds were incubated at 4°C, while *Bromus* seeds were incubated at 22°C in the dark except for an occasional, brief exposure to fluorescent lights. Radicle emergence $\geq$ 1 mm was the criterion for seed germination (Lei 1997). Germination occurred between 2–3 weeks at a 87% rate for *Coleogyne,* and occurred within two weeks at a 90% rate for *Bromus.*

Pot Trial Experiments

Transplanting commenced on November 14, 2004 for the early germinating *Bromus* and completed on January 9, 2005 for the later *Bromus* in the glasshouse. All other seedlings were introduced into pots on December 12. *Bromus* was selected because it has often coexisted with *Coleogyne* as a common herbaceous species at mid-elevations of southern Nevada. Three densities of *Bromus*: low, medium, and high were represented by two, four, and six individual plants, respectively, with a single *Coleogyne* seedling.

Five-week old *Coleogyne* and three-week old *Bromus* seedlings were transplanted into small, cone-shaped containers (plastic pots) that were 6.5 cm in diameter and 35 cm tall. Pots were placed in a glasshouse at the Henderson Campus of Community College of Southern Nevada (CCSN) from mid-November 2004 through early June 2005. Each pot contained one-third perlite and two-thirds natural field soil, without adding fertilizers in order to maintain a low soil fertility level. Perlite was used to improve aeration and drainage (Lei 2004).

Plantings of *Coleogyne* and *Bromus* were made on three different dates. The first planting date was on the ''same day'' when both *Coleogyne* and *Bromus* were introduced into pots simultaneously on December 12, 2004. The second planting date was ''early grass'', in which *Bromus* was initially introduced into pots on December 12, and 28 days later *Coleogyne* was introduced (January 9, 2005). The third date was ''late grass', in which *Coleogyne* was planted first on November 14, 2004, and the *Bromus* was planted later on December 12. *Coleogyne* was planted first in order to promote seedling survival and growth. *Coleogyne* seedlings were placed in the center of each pot, while individuals of *Bromus* were placed on the periphery. All 15 replicates of each treatment received the same amount of irrigation and liquid fungicide, as well as the same intensity of incoming sunlight (experimental populations). Single *Coleogyne* seedlings without the presence of *Bromus* were served as a control population, and were used to compare with various density levels and times of planting (experimental populations).

Prior to planting, care was taken to allocate seedlings by size to various experimental treatments, so that no single treatment had disproportionally large or small seedlings. Pots were lightly moistened with tap water for 20 weeks (five months) in the glasshouse. Initially, seedlings were watered twice a week for the first three weeks, and thereafter once a week until the end of pot trial experiments. A small amount of liquid fungicide was applied monthly. Any deaths observed during the first few days were immediately replaced with new *Coleogyne* seedlings. A mortality rate in each experimental treatment was recorded.

Water status of each *Coleogyne* seedling was determined using a portable pressure chamber (Plant Moisture Stress Instrument Company; Covallis, OR) as described by Scholander et al. (1965) in order to quantify the soil water environment encountered by the root system. The chamber was pressurized with nitrogen gas. Once the shoots were incised, water potential measurements were made immediately in the glasshouse to decrease evaporation loss. Shoots were sealed into the chamber, and the pressure indicated at the first sign of water at the cut end was recorded as an estimate of shoot water potential (Lei 2004).

All surviving *Coleogyne* seedlings were harvested five months after planting by carefully removing them from pots, and soil was gently rinsed away with slow-flowing tap water. Intertwined roots of *Bromus* and *Coleogyne* were carefully separated while their roots were submerged in water. *Coleogyne* were separated into root and shoot components. Root length, shoot length, and basal shoot diameter were measured with a metric ruler. Root and shoot biomass were obtained after oven-drying at 65°C for 36 hours.

Statistical Analyses

Germination was computed on the basis of percentages of potentially viable seeds. Mortalities of *Coleogyne* seedlings with respect to neighboring *Bromus* density and time of planting were expressed with percentages. A two-way Analysis of Variance (ANOVA; Analytical Software 1994) was conducted to detect significant differences in shoot height, root/shoot ratio, basal shoot diameter, root and shoot biomass, leaf length, and shoot water potential (growth characteristics) of *Coleogyne* seedlings, with neighboring *Bromus* density and time of planting

Table 1. Mortality and harvest values (mean ± SE, n = 15 per density level per growth characteristic) of *Coleogyne* seedlings grown in mixed cultures with *Bromus* when Bromus individuals were planted four weeks earlier. Low, medium, and high densities represent two, four, and six individuals of *Bromus* per pot, respectively. Statistical comparisons and significance are indicated in Table 4.

Growth variable	Number of *Bromus* individuals per pot			
	Control	2	4	6
Mortality (%)	13.3	26.7	46.7	53.3
Shoot height (cm)	6.7 ± 1.2	5.7 ± 1.3	4.4 ± 1.1	3.8 ± 1.2
Root/shoot ratio	1.9 ± 0.1	2.2 ± 0.2	2.4 ± 0.2	2.6 ± 0.1
Shoot diameter (mm)	3.6 ± 0.2	2.8 ± 0.2	2.4 ± 0.1	2.0 ± 0.1
Shoot biomass (g)	0.17 ± 0.05	0.15 ± 0.06	0.11 ± 0.05	0.09 ± 0.04
Root biomass (g)	0.04 ± 0.01	0.05 ± 0.01	0.07 ± 0.01	0.09 ± 0.01
Leaf length (mm)	6.2 ± 0.8	5.8 ± 0.7	5.3 ± 0.6	4.8 ± 0.5
Water potential (MPa)	−1.7 ± 0.1	−2.3 ± 0.2	−2.7 ± 0.1	−3.1 ± 0.2

as main effects. Mean values were presented with standard errors, and statistical significance was determined at $p \leq 0.05$ level.

Results

Low mortality was observed when *Coleogyne* seedlings grew alone in the absence of interspecific competition (13.3%; Table 1). Highest mortality was found (53.3%) when individuals of *Bromus* were established four weeks before *Coleogyne* in high density than in low density of control pots (Table 1). All *Coleogyne* growth parameters with medium *Bromus* density had intermediate values (Table 2) between high and low densities (Tables 1 and 3, respectively). When *Coleogyne* was planted four weeks before *Bromus,* substantial deaths still occurred at the high density level (26.7%; Table 3).

Density of neighboring *Bromus* had a significant effect on growth of experimental *Coleogyne* populations irrespective of establishment time. High *Bromus* density significantly increased root/shoot ratio, but decreased shoot height, basal shoot diameter, root and shoot biomass, leaf length, and shoot water potential of experimental populations compared to the control population ($p \leq 0.05$; Table 4).

Table 2. Mortality and harvest values (mean ± SE, n = 15 per density level per growth characteristic) of *Coleogyne* seedlings grown in mixed cultures with *Bromus* when both species were planted simultaneously. Low, medium, and high densities represent two, four, and six individuals of *Bromus* per pot, respectively. Statistical comparisons and significance are indicated in Table 4.

Growth variable	Number of *Bromus* individuals per pot			
	Control	2	4	6
Mortality (%)	13.3	20.0	33.3	40.0
Shoot height (cm)	6.7 ± 1.2	6.1 ± 1.3	5.5 ± 1.1	5.0 ± 1.2
Root/shoot ratio	1.9 ± 0.1	2.1 ± 0.2	2.5 ± 0.2	2.7 ± 0.1
Shoot diameter (mm)	3.6 ± 0.2	3.1 ± 0.2	2.7 ± 0.1	2.3 ± 0.2
Shoot biomass (g)	0.17 ± 0.05	0.15 ± 0.04	0.13 ± 0.03	0.11 ± 0.02
Root biomass (g)	0.04 ± 0.01	0.05 ± 0.01	0.07 ± 0.01	0.08 ± 0.02
Leaf length (mm)	6.2 ± 0.8	5.9 ± 0.7	5.6 ± 0.6	5.0 ± 0.5
Water potential (MPa)	−1.7 ± 0.1	−2.2 ± 0.2	−2.5 ± 0.1	−2.8 ± 0.2

Table 3. Mortality and harvest values (mean ± SE, n = 15 per density level per growth characteristic) of *Coleogyne* seedlings grown in mixed cultures with *Bromus* when *Coleogyne* individuals were planted four weeks earlier. Low, medium, and high densities represent two, four, and six individuals of *Bromus* per pot, respectively. Statistical comparisons and significance are indicated in Table 4.

	Number of *Bromus* individuals per pot			
Growth variable	Control	2	4	6
Mortality (%)	13.3	20.0	20.0	26.7
Shoot height (cm)	6.7 ± 1.2	6.4 ± 1.3	6.0 ± 1.3	5.7 ± 1.2
Root/shoot ratio	1.9 ± 0.1	2.0 ± 0.2	2.2 ± 0.2	2.4 ± 0.1
Shoot diameter (mm)	3.6 ± 0.2	3.3 ± 0.2	2.9 ± 0.1	2.7 ± 0.2
Shoot biomass (g)	0.17 ± 0.05	0.16 ± 0.06	0.15 ± 0.05	0.13 ± 0.04
Root biomass (g)	0.04 ± 0.01	0.05 ± 0.01	0.06 ± 0.01	0.07 ± 0.01
Leaf length (mm)	6.2 ± 0.8	6.0 ± 0.7	5.8 ± 0.6	5.5 ± 0.5
Water potential (MPa)	−1.7 ± 0.1	−1.9 ± 0.2	−2.1 ± 0.1	−2.3 ± 0.2

Time of planting also had a significant effect on certain growth parameters of experimental *Coloegyne* seedlings irrespective of neighboring *Bromus* density. Early *Bromus* establishment significantly reduced shoot height, shoot biomass, leaf length, and water potential, but increased root/shoot ratio of *Coleogyne* seedlings compared to *Bromus* established four weeks after *Coleogyne* ($p \leq 0.05$; Table 4). Nevertheless, basal shoot diameter, as well as root and shoot biomass of did not differ significantly between control and experimental populations, with respect to time of planting ($p > 0.05$; Table 4).

Growth of *Coleogyne* seedlings was significantly affected by interactive effects of neighboring *Bromus* density and time of establishment. A two-way ANOVA revealed that neighboring *Bromus* density * time of planting interaction was statistically significant for shoot height, root/shoot ratio, leaf length, and shoot water potential of *Coleogyne* seedlings ($p \leq 0.05$; Table 4). A combination of high *Bromus* density and early *Bromus* emergence significantly decreased these four growth parameters of experimental seedlings ($p \leq 0.05$; Table 4). However, the *Bromus* density * time of time was not statistically significant for basal shoot diameter, as well as root and shoot biomass of *Coleogyne* seedlings ($p > 0.05$; Table 4).

Table 4. Summary of two-way ANOVA showing effects of neighboring *Bromus* density, time of planting, and their interactions on various growth characteristics of *Coleogyne* seedlings. Statistical significance was determined at $p \leq 0.05$. df = 2 for time of planting, df = 3 for neighboring *Bromus* density, and df = 6 for *Bromus* density and time of planting combination.

	Bromus density		Time of planting		Density * time	
Variable	F	P	F	P	F	P
Shoot height	198.65	<0.0001	72.95	<0.0001	14.39	0.0001
Root/shoot ratio	173.44	<0.0001	27.00	0.0001	5.22	0.0090
Shoot diameter	21.78	0.0006	1.78	0.2297	0.44	0.7740
Shoot biomass	68.40	<0.0001	14.93	0.0007	2.15	0.1285
Root biomass	17.68	0.0002	2.00	0.1810	1.64	0.2247
Leaf length	102.45	<0.0001	13.94	0.0010	5.63	0.0068
Water potential	101.17	<0.0001	42.51	<0.0001	3.53	0.0337

Discussion

This study demonstrated that some *Coleogyne* mortalities occurred in the absence of interspecific competition, but that early emergence of *Bromus* at the high density level significantly reduced the performance of experimental *Coleogyne* seedlings compared to control seedlings. Due to different life history strategies, experimental *Coleogyne* populations experienced major disadvantages in competing for space and moisture when planting simultaneously with *Bromus* seedlings, or when planted four weeks after *Bromus* establishment.

In this study, *Bromus* at high density was shown to have early, adverse impact on various growth parameters of experimental *Coleogyne* seedling populations, including increased root/shoot ratio, and decreased shoot growth and water potential values. Increased mortality and decreased growth among experimental populations were indications of water stress, as evidenced by significantly lower (more negative) shoot water potential values under local crowding compared to the control population.

Time of planting also played a major role in early *Coleogyne* mortality and reduced growth of experimental seedling populations. Among the three periods of planting, mortality of experimental *Coleogyne* seedlings was highest when established four weeks after *Bromus*. The species that germinates first is likely to have a competitive advantage (Florentine and Fox 2003). In this study, *Coleogyne* must become established at least four weeks prior to the emergence of Bromus in order to gain a competitive advantage. Earlier establishment of *Coleogyne* seedlings than the competing *Bromus* suggested that early germination of *Coleogyne* would enhance seedling survival and subsequent growth, primarily through a more rapid development of root biomass. For this reason, early germinants would be superior competitors relative to later germinants (Fowler 1986; Florentine and Fox 2003).

One reason for the observed reduction of *Coleogyne* shoot growth in the presence of *B. tectorum* may be found in the biomass allocation patterns (Pendleton et al. 1999). Interspecific competition resulted in an altered allocation pattern for *Coleogyne* (Pendleton et al. 1999). In mixture with *Bromus, Coleogyne* root length and root/shoot ratio increased when grown with *Bromus* in this study. In the absence of competition from *Bromus,* root/shoot ratio of *Coleogyne* was reduced. However, when competition was introduced, the root/shoot ratio of *Coleogyne* actually increased (Pendleton et al. 1999), which is in agreement with this study. Therefore, root competition in the very early stages of seedling growth would be an important factor contributing to the death of *Coleogyne* seedlings (Lei 2004).

The timing of germination in *Coleogyne* varies in time and space, depending on the seasonal moisture availability. Under field conditions where soil moisture is sufficient for seedling recruitment of *Coleogyne, Bromus* is also stimulated (Lei, personal observation). Consequently, newly emerged *Coleogyne* seedlings are often concealed among dense carpets of *Bromus* and other herbaceous plant species. Early emergence would give *Coleogyne* seedlings the best possible opportunity to gain more control of available space and resources compared to establishment of *Bromus* four weeks after, or at the same time as, *Coleogyne* seedlings. Availability of soil moisture, along with early seed germination at least four weeks prior to *Bromus* emergence would be two ideal conditions for *Coleogyne* seedlings to establish and survive with low mortality rates.

This pot trial study demonstrated that interactive effects of *Bromus* density and time of planting significantly, reduce the early survival and growth of experimental *Coleogyne* seedlings. A combination of increasing neighboring *Bromus* density and early *Bromus* emergence resulted in a direct reduction in the survival and growth of *Coleogyne* seedlings. Competition is ubiquitous, and can be examined directly in both monocultures and mixed cultures. This study also revealed that single seedlings of *Coleogyne* that grew alone had the lowest mortality rate, grew significantly better, and produced more biomass than *Coleogyne* seedlings that were locally crowded and/or established four weeks after *Bromus* emergence. However, the *Bromus* density * time of planting interaction was not statistically significant for basal shoot diameter, as well as root and shoot biomass of *Coleogyne* seedlings, indicating that both high density and early emergence of *Bromus* had a similar adverse effect on biomass and shoot diameter of early *Coleogyne* seedling populations.

Ecological Implications

In this pot trial study, early mortality and limited growth reflect the poor competitive ability of *Coleogyne* seedlings in the natural field. Attempting to revegetate *Coleogyne* in natural habitats has a limited success. Two contributing factors are competition with invasive, ruderal (exotic) species and the extremely slow growth of *Coleogyne* (Pendleton et al. 1999). Because of different life history strategies, *Coleogyne* seedlings generally did not compete well with species of *Bromus.*

Although a common reclamation practice, fertilization may place slow-growing *Coleogyne* at a competitive disadvantage (Pendleton et al. 1999). Laboratory studies also demonstrate that *Coleogyne* seedlings exhibited reduced survivorship and competitive ability when grown in competition with neighboring *B. tectorum* under high level of fertilization. The rapid growth of *B. tectorum* in response to fertilization shaded out the slow-growing *Coleogyne,* resulting in stunted growth or death of *Coleogyne* (Pendleton et al. 1999). For these reasons, early seed germination and seedling establishment of *Coleogyne* at least four weeks prior to the emergence of *Bromus* and other ruderal species at low soil fertility would be ideal conditions for them to establish and survive.

Finally, one must realize that *Coleogyne* seedlings grown in mixed cultures were at densities lower than those normally encountered in field situations. Extrapolating from controlled experimental results to field conditions should be done with caution because there are many biotic and abiotic factors interacting with each other, and because there are multiple limiting factors in the field (Florentine and Fox 2003; Lei 2004). During the period of growth associated with establishment, competition for limited space and resources (water, nutrients, and light) may intensify as individual plants develop (Florentine and Fox 2003). Although *Coleogyne* are at a competitive disadvantage in disturbed sites dominated by ruderal vegetation, long-term field and laboratory research studies are required to determine exactly which resources these *Coleogyne* and *Bromus* are competing for. This study, however, is an attempt to mimic natural field conditions, and to understand how newly recruited *Coleogyne* seedlings compete with various cohorts of *Bromus,* with respect to neighboring density and time of planting.

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