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GROWTH AND WATER RELATIONS OF NATIVE WHEATGRASS  
POPULATIONS

by

Brian P. Bell

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

UTAH STATE UNIVERSITY  
Logan, Utah

2008

## ABSTRACT

## Growth and Water Relations of Native Wheatgrass Populations

by

Brian P. Bell, Master of Science

Utah State University, 2008

Major Professor: Dr. Christopher A. Call  
Department: Wildland Resources

Screening populations for development into released plant materials can be done inexpensively and in a timely manner. A common approach has been to quantify the amount of shoot dry mass produced as a surrogate for competitiveness. Besides dry mass production, other morphological characteristics have been employed, but physiological parameters have received less emphasis. Dry mass production may be an important characteristic, but identifying the traits responsible can be just as imperative. Populations with greater drought tolerance may be less impacted by competition for water from weeds, which could lead to greater establishment of desirable grasses on disturbed landscapes.

The objective for chapter 2 was to evaluate the effects of cheatgrass competition on the growth and water relations of three Snake River wheatgrass (*Elymus wawawaiensis*) populations and two bluebunch wheatgrass (*Pseudoroegneria spicata*) populations in the seedling stage in a greenhouse setting. The treatments were 1) containers with a single wheatgrass plant or 2) containers with one wheatgrass and one

cheatgrass plant. Containers were watered gravimetrically to 11.5% soil-water content, regardless of treatment, every few days until harvested on day 35. Cheatgrass competition reduced root dry mass, shoot dry mass, leaf area, leaf number, tiller number, xylem pressure potential, and stomatal conductance. The bluebunch wheatgrass populations generally had more negative xylem pressure potential, higher stomatal conductance, and higher shoot dry mass, while the Snake River populations had higher specific leaf area and less negative xylem pressure potentials.

The objective for chapter 3 was to evaluate the effects of planting density on the growth and water relations over a 2-year period among five Snake River wheatgrass populations, one thickspike wheatgrass (*Elymus lanceolatus*) population, and three interspecific hybrids. High (25 plants/m<sup>2</sup>) and low-density (7.8 plants/m<sup>2</sup>) plots of each grass were transplanted to Millville, Utah in the spring of 2005 and 2006 intended to generate low and high resource availability environments, respectively. Thickspike wheatgrass had the highest shoot dry mass and least negative xylem pressure potential, the hybrids were intermediate, and the Snake River wheatgrasses were least productive and more water stressed.

The primary benefit of this thesis will be through identifying the potential for developing these populations into improved plant materials and releasing them for commercial use in degraded rangelands across the Intermountain West. These new plant materials may also help transition damaged rangelands towards more desirable stable states composed of lower abundances of invasive annual grasses.



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Brian P. Bell

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## CHAPTER 1

### INTRODUCTION

Rangelands cover approximately 445 million ha in the United States, of which 283 million are administered by public agencies (Holechek 2001). Prior to European settlement, the rangelands of the Great Basin were comprised of shrubs with perennial bunchgrasses and forbs in the understory (Miller et al. 1994). Fire always played an important role in shaping rangeland ecosystems, but post-European settlement modified fire frequency, altering ecosystem composition and function (Norton et al. 2004; Bradley et al. 2006). Europeans introduced livestock as well as exotic species, particularly the winter annual grass *Bromus tectorum* L. (cheatgrass), which thrived in its newly adopted landscape. Cheatgrass has been estimated to dominate about 1.3 million ha of public land in the Great Basin with another 31 million ha infested or vulnerable to cheatgrass invasion (Pellant and Hall 1994). Monodominant stands of cheatgrass form a continuous fuel load upon senescence, awaiting potential wildfire when environmental conditions comply. The presence of cheatgrass lengthens the fire season (Pellant 2002) and increases fire frequency (Whisenant 1990), thereby reducing establishment opportunities for other vegetation.

On federally administered lands of the Great Basin, the number of fires occurring per unit area has doubled from 1988 to 1999, and the average area burned has increased almost five-fold (Pyke et al. 2003). Not all the burned lands are reseeded or rehabilitated, but rehabilitation projects increased from 180 to 720 projects per million ha within the Great Basin region over the same period (Pyke et al. 2003). Rehabilitation success is dependent upon reseeding with the proper technique when environmental conditions

favor seedling establishment. The choice of species for reseeding efforts varies, depending primarily on climate and vegetation habitat type.

Demand for native and non-native species in the Great Basin originates primarily from federal land management agencies like the U.S. Forest Service (USFS) and the Bureau of Land Management (BLM). These agencies use seed to rehabilitate areas disturbed by a variety of agents ranging from fire to mining. In fiscal year 2008 the BLM centralized seed buy (Denver, Colorado) alone purchased 149,628 kg of 'Secar' Snake River wheatgrass (*Elymus wawawaiensis* J. Carlson and Barkworth) at a price of \$4,867,000 (Elaine Flick, BLM, personal communication). With many different grass, forb, shrub, and tree species available, the market for available species is diverse and the demand can be quite high. A 2003 survey of the National Forests in Oregon and Washington reported that 336,487 kg of 20 different native and introduced grasses were used for reseeding efforts (Aubry et al. 2005). Annual demand may fluctuate, but seed will be in demand as long as a procurement budget is available and a workforce is in place to manage the projects.

The question asked by land managers is what kinds of species should be used when reseeding a landscape after a disturbance, native or non-native? If the species is native, should it come from a local population source, or will any population suffice? Surveys done on BLM lands of the Great Basin found an average of 4 to 5 species used per reseeding, with 1 or 2 of those species being native (Richards et al. 1998; Pyke et al. 2003). The most common native species used for reseeding are *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young, *Atriplex canescens* (Pursh) Nutt., and *Leymus cinereus* (Scribn. & Merr.) A. Löve, while the most common introduced species are

*Medicago sativa* L., *Sanguisorba minor* Scop., and *Agropyron desertorum* (Fisch. ex Link) Schult. (Richards et al. 1998; Pyke et al. 2003). Of the six species mentioned above, only one is a native grass.

A few reasons why native grasses are used less frequently than introduced species are poor establishment, more expensive seed, and limited adaptation (Pellant and Monsen 1993; Lesica and DeLuca 1996). Despite these limitations, the percentage of native seed in seed mixtures has increased over time on BLM-administered lands (Pyke et al. 2003). The same meta-analysis reported that, by the fifth year following reseeding, the percentage composition of native species exceeded introduced species on BLM lands of the Great Basin (Pyke et al. 2003). Using native species on rehabilitated landscapes in the Intermountain Region is increasing (Pellant and Monsen 1993; Lesica and DeLuca 1996), so developing new plant materials with higher competitiveness and productivity than current materials may help counter the dominance of invasives.

Besides altering the fire regime, cheatgrass may come to dominate rangelands and displace native grasses as it gains a competitive advantage due to earlier fall germination and superior low-temperature growth than native cool-season perennial grasses (Harris and Wilson 1970; Aguirre and Johnson 1991; Pyke and Novak 1994). Cheatgrass produces more root biomass in winter and possesses a higher relative growth rate than other cool-season grasses commonly found in the western U.S. (Harris and Wilson 1970; Aguirre and Johnson 1991; Pyke and Novak 1994; Arredondo et al. 1998). Grasses can effectively compete for resources through a combination of mechanisms by decreasing the availability of light, water, and nutrients.



Plant populations developed for western rangelands need to be competitive against cheatgrass and other exotic weeds, while utilizing resources efficiently and producing adequate amounts of seed for perpetuating stands and forage for wildlife and livestock. Reducing resource availability to other species by preempting resources enhances the competitive outcome of the species that first uses that resource. Higher resource acquisition and higher competitive ability against invasives may prove to be valuable criteria when selecting native grass populations for their rangeland revegetation potential.

Grasses have been shown to reduce photosynthetically active radiation at the soil surface, thus reducing available light to potential competitors (Tang et al. 1988; Thompson and Harper 1988). Tang et al. (1988) found that the grass *Miscanthus sinensis* Anderson reduced available light and carbon gain of oak seedlings (*Quercus serrata* Thunb.), thereby constraining the oaks' ability to encroach into grassland-dominated communities. Reducing available light by shading one's opponent is primarily achieved through production of above-ground biomass, but this may not be important in western rangelands where light is not the limiting factor.

Exotic grasses have been shown to be effective competitors for water with native species. Davis and Mooney (1985) found that seedling growth of the native shrub *Baccharis pilularis* DC. was inhibited by competition with exotic annual grasses for soil moisture. Elliott and White (1987) partially attributed declining ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) reestablishment following wildfire to soil-water competition from two exotic perennial grasses, *Agropyron desertorum* and *Dactylis glomerata* L. Eissenstat and Caldwell (1988) have shown that *A. desertorum* depletes soil



water content faster, and to a greater degree, than does the native bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve). In addition, they found that *A. desertorum* more effectively competed for water than the dominant shrub *Artemisia tridentata* Nutt. ssp. *wyomingensis*.

Cheatgrass is generally more profuse in stands of *P. spicata* than in stands of *A. desertorum* because root proliferation of cheatgrass occurs when *A. desertorum* is actively reducing available soil moisture, which occurs faster than its counterpart, *P. spicata* (Eissenstat and Caldwell 1988). Another study showed that stands of the native species *Hesperostipa comata* (Trin. & Rupr.) Barkworth and *Chrysothamnus viscidiflorus* (Hook.) Nutt. had lower soil-water content when cheatgrass was present than when it was absent (Melgoza et al. 1990). A similar study (Booth et al. 2003a) showed faster soil moisture reduction in monodominant cheatgrass stands than in stands of *Elymus elymoides* (Raf.) Swezey and *A. tridentata*. Kulmatiski et al. (2006) also found that shallow soils in fields of exotics dry out earlier in the growing season than fields of natives. These results suggest that reducing soil water content may enhance overall competitive ability by limiting water available to germinating seedlings and coexisting species.

Exotic grasses have also been shown to acquire nitrogen resources faster than native grasses and shrubs, thus contributing to their persistence on western rangelands. Elliot and White (1987) found lower soil nitrate concentrations in stands of the exotic *Dactylis glomerata* than in stands of the native *Bouteloua gracilis* (Kunth) Lag. ex Griffiths. Nitrogen utilization by cheatgrass in concentrated patches was higher than for native shrub and perennial grasses (Duke and Caldwell 2001). *Agropyron desertorum*

acquired  $^{15}\text{N}$  faster than *Artemisia* in a simulated rainfall event (Ivans et al. 2003). Cheatgrass was the most effective in acquiring  $^{15}\text{N}$  in spring and autumn when competing against *A. tridentata* and *E. elymoides* (Booth et al. 2003a). Gross rates of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  consumption were higher in cheatgrass stands than in *Artemisia* stands (Booth et al. 2003b). Greater nitrogen uptake of cheatgrass may also be an important mechanism limiting native perennial establishment.

The traits responsible for greater competitive ability of cheatgrass relative to native perennial grasses include high rates of water and nitrogen extraction (Eissenstat and Caldwell 1988; Melgoza et al. 1990; Duke and Caldwell 2001; Booth et al. 2003a, 2003b; Kulmatiski et al. 2006), which are likely due to superior shoot and root growth (Harris and Wilson 1970; Aguirre and Johnson 1991; Pyke and Novak 1994; Arredondo et al. 1998). Thus, these are traits that should be considered for selecting plant materials that effectively compete with cheatgrass. Possession of only one or two traits may not fully assure that a species will be an effective competitor.

Native grass populations displaying attributes similar to cheatgrass may have the most potential to compete with it. Designing a screening protocol to determine the effects cheatgrass has on growth, while simultaneously understanding the physiological mechanisms enhancing growth, may elucidate more practical methods of identifying populations with greater competitive ability. Populations intended for commercial use may be selected for traits varying from seed production to salt tolerance. However, these may not be the most important criteria when developing plants for rangelands.

Competitive ability may be more important for combating the current procession of invasive species. Studies have shown that, regardless of neighbor species identity,

increasing neighbor mass results in greater competitive suppression (Goldberg 1987; Miller and Werner 1987; Wilson and Tilman 1991; Gerry and Wilson 1995; Francis and Pyke 1996; Dyer and Rice 1999; Mulligan and Kirkman 2002). Above-ground biomass production may be an important means of quantifying a plant's response to increasing competition from neighbors.

Screening populations for development into released plant materials can be done inexpensively and in a timely manner. A common approach has been to quantify the amount of shoot dry mass produced as a surrogate for competitiveness. Besides dry-mass production, other morphological characteristics have been employed, but physiological parameters have received less emphasis mainly due to time and budget constraints. Dry-mass production may be an important characteristic, but understanding which traits are responsible for greater biomass production may be more insightful.

Below-ground processes are also important to resource acquisition in dryland environments because soil moisture can be the limiting resource. In semi-arid ecosystems competitive ability of grasses has been associated with rates of water extraction (Eissenstat and Caldwell 1988; Melgoza et al. 1990; Kremer and Running 1996; Duke and Caldwell 2001; Booth et al. 2003a, 2003b). If plants are not competitive for below-ground resources, this will be manifested in limited above-ground dry-mass production. By acquiring limited water resources, the rooting system of a plant in a semi-arid environment plays an integral role in maintaining favorable water balance for maximum photosynthesis. Below-ground processes cannot be ignored when screening populations for resource acquisition and competitive ability, but measuring uptake of stable isotopes is costly. Other methods include quantifying root biomass production and rooting

morphology and phenology. Measuring a single variable can't determine whether a population has a competitive advantage, but defining a suite of variables may be an informative approach for selecting populations for competitive ability.

The USDA-Agricultural Research Service (ARS) plays a role in developing improved plant materials for a wide variety of applications on public and private lands. These materials may be selected for such traits as salt tolerance, drought tolerance, seedling vigor, seed and forage production, grazing preference, and grazing tolerance. The focus of this research is to evaluate and compare native wheatgrass populations of *Elymus wawawaiensis*, *E. lanceolatus* (Scribner & J.G. Smith) Gould, and *P. spicata*, including some cultivars. The released cultivars serve as standards to which experimental populations may be compared. One component of the study will address the effects of competition at the seedling stage, while the other will look at the effects of density on growth and water relations of established plants.

Specifically, I will characterize: 1) the effects of cheatgrass competition on the growth and leaf water relations of native wheatgrasses being developed used for reseeding, and 2) the productivity of native wheatgrasses under contrasting levels of resource availability, as induced by two planting densities. The ability of native wheatgrasses to compete will be assessed by comparing shoot and root biomass production, while simultaneously maintaining a favorable water balance. Resource acquisition of the populations used in this study will be assessed by quantifying shoot and root biomass production, xylem water potential, and stomatal conductance.

The primary benefit of this study will be through identifying the potential for developing these populations into improved plant materials and their release for

commercial use on degraded rangelands across the Intermountain West. These new plant materials may also help transition damaged rangelands toward a more desirable stable state composed of lower abundances of invasive annual species.

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## CHAPTER 2

EFFECTS OF CHEATGRASS COMPETITION ON GROWTH AND  
WATER RELATIONS OF PERENNIAL WHEATGRASS POPULATIONS

## ABSTRACT

I investigated the effects of cheatgrass (*Bromus tectorum* L.) competition on one released cultivar and one experimental population of bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love), and one released cultivar and two experimental populations of Snake River wheatgrass (*Elymus wawawaiensis* J. Carlson & Barkworth) at the seedling stage in three trials under a greenhouse setting. The treatments were 1) 0.5-L containers with a single wheatgrass plant or 2) 0.5-L containers with one wheatgrass and one cheatgrass plant. Containers were watered to 11.5% soil-water content every few days regardless of planting treatment, until harvested on day 35. Cheatgrass competition reduced root dry mass, shoot dry mass, leaf area, leaf number, tiller number stomatal conductance, and xylem pressure potential of perennial wheatgrasses. The bluebunch wheatgrass populations generally had more negative xylem water potential, higher stomatal conductance, and higher shoot dry mass, while the Snake River wheatgrass populations had higher specific leaf area and greater leaf number. 'Goldar' bluebunch wheatgrass had the highest stomatal conductance and shoot dry mass with cheatgrass, and 'Secar' Snake River wheatgrass was most similar to Goldar. Identifying populations with traits least affected by cheatgrass competition during the seedling stage may prove most useful for developing plant materials to combat the current dominance of this invasive species.

## INTRODUCTION

Problems facing rangeland resource managers continue to escalate, especially in the areas of recent land conversion due to wild fires, but controlling the expansion of exotic species across rangelands has been and should remain a high priority. The invasive annual, cheatgrass (*Bromus tectorum* L.), dominates approximately 1.3 million ha in the Great Basin, with another 31 million ha infested or vulnerable to cheatgrass invasion (Pellant and Hall 1994). Cheatgrass has damaged ecosystem function and composition, perhaps irreversibly (Norton et al. 2004; Bradley et al. 2006). The cheatgrass threat may never cease, so plant materials with traits that confer greater competitive ability must be developed to thwart the current procession.

One reason cheatgrass gains a competitive advantage over native perennial grass seedlings is that it germinates earlier and faster in both autumn and spring, being able to grow at colder temperatures (Harris and Wilson 1970; Aguirre and Johnson 1991; Pyke and Novak 1994). It is also able to produce more root biomass over winter, and it has a higher relative growth rate than other western range grasses (Harris and Wilson 1970; Svejcar 1990; Aguirre and Johnson 1991; Pyke and Novak 1994; Arredondo et al. 1998; Peek et al. 2005). Plant materials developed for western rangelands need to be competitive against cheatgrass and other exotic weeds, while utilizing resources efficiently and producing adequate amounts of seed and forage for both wild and domestic foragers.

Many studies (Hull 1963; Buman et al. 1988; Melgoza et al. 1990; Jaindl et al. 1994; Nasri and Doescher 1995; Francis and Pyke 1996; Goodwin et al. 1999; Booth et al. 2003a) have reported a reduction in above-ground perennial biomass in response to

cheatgrass competition, but only two have documented the effects of cheatgrass competition on seedling establishment (Hull 1963; Buman et al. 1988). Both of these studies used the introduced bunchgrass, crested wheatgrass (*Agropyron desertorum* [Fisch. ex Link] Schult.). The seedling stage is the most vulnerable period for establishment, and populations displaying traits least affected by cheatgrass during this period may prove to be valuable for plant material developers.

Grasses can effectively compete for resources through a combination of mechanisms, e.g., by decreasing the availability of light, water, and nutrients to competitors. Reducing resources of other species by preemptive uptake will enhance competitive ability. Grasses have been shown to reduce photosynthetically active radiation reaching the soil surface, thus limiting available light to potential competitors (Tang et al. 1988; Thompson and Harper 1988). However, in semi-arid ecosystems this may not be the most important mechanism limiting the establishment of native perennial wheatgrasses. In arid and semi-arid ecosystems water is the limiting resource inhibiting plant growth.

Exotic grasses effectively outcompete native species for water and nutrients. Research has shown that invasive grasses deplete soil water faster and to lower levels than native grasses and shrubs (Davis and Mooney 1985; Elliott and White 1987; Eissenstat and Caldwell 1988; Melgoza et al. 1990; Kremer and Running 1996; Booth et al. 2003a; Kulmatiski et al. 2006). Research has also documented the superior ability of invasive grasses to acquire nitrogen when competing against native grasses and shrubs (Duke and Caldwell 2001; Booth et al. 2003a, 2003b; Ivans et al. 2003). The superior capacity of cheatgrass to acquire water and nitrogen leads to its dominance over native

species commonly found on rangelands. Identifying native species that rival cheatgrass for resource use may diminish this annual's preeminence on western rangelands. However, measuring resource acquisition using stable isotope methodologies can be cost prohibitive.

An economical method to identify native grass populations that may adequately compete against cheatgrass may be to look for similar morphological characteristics. Cheatgrass has higher specific leaf area and higher root and shoot relative growth rates than native perennial grasses (Harris and Wilson 1970; Svejcar 1990; Aguirre and Johnson 1991; Pyke and Novak 1994; Arredondo et al. 1998). Traits of native perennial grasses that may be similar to cheatgrass need to be identified and quantified to help direct the development of plant materials that can potentially compete on cheatgrass-infested landscapes. Possession of one or two traits cannot fully assure that a species will be an effective competitor.

For this study, I have chosen not only to document various physiological and morphological traits of native wheatgrass populations, but also to examine the impact of cheatgrass competition on these traits. Numerous studies have already documented the expedient growth and resource acquisition of cheatgrass, but few have looked at the effects cheatgrass has on growth and water-relations of competing seedlings. I chose to use a widespread species of the Intermountain West, bluebunch wheatgrass (BBWG) (*Pseudoroegneria spicata* [Pursh] A. Love), and a functionally similar species once thought to be synonymous with it, Snake River wheatgrass (SRWG) (*Elymus wawawaiensis* J. Carlson and Barkworth). Both of these cool-season bunchgrasses are commonly used to restore landscapes where cheatgrass may already occur, but SRWG

has been found to be more drought and grazing tolerant (Morrison and Kelley 1981; Jones and Nielson 1997; Kindiger and Conley 2002).

Three greenhouse trials investigating the effects of cheatgrass on the water relations and growth of BBWG and SRWG populations were conducted to determine their competitiveness when grown with cheatgrass. The objective of this study is to identify populations least affected by competition with cheatgrass, defined as minimal percentage reduction of shoot and root dry mass, xylem pressure potential, and stomatal conductance in the presence of cheatgrass. I hypothesized the Snake River wheatgrasses would be less affected than the bluebunch wheatgrasses as demonstrated by greater productivity and more favorable water-relations.

## METHODS

Three 5-week trials were conducted in the USDA-ARS greenhouse on the Utah State University campus, Logan, UT, from 12 Jan. 2005 to 17 Feb. 2005 (Trial 1), 20 June 2005 to 26 July 2005 (Trial 2), and 12 Jan. 2006 to 17 Feb. 2006 (Trial 3). Plant materials for Trial 1 were cheatgrass, Goldar and P-24 BBWGs, and E-45 SRWG. Plant materials for Trial 2 were cheatgrass, Goldar and P-24 BBWGs, and Secar and E-45 SRWGs. Plant materials for Trial 3 were cheatgrass, Goldar and P-24 BBWGs; and Secar, Discovery, and E-45 SRWGs. Both wheatgrass species are perennial tussock grasses native to western North America, and cheatgrass is an exotic annual native to Eurasia. Goldar BBWG, released in 1989, was selected from a 1934 collection made on Mallery Ridge in the Umatilla National Forest near Asotin, WA (Native Seed Network 2004). The P-24 BBWG experimental population was developed from a population

collected near Lind, WA by three cycles of selection for seedling vigor and seed-head production. Secar SRWG was released in 1980 by the Pullman, WA, USDA-NRCS Plant Materials Center. It originated from a population collected in the Snake River gorge in close proximity to Lewiston, ID (USDA, NRCS 2007). 'Discovery' SRWG was developed by intermating collections made in southeastern Washington and adjacent central Idaho. The E-45 SRWG experimental population was developed from Discovery by two cycles of selection for seedling vigor and seed-head production. Seed of P-24, Discovery, and E-45 were harvested in 2003 from USDA-ARS plots located in Millville, UT, while seed of Goldar and Secar was purchased from a seed company in 2004. Cheatgrass seed was collected approximately 10 km west of Logan, UT in the summer of 2003.

All trials were conducted in a greenhouse without artificial light. Average daily temperature for Trial 1 was 18.5° C, with a low of 13.5° C and a high of 28° C. For Trial 3 average daily temperature was 21.4° C, with a low of 17° C and a high of 32° C. Trial 2 has no temperature data due to equipment malfunction. Wheatgrass seed was wetted 2 days earlier than cheatgrass seed to adjust for the latter's faster germination. The monoculture treatment consisted of containers with one wheatgrass plant, and the mixture treatment consisted of containers with one wheatgrass plant and one cheatgrass plant. Containers used for the study were 0.5 L, red-colored plastic cups filled with 525 g of Kidman fine sandy loam (coarse-loamy, mixed, mesic Calcic Haploxerolls, Amalga, UT) sifted through a 2-mm brass screen. Each container received 110 ml of tap water to facilitate the subsequent transplanting of seedlings. Containers were gravimetrically weighed every 2 to 4 days and maintained at 11.5% soil-water content regardless of



treatment. Containers were watered a total of 10 times throughout the trial period. Each container received a single 20.0-ml fertilization treatment of Miracle-Grow (Stern's Nurseries, Geneva, NY; 20:20:20 N-P<sub>2</sub>O<sub>5</sub>-K<sub>2</sub>O) 2 weeks (2 Feb. 2005, 7 July 2005, and 2 Feb. 2006) after planting.

Leaves and tillers were counted at harvest on 17 Feb. 2005, 26 July 2005, and 17 Feb. 2006. Leaf area was measured three times on the same sample using a LI-3000 portable leaf-area meter (Li-Cor Inc., Lincoln, NE). Roots were rinsed with water to remove soil. For Trial 1 roots were only analyzed for wheatgrasses grown alone. Roots were not collected for Trial 2. Wheatgrass and cheatgrass roots were separated in Trial 3. Perennial shoot and root dry weights were measured after oven-drying at 60° C for 48 hours. Specific leaf area (SLA) was calculated by dividing leaf area by shoot dry weight.

Stomatal conductance was measured between 1000 and 1400 hours on each plant before harvest using a LI-1600 steady-state porometer (Li-Cor Inc., Lincoln, NE) in Trial 1 (12 replications) and Trial 2 (12 replications), and with a leaf porometer Model SC-1 (Decagon Devices, Inc., Pullman, WA) in Trial 3 (11 replications). For both Trials 1 and 3, xylem pressure potential was measured between 1000 and 1400 hours on each target (native wheatgrass) plant (12 replications) before harvest using a Scholander-type pressure chamber according to Boyer (1967). Xylem pressure potential was not measured in Trial 2.

All data were tested for normality by examining histograms and normal probability plots of residuals. For non-normal data, a transformation was chosen to maximize the *P*-value for the Shapiro-Wilk test (Zar 1984). Stomatal conductance (Trial 3), xylem pressure potential (Trial 3), and root-to-shoot dry-mass ratio (Trials 1 and 3)

data were normalized by using a natural-log transformation. Root dry mass (Trials 1 and 3) and stomatal conductance (Trials 1 and 2) data were normalized by a cube-root transformation. Leaf area (Trial 2) data were normalized by a square-root transformation. No other variables required transformation. All trials were analyzed as completely randomized designs. Data were analyzed with SAS (SAS Institute 1998) using the MIXED procedure with treatment and population as fixed effects. Least-squares means were calculated from non-transformed data, but mean separations (least significant difference = 0.05) were based on transformed data as required. Differences were considered nonsignificant if  $P$  exceeded 0.05.

## RESULTS

### **Trial 1 (winter 2005)**

Xylem pressure potential for E-45 SRWG was less negative than for Goldar or P-24 BBWGs ( $P < 0.05$ ), but the treatment and interaction effects were not significant (Tables 2-1, 2-2). Cheatgrass reduced stomatal conductance by 30% ( $P < 0.001$ ), and Goldar and P-24 BBWGs were higher than E-45 SRWG ( $P < 0.05$ ) (Table 2-2). The population x treatment interaction was not significant (Table 2-1).

Cheatgrass competition reduced shoot dry mass production by 28% ( $P < 0.001$ ), and Goldar BBWG produced more dry mass than P-24 BBWG and E-45 SRWG ( $P < 0.01$ ) (Tables 2-1, 2-2). The population x treatment interaction was not significant (Table 2-1). Cheatgrass competition reduced tiller number by 19% ( $P < 0.01$ , Table 2-2). Populations E-45 SRWG and P-24 BBWG produced more tillers than Goldar BBWG ( $P < 0.01$ , Table 2-2), but the interaction was not significant (Table 2-1). Goldar BBWG



had more leaves per tiller than both P-24 BBWG and E-45 SRWG ( $P < 0.001$ , Table 2-2), but the treatment effect and interaction were not significant (Table 2-1).

Cheatgrass competition reduced leaf area by 36% ( $P < 0.001$ ), and E-45 SRWG and Goldar BBWG produced more leaf area than P-24 BBWG ( $P < 0.01$ ) (Tables 2-1, 2-2). The population x treatment interaction was not significant (Table 2-1). Cheatgrass competition reduced SLA by 11% ( $P < 0.01$ ), and E-45 SRWG had higher SLA than Goldar and P-24 BBWGs ( $P < 0.001$ ) (Table 2-2). The population x treatment interaction was not significant (Table 2-1).

Target plant roots were not separated from the cheatgrass roots in Trial 1, so only the treatment where the wheatgrasses were grown alone is presented. The population effect for root dry mass was not significant and neither was the root-to-shoot ratio (Table 2-1).

### **Trial 2 (summer 2005)**

Population P-24 BBWG had the highest stomatal conductance, Goldar BBWG and Secar SRWG were intermediate, and E-45 SRWG had the lowest ( $P < 0.001$ , Table 2-3), but there was no significant effect for treatment or population x treatment interaction (Table 2-1).

Goldar BBWG and Secar SRWG had the highest shoot dry mass, P-24 BBWG was intermediate, and E-45 SRWG had the lowest when grown without cheatgrass ( $P < 0.05$ , Table 2-3). When the populations were grown with cheatgrass they were not statistically different from one another (Table 2-3). However, cheatgrass competition reduced shoot dry mass production by 33% ( $P < 0.001$ , Table 2-3), and shoot dry mass had a significant population x treatment interaction ( $P < 0.05$ , Table 2-1). Percentage reduction

in shoot dry mass due to cheatgrass was 7% for E-45 SRWG, 29% for P-24 BBWG, 30% for Secar SRWG, and 50% for Goldar BBWG (Figure 2-1). Overall, the SRWGs had 11% more shoot dry mass than the BBWGs when grown with cheatgrass ( $P < 0.05$ , Table 2-3). Cheatgrass competition reduced tiller number by 30% ( $P < 0.001$ , Table 2-3), but the population and interaction effects were not significant (Table 2-1).

Goldar BBWG and Secar SRWG had the highest leaf area when grown without cheatgrass, E-45 SRWG was intermediate, and P-24 BBWG had the lowest ( $P < 0.05$ , Table 2-3). Population E-45 SRWG had the highest leaf area when grown with cheatgrass, and Secar SRWG, Goldar BBWG and P-24 BBWG had the lowest ( $P < 0.05$ , Table 2-3). Cheatgrass competition reduced leaf area by 33% ( $P < 0.001$ , Table 2-3). Leaf area had a significant interaction for population and treatment effects ( $P < 0.05$ , Table 2-1). Percentage reduction in leaf area due to cheatgrass competition was 9% for E-45 SRWG, 29% for Secar SRWG, 35% for P-24 BBWG, and 52% for Goldar BBWG (Table 2-3). Overall, the SRWGs had 39% more leaf area than the BBWGs when grown with cheatgrass ( $P < 0.05$ , Table 2-3). Population E-45 SRWG had a higher SLA than P-24 BBWG ( $P < 0.001$ , Table 2-3) with Goldar BBWG and Secar SRWG intermediate, but the treatment and interaction effects were not significant (Table 2-1). Overall, SLA was 20% greater for the SRWGs than for BBWGs ( $P < 0.001$ , Table 2-3).

### **Trial 3 (winter 2006)**

Cheatgrass competition reduced xylem pressure potential by 7% ( $P < 0.05$ , Table 2-4). Xylem pressure potential for Secar SRWG was less negative than Goldar or P-24 BBWGs ( $P < 0.05$ , Table 2-4), but E-45 and Discovery SRWGs were not significantly different from the other populations. The population x treatment interaction was not

significant (Tables 2-1). Cheatgrass reduced stomatal conductance by 15% ( $P < 0.001$ ). Goldar BBWG was higher than E-45 SRWG, and Discovery and Secar SRWGs and P-24 BBWG were intermediate ( $P < 0.05$ , Table 2-4). Overall, the BBWGs had 12% higher stomatal conductance than the SRWGs ( $P < 0.05$ , Table 2-4). The population  $\times$  treatment interaction was not significant (Table 2-1).

Cheatgrass competition reduced shoot dry-mass by 31% ( $P < 0.001$ , Table 2-4). Shoot dry mass had a significant interaction for population and treatment ( $P < 0.05$ , Table 2-1). The BBWGs produced 13% more shoot dry mass than SRWGs ( $P < 0.01$ , Table 2-4). Cheatgrass reduced shoot dry mass by 8% for Goldar BBWG, 28% for Discovery SRWG, 33% for Secar SRWG, 37% for E-45 SRWG, and 45% for P-24 BBWG (Figure 2-1). Cheatgrass competition reduced tiller number by 13% ( $P < 0.05$ , Table 2-4). P-24 BBWG and Secar SRWG produced the most tillers, and Goldar BBWG and E-45 and Discovery SRWGs had the least ( $P < 0.05$ , Table 2-4), but Secar and E-45 SRWGs were not significantly different from one another. The population  $\times$  treatment interaction was not significant (Table 2-1). Goldar produced more leaves per tiller than all the other populations ( $P < 0.01$ , Table 2-4); however, there was no treatment effect or interaction (Table 2-1). Overall, the BBWGs produced 13% more leaves per tiller than the SRWGs ( $P < 0.001$ , Table 2-4).

Cheatgrass competition reduced leaf area by 36% ( $P < 0.001$ , Table 2-4), but the population and interaction effects were not significant (Table 2-1). Secar, E-45, and Discovery SRWGs had higher SLA than Goldar and P-24 BBWGs ( $P < 0.001$ , Table 2-4), but the treatment and interaction effects were not significant (Table 2-1). Overall, SLA was 19% greater for the SRWGs than for the BBWGs.

Cheatgrass competition reduced perennial root dry mass by 22% ( $P < 0.001$ , Table 2-4), but the population effect and interaction were not significant (Table 2-1). No significant population, treatment, or interaction effects were found for perennial root-to-shoot ratio (Table 2-1).

## DISCUSSION

Cheatgrass competition reduced shoot dry mass, leaf area, tiller number, root dry mass, specific leaf area, water potential, and stomatal conductance of the bluebunch and Snake River wheatgrasses. Many other studies have also reported a reduction in shoot dry mass of perennials due to cheatgrass competition (Hull 1963; Buman et al. 1988; Melgoza et al. 1990; Jaendl et al. 1994; Nasri and Doescher 1995; Francis and Pyke 1996; Goodwin et al. 1999; Booth et al. 2003a). However, data from experiments reported here do not support the hypothesis that SRWG was less affected by competition from cheatgrass than BBWG. In both winter trials (Trial 1 and 3), Goldar BBWG had the highest shoot dry mass and stomatal conductance, and E-45 SRWG had the lowest. In the summer trial (Trial 2), Secar SRWG had the highest shoot dry mass when competing with cheatgrass, but was not significantly different from any of the other populations. The major difference between the summer trial and winter trials was the former's lower SLA. For all variables, the species had similar ranking across trials.

The SRWGs maintained more favorable (less negative) xylem pressure potential and greater SLA than the BBWGs. More favorable xylem pressure potential of the SRWGs could have resulted from stomatal control of water loss through transpiration because SRWG had lower leaf conductance rates. However, a plant may be more

competitive with cheatgrass if it can pre-empt soil water by depleting soil moisture that cheatgrass may potentially use, while simultaneously maintaining a favorable pressure potential. As long as physiological utility and growth are not hindered by desiccation, pre-emption of soil water may be an important cheatgrass competition mechanism.

In all trials the SRWGs had higher SLA than the BBWGs. High SLA is associated with rapid early-season growth, high leaf-surface area, thin leaves, and high leaf-nitrogen concentration (Field and Mooney 1986; Körner 1989; Schulze et al. 1994; Poorter and Evans 1998; Evans and Poorter 2001; Rebetzke et al. 2004; Hoffman et al. 2005). Low SLA values result in reduced leaf area available for light interception, and thus photosynthesis, which may reduce overall growth. However, this was not the case for BBWG compared to SRWG. Even though BBWG had lower SLA, it had higher shoot dry mass. This may be explained by its higher stomatal conductance, which could be interpreted as higher photosynthetic output, resulting in more plant growth. Specific leaf area in the summer trial was almost half that of the two winter trials. Greater photosynthetically active radiation during the summer trial may have caused a reduction in leaf area available for photosynthesis because it was not needed. However, shoot dry mass among all three trials was similar.

In Trial 3 (winter 2006) Goldar BBWG showed the smallest percentage reduction (8%) in shoot dry-mass when grown with cheatgrass. However, in Trial 2 (summer 2005) Goldar BBWG had the lowest shoot dry mass and highest percentage reduction (52%) in shoot dry mass due to cheatgrass competition. This discrepancy may have been due to greater environmental stress from higher light and heat loads during the summer months, exacerbating stress from competition. The Secar SRWG population had the highest shoot

dry mass and second highest percentage reduction (31%) due to cheatgrass competition in Trial 2.

Cheatgrass competition is most critical at the seedling stage. Evaluation for seedling competition may prove to be critical for developing better plant materials for revegetating western rangelands. Compared to greenhouse experiments, effects of cheatgrass competition will be drastically greater under field conditions where cheatgrass seedlings can number in the thousands per  $m^2$  (Young and Evans 1978). Populations co-occurring with cheatgrass may not necessarily have any greater competitive ability than populations occurring in the absence of cheatgrass. Some have postulated that native perennial grass populations co-occurring with cheatgrass may be more tolerant of cheatgrass competition than populations found in the absence of cheatgrass. However, evaluation of Idaho fescue (*Festuca idahoensis* Elmer) populations showing persistence on degraded cheatgrass sites did not indicate a competitive advantage over populations found on pristine uninvaded sites (Nasri and Doescher 1995; Goodwin et al. 1999). In the field, cheatgrass usually germinates in the fall, and native perennial grasses germinate in the spring, giving cheatgrass a competitive advantage over native perennial grasses. It may be more informative to conduct a similar experiment using established cheatgrass plants with varying densities to document the effects of competition on the seedlings of native perennial grass populations.



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Table 2-1. Summary statistics for three greenhouse trials for xylem pressure potential, stomatal conductance, shoot dry mass, tiller number, leaves per tiller, leaf area, specific leaf area, root dry mass, and root-to-shoot ratio.

Xylem pressure potential (mPA)	Trial 1		Trial 2		Trial 3	
	df	F-Value	df	F-Value	df	F-Value
Treatment	1, 71	0.26 <sup>ns</sup>			1, 118	4.51*
Population	2, 71	4.57*			4, 118	3.05*
Trt*Pop	2, 71	0.02 <sup>ns</sup>			4, 118	0.41 <sup>ns</sup>
Stomatal conductance (mol m <sup>-2</sup> s <sup>-1</sup> )						
Treatment	1, 70	17.10***	1, 187	0.21 <sup>ns</sup>	1, 104	11.83***
Population	2, 70	3.17*	3, 187	9.22***	4, 104	5.36***
Trt*Pop	2, 70	0.67 <sup>ns</sup>	3, 187	0.42 <sup>ns</sup>	4, 104	0.53 <sup>ns</sup>
Shoot dry mass (mg)						
Treatment	1, 71	31.53***	1, 187	33.30***	1, 192	54.20***
Population	2, 71	5.59**	3, 187	2.79*	4, 192	2.50*
Trt*Pop	2, 71	0.98 <sup>ns</sup>	3, 187	3.79*	4, 192	2.77*
Tiller number						
Treatment	1, 71	8.24**	1, 187	21.91***	1, 174	8.56**
Population	2, 71	5.71**	3, 187	1.87 <sup>ns</sup>	4, 174	5.55***
Trt*Pop	2, 71	0.20 <sup>ns</sup>	3, 187	0.33 <sup>ns</sup>	4, 174	0.40 <sup>ns</sup>
Leaves per tiller						
Treatment	1, 71	1.26 <sup>ns</sup>			1, 173	0.17 <sup>ns</sup>
Population	2, 71	7.94***			4, 173	4.19**
Trt*Pop	2, 71	0.27 <sup>ns</sup>			4, 173	0.32 <sup>ns</sup>
Leaf area (cm <sup>2</sup> )						
Treatment	1, 71	44.42***	1, 187	31.54***	1, 188	61.95***
Population	2, 71	5.63**	3, 187	1.99 <sup>ns</sup>	4, 188	0.88 <sup>ns</sup>
Trt*Pop	2, 71	2.68 <sup>ns</sup>	3, 187	3.83*	4, 188	2.24 <sup>ns</sup>
Specific leaf area (m <sup>2</sup> kg <sup>-1</sup> )						
Treatment	1, 71	9.74**	1, 187	2.02 <sup>ns</sup>	1, 184	1.38 <sup>ns</sup>
Population	2, 71	28.87***	3, 187	21.20***	4, 184	8.07***
Trt*Pop	2, 71	0.51 <sup>ns</sup>	3, 187	0.42 <sup>ns</sup>	4, 184	0.58 <sup>ns</sup>
Root dry mass (g)						
Treatment	na	na			1, 161	13.20***
Population	2, 71	1.92 <sup>ns</sup>			4, 161	0.07 <sup>ns</sup>
Trt*Pop	na	na			4, 161	1.61 <sup>ns</sup>
Root-to-shoot ratio (g g <sup>-1</sup> )						
Treatment	na	na			1, 161	1.95 <sup>ns</sup>
Population	2, 71	0.01 <sup>ns</sup>			4, 161	1.22 <sup>ns</sup>
Trt*Pop	na	na			4, 161	0.48 <sup>ns</sup>

\*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001, ns - P > 0.05

Table 2-2. Xylem pressure potential ( $\Psi$ ), stomatal conductance ( $g_s$ ), shoot dry mass (DM), tiller number, leaves per tiller, leaf area, specific leaf area (SLA), root dry mass, and root-to-shoot ratio (Root:Shoot) of plants grown alone or with cheatgrass (w/ CG) for 3 wheatgrasses in Trial 1 (winter 2005).

Trial 1									
Population	$\Psi$ mPA	$g_s$ mol m <sup>-2</sup> s <sup>-1</sup>	Shoot DM mg	Tiller Number no.	Leaves per tiller no.	Leaf Area cm <sup>2</sup>	SLA m <sup>2</sup> kg <sup>-1</sup>	Root DM g	Root:Shoot g g <sup>-1</sup>
Goldar BBWG	-1.45b*	0.098a*	56.08a**	2.10b**	4.15a***	11.38a**	20.35b***	0.042 <sup>ns</sup>	0.72 <sup>ns</sup>
P-24 BBWG	-1.44b	0.097a	47.78b	2.70a	3.24b	9.04b	18.83b	0.036	0.72
E-45 SRWG	-1.27a	0.076b	44.26b	2.81a	2.74b	11.51a	25.79a	0.034	0.61
Trt Means									
alone	-1.37 <sup>ns</sup>	0.106a***	57.47a***	2.79a**	3.22 <sup>ns</sup>	12.97a***	22.89a**	0.037	0.68
w/ CG	-1.40	0.074b	41.27b	2.27b	3.54	8.31b	20.43b	na	na

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ;  $ns - P > 0.05$

Table 2-3. Stomatal conductance ( $g_s$ ), shoot dry mass (DM), tiller number, leaf area, and specific leaf area (SLA) of plants grown alone or with cheatgrass (w/CG) for 4 wheatgrasses in Trial 2 (summer 2005).

Trial 2							
Population	$g_s$	Shoot DM		Tiller Number	Leaf Area		SLA
	mol m <sup>-2</sup> s <sup>-1</sup>	alone	w/ CG		alone	w/ CG	
		mg	no.		cm <sup>2</sup>	m <sup>2</sup> kg <sup>-1</sup>	
Goldar BBWG	0.124b <sup>***</sup>	72.52a <sup>*</sup>	35.51a <sup>*</sup>	1.45 <sup>ns</sup>	8.04a <sup>*</sup>	3.82b <sup>*</sup>	11.05bc <sup>***</sup>
P-24 BBWG	0.157a	57.17bc	39.93a	1.81	5.76b	3.78b	9.97c
Secar SRWG	0.115b	64.77ab	44.83a	1.77	7.16ab	5.06ab	11.44b
E-45 SRWG	0.088c	43.40c	38.90a	1.61	6.10b	5.57a	14.94a
Trt Means							
alone	0.124a <sup>***</sup>	59.47a <sup>***</sup>		1.95a <sup>***</sup>	6.76a <sup>***</sup>		12.06 <sup>ns</sup>
w/ CG	0.119b	39.79b		1.36b	4.56b		11.64
Species							
BBWG	0.142a <sup>***</sup>	65.56a <sup>*</sup>	38.74b <sup>*</sup>	1.64 <sup>ns</sup>	6.99a <sup>*</sup>	3.84b <sup>*</sup>	10.35b <sup>***</sup>
SRWG	0.103b	56.21b	43.04a	1.70	6.74b	5.33a	12.86a

\*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001; ns - P > 0.05

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; ns -  $P > 0.05$

Table 2-4. Xylem pressure potential ( $\Psi$ ), stomatal conductance ( $g_s$ ), shoot dry mass (DM), tiller number, leaves per tiller, leaf area, specific leaf area (SLA), root dry mass, and root-to-shoot ratio (Root:Shoot) of plants grown alone or with cheatgrass (w/ CG) for 5 wheatgrasses in Trial 3 (winter 2006).

Population	Trial 3									
	$\Psi$	$g_s$	Shoot DM		Tiller Number	Leaves per tiller	Leaf Area	SLA	Root DM	Root:Shoot
	mPA	$\text{mol m}^{-2} \text{s}^{-1}$	alone	w/ CG	no.	no.	$\text{cm}^2$	$\text{m}^2 \text{kg}^{-1}$	g	$\text{g g}^{-1}$
Goldar BBWG	-1.50b*	0.130a***	59.35ab*	54.38a*	2.38c***	3.56a**	12.12 <sup>ns</sup>	21.57b***	0.054 <sup>ns</sup>	1.05 <sup>ns</sup>
P-24 BBWG	-1.54b	0.113b	70.28a	38.74b	3.17a	3.15b	12.12	22.62b	0.055	1.11
Secar SRWG	-1.31a	0.113b	60.95ab	40.58b	2.85ab	2.90b	13.75	26.82a	0.051	1.03
E-45 SRWG	-1.39ab	0.091c	56.30b	35.54b	2.50bc	2.99b	12.24	25.87a	0.055	1.00
Discovery SRWG	-1.39ab	0.113ab	55.98b	40.48b	2.43c	2.94b	12.60	25.87a	0.051	1.16
Trt Means										
alone	-1.38a*	0.121a***	60.57a***		2.85a**	3.13 <sup>ns</sup>	15.17a***	24.99 <sup>ns</sup>	0.058a***	1.03 <sup>ns</sup>
w/ CG	-1.47b	0.103b	41.95b		2.48b	3.09	9.97b	24.13	0.045b	1.10
Species										
BBWG	-1.52b**	0.121a**	55.67a**		2.60 <sup>ns</sup>	3.36a***	12.86 <sup>ns</sup>	22.10b***	0.049 <sup>ns</sup>	1.06 <sup>ns</sup>
SRWG	-1.37a	0.106b	48.27b		2.78	2.94b	12.13	26.20a	0.055	1.08

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; <sup>ns</sup> -  $P > 0.05$



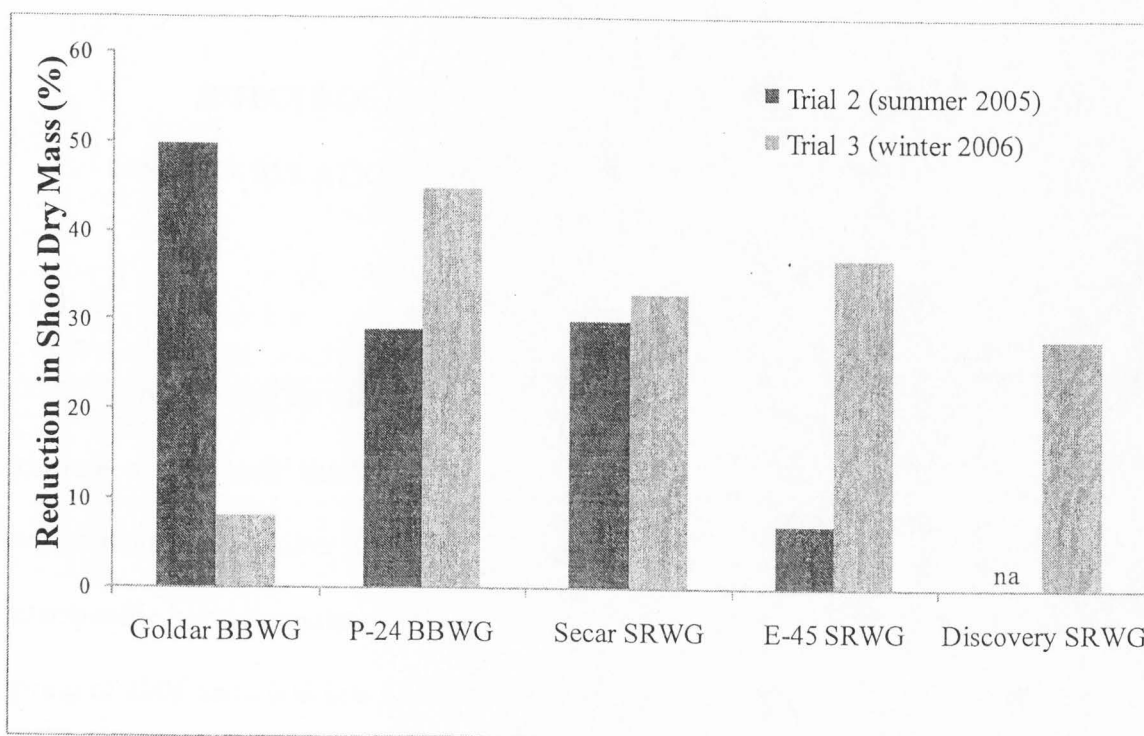


Figure 2-1. The percentage reduction in shoot dry mass due to cheatgrass competition for two BBWG and three SRWG populations in Trial 2 and two BBWG and two SRWG populations in Trial 3.

CHAPTER 3

EFFECTS OF PLANT DENSITY ON THE GROWTH AND  
WATER RELATIONS OF NINE NATIVE WHEATGRASS POPULATIONS

ABSTRACT

I investigated the effects of two planting densities on the growth and water relations of 'Bannock' thickspike wheatgrass (*Elymus lanceolatus*), 'Secar' and four experimental Snake River wheatgrass (*Elymus wawawaiensis*) populations, and three interspecific hybrid populations. Seedlings were transplanted to Millville, Utah in the spring of 2005 and 2006 into high (25 plants/m<sup>2</sup>) and low-density (7.8 plants/m<sup>2</sup>) plots to generate differential intraspecific competition. Shoot dry mass per plant was quantified in November 2005 and July 2006 for the 2005 experiment and in October 2006 for the 2006 experiment. In July 2006, shoot dry mass per plant in low-density plots was twice that in high-density plots. At both densities, Bannock had the highest shoot mass per plant followed by the hybrids. In June 2006, Bannock had the lowest conductance averaged across both densities, followed closely by the hybrids. Both pre-dawn and mid-day xylem pressure potentials were less negative for Bannock than the other populations in May, June, and July 2006 averaged across both densities. The remaining populations were similar at pre-dawn for all 3 months, but the hybrids were more similar to Bannock at mid-day. Bannock and the hybrids appear to have greater shoot productivity and more favorable water relations than Snake River wheatgrass. The prolific root production and the rhizomatous nature of thickspike wheatgrass may possibly account for its superior ability to exploit limited soil water.

## INTRODUCTION

Selection criteria for native perennial grass populations to be sold commercially for restoration purposes may vary from seed production to salt tolerance. However, a plant's ability to remain productive and physiologically active during the growing season may prove to be the most important characteristic for selecting plant materials for western rangelands. High productivity, despite relatively low resource availability, is an important trait because it identifies plants capable of persisting under both drought and competition from neighboring vegetation. Invasive weeds rapidly deplete soil water early in the growing season (Holmes and Rice 1996; Kremer and Running 1996; Dyer and Rice 1999; Booth et al. 2003a; Kulmatiski et al. 2006), elevating the need for plant materials capable of not only high water use in the spring but also continuing productivity as soil water decreases in the summer. Selecting for favorable response to these extremes in water availability can be accomplished by examining a plant's response to contrasting soil resources, as experimentally induced by altering plant density.

Drought and preemptive resource capture by invasive weeds complicate the ability of native perennial grasses to establish and subsist on western rangelands. Upon establishment, native perennial grasses need to respond quickly when high-resource patches are encountered in order to overcome periods of low resource availability. Numerous studies have shown that increasing neighbor mass reduces resource availability and productivity (Goldberg 1987; Miller and Werner 1987; Wilson and Tilman 1991; Gerry and Wilson 1995; Francis and Pyke 1996; Dyer and Rice 1999; Mulligan and Kirkman 2002). Productivity, despite low resource availability, may be an

important selection criterion for plant materials destined for western rangelands where low resource availability is the norm.

The potential of plants to grow when moisture availability is high, as in spring and after rainfall events, may be associated with traits that facilitate effective resource acquisition. Plants are capable of adjusting growth towards areas of high resource availability and reducing or restricting growth to areas where resources are low (Gersani and Sachs 1992; Jackson and Caldwell 1992; Bilbrough and Caldwell 1995; Cui and Caldwell 1997; Linkohr et al. 2002). Plant materials displaying favorable responses to both high and low-density planting regimes may be better competitors because they are suited to cope with a variable array of resource availabilities.

Trade-offs exist when selecting plants for greater productivity under high and low resource availability. Selecting populations for high productivity under high resources may be disadvantageous because resources are not always readily available, and these populations may not be as productive when resources become limiting. Conversely, populations displaying high productivity when resources are low may not necessarily be the most productive when resources are high. Plant materials developed for western rangelands need to be flexible in their response to resources. They need to be as productive as possible when resource availability is both high and low because this is a feature of the environment in which they will be competing.

Below-ground processes play an integral role in determining the productivity of species in dryland environments because soil moisture and nutrients inevitably limit growth. Productivity of grasses in semi-arid ecosystems has been associated with high rates of water and nutrient extraction (Eissenstat and Caldwell 1988; Melgoza et al. 1990;

Kremer and Running 1996; Duke and Caldwell 2001; Hendon and Briske 2002; Booth et al. 2003a, 2003b). If plants are not competitively foraging for below-ground resources, this will be manifested in reduced above-ground biomass production.

Snake River wheatgrass is found in the valleys of the Columbia River, the Snake River, and their tributaries in eastern Washington, eastern Oregon, and northern and central Idaho. At one time, SRWG was thought to be synonymous with bluebunch wheatgrass (BBWG; *Pseudoroegneria spicata* [Pursh] A. Löve), a widespread species found throughout the Intermountain West (Carlson and Barksworth 1997). Both are commonly used to restore landscapes disturbed by a variety of agents. However, Snake River wheatgrass may be better adapted to grazing and drier conditions than bluebunch wheatgrass (Morrison and Kelley 1981; Jones and Nielson 1997; Kindiger and Conley 2002). Thickspike wheatgrass [TSWG; *Elymus lanceolatus* (Scribner & J.G. Smith) Gould ssp. *lanceolatus*], another species commonly found throughout the Intermountain West and widely used in restoration efforts, is SRWG's closest relative and is more distantly related to bluebunch wheatgrass (Carlson and Barksworth 1997). However, unlike SRWG or BBWG, TSWG possesses a highly rhizomatous growth habitat.

Several studies have been conducted on Snake River wheatgrass (SRWG; *Elymus wawawaiensis* J. Carlson and Barksworth) to evaluate clipping tolerance, grazing preference, productivity, and effectiveness for seeding on disturbed landscapes (Goebel et al. 1988; Ganskopp et al. 1993; Jones and Nielson 1993; Jones et al. 1994; Ganskopp et al. 1997; Jones and Nielson 1997; Humphrey and Pyke 1998; Thorne et al. 1998), but most have examined only 'Secar'. Here, multiple populations were included to identify a SRWG population that may be more productive than Secar.

I designed a study to evaluate the effects of modifying intraspecific competition on the growth and water relations of nine populations of SRWG, TSWG, and interspecific hybrids. High and low plant density were used to induce low and high intraspecific competition, respectively. The objectives of this experiment are i) to determine which populations experience the greatest differential in biomass and stomatal conductance between high and low density, and ii) to elucidate the relationship between shoot dry mass production, stomatal conductance, and xylem pressure potential. I hypothesize that i) TSWG will display greater shoot dry mass than SRWG, with hybrids intermediate, and that ii) shoot dry mass production will be associated with maintenance of favorable stomatal conductance and xylem pressure potential under conditions of low moisture availability.

## METHODS

### **Plant Materials and Experimental Design**

The plant materials for this study are 'Bannock' TSWG; 'Secar' SRWG; E-45, 'Discovery', E-46, and SERDP experimental SRWG populations; and E-38X, E-48X, and E-49X experimental SRWG X TSWG populations (Figure 3-1). Seeds of Discovery, E-45, E-46, E-38X, E-48X, and E-49X were harvested in 2003 from USDA-ARS plots located in Millville, Utah, while seeds of Bannock and Secar were obtained commercially.

Individual plants were germinated and transplanted into a 3:1 sand:peat moss mixture in opaque, round plastic tubes (20-cm long by 5-cm diameter) in the USDA-ARS greenhouse on the Utah State University campus in Logan, Utah. Plants were trimmed



regularly to 10-cm height until planting at Millville, UT about 3 months after greenhouse transplanting. The plants received a 10-ml fertilization treatment of Peter's Professional Water-Soluble Fertilizer (Scotts-Sierra Horticultural Products Co., Marysville, Ohio; 20:20:20: N-P<sub>2</sub>O<sub>5</sub>-K<sub>2</sub>O) approximately every 2 weeks. Peter's fertilizer was alternated with another nutrient solution containing: 20.2 mM Ca, 67.5 mM N, 47.0 mM K, 17.5 mM P, 24.6 mM S, 17.5 mM Mg, 12.8 mM Cl, 537  $\mu$ M Fe, 68.5  $\mu$ M B, 0.800  $\mu$ M Cu, 22.5  $\mu$ M Mn, 0.35  $\mu$ M Mo, and 1.70  $\mu$ M Zn.

The planting design consisted of two planting densities (whole plots) and nine populations (split plots) arranged in a split-plot design. Low-density plots consisted of five plants per 3600 cm<sup>2</sup>, planted with one plant on each corner of the square and one directly in the center. High-density plots consisted of 16 plants per 3600 cm<sup>2</sup> in a 4-by-4 arrangement, each 20 cm from its nearest neighbor. Forty-cm aisles separated plots in both directions, and a single-row border formed a perimeter 40 cm outside the experimental area. Soil at the Millville site is a Ricks gravelly loam (coarse-loamy over sandy or sandy-skeletal, mixed, superactive, mesic Calcic Haploxerolls).

The study period for the 2005 experiment began shortly after transplanting, 16 and 18 May 2005, and ended in November when shoot biomass was harvested. The study period for 2006 started in May and ended in August after root samples were collected. Measurements for both field seasons were taken on the same plot throughout the experiment. A total of 16 replications were planted for the 2005 experiment. A duplicate experiment was transplanted 15 and 16 May 2006 and ended in October 2006 when shoot biomass was harvested. A total of 12 replications were planted for the 2006 experiment.

Secar was dropped from analysis of the 2005 experiment when it was discovered that the seed lot used was contaminated.

### **Physiological Measurements**

Physiological measurements were taken on various dates during spring, summer, and autumn, depending on the measurement and weather. Stomatal conductance was measured on 12 replications with a LI-1600 steady-state porometer (Li-Cor Inc., Lincoln, NE) between 1000 and 1400 hours on 15 to 17 June 2005 and 27 to 29 July 2005. Stomatal conductance was measured on 12 replications with a Model SC-1 leaf porometer (Decagon Devices, Inc., Pullman, WA) on 18 and 19 May, 21 and 22 June, and 11 and 12 July 2006 for the 2005 experiment. Stomatal conductance was measured on 12 replications with a Model SC-1 leaf porometer (Decagon Devices, Inc., Pullman, WA) on 22 June and 11 and 12 July 2006 for the 2006 experiment. Taking porometer measurements across multiple days with 3 to 6 replications measured per day reduces daily environmental variability that would otherwise result if all data were collected on a single day from early morning to late afternoon. Measurements were taken on one of the four center target plants for the high-density plots and on the center target plant for the low-density plots. If the center plant of a low-density plot was missing, then a porometer measurement was taken on one of the four corner plants.

For the 2005 experiment, xylem pressure potential was measured in 2006 on 8 replications on the same sampling days as conductance measurements using a Scholander-type pressure bomb (Boyer 1967). Pre-dawn xylem pressure potentials were measured between 300 and 530 hours and mid-day water potentials between 1200 and 1400 hours using the center target plants for each density.

### Morphological Measurements

For the 2005 experiment, morphological measurements for 2005 were limited to leaf-area index, percentage of plants producing spikes, and shoot dry mass per plant. Leaf-area index (LAI) was measured on 11 Oct. 2005 and 10 May 2006 using a PAR-80 line-quantum sensor (AccuPAR, Decagon Devices, Inc., Pullman, WA). For all 16 replications, I counted the number of plants producing reproductive tillers per plot for the first year and the number of plants surviving at the end of the second year. To determine shoot dry mass, all plants were harvested on 23 or 25 Nov. 2005 at a 5-cm height. Second-year shoot dry mass was harvested at 10 cm on 27 July 2006. Shoot dry mass was measured after oven-drying at 60° C for 48 hours. Second-year seed yield was obtained by shaking the seed heads of the plants into buckets for each plot on 11 and again on 19 July 2006. Seed for each plot was combined across the two dates, cleaned with a South Dakota Seed Blower (Seedburo Equipment Co., Chicago, IL), and weighed to quantify seed yield.

On 1 and 2 Aug. 2006, four soil cores (10-cm diameter x 17-cm, 1450 cm<sup>3</sup>) were removed equidistant from the center of each plot (approximately 15 cm) in the 2005 experiment using a golf cup cutter (H10 Hole Cutter, KSAB Golf Equipment, Västerås, Sweden). Root biomass of the combined sample was measured after washing and oven-drying the roots at 60° C for 48 hours. A random sub-sample of the roots was taken to analyze for root surface area, root length, and root diameter using WinRHIZO Pro Version 2005b (Regent Instrument Inc., Quebec, Canada). Specific root length was calculated by dividing root length by root dry mass.

For the 2006 experiment, five leaves were removed from one of the centrally located plants of 12 replications of the high-density plots on 22 August 2006 and placed into a press. Leaf area was measured three times on the same sample using a Li-3000 portable leaf-area meter (Li-Cor Inc., Lincoln, NE), and dry mass of the samples was measured after oven-drying at 60° C for 48 hours. Specific leaf area (SLA) was calculated as dry mass divided by leaf area. Shoot dry mass was harvested on 17 Oct. 2006 at 5-cm, as in the first year of the 2005 experiment, and weighed after oven-drying at 60° C for 48 hours.

### Statistical Analysis

Statistical significance of effects was determined with the SAS (SAS Institute 1999) MIXED procedure using treatment and population as fixed effects and replication as a random effect. For both experiments correlation coefficients were determined with the SAS CORR procedure using the means for each population of every variable measured. All data were tested for normality by examining histograms and normal probability plots of residuals. For non-normal data, I applied the transformation that produced the highest normality and *P*-value according to the Shapiro-Wilk test (Zar 1984). For the 2005 experiment, stomatal conductance for June 2005, seed yield, and root-to-shoot dry mass ratio were normalized with a natural-log transformation. Stomatal conductance for May, June, and July 2006, and root dry mass were normalized with a cube-root transformation. For the 2006 experiment, stomatal conductance for July 2006 was normalized with a natural-log transformation, and stomatal conductance for June 2006 was normalized with a cube-root transformation. Other variables did not require transformation. Least-squares means were calculated from the GLM procedure on non-

transformed data, but mean separations (least significant difference = 0.05) were based on transformed data as required.

## RESULTS

### Water Relations

#### *2005 Experiment*

High density reduced stomatal conductance ( $g_s$ ) by 16% in June 2005 ( $P < 0.05$ , Table 3-4). Populations E-48X, Bannock TSWG, and Discovery SRWG had the highest  $g_s$ , and E-45 SRWG had the lowest  $g_s$  ( $P < 0.001$ , Table 3-4). However, the population  $\times$  density interaction was absent in June 2005. In July 2005, high density reduced  $g_s$  by 19% ( $P < 0.05$ , Table 3-4), and a population  $\times$  density interaction was present ( $P < 0.05$ , Table 3-1). For high density, E-46 SRWG, SERDP SRWG, Bannock TSWG, and E-49X had the highest  $g_s$ , and E-48X, E-38X, and Discovery SRWG had the lowest (Table 3-4). For low density, SERDP, Discovery, and E-45 SRWG had the highest  $g_s$ , and E-38X had the lowest (Table 3-4).

High density reduced  $g_s$  by 44% in May 2006 ( $P < 0.001$ , Table 3-5), but the population effect and interaction were not significant (Table 3-2). In June 2006, high density reduced  $g_s$  by 38% ( $P < 0.01$ , Table 3-5). Discovery, E-46, and SERDP SRWGs had the highest  $g_s$ , and Bannock TSWG and E-49X had the lowest ( $P < 0.05$ , Table 3-5). The population  $\times$  density interaction was not significant (Table 3-2). In July 2006,  $g_s$  was highest for Discovery, SERDP, and E-45 SRWGs and E-38X, and E-48X and E-49X were lowest ( $P < 0.01$ , Table 3-5). The density effect and interaction were not significant (Table 3-2).

In May 2006, xylem pressure potential differed for the populations at both pre-dawn ( $\Psi_{pd}$ ) and mid-day ( $\Psi_{md}$ ) ( $P < 0.001$  for both, Table 3-2), but the density effect and interaction were not significant. Bannock TSWG had the least negative  $\Psi_{pd}$ , and Bannock TSWG and E-49X had the least negative  $\Psi_{md}$  (Table 3-5). The SERDP, Discovery, E-45 SRWG populations and the hybrids had the most negative  $\Psi_{pd}$ , while SERDP, Secar, and E-45 SRWGs and the E-38X hybrid had the most negative  $\Psi_{md}$  (Table 3-5). In June 2006, populations differed for both  $\Psi_{pd}$  and  $\Psi_{md}$  ( $P < 0.001$  for both, Table 3-2), but the density effect and interaction were not significant. Bannock TSWG and E-49X had the least negative  $\Psi_{pd}$ , and SERDP, Discovery, and E-45 SRWGs and E-48X were the most negative (Table 3-5). For  $\Psi_{md}$ , Bannock TSWG was the least negative of all populations, the remainder of which were not different from one another (Table 3-5). In July 2006, populations differed for both  $\Psi_{pd}$  ( $P < 0.01$ ) and  $\Psi_{md}$  ( $P < 0.001$ , Table 3-2). Bannock TSWG had the least negative  $\Psi_{pd}$ , and all other populations were not different from one another (Table 3-5). Bannock TSWG and the three hybrids had the least negative  $\Psi_{md}$ , and the four SRWGs had the most negative  $\Psi_{md}$  (Table 3-5). Density and interaction effects were not significant (Table 3-2).

### ***2006 Experiment***

Density reduced  $g_s$  by 15% in June 2006 ( $P < 0.01$ ) and 17% in July 2006 for the 2006 experiment ( $P < 0.01$ , Table 3-4). For both months, the population effect and interaction were not significant (Table 3-1).



## Growth

### 2005 Experiment

Shoot dry mass per plant for November 2005 was highly significant among populations ( $P < 0.001$ ) and between densities ( $P < 0.001$ , Table 3-1), but the interaction was not significant. High density reduced shoot dry mass per plant by 37% (Table 3-4). Bannock TSWG produced the most dry mass, followed by the three hybrids, with E-45 SRWG having the least dry mass (Table 3-4). High density increased LAI by 64% ( $P < 0.001$ , Table 3-4). Bannock TSWG, E-48X, and E-49X had the highest LAI, and E-45 and SERDP SRWGs had the lowest ( $P < 0.001$ , Table 3-4). However, the interaction for LAI was not significant (Table 3-1). High density decreased reproductive plant percentage by 16% ( $P < 0.05$ , Table 3-4). Hybrids E-38X and E-48X had the highest reproductive plant percentage, and Bannock TSWG and E-45 SRWG had the lowest ( $P < 0.001$ , Table 3-4). The interaction was not significant (Table 3-1).

In contrast to November 2005, shoot dry mass per plant in July 2006 had a highly significant population x density interaction ( $P < 0.001$ , Table 3-3). Overall, high density reduced shoot dry mass 48% ( $P < 0.001$ , Table 3-6). At low density, Bannock TSWG produced the most dry mass, and Discovery, E-46, and E-45 SRWGs produced the least (Table 3-6). At high density, Bannock TSWG and the hybrids E-49X, E-38X, and E-48X produced the most dry mass, and E-45 SRWG produced the least (Table 3-6). High density reduced seed yield per plant by 59% ( $P < 0.01$ , Table 3-6). Bannock TSWG, SERDP SRWG, and E-38X produced the most seed, and E-49X and E-45 SRWG produced the least ( $P < 0.001$ , Table 3-6). The interaction was not significant (Table 3-3).

The only population differing from the others in survivorship after two years was E-45 SRWG, which had the lowest survival rate at 91% ( $P < 0.05$ , Table 3-6). Density and interaction effects were not significant (Table 3-3).

The SERDP and Discovery SRWGs and E-48X produced the most root mass per sample, and Bannock TSWG, E-45 and E-46 SRWGs, E38X, and E-49X produced the least ( $P < 0.05$ , Table 3-6). The root dry mass data may be biased against the rhizomatous populations because they are better able to forage for resources outside the sampled area. The density effect and interaction were not significant (Table 3-3). Bannock TSWG and SERDP SRWG had the highest specific root length, and the remaining populations were not significantly different from each other ( $P < 0.05$ , Table 3-6). There was no significant density effect or interaction (Table 3-3).

### *2006 Experiment*

Shoot dry mass per plant had a highly significant density x population interaction in October 2006 ( $P < 0.001$ , Table 3-1). At high density, Bannock TSWG, the top population, produced 113% more shoot dry mass per plant than Secar SRWG, the bottom population ( $P < 0.001$ , Table 3-4). At low density, Bannock TSWG, again the top population, produced 274% more shoot dry mass per plant than Secar, again the bottom population ( $P < 0.001$ , Table 3-4). Overall, density reduced shoot dry mass per plant by 54% ( $P < 0.001$ , Table 3-4). The SERDP, E-46, Secar, and Discovery SRWGs and E-38X had the highest SLA, and Bannock TSWG, E-45 SRWG, E-48X, and E-49X had the least ( $P < 0.001$ , Table 3-4).

## Correlations

### 2005 Experiment

With Bannock TSWG included in the data set, shoot dry mass per plant was highly correlated with LAI for 2005 ( $r=0.92$ ,  $P<0.01$ , Table 3-7). Shoot dry mass per plant ( $r=0.77$ ,  $P<0.05$ , Figure 3-2) and LAI ( $r=0.76$ ,  $P<0.05$ , Table 3-7) were also positively correlated with  $g_s$  in June 2005. In 2006, populations having high shoot dry mass at high density also had high values at low density ( $r=0.94$ ,  $P<0.001$ , Table 3-8). When Bannock was removed from the 2005 data set, the relationship between LAI and shoot dry mass per plant was unchanged ( $r=0.92$ ,  $P<0.01$  vs.  $r=0.89$ ,  $P<0.01$ ), but the correlations between LAI and June stomatal conductance ( $r=0.76$ ,  $P<0.05$  vs.  $r=0.73$ ,  $P<0.10$ ) and between shoot dry mass per plant and June stomatal conductance ( $r=0.77$ ,  $P<0.05$  vs.  $r=0.75$ ,  $P<0.10$ ) became nonsignificant. The relationships between root dry mass and high-density and low-density shoot dry mass are positive ( $r=0.52$ ,  $0.24$ , respectively) when Bannock is included (Table 3-8), but when Bannock is removed the relationships become negative ( $r=-0.51$ ,  $-0.17$ , respectively); however, none of the relationships are significant.

Measurements in 2006 of  $\Psi_{pd}$  and  $\Psi_{md}$  were positively correlated with each other in 7 out of 15 possible pairwise combinations (Table 3-8). However, May  $\Psi_{pd}$  is negatively related to all the other xylem pressure potentials, although not significantly. The only significant correlation between  $\Psi_{pd}$  and  $g_s$  was negative, in June 2006 ( $r=-0.73$ ,  $P<0.05$ , Figure 3-3). June and July 2006  $\Psi_{md}$  were negatively correlated with May 2006  $g_s$  ( $r=-0.80$ ,  $P<0.05$ ,  $r=-0.77$ ,  $P<0.05$ , respectively). June and July 2006  $\Psi_{md}$  were also negatively correlated with June 2006  $g_s$  ( $r=-0.73$ ,  $P<0.05$ ,  $r=-0.89$ ,  $P<0.01$ , respectively,

Figure 3-4). Without Bannock, the number of significant correlations between the pre-dawn and mid-day xylem pressure potential measurements in 2006 fell from 7 to 2 out of 15 possible pairwise combinations (Table 3-8). The relationship lost strength, though remaining positive, when Bannock TSWG was excluded. The same was true for the relationship between stomatal conductance and xylem pressure potential.

In 2006, shoot dry mass per plant was positively correlated with  $\Psi_{md}$  for 5 out of 6 measurements, but only once, in June, with  $\Psi_{pd}$  (Table 3-8). The number of significant correlations for shoot dry mass and  $\Psi_{md}$  was reduced from 5 out of 6 times to 3 without Bannock in the data set. The correlation between May 2006  $g_s$  and July 2006 shoot dry mass per plant was strongly negative for high density ( $r=-0.92$ ,  $P<0.01$ , Figure 3-4) and low density ( $r=-0.96$ ,  $P<0.001$ , Figure 3-4), and remained so when Bannock was removed from the data set. Leaf area index was negatively correlated with May  $\Psi_{pd}$  ( $r=-0.73$ ,  $P<0.05$ ) and  $g_s$  ( $r=-0.72$ ,  $P<0.05$ ). However, when Bannock was removed, the correlation of LAI with May  $\Psi_{pd}$  ( $r=-0.73$ ) becomes nonsignificant, while the correlation with  $g_s$  remains negative ( $r=-0.77$ ,  $P<0.05$ ). Plant survivorship was negatively correlated with May  $\Psi_{pd}$  ( $r=-0.93$ ,  $P<0.001$ ), and it remained so when Bannock was removed from the data set.

Root dry mass was negatively correlated with  $\Psi_{pd}$  in June ( $r=-0.82$ ,  $P<0.05$ ) and also for  $\Psi_{pd}$  the other months, but not significantly. Root dry mass was positively related to June  $g_s$  ( $r=0.72$ ,  $P<0.05$ ), but not on other sample dates. The relationships between root dry mass and June  $\Psi_{pd}$  or  $g_s$  did not change when Bannock was removed from the data set.

The correlation between May 2006  $g_s$  and July 2006 shoot dry mass per plant was strongly negative for high density ( $r=-0.92$ ,  $P<0.01$ ) and low density ( $r=-0.96$ ,  $P<0.001$ ) and remained so when Bannock was removed from the data set (Table 3-8). Leaf area index was negatively correlated with May 2006  $g_s$  ( $r=-0.72$ ,  $P<0.05$ ) and remained so when Bannock was removed from the data set. Root dry mass was positively related to June 2006  $g_s$  ( $r=0.72$ ,  $P<0.05$ ), but not on other sample dates. The relationships between root dry mass and June  $g_s$  did not change when Bannock was removed from the data set.

### *2006 Experiment*

For the 2006 planting, there was a significantly positive correlation between shoot dry mass per plant at high density and low density ( $r=0.96$ ,  $P<0.001$ , Table 3-7). When Bannock was removed from the data set, the relationship between shoot dry mass per plant of high density and low density remained, although slightly weaker ( $r=0.86$ ,  $P<0.01$ ). The relationship between high-density shoot dry mass per plant and SLA was negative ( $r=-0.69$ ,  $P<0.05$ ), but it became nonsignificant ( $r=0.22$ ) when Bannock was removed from the data set (Table 3-7). Stomatal conductance was not correlated with shoot dry mass per plant, as was the case in both field years of the 2005 planting.

## DISCUSSION

For all harvests, increasing density decreased per-plant productivity, which is consistent with other studies (Goldberg 1987; Miller and Werner 1987; Wilson and Tilman 1991; Gerry and Wilson 1995; Francis and Pyke 1996; Dyer and Rice 1999; Mulligan and Kirkman 2002). The negative correlations between shoot dry mass per plant and  $g_s$ , and the positive correlations between shoot dry mass per plant and xylem

pressure potential support the hypothesis that greater productivity is associated with the ability to regulate stomatal closure and maintain favorable water relations. Bannock TSWG's superior productivity under both densities suggest that it responds to low and high resource availability better than the SRWG and SRWG X TSWG populations in the first 2 years.

In June 2005, when water may not have been limiting, Bannock had the second highest  $g_s$ , suggesting that it was actively engaged in photosynthesis, and possibly had access to relatively high amounts of soil water. However, by July 2005 when soil moisture may have become limiting,  $g_s$  showed a different pattern. Bannock's stomatal conductance did not differ between high and low density, whereas other populations had reduced  $g_s$  at high density. This suggests that either 1) competition for water was low and plants were not large enough to be actively competing for below-ground resources, or that 2) Bannock is better able to acquire below-ground resources, possibly due to its rooting structure and rhizomatous morphology. The latter scenario seems more likely because increased density reduced  $g_s$  and November shoot dry mass per plant, suggesting that competition does indeed play a role in the establishment year. Humphrey and Pyke (1998) found that TSWG exploited resources more quickly than SRWG during the first year, as measured by faster growth and greater ramet production.

Populations limited by water at high density may have responded by reducing their stomatal apertures to conserve water, thus reducing  $g_s$ . The SRWGs may tolerate water stress by this mechanism, but photosynthesis and overall plant growth may be curtailed in the process. Conversely, at low density, where competition for water may have been less severe, the populations maintained high stomatal conductance. A similar



pattern was found in the greenhouse and field by Read et al. (1991, 1992). Plants grown in well-watered treatments had higher stomatal conductance than plants grown under drought conditions. Even though no specific mention was made of a correlation between stomatal conductance and shoot dry mass, plants producing the most shoot dry mass under drought conditions had the lowest conductance (Read et al. 1991). Gibson and Skeel (1996) also found that stomatal conductance decreased with increasing neighbor density in the greenhouse.

The positive correlation between June 2005  $g_s$  and November 2005 shoot dry mass per plant (Figure 3-1) could be due to more favorable soil moisture levels caused by larger plants reducing evaporation through shading of the soil surface. In contrast, July 2005  $g_s$  and November shoot dry mass per plant were negative, though not significant, possibly suggesting that larger plants could not attain enough water to maintain open stomata due to increasing competition from neighbors.

For the 2006 experiment, Bannock had the highest shoot dry mass at both densities. Bannock displayed the greatest increase (65%) in dry mass from high density to low density, followed closely by SERDP SRWG (57%), with Secar SRWG having the least (38%). Stomatal conductance did not differ between populations for either June or July 2006, but increased density did reduce stomatal conductance both months. Bannock had the lowest SLA, which was negatively correlated with high-density shoot dry mass per plant ( $r=-0.69$ ,  $P<0.05$ ), though not significantly with low-density shoot dry mass per plant ( $r=-0.58$ , Table 4-7). However, when Bannock TSWG was removed from the data set the correlations of SLA with high and low-density shoot dry mass per plant became lower and nonsignificant, but remained negative ( $r=-0.51$ ,  $-0.22$ , respectively).

A similar pattern emerged for growth and water relations of Bannock TSWG in 2006 for the 2005 experiment. Bannock TSWG had the highest shoot dry mass at both densities. Bannock and SERDP SRWG had the greatest increase of shoot dry mass in response to density (54%), and E-46 SRWG had the lowest (41%).

For the 2005 experiment, the relationship between July 2006 shoot dry mass per plant and May, June, and July 2006  $g_s$  was always negative, but was stronger in May (Table 3-8). This may be explained by the fact that larger plants have a greater demand for soil moisture. In order to compensate, larger plants must lower their  $g_s$  to conserve water and maintain growth. This is evident in the positive correlation between xylem pressure potential and shoot dry mass per plant. Plants having less negative xylem pressure potentials are less stressed and more productive in drought-stressed environments. This could be an important relationship to use in designing selection criteria for plant material development. However, it may be that SRWG is better able to tolerate lower xylem pressure potentials while still maintaining photosynthetic function than TSWG.

For all three summer 2006 measurements, Bannock consistently had the least negative  $\Psi_{pd}$  and  $\Psi_{md}$  of the eight populations. Ideally, a plant would be able to simultaneously keep its stomata open to assimilate  $CO_2$  and maintain a favorable water balance, permitting high day-time  $g_s$  and photosynthesis (Rodríguez et al. 2005). However, this was not the case for Bannock. Even though it had the least negative xylem pressure potential it consistently had one of the lowest  $g_s$ . This pattern was similar for the hybrid populations, but completely the reverse of the SRWG populations. The SRWG populations consistently had more negative  $\Psi_{pd}$  and  $\Psi_{md}$  than Bannock, but they had

higher stomatal conductance despite starting the day with less internal water. The two species, TSWG and SRWG, seem to have different ecophysiological adaptations, and thus plant strategies, that condition their response to limited soil water.

Another possible explanation for SRWG's more negative xylem pressure potential and higher conductance could be a greater need for increased root water uptake to increase the mass flow of nutrients, expressed by transpiration. Essentially, if SRWG has a higher nutrient requirement than TSWG, a strategy to obtain more nutrients might be to actively draw down the soil moisture in order to facilitate nutrient transportation to the soil-root interface. Ganskopp et al. (1997) reported that SRWG has higher crude protein and mineral nutrient levels (P, K, Ca, and Mg) than TSWG at both the boot stage and quiescent stage, suggesting that it may have a higher nutrient requirement. The contention that SRWG growth is limited in part by nutrient uptake may be supported by its lower shoot dry mass production. If this indeed were the case, more resources might be allocated to root growth in order to acquire more water and nutrient resources. Others have suggested that plants that have evolved in low-nutrient environments tend to grow slowly (Chapin 1980; Wilson and Tilman 1991), which could be the case for SRWG.

Even though xylem pressure potential never differed ( $P > 0.05$ ) between densities,  $g_s$  was lower at high density for six of the seven measurements. Lower  $g_s$  could result from lower water availability at high density. Because soil moisture was not measured, however, this possibility cannot be evaluated. It is important to note that Bannock and the hybrid populations consistently had lower  $g_s$  and less negative xylem pressure potentials than SRWG in 2006 for the 2005 experiment. The higher specific root length of Bannock indicates there was more root length for a given root mass, which may be a possible

mechanism explaining Bannock's less negative xylem pressure potential. With greater root length per root mass, Bannock was likely better able to exploit resources patches.

Of all populations in both experiments, Bannock TSWG had the highest shoot dry mass per plant at all three harvests, the most favorable stomatal conductance and xylem pressure potential, highest SRL, lowest SLA, and the greatest increase of shoot dry-mass from high to low density. The Snake River wheatgrass populations did not perform as well as the TSWG x SRWG hybrids, indicating the contribution of TSWG to the cross. Similar results for shoot dry-mass production of the same two species have been reported based on measurements taken 2 and 3 years after initial planting (Jones and Nielson 1993; Humphrey and Pyke 1998).

These results may be inconclusive because the limited difference between densities did not allow for a dramatic response, perhaps resulting in an absence of interaction. As the plants mature and the amount of space between them decreases, the effects of decreased resource availability should become more severe. However, the results do show that Bannock and the hybrids are more productive than SRWG for the first 2 years. The hybrid populations may not be widely accepted among land managers trying to maintain genetic integrity of remnant SRWG or TSWG populations, if they are present. However, if performance is paramount then the hybrids may be preferred over SRWG due to their higher productivity and more favorable water relations.

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Table 3-1. Summary statistics for June and July stomatal conductance ( $g_s$ ), shoot dry mass (DM), leaf area index (LAI) (2005 only), percentage plants reproducing (2005 only), and specific leaf area (SLA) (2006 high-density only) for the first year of the 2005 and 2006 experiments.

2005 Experiment			2006 Experiment		
June 2005 $g_s$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	df	F-Value	June 2006 $g_s$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	df	F-Value
Density	1, 11	8.58*	Density	1, 11	6.45*
Population	7, 119	4.70***	Population	8, 176	0.37 <sup>ns</sup>
Den*Pop	7, 119	1.00 <sup>ns</sup>	Den*Pop	8, 176	0.60 <sup>ns</sup>
July 2005 $g_s$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )			July 2006 $g_s$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )		
Density	1, 11	11.42**	Density	1, 11	11.09**
Population	7, 136	2.49*	Population	8, 175	1.29 <sup>ns</sup>
Den*Pop	7, 136	2.21*	Den*Pop	8, 175	1.40 <sup>ns</sup>
Nov 2005 Shoot DM (mg)			Oct 2006 Shoot DM (mg)		
Density	1, 15	69.26***	Density	1, 11	468.13***
Population	7, 189	10.13***	Population	8, 174	50.18***
Den*Pop	7, 189	1.23 <sup>ns</sup>	Den*Pop	8, 174	17.77***
Oct 2005 LAI ( $\text{m}^2 \text{m}^{-2}$ )			Aug 2006 SLA ( $\text{m}^2 \text{kg}^{-1}$ )		
Density	1, 15	171.08***	Population	8, 88	4.38***
Population	7, 189	6.13***			
Den*Pop	7, 189	1.33 <sup>ns</sup>			
Aug 2005 Reproducing (%)					
Density	1, 7	44.42***			
Population	2, 71	5.63**			
Den*Pop	2, 71	2.68 <sup>ns</sup>			

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , <sup>ns</sup>  $P > 0.05$

Table 3-2. Summary statistics for second-year (2006) pre-dawn ( $\Psi_{pd}$ ) and mid-day ( $\Psi_{md}$ ) xylem pressure potential and stomatal conductance ( $g_s$ ) measured in May, June, and July for the 2005 experiment.

	May 2006					
	$\Psi_{pd}$ (mPA)		$\Psi_{md}$ (mPA)		$g_s$ (mol m <sup>-2</sup> s <sup>-1</sup> )	
	df	F-Value	df	F-Value	df	F-Value
Density	1, 7	0.32 <sup>ns</sup>	1, 7	0.56 <sup>ns</sup>	1, 11	20.64 <sup>***</sup>
Population	7, 95	3.94 <sup>***</sup>	7, 95	4.95 <sup>***</sup>	7, 142	0.47 <sup>ns</sup>
Den*Pop	7, 95	1.32 <sup>ns</sup>	7, 95	0.46 <sup>ns</sup>	7, 142	1.22 <sup>ns</sup>

	June 2006					
	$\Psi_{pd}$ (mPA)		$\Psi_{md}$ (mPA)		$g_s$ (mol m <sup>-2</sup> s <sup>-1</sup> )	
	df	F-Value	df	F-Value	df	F-Value
Density	1, 7	4.07 <sup>ns</sup>	1, 7	1.06 <sup>ns</sup>	1, 7	15.65 <sup>**</sup>
Population	7, 95	6.92 <sup>***</sup>	7, 95	3.92 <sup>***</sup>	7, 95	2.54 <sup>*</sup>
Den*Pop	7, 95	0.85 <sup>ns</sup>	7, 95	1.42 <sup>ns</sup>	7, 95	1.51 <sup>ns</sup>

	July 2006					
	$\Psi_{pd}$ (mPA)		$\Psi_{md}$ (mPA)		$g_s$ (mol m <sup>-2</sup> s <sup>-1</sup> )	
	df	F-Value	df	F-Value	df	F-Value
Density	1, 7	0.90 <sup>ns</sup>	1, 7	0.81 <sup>ns</sup>	1, 7	3.96 <sup>ns</sup>
Population	7, 95	3.04 <sup>**</sup>	7, 95	3.88 <sup>***</sup>	7, 95	3.73 <sup>**</sup>
Den*Pop	7, 95	0.26 <sup>ns</sup>	7, 95	0.63 <sup>ns</sup>	7, 95	0.44 <sup>ns</sup>

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , ns  $P > 0.05$

Table 3-3. Summary statistics for second-year (2006) shoot dry mass (DM), leaf area index (LAI), root dry mass, specific root length (SRL), seed yield, and percentage plants surviving after two years for the 2005 experiment.

2006 Growth Parameters		
July Shoot DM (g)	DF	F-Value
Density	1, 15	367.95 <sup>***</sup>
Population	7, 191	21.81 <sup>***</sup>
Den*Pop	7, 191	4.97 <sup>***</sup>
<hr/> July LAI (m <sup>2</sup> m <sup>-2</sup> )		
Density	1, 11	28.54 <sup>***</sup>
Population	7, 143	5.22 <sup>***</sup>
Den*Pop	7, 143	1.25 <sup>ns</sup>
<hr/> Aug Root DM (g)		
Density	1, 6	1.18 <sup>ns</sup>
Population	7, 78	2.78 <sup>*</sup>
Den*Pop	7, 78	1.52 <sup>ns</sup>
<hr/> Aug SRL (m kg <sup>-1</sup> )		
Density	1, 6	1.92 <sup>ns</sup>
Population	7, 82	2.44 <sup>*</sup>
Den*Pop	7, 82	0.56 <sup>ns</sup>
<hr/> July Seed Yield (g)		
Density	1, 15	208.39 <sup>***</sup>
Population	7, 189	15.14 <sup>**</sup>
Den*Pop	7, 189	1.28 <sup>ns</sup>
<hr/> Sept Surviving (%)		
Density	1, 15	0.88 <sup>ns</sup>
Population	7, 189	4.56 <sup>***</sup>
Den*Pop	7, 189	0.78 <sup>ns</sup>

\*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001, ns P > 0.05

Table 3-4. First-year June and July stomatal conductance ( $g_s$ ), shoot dry mass (DM), leaf area index (LAI) (2005 only), percentage plants reproducing, and specific leaf area (SLA) (2006 only) for eight wheatgrass populations in the 2005 experiment and nine wheatgrass populations in the 2006 experiment.

Population	2005 Experiment (2005 data)					
	June $g_s$	July $g_s$		Shoot DM	LAI	Reproducing
		High Density	Low Density			
	$\text{mol m}^{-2} \text{s}^{-1}$	$\text{mol m}^{-2} \text{s}^{-1}$	$\text{mol m}^{-2} \text{s}^{-1}$	$\text{g plant}^{-1}$	$\text{m}^2 \text{m}^{-2}$	%
Bannock TSWG	0.139a***	0.090abc*	0.090bc*	13.28a***	0.72a***	13.79f***
E-38X	0.110b	0.068cd	0.080c	11.44bc	0.55bc	57.53a
E-48X	0.143a	0.064d	0.098bc	11.79ab	0.70a	48.55ab
E-49X	0.127ab	0.090a	0.084bc	11.68ab	0.59ab	31.81d
Discovery SRWG	0.137a	0.067bcd	0.112ab	10.36bcd	0.52bc	44.22bc
E-46 SRWG	0.124ab	0.099a	0.100bc	9.59d	0.50bc	37.85cd
E-45 SRWG	0.084c	0.078abcd	0.104abc	6.85e	0.35d	20.3ef
SERDP SRWG	0.126ab	0.096ab	0.138a	9.76cd	0.42cd	32.86de
Treatment						
High Density	0.134a*	0.082b**		8.21b***	0.80a***	32.78b*
Low Density	0.113b	0.101a		12.97a	0.29b	38.95

Population	2006 Experiment (2006 data)				
	June $g_s$	July $g_s$	Shoot DM	Shoot DM	SLA
			High Density	Low Density	High Density
	$\text{mol m}^{-2} \text{s}^{-1}$	$\text{mol m}^{-2} \text{s}^{-1}$	$\text{g plant}^{-1}$	$\text{g plant}^{-1}$	$\text{m}^2 \text{kg}^{-1}$
Bannock TSWG	0.167 <sup>ns</sup>	0.112 <sup>ns</sup>	12.75a***	36.17a***	6.97c***
E-38X	0.166	0.119	8.53bc	18.12bc	9.77a
E-48X	0.157	0.124	8.59b	15.95cd	7.69bc
E-49X	0.175	0.112	8.89b	19.49b	7.55bc
Discovery SRWG	0.186	0.121	7.86bc	14.73d	8.65ab
E-46 SRWG	0.172	0.115	7.43bc	15.81cd	9.41a
E-45 SRWG	0.154	0.093	7.47bc	15.13d	7.93bc
SERDP SRWG	0.170	0.098	6.39bc	14.72d	10.10a
Secar SRWG	0.162	0.109	5.98c	9.68e	8.96ab
Treatment					
High Density	0.154b*	0.101b*	8.21b***		na
Low Density	0.181a	0.122b	17.75a		na

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; ns -  $P > 0.05$

Table 3-5. Second-year (2006) pre-dawn ( $\Psi_{pd}$ ) and mid-day ( $\Psi_{md}$ ) xylem pressure potential and stomatal conductance ( $g_s$ ) for eight wheatgrass populations in the 2005 experiment.

2005 Experiment									
Population	May 2006			June 2006			July 2006		
	$\Psi_{pd}$	$\Psi_{md}$	$g_s$	$\Psi_{pd}$	$\Psi_{md}$	$g_s$	$\Psi_{pd}$	$\Psi_{md}$	$g_s$
	mPA	mPA	$\text{mol m}^{-2} \text{s}^{-1}$	mPA	mPA	$\text{mol m}^{-2} \text{s}^{-1}$	mPA	mPA	$\text{mol m}^{-2} \text{s}^{-1}$
Bannock TSWG	-0.55a <sup>***</sup>	-2.71a <sup>***</sup>	0.181 <sup>ns</sup>	-0.55a <sup>***</sup>	-2.83a <sup>***</sup>	0.072b <sup>*</sup>	-0.58a <sup>**</sup>	-3.24a <sup>***</sup>	0.081ab <sup>**</sup>
E-38X	-0.71bc	-3.05bcd	0.188	-0.73b	-3.09b	0.095ab	-0.72b	-3.47abcd	0.102a
E-48X	-0.73bc	-2.94bc	0.188	-0.78bc	-3.24b	0.093ab	-0.74b	-3.41abc	0.045c
E-49X	-0.70bc	-2.86ab	0.187	-0.55a	-3.11b	0.075b	-0.74b	-3.40ab	0.062bc
SERDP SRWG	-0.77c	-3.25d	0.192	-0.88c	-3.19b	0.107a	-0.83b	-3.66cde	0.112a
E-46 SRWG	-0.66b	-3.01bc	0.204	-0.71b	-3.31b	0.112a	-0.75b	-3.76e	0.084ab
Discovery SRWG	-0.72bc	-2.99bc	0.205	-0.81bc	-3.32b	0.120a	-0.74b	-3.69de	0.116a
E-45 SRWG	-0.70bc	-3.09cd	0.212	-0.78bc	-3.29b	0.087ab	-0.76b	-3.57bcde	0.110a
Treatment									
High Density	-0.70 <sup>ns</sup>	-2.97 <sup>ns</sup>	0.140 <sup>***</sup>	-0.76 <sup>ns</sup>	-3.14 <sup>ns</sup>	0.080 <sup>**</sup>	-0.74 <sup>ns</sup>	-3.50 <sup>ns</sup>	0.079 <sup>ns</sup>
Low Density	-0.69	-3.01	0.249	-0.69	-3.19	0.110	-0.72	-3.57	0.101

\*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001; ns - no significance



Table 3-6. Second-year data (2006) for shoot dry mass (DM) at high and low density, leaf area index (LAI), root DM, specific root length (SRL), seed yield, and survivorship for eight wheatgrass populations in the 2005 experiment.

2005 Experiment							
Population	Shoot DM	Shoot DM	LAI	Root DM	SRL	Seed Yield	Surviving
	High Density	Low Density					
	g plant <sup>-1</sup>	g plant <sup>-1</sup>	m <sup>2</sup> m <sup>-2</sup>	g sample <sup>-1</sup>	m kg <sup>-1</sup>	g plant <sup>-1</sup>	%
Bannock TSWG	21.81a <sup>***</sup>	47.46a <sup>***</sup>	1.39abc <sup>***</sup>	0.188bcd <sup>*</sup>	15.45a <sup>*</sup>	1.75a <sup>***</sup>	98.36a <sup>*</sup>
E-38X	19.96abc	37.58b	1.47ab	0.191bcd	12.43bc	1.43ab	96.69a
E-48X	19.11abcd	37.96b	1.55a	0.206abc	12.56bc	1.13bc	97.75a
E-49X	20.18ab	37.61b	1.28bc	0.154d	12.61bc	0.73e	96.90a
SERDP SRWG	15.54bcde	33.84b	1.42ab	0.260a	14.71ab	1.75a	99.23a
E-46 SRWG	15.43cde	26.34c	1.36c	0.194bcd	11.95c	0.97cd	96.84a
Discovery SRWG	14.84de	27.48c	1.23c	0.238ab	12.36bc	1.01c	99.10a
E-45 SRWG	13.85e	23.84c	1.08c	0.189cd	13.91abc	0.84de	90.59b
Treatment							
High Density	17.59b <sup>***</sup>		1.51a <sup>***</sup>	0.188 <sup>ns</sup>	13.82 <sup>ns</sup>	0.70 <sup>***</sup>	96.62 <sup>ns</sup>
Low Density	34.01a		1.18b	0.217	12.67	1.71	97.50

\*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001; ns - no significance

Table 3-7. Correlation coefficients and significance levels for all pairs of variables measured the first year for experiments transplanted in 2005 and 2006 including stomatal conductance ( $g_s$ ), dry mass (DM), leaf area index (LAI) (2005 only), percentage reproducing (2005 only), and specific leaf area (SLA) (2006 only). High density (HD) and low density (LD) are reported separately for stomatal conductance in the 2005 experiment and for dry mass in the 2006 experiment because of a density x population interaction. Correlations above the diagonal are with Bannock TSWG included, and those below the diagonal are with Bannock TSWG excluded.

2005 Experiment						
Correlations with Bannock						
	June $g_s$	HD July $g_s$	LD July $g_s$	DM	LAI	Reproducing
June $g_s$	-	-0.01	0.05	0.77 <sup>*</sup>	0.76 <sup>*</sup>	0.17
HD July $g_s$	-0.09	-	0.25	-0.07	-0.20	-0.57
LD July $g_s$	0.13	0.33	-	-0.45	-0.53	-0.13
DM	0.75 <sup>+</sup>	-0.26	-0.40	-	0.92 <sup>**</sup>	0.14
LAI	0.73 <sup>+</sup>	-0.42	-0.42	0.89 <sup>**</sup>	-	0.09
Reproducing	0.49	-0.55	-0.55	0.74 <sup>+</sup>	0.67	-

Correlations without Bannock

2006 Experiment					
Correlations with Bannock					
	June $g_s$	July $g_s$	HD DM	LD DM	SLA
June $g_s$	-	0.35	0.04	0.05	0.19
July $g_s$	0.36	-	0.29	0.11	-0.11
HD DM	0.12	0.55	-	0.96 <sup>***</sup>	-0.69 <sup>*</sup>
LD DM	0.21	0.24	0.86 <sup>**</sup>	-	-0.58
SLA	0.21	-0.11	-0.51	-0.22	-

Correlations without Bannock

<sup>+</sup> $P < 0.10$ ;  $^*P < 0.05$ ;  $^{**}P < 0.01$ ;  $^{***}P < 0.001$ ; coefficients without superscripts are not significant ( $P > 0.10$ )

Table 3-8. Correlation coefficients and significance levels for all pairs of variables measured in 2006 for the 2005 experiment including May, June, July pre-dawn water potential ( $\Psi_{pd}$ ), mid-day water potential ( $\Psi_{md}$ ), and stomatal conductance ( $g_s$ ); high-density (HD) and low-density (LD) dry mass (DM); seed yield; root dry mass, specific root length (SRL); leaf area index (LAI); and survivorship. Correlations above the diagonal are with Bannock TSWG included, and those below the diagonal are with Bannock TSWG excluded.

	Correlations with Bannock															
	May $\Psi_{pd}$	June $\Psi_{pd}$	July $\Psi_{pd}$	May $\Psi_{md}$	June $\Psi_{md}$	July $\Psi_{md}$	May $g_s$	June $g_s$	July $g_s$	HD DM	LD DM	Seed Yield	Root DM	SRL	LAI	Survivorship
May $\Psi_{pd}$	-	-0.19	-0.16	-0.26	-0.29	-0.10	0.65 <sup>+</sup>	-0.19	0.33	-0.50	-0.53	-0.37	-0.17	0.21	-0.73 <sup>+</sup>	-0.93 <sup>***</sup>
June $\Psi_{pd}$	-0.13	-	0.74 <sup>+</sup>	0.86 <sup>**</sup>	0.69 <sup>+</sup>	0.68	-0.51	-0.75 <sup>+</sup>	-0.51	0.73 <sup>+</sup>	0.58	-0.11	-0.82 <sup>+</sup>	0.10	-0.02	0.01
July $\Psi_{pd}$	-0.07	0.56	-	0.88 <sup>**</sup>	0.77 <sup>+</sup>	0.72 <sup>+</sup>	-0.47	-0.57	-0.28	0.68 <sup>+</sup>	0.66 <sup>+</sup>	0.27	-0.46	0.33	0.11	0.11
May $\Psi_{md}$	-0.22	0.78 <sup>+</sup>	0.79 <sup>+</sup>	-	0.63 <sup>+</sup>	0.73 <sup>+</sup>	-0.49	-0.61	-0.58	0.72 <sup>+</sup>	0.62	-0.06	-0.62 <sup>+</sup>	0.09	0.08	0.16
June $\Psi_{md}$	-0.32	0.44	0.10	0.09	-	0.83 <sup>+</sup>	-0.80 <sup>+</sup>	-0.73 <sup>+</sup>	-0.22	0.84 <sup>**</sup>	0.90 <sup>**</sup>	0.61	-0.34	0.61	0.31	0.26
July $\Psi_{md}$	-0.01	0.48	0.41	0.49	0.68 <sup>+</sup>	-	-0.77 <sup>+</sup>	-0.89 <sup>**</sup>	-0.55	0.88 <sup>**</sup>	0.86 <sup>**</sup>	0.27	-0.53	0.41	0.29	0.04
May $g_s$	0.67	-0.30	-0.07	-0.22	-0.82 <sup>+</sup>	-0.67 <sup>+</sup>	-	0.56	0.54	-0.92 <sup>**</sup>	-0.96 <sup>***</sup>	-0.55	0.21	-0.30	-0.72 <sup>+</sup>	-0.56
June $g_s$	-0.32	-0.63	-0.23	-0.39	-0.60	-0.84 <sup>+</sup>	0.39	-	0.49	-0.70 <sup>+</sup>	-0.64 <sup>+</sup>	-0.05	0.72 <sup>+</sup>	-0.45	0.01	0.29
July $g_s$	0.32	-0.54	-0.35	-0.70 <sup>+</sup>	-0.22	-0.62	0.55	0.51	-	-0.61	-0.49	0.22	0.54	0.21	-0.49	-0.14
HD DM	-0.52	0.59	0.47	0.54	0.81 <sup>+</sup>	0.82 <sup>+</sup>	-0.89 <sup>**</sup>	-0.57	-0.66	-	0.94 <sup>***</sup>	0.33	0.52	0.17	0.56	0.34
LD DM	-0.60	0.29	0.14	0.26	0.82 <sup>+</sup>	0.75 <sup>+</sup>	-0.99 <sup>***</sup>	-0.44	-0.56	0.92 <sup>**</sup>	-	0.59	0.24	0.44	0.61	0.48
Seed Yield	-0.35	-0.66	-0.57	-0.76 <sup>+</sup>	0.30	-0.16	-0.38	0.37	0.35	0.02	0.34	-	0.48	0.68 <sup>+</sup>	0.55	0.50
Root DM	-0.20	-0.91 <sup>**</sup>	-0.65	-0.71 <sup>+</sup>	-0.35	-0.56	0.14	0.76 <sup>+</sup>	0.53	-0.51	-0.17	0.71 <sup>+</sup>	-	0.21	0.16	0.45
SRL	0.43	-0.53	-0.85 <sup>+</sup>	-0.78 <sup>+</sup>	0.07	-0.08	0.09	-0.11	0.42	-0.39	-0.09	0.48	0.47	-	-0.06	0.01
LAI	-0.73 <sup>+</sup>	-0.11	0.02	0.01	0.40	0.28	-0.77 <sup>+</sup>	0.09	-0.48	0.61	0.74 <sup>+</sup>	0.59	0.19	-0.20	-	0.63 <sup>+</sup>
Survivorship	-0.93 <sup>**</sup>	-0.15	-0.17	0.02	0.15	-0.14	-0.54	0.50	-0.12	0.28	0.47	0.48	0.50	-0.20	0.63	-

Correlations without Bannock

\* $P < 0.10$ ; \*\* $P < 0.05$ ; \*\*\* $P < 0.01$ ; \*\*\*\* $P < 0.001$ ; coefficients without superscripts are not significant ( $P > 0.10$ )

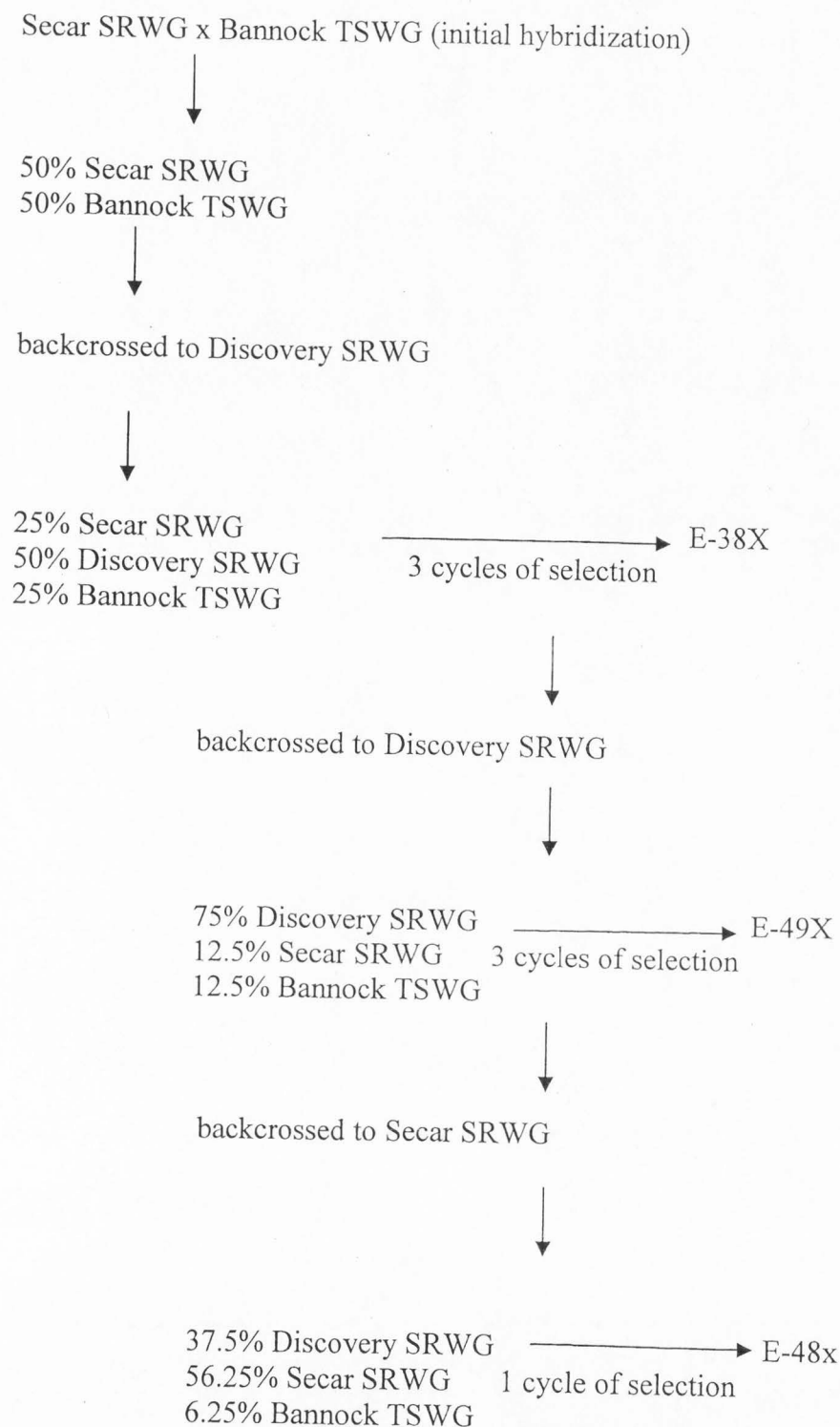


Figure 3-1. Breeding history of three Snake River wheatgrass (SRWG) x thickspike wheatgrass (TSWG) hybrid populations.

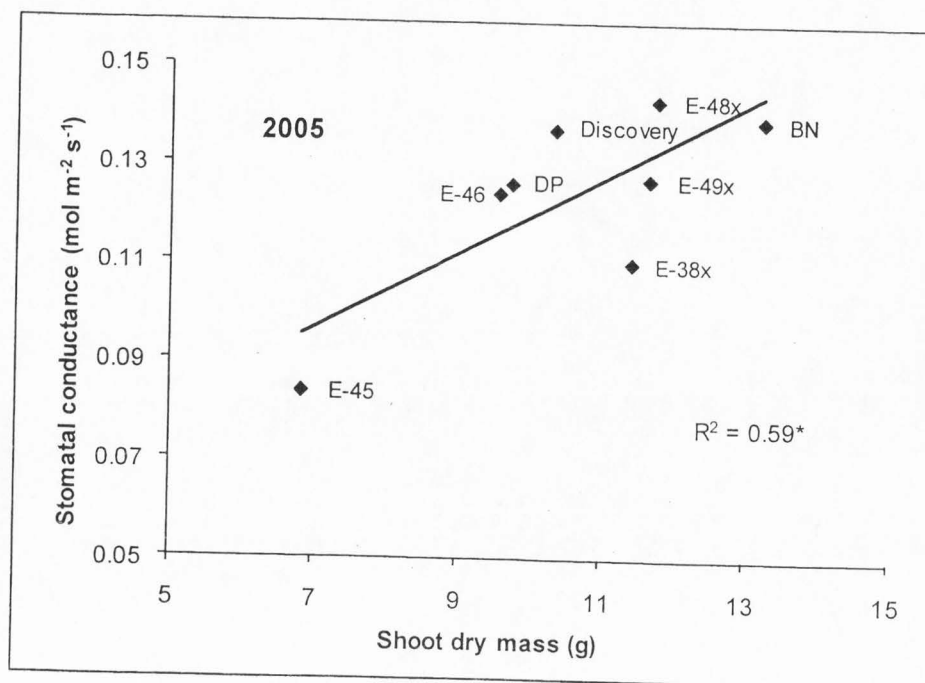


Figure 3-2. Relationship between shoot dry mass and June stomatal conductance measured in 2005 for the 2005 experiment.

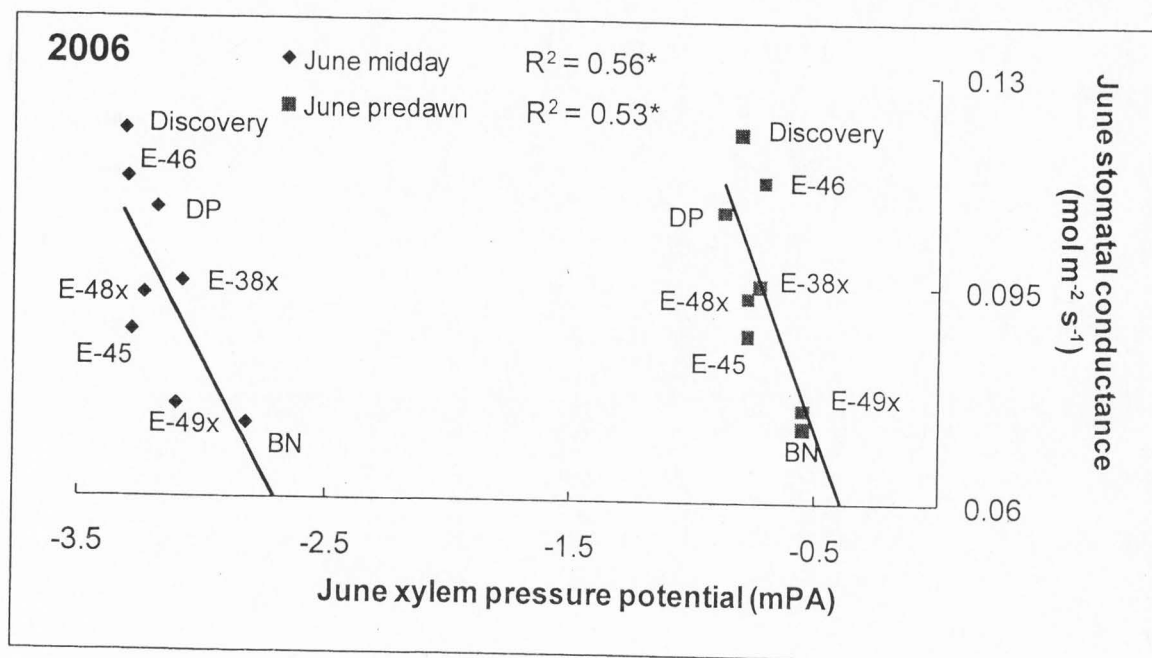


Figure 3-3. Relationship between June pre-dawn and mid-day xylem pressure potential and stomatal conductance for plants measured in 2006 for the 2005 experiment.



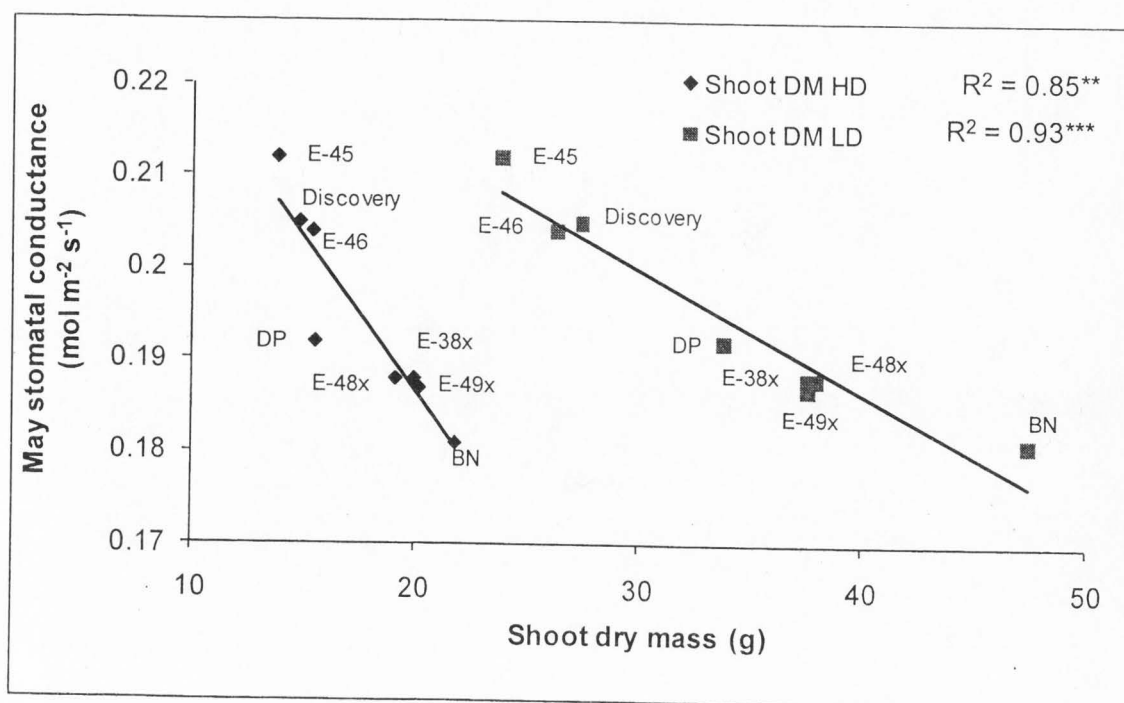


Figure 3-4. Correlation coefficients and significance levels between shoot dry mass (DM), for both high density (HD) and low density (LD), and May stomatal conductance for plants measured in 2006 for the 2005 experiment

## CHAPTER 4

## CONCLUSION

Identifying morphological and physiological traits responsible for greater productivity may help elucidate the reasons why certain plants have superior shoot dry mass production. Productive plants may be more competitive and better able to co-exist with invasive weeds. Using populations displaying the greatest resource acquisition, as evidenced by shoot dry-mass production, may help reduce the dominance of undesirable species and transition the invaded landscapes towards systems consisting of a higher percentage of native perennial wheatgrasses.

Effects of cheatgrass competition on seedling growth and water relations were most pronounced in the SRWG populations compared to the BBWG populations. Of the SRWGs, Secar did fairly well, but it performed the worst in the field study. Of the SRWGs, Discovery had the smallest percentage reduction in shoot dry mass due to cheatgrass competition, and in the field study it was one of the better-performing SRWG populations. Greenhouse studies are good for developing hypotheses, but should be supplemented in a field setting to test them under more naturalized conditions.

The greenhouse results were collected once after a five-week period. The results may have been different if a temporal component was also addressed to examine how the effects of cheatgrass competition changed throughout a longer time frame. In most natural situations cheatgrass is well established before native perennial grasses germinate. Future studies investigating the effects of cheatgrass competition on seedling establishment should determine how different densities of cheatgrass affect germination

rates and how seedlings cope with competition from cheatgrass under varying densities of cheatgrass at different ages.

As for the field study portion, Bannock TSWG was the most productive out of all nine populations examined for all data sets and the hybrid populations consistently outperformed the SRWG populations. Of the SRWGs, E-45 had the lowest shoot dry mass for 2005 and 2006 in the 2005 field planting, but one of the higher shoot dry masses in 2006 for the 2006 field planting. The results of the field study give an idea of future directions that can be taken. For example, Bannock and the hybrids had more favorable water relations and greater productivity, but what are some of the micro-morphological characteristics of TSWG that allow its water relations to be more favorable? Does TSWG have fewer stomata per unit area, is it more glaucous, and does it have a thicker or thinner boundary layer? The applicability of this research will help to identify possible populations that may be implemented in management years in the future.

If we wish to select for productivity/competitiveness, then we need to screen populations throughout their whole life cycle. By starting the plants in a greenhouse setting under favorable environmental conditions we are already working against natural selection. When seed germination and establishment traits are ignored, we may inadvertently select populations with inferior germination and seedling establishment. The most critical phase in a plants' life cycle is the seedling stage (if it germinates), and when we bypass this, we may be selecting plants that are the most productive but with poor germination or seedling establishment.

The impact of these findings will aid in the advancement of some of these populations into possible cultivars that will be released for rehabilitation efforts. The

results also determined that some of the populations warrant no further advancement. As for plant material developers, this study may help explain why some species/populations perform better than others. Elucidating the mechanisms some plants employ to produce more shoot dry-mass permit population screening in a more enlightened fashion.

