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Crested wheatgrass-cheatgrass seedling competition in a mixed-density design

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Abstract

Plant competition experiments have historically used designs that are difficult to interpret due to confounding problems. Recently, designs based on a "response function" approach have been proposed and tested in various plant mixture settings. For this study, 3 species were used that are important in current revegetation practices in the Intermountain West. 'Nordan' (*Agropyron desertorum* [Fish. ex Link] Shult.) and 'Hycrest' (*A. cristatum* [L.] Gaertn. x *desertorum*) crested wheatgrass are commonly-used revegetation species on rangelands susceptible to cheatgrass (*Bromus tectorum* L.) invasion, although little quantitative data exist that compare their competitive abilities. We evaluated the competitive ability of Hycrest and Nordan seedlings in 2-species mixtures with cheatgrass in a greenhouse study. Linear and nonlinear models were developed for a range of densities (130-520 seeds m^{-2}) for each species to predict median above-ground biomass and tiller numbers and to further test the usefulness of this design for evaluating species to rehabilitate rangelands. In both experiments, increasing Hycrest and Nordan densities reduced their own biomass and tiller production while increasing Hycrest densities reduced cheatgrass biomass and tiller production. Nordan did not affect cheatgrass biomass and tiller production. However, increasing cheatgrass densities reduced Hycrest and Nordan biomass and tiller production, and its own biomass and tiller production. The competition index i.e. substitution rate, indicated that Hycrest seedlings were better competitors with cheatgrass than Nordan, although in all mixtures, cheatgrass plants were the superior competitors. Further field research using this design, where environmental inputs are less optimal and diverse, is needed to validate these results and to further evaluate the use of this approach in examining effects of intra- and interspecific competition.

Key Words: competition index, mixture ratios, 'Hycrest', 'Nordan', aboveground biomass, tiller production

The need for successful revegetation practices to control the spread of undesirable plants has motivated ecologists to understand intra- and interspecific interactions among plants. Recent criticism of competition designs (Firbank and Watkinson 1985, Connolly 1986a, 1986b, Snaydon 1994) has led to alternative techniques that relate yield to density in mixtures (Connolly and Nolan 1976, Firbank and Watkinson 1985, Connolly 1987, Law and Watkinson 1987, Connolly et al. 1990, Menchaca and Connolly 1990).

To test this approach, a seedling competition study was conducted using 3 species that often interact during revegetation of rangelands in the western U.S. (Pellant and Monsen 1993). One of these, cheatgrass (*Bromus tectorum* L.), is a competitive annual from Eurasia (Hulbert 1955, Klemmedson and Smith 1964, Harris 1967, Pyke 1987). To help counter this plant, crested wheatgrasses (*Agropyron desertorum* [Fish. ex Link] Shult. and *A. cristatum* [L.] Gaertn.) are sown in most revegetation projects. The commonly sown cultivars include 'Nordan,' a natural tetraploid of *A. desertorum*, and 'Fairway,' a natural diploid of *A. cristatum* (Asay et al. 1985a). 'Hycrest,' the first commercially released interspecific hybrid between *A. cristatum* and *A. desertorum*, produces a greater amount of aboveground biomass than either parent (Asay et al. 1985b). Initial seeding trials with Hycrest provided qualitative observations concerning its apparent superior ability to compete with highly invasive annuals such as cheatgrass and halogeton (*Halogeton glomeratus* Meyer.) (Asay et al. 1985a).

We compared the ability of Hycrest and Nordan to compete as young plants with cheatgrass. Aboveground biomass and tiller numbers were used as yield parameters for comparing among these plants using mixed-density regression models. This study also provides a useful comparison of Connolly's (1987) indices for competitive interactions as they relate to revegetation.

Materials and Methods

Hycrest seeds were harvested in 1987 from USDA-ARS plots located in Logan, Utah, U.S.A. (41° 48' N, 111° 51' W), while Nordan seeds were purchased the same year from a local seed company. Cheatgrass seeds were collected in 1987 from the Utah State University Tintic Research site, 8 km south of Eureka, Utah (39° 2' N, 112° 8' W).

This study was conducted in a controlled, glasshouse environment. Experimental units were large fiber pots (33-cm upper diameter × 30-cm lower diameter × 36-cm depth). Ground fritted clay was used as the growth medium because of its excellent water- and nutrient-holding capacity (van Bavel et al. 1978). Each fritted clay-filled pot was rinsed with water to remove impurities and establish available water content for imbibition.

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A preliminary germination study was conducted to establish seeding rates to achieve the desired seedling densities. Differences in densities persisted without thinning throughout the experiment and were used in developing multiple regression equations. Four approximate densities were established for each species, 12, 24, 36, and 48 Pure Live Seed (PLS) species^{-1} pot^{-1}, equivalent to 130, 260, 390, and 520 seeds m^{-2}. The recommended seeding rate of the crested wheatgrass species is approximately 260 seeds m^{-2} (Asay et al. 1985b).

Seeds were sown between 11–15 October 1989. All species in an individual pot were sown on the same day. Crested wheatgrass seeds were hand sown in a 2-cm deep furrow extending across the diameter of the pot's soil surface and running north-south to minimize shading from adjacent plants. Seed was distributed evenly across the furrow and covered to simulate drilling. To further simulate naturally-occurring conditions, cheatgrass seeds were hand sown randomly across the soil surface, including the area of the furrow where the crested wheatgrass seeds were sown. Cheatgrass seeds were covered with approximately 1 cm of clay to insure adequate contact with the clay and available water.

The experimental design was a randomized-complete-block using 4 blocks (replicates) with 44 pots (treatments) block^{-1}, for a total of 176 pots. Treatments included monocultures of all 3 species at each density, and mixtures of Hycrest or Nordan and cheatgrass at all 4 densities for each species in the mixture (16 combinations).

Naturally occurring photoperiods were used through the 176-day experiment that extended from 11 October 1989 to 4 April 1990. Glasshouse day/night temperatures were maintained at 24/7 °C. Soil water was maintained near field capacity throughout the experimental period. A commercial fertilizer, Peter's™ 20-20-20 (N-P-K), was applied in water at 2.4 g fertilizer liter^{-1} of water, yielding 0.5 mg m^{-3} of N, P, and K. Fertilizer solution (0.95 liter) was applied to each pot 3 times during the experiment: 16, 38, and 70 days from the date of seeding. In February 1990, 1 application of Ortho Malathion™ was applied to plants in all pots to control aphids. Seedling emergence was monitored to determine densities and no adjustments were necessary.

Plants were harvested in April and May 1990. Aboveground biomass of each plant was harvested and stored in envelopes. Tiller counts for each plant were recorded at the same time. Plants were dried at 70° C for 48 hours. Aboveground biomass for each plant was recorded to the nearest 0.1 mg. Because cheatgrass seed production was limited due to phenological variability, seed weight was not recorded, but was included as aboveground biomass. Roots were not quantified because roots of individual plants could not be separated. Aboveground biomass and tiller counts exhibited skewed distributions for each species. Median values were used as the measure of central tendency since log and square root transformations did not normalize the data.

Based on Connolly's (1987) 'response function' approach, several multiple regression equations were fitted to the data (Table 1). The adequacy of fit of each model was tested using both its resulting R^2 value and Mallow's C_p statistic, which measures the sum of the squared biases plus the squared random errors in Y at all N data points (Daniel and Wood 1980). Additionally, the ability to explain biologically the parameters of each model was important in the selection process.

A substitution rate, i.e., a competition index, was calculated from the selected model for each variable to evaluate the effects of species interactions and densities. The substitution rate (S) is a quantitative, model-dependent measurement comparing the degree of influence that 1 species has on another species relative to its influence on itself. At mixed density (d_1, d_2), the substitution rates S_1 and S_2, are:

$$S_1 = (\delta f_1/\delta d_2) / (\delta f_1/\delta d_1) \quad \text{and} \quad S_2 = (\delta f_2/\delta d_1) / (\delta f_2/\delta d_2), \tag{1}$$

where $\delta f_i/\delta d_j$ is the partial derivative of the model (f_i) explaining the yield of species *i* with respect to the density of species *j* (d_j) (Maynard Smith 1974). When linear or inverse linear models were used, substitution rates were calculated following the form of Menchaca and Connolly (1990), while the form put forth by Law and Watkinson (1987) was followed when nonlinear models were used. This index was calculated across mixtures and densities if the necessary information was provided by the selected model and graphed to evaluate their trend with changing densities. This index is used as a competition coefficient, sensu Firbank and Watkinson (1985), and was not interpreted in a fitness sense.

Table 1. Models tested for 2-species mixtures where yield(Y) is a function of the densities (X) of Hycrest or Nordan crested wheatgrass (i) and cheatgrass (j), and where B_1, B_2 and B_3 are density coefficients and A, C, D and W are competition coefficients.

Model Tested	Source
$Y_i = B_0 + B_1X_i + B_2X_j$	Standard
$1/Y_i = B_0 + B_1X_i + B_2X_j + B_3(X_i*X_j)$	Wright 1981; Spitters 1983; Firbank and Watkinson 1985; Menchaca and Connolly 1990;
$Y_i = X_iW_i/(1 + C_iX_i + C_iA_{ij}X_j)$	Law and Watkinson 1987
$Y_i = X_iW_i/(1 + (X_i + A_{ij}X_j)^{Di})$	Law and Watkinson 1987
$Y_i = X_iW_i/(1 + X_i + A_{ij}X_j)^{Di}$	Law and Watkinson 1987
$Y_i = X_iW_i/(1 + C_iX_i + C_iA_{ij}X_j)^{Di}$	Law and Watkinson 1987
$Y_i = X_iW_i/(1 + X_i^{Dii} + X_j^{Dij})$	Law and Watkinson 1987

Results

An inverse linear model best described biomass of all species in the 2 mixture experiments (Table 2). The combined densities of the crested wheatgrass and cheatgrass influenced the biomass of Hycrest or Nordan grown in mixtures with cheatgrass and they influenced the biomass of cheatgrass grown in mixtures with Hycrest. Cheatgrass biomass was explained by changes in intraspecific density alone when grown in mixtures with Nordan.

In contrast, a nonlinear model best described tiller production for both Hycrest and cheatgrass in mixture and for Nordan in mixture, and a linear model best described cheatgrass mixed with Nordan (Table 2). Although slightly lower in their explained variation (R^2 value) than several linear models, the nonlinear models' C_p values equaled those of their linear counterparts. These nonlinear models demonstrated that numbers of tillers of both species in a mixture were reduced when densities increased regardless of the species. Lastly, a linear model best described the tiller count data for cheatgrass in the Nordan and cheatgrass mixture, indicating tiller production was affected only by changes in intraspecific density.

Table 2. **Best-fit models for individual plant biomass and tiller production (Y) for each species in a mixture where D represents density (plants per pot) of Hycrest or Nordan (i) grown in a mixture with cheatgrass (j).**

Mixture & Species	Variable	Best-fit Model	Coefficient Determination (R^2)	Mallows C_p[1]
Hycrest X cheatgrass				
Hycrest	Biomass	$1/Y_i = -0.22 + 0.2D_i + 0.12D_j - 0.002D_i^2$	0.72	2.5
Cheatgrass	Biomass	$1/Y_j = 0.35 + 0.01D_j + 0.007D_i + 0.0002D_j^2$	0.70	3.5
Hycrest	Tiller number	$Y_i = D_i 22.61/(1 + D_i^{1.52} + D_j^{1.16})$	0.67	2.9
Cheatgrass	Tiller number	$Y_j = D_j 68.64/(1 + D_j^{1.56} + D_i^{0.59})$	0.50	2.9
Nordan X cheatgrass				
Nordan	Biomass	$1/Y_i = 5.37 + 0.14D_i + 0.64D_j$	0.67	1.3
Cheatgrass	Biomass	$1/Y_j = 0.2 + 0.03D_j - 0.0002D_j^2$	0.59	2.0
Nordan	Tiller number	$Y_i = D_i 51.15/(1 + D_i^{1.8} + D_j^{1.59})$	0.84	2.9
Cheatgrass	Tiller number	$Y_j = 21.28 - 0.43D_j + 0.004D_j^2$	0.58	0.4

[1] "Total squared error" - measures the sum of the *squared biases* plus the *squared random errors* in Y at all N data points (Daniel and Wood 1980).

Both Hycrest and cheatgrass densities influenced the biomass plant^{-1} of Hycrest (Fig. 1A) and cheatgrass (Fig. 1B). While Hycrest and cheatgrass biomass plant^{-1} were both highest at the lowest monoculture and mixture densities (Fig. 1A and 1B), biomass area^{-1} exhibited opposite trends for the 2 species (Fig. 2A and 2B). Tiller numbers of Hycrest (Fig. 3A) and cheatgrass (Fig. 3B) exhibited different trends from the biomass data. Although increases in cheatgrass density reduced tiller numbers of both species, the reduction was the greatest at the lowest Hycrest densities and diminished as Hycrest density increased (Fig. 3A). At low cheatgrass densities, low Hycrest densities allowed Hycrest tiller numbers to increase. As cheatgrass densities increased, a threshold density for Hycrest (24 plants pot^{-1}) appeared where tiller numbers were maximized for both species. In contrast, changes in Hycrest densities had smaller effects on cheatgrass tiller numbers (Fig. 3B).

Trends in biomass (both on a plant^{-1} and area^{-1} basis) and tiller numbers (plant^{-1}) for mixtures of Nordan and cheatgrass showed similar response figures to mixtures of Hycrest and cheatgrass, yet they differed in magnitude (Figs. 1, 2, and 3). On a plant^{-1} basis, Nordan generally produced less biomass than Hycrest with increasing cheatgrass densities (Fig. 1A and 1C). Cheatgrass biomass was not influenced by increasing Nordan densities (Fig. 1D), whereas increasing Hycrest densities reduced cheatgrass biomass when cheatgrass densities were low (Fig. 1B). As cheatgrass densities increased, cheatgrass yielded similar biomass regardless with which cultivar of crested wheatgrass it was grown.

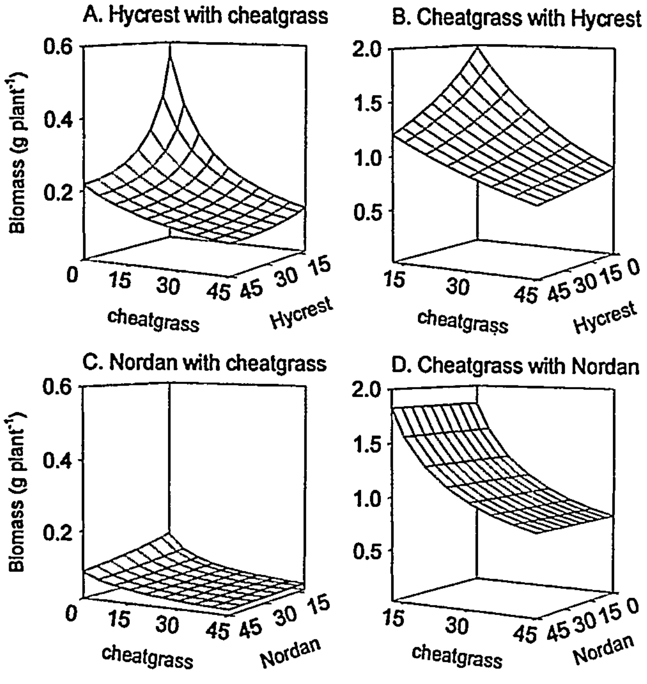

Fig. 1 Modeled biomass per plant for Hycrest (A), Nordan (C) and cheatgrass (B and D) in 2-species mixtures of Hycrest or Nordan with cheatgrass.

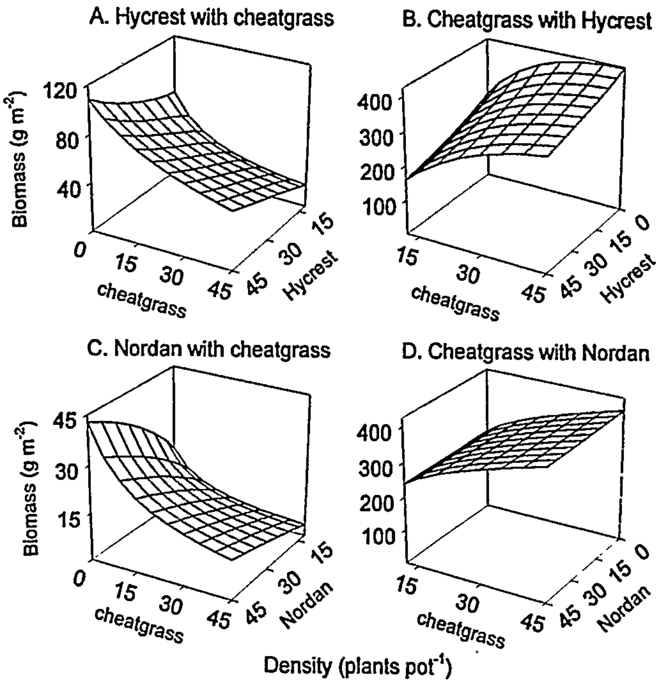

Fig. 2 Modeled biomass per area for Hycrest (A), Nordan (C) and cheatgrass (B and D) in 2-species mixtures of Hycrest or Nordan with cheatgrass.

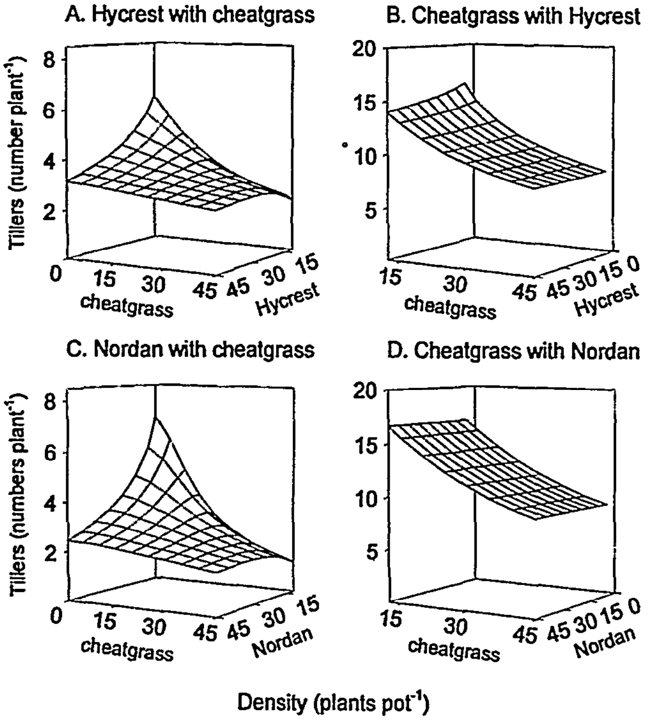

Fig. 3 Modeled tiller production per plant for Hycrest (A), Nordan (C) and cheatgrass (B and D) in 2-species mixtures of Hycrest or Nordan with cheatgrass.

Tiller counts for Hycrest and Nordan were similar at lower densities (6.1 vs. 6.9 plant^{-1}), but Hycrest produced more tillers at the higher densities (2.4 vs. 1.6 plant^{-1}), indicating a greater effect of cheatgrass on Nordan at higher densities than on Hycrest (Fig. 3A and 3C). Response surfaces for cheatgrass tiller numbers were similar in shape in the Hycrest and Nordan mixtures, providing further evidence that intraspecific competition has the greatest effect in determining tiller production for cheatgrass (Fig. 3B and 3D).

Substitution rates for Hycrest based on biomass increased as a result of increasing Hycrest density, demonstrating that cheatgrass individuals were increasingly more influential than Hycrest individuals in the mixture (Fig. 4A). In an opposite effect, cheatgrass substitution rates decreased with increases in cheatgrass density indicating that the influence of Hycrest individuals over individuals of cheatgrass was decreased as cheatgrass densities increased (Fig. 4B).

Substitution rates for Nordan remained constant as each cheatgrass individual had an effect equivalent to 4.6 individuals of Nordan (Fig. 4C). This result was due to the parameters of the selected model which produced a constant rate. For cheatgrass in the mixture with Nordan, a substitution rate could not be calculated due to model constraints indicating that cheatgrass was not affected by Nordan.

For Hycrest and cheatgrass tiller production, substitution rates ranged from 0.16 to 0.34 for Hycrest and from 0.01 to 0.03 for cheatgrass, with the lowest rates for Hycrest and cheatgrass occurring at the 48 Hycrest and 12 cheatgrass plants pot^{-1}, and at the 48 Hycrest and 48 cheatgrass plants in mixtures, respectively (Fig. 5A and 5B). For both Hycrest and cheatgrass, substitution rates decreased as intraspecific densities increased. Conversely, as interspecific densities increased, substitution rates increased for Hycrest and decreased for cheatgrass (Fig. 5A and 5B). In the Nordan and cheatgrass mixtures, substitution rates for tiller production could only be calculated for Nordan, which ranged from 0.51 to 0.97 (Fig. 5C), since cheatgrass tiller production was not influenced by Nordan. Results for tiller production substitution rates for all 3 species were less than 1, regardless of densities and mixture ratios, indicating that each species was more influenced by its own individuals than by the other species within the mixture. Thus, intraspecific competition was the main influence in tiller production for all species.

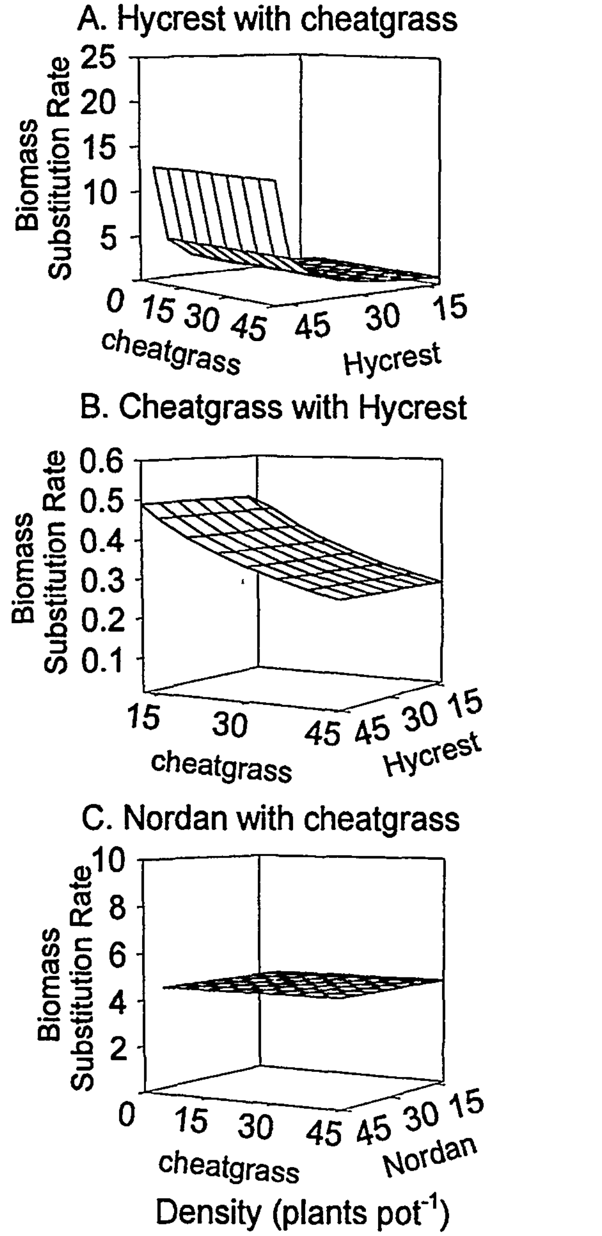

Fig. 4 Biomass substitution rates for Hycrest (A) and cheatgrass (B) for the Hycrest and cheatgrass mixture, and for Nordan (C) in the Nordan and cheatgrass mixture.

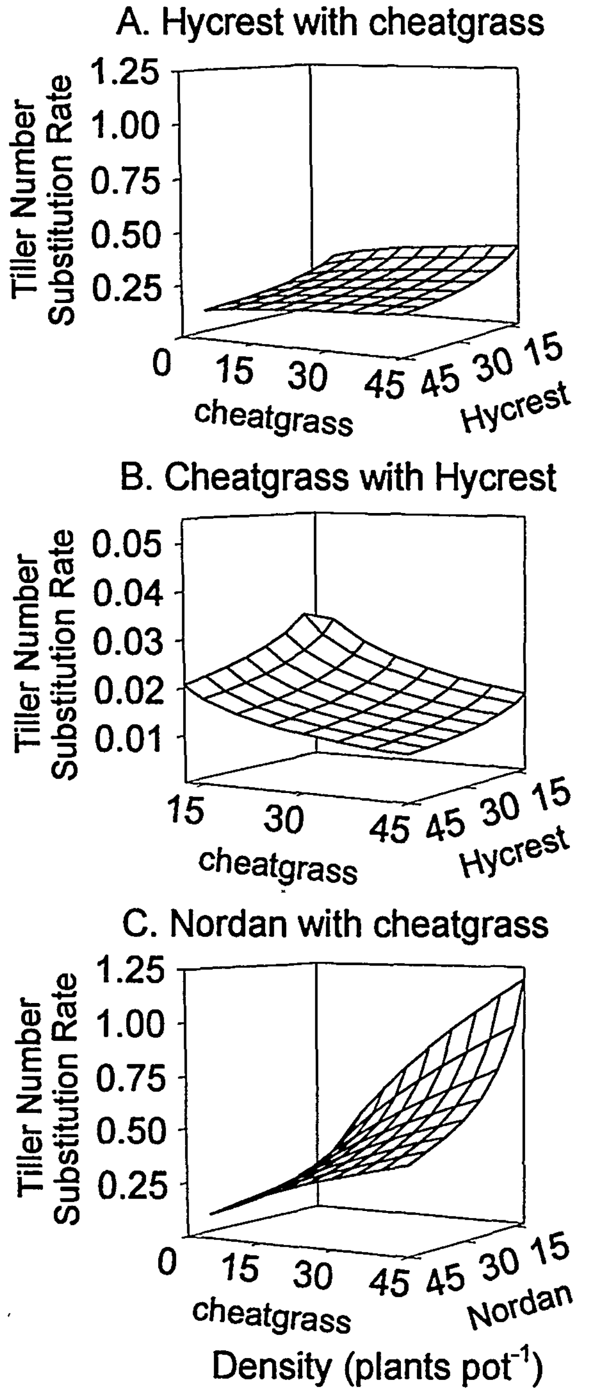

Fig. 5 Tiller number substitution rates for Hycrest (A) and cheatgrass (B) for the Hycrest and cheatgrass mixture, and for Nordan (C) in the Nordan and cheatgrass mixture.

Discussion

Previous work evaluating competition between crested wheatgrass and cheatgrass produced varied results with most citing cheatgrass as the dominant competitor (Evans 1961, Hull 1963, Harris 1967, Harris 1977, Young and Evans 1985, Buman et al. 1988, Aguirre and Johnson 1991b). However, problematic in each of these studies is the provision for ranges of densities and mixture ratios of each species. Real plant populations exhibit varying densities and mixture ratios of species, and a more realistic evaluation across a range of population densities and mixture ratios is required (Call and Roundy 1991, Pyke and Archer 1991).

Comparative results for Hycrest or Nordan competition with cheatgrass from other work is very limited and hard to apply since most have the same design problem. However, results of the current study are consistent with field studies by Rummel (1946) and Hull (1963), who found that as cheatgrass density increased, crested wheatgrass (pre-Hycrest era) shoot weight decreased. Results are also consistent with greenhouse results of Aguirre and Johnson (1991a, 1991b), who found young cheatgrass was superior to Hycrest in several seedling characteristics at 1:1 and 1:4 mixture ratios. In contrast, Buman et al. (1988) found that 6-week-old Hycrest seedlings were equal to cheatgrass seedlings in shoot biomass when competing in a 1:1 mixture. Reasons for the greater competitive ability of cheatgrass over other grasses including cultivars of crested wheatgrass include morphological and physiological characteristics such as: 1) a more efficient root system in exploiting soil moisture (Evans 1961, Harris 1967, Melgoza and Nowak 1991); 2) earlier branching of the primary root, a greater number and order of branching of seminal roots, and earlier elongation and branching of adventitious roots; 3) greater total root length and root dry weight at higher cumulative growing degree days; 4) faster leaf and tiller development; 5) greater leaf area (Aguirre and Johnson 1991a); and 6) greater efficiency (per unit of biomass) in producing leaf area and root length (Svejcar 1990).

Given this information, some have suggested that lower densities of aggressive perennials may enable the perennials to better compete with invasive annuals such as cheatgrass (Buman et al. 1988, Pyke and Archer 1991). This premise rests in the ability of fewer individuals having access to more resources by reducing the amount of intraspecific competition. While limited, results of this study support this suggestion with quantifiable evidence using a design that allows for natural population variations with ranges of mixed densities and mixture ratios. This ability to quantify competition among species provides more diverse and usable information for understanding plant interactions.

Hycrest and Nordan appear to have a greater chance for exploiting resources in less crowded populations. Comparisons of maximum biomass and tiller production as measured on a individual^{-1} and area^{-1} basis demonstrated opposite trends, with all 3 species maximizing biomass production area^{-1} at the highest crested wheatgrass-cheatgrass mixtures. Although it appears that plant densities compensate for lower individual plant biomass at the higher densities, what is not known is how many of these individuals survive to the next year. In addition, how environmental inputs, i.e. soil types, precipitation regimes, microsites, etc., at field sites will affect both survival and competitive relationships between species should be further investigated. Thus, the important relationship to seek out through additional research is how the plant-to-plant relationship relates to individual establishment and survival with a diversity of environmental inputs.

While the modeled data provided important insight and evidence for seeding Hycrest and Nordan at lower densities for increased competitive ability, the substitution rate provided the means to evaluate the competitive interactions as densities and mixtures ratios changed. It became evident from this index that lower densities of the crested wheatgrasses allowed it to compete better with cheatgrass. In all cases, lower densities of Hycrest and Nordan are less affected by cheatgrass as a competitor. However, as crested wheatgrass and cheatgrass densities increase, the compounding effect of intra- and interspecific competition led to cheatgrass becoming more competitive. Thus, the morphological and physiological advantages of cheatgrass in crowded stands of mixed species allow it to exploit resources more effectively than the crested wheatgrass.

Since neither Hycrest nor Nordan appears to effectively suppress cheatgrass at any of the examined densities during the first-year establishment phase, recommendations for appropriate seeding rates will require field oriented studies conducted under a variety of environmental inputs, and extended beyond 1 year. Recognizing these limitations, however, results of this experiment provides a view of the role of intra- and interspecific competition on first-year growth of these crested wheatgrasses. As such, comparison of the 2 crested wheatgrasses demonstrated that Hycrest was more competitive than Nordan when grown with cheatgrass.

Given these results, establishment of a perennial grass seedling such as crested wheatgrass, can be enhanced by producing multiple-tillered individuals because of the multiple buds for daughter tiller production in the following year. Thus, sowing crested wheatgrasses at densities that maximize tiller production as well as biomass may prove beneficial in subsequent years. One possible negative outcome of this decision may entail a more intense seedbed preparation regime to help offset the risk of seedling establishment failure. Thus, inherently important to this process is the season of sowing. This experiment used a autumn-winter-spring growing season rather than the typical spring growing season for crested wheatgrass. Recognizing that cheatgrass may germinate in autumn, some of these seedlings could be displaced during a late-autumn seeding process (e.g., using deep-furrow drills). Klomp and Hull (1972) demonstrated that crested wheatgrass stand ratings were highest using a deep-furrow drill after autumn germination of cheatgrass. Regardless, real populations of interacting individuals of cheatgrass and crested wheatgrass are likely to germinate in the same season (e.g., late winter). Given this reality, perennial grasses should be managed to give them the greatest advantage. In this case, in order for Hycrest to achieve optimum growth in the first year as the better competitor, it would seem more advantageous to prescribe Hycrest seeding rates at or below recommended densities (approximately 260 seeds m^{-2}) when cheatgrass is present. This in turn may allow Hycrest to better exploit available resources, reduce intraspecific competition, and reduce the compounding effect of interspecific competition.

The ultimate goal of seeding competitive perennials on cheatgrass-dominated rangelands is to reduce cheatgrass abundance while simultaneously establishing perennials that remain green later in the summer to reduce the threat of wildfires that are common on cheatgrass rangelands (Pellant 1990). If lower seeding rates of crested wheatgrass can ultimately maintain their competitive advantage into subsequent years, then cheatgrass densities may decline quicker than with current seeding rates; however most studies document the establishment of the perennial, but rarely determine the long-term impact on cheatgrass densities. Hull and Stewart (1948) provide some evidence for effective reductions of cheatgrass when crested wheatgrass is sown in late-autumn, after cheatgrass germination, using a deep-furrow drill. In a broader context, these results emphasize the need for knowledge of seed pool sizes of undesirable species as well as the diverse environmental inputs and their affects in the competitive relationships. With this knowledge, seeding rates can be better calculated to help increase establishment and growth of desirable species in subsequent years.

In addition to producing insight into the interactions of these 2 wheatgrasses with cheatgrass, the results of this study also provide evidence supporting the use of this approach in other plant competition studies, whether in desirable-undesirable or desirable multiple-species mixtures. When concerned with the latter type of mixture, especially when formulating seeding rates, this experimental design provides information on overlap in plant resource requirements and acquisition strategies that can help determine: 1) which species are likely to directly compete and therefore be inherently incompatible; 2) which species may effectively partition site resources to minimize competitive exclusion and therefore promote coexistence and diversity; and 3) which species may modify site characteristics to facilitate succession and establishment of additional species (Pyke and Archer 1991). While answers to these questions are both important and vital in attaining a successful revegetation strategy, this design also helps produce a clearer understanding of various plant interactions that occur not only among species, but also through time.

While revegetation technology apparently has progressed more rapidly than revegetation science over the past decades (Call and Roundy 1991), steps are being taken to establish the science involved in the revegetation process. The goal for future work should involve determining requirements and positive characteristics of different species (Aber 1987, Call and Roundy 1991), while simultaneously preparing for potential secondary problems such as undesirable plant invasions (Pyke and Archer 1991). Plant competition is a vital and important factor in any revegetation effort and nontraditional approaches for the design and quantification of interactions can provide information needed to produce stable and diverse plant communities for the future.

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