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COMPETITIVE INTERACTIONS BETWEEN CRESTED WHEATGRASSES  
AND CHEATGRASS

by

Mark G. Francis

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

of

MASTER OF SCIENCE

in

Range Ecology

Approved:

UTAH STATE UNIVERSITY  
Logan, Utah

1993

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Mark G. Francis

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## ABSTRACT

Competitive Interaction between Crested Wheatgrasses  
and Cheatgrass

by

Mark G. Francis, Master of Science

Utah State University, 1993

Major Professor: Dr. David A. Pyke  
Department: Range Science

Current revegetation practices in the Intermountain West include the use of Nordan (Agropyron desertorum) and Hycrest (A. cristatum x desertorum) crested wheatgrass on rangeland susceptible to cheatgrass (Bromus tectorum) invasion, although little quantitative data exists that compares their competitive abilities. We evaluated both the competitive ability of Hycrest and Nordan in two-species mixtures with cheatgrass, and evaluated seedling establishment characteristics for all three species in a greenhouse study. Linear and nonlinear models were developed for a range of densities for each species to predict median above-ground biomass and tiller numbers. In both experiments, increasing Hycrest and Nordan densities reduced their own biomass and tiller production while cheatgrass biomass and tiller production was not influenced. However, increasing cheatgrass densities reduced both Hycrest and Nordan biomass and tiller production, as well as its own biomass and tiller production. Examination of trends in competition indices, such as relative resources totals,

substitution rates and perceived densities indicated that as seedlings, Hycrest was a better competitor with cheatgrass than Nordan at lower crested wheatgrass densities (130 plants/m<sup>2</sup>). Results from this experiment indicate that Hycrest is a better competitor than Nordan with cheatgrass and suggest that seeding Hycrest at lower densities than currently recommended may optimize its seedling growth when competing with cheatgrass. Future research concerning competition in these species using similar designs should focus on competition in successive years after establishment and on field experiments to verify these results.

(69 pages)



## INTRODUCTION

In the Intermountain West, highly plastic annual plants have invaded and established their dominance on both disturbed and undisturbed land.

Cheatgrass (Bromus tectorum L.) is one such autogamous annual from Eurasia that was introduced several times in the Intermountain West prior to 1900 (Mack 1981). Its invasive ability centers around several growth characteristics, including autumn germination, a lack of dormancy, rapid autumn and spring growth, a plastic response to competition (Harris 1967), the potential production of more than 300 seeds per parent (Hulbert 1955), and persistence when grazed (Hulbert 1955, Klemmedson and Smith 1964, Pyke 1987).

To help counter these invasive plants, widely adapted cool-season perennials such as the crested wheatgrasses (Agropyron desertorum [Fish. ex Link] Shult. and A. cristatum [L.] Gaertn.) have been used in most of the revegetation efforts on western rangelands. The cultivars 'Nordan,' a natural tetraploid of A. desertorum, and 'Fairway,' a natural diploid of A. cristatum, have been widely used in revegetation programs (Asay et al. 1985b). 'Hycrest,' the first commercially released interspecific hybrid between A. cristatum and A. desertorum, is a taller statured plant that produces a greater amount of aboveground biomass than either parent (Asay et al. 1985a). Initial seeding trials with Hycrest demonstrated its ability to survive and grow on arid sites, while a qualitative observation was made concerning its apparent superior ability to compete with highly invasive annuals such as cheatgrass and Halogeton glomeratus Meyer. (Asay et al. 1985b). Hycrest's ability to survive, grow, and propagate on degraded lands depends on its ability as a young plant

to compete with less desirable species. (Francis, 1993)

Typical competition experiments involving two-species mixtures have used either an additive or a substitutive experimental design (Silvertown 1987). However, the constraints of each design inherently confound or make interpretations of the results very difficult (Harper 1977, Mead 1979, Inouye and Schaffer 1981, Joliffe et al. 1984, Firbank and Watkinson 1985, Connolly 1986a,b). In light of these difficulties, recent studies of competition between two species have used alternative techniques that relate yield (biomass or seed production) for each species to the densities of both species in the mixtures (Connolly and Nolan 1976, Suehiro and Ogawa 1980, Wright 1981, Spitters 1983, Firbank and Watkinson 1985, Law and Watkinson 1987, Roush et al. 1989, Connolly et al. 1990, Menchaca and Connolly 1990). Connolly (1987) further developed this approach allowing a quantitative assessment of the degree that environmental factors affect an individual plant's response to its environment.

In light of the qualitative observations concerning the competitive ability of Hycrest, and to better understand the competitive abilities of desired and undesired plant species, a controlled glasshouse study was conducted using Connolly's (1987) techniques to evaluate the interactions among Nordan, Hycrest, and cheatgrass. The objectives of this study were to (1) evaluate both the competitive abilities of Hycrest and Nordan in two-species mixtures with cheatgrass and (2) evaluate seedling establishment characteristics of all three species based on aboveground biomass and tiller number. A third objective

was to further evaluate the usefulness of Connolly's (1987) techniques and indices for describing competitive interactions between species. For each objective, densities and mixture rates were varied to provide a range of population sizes for predicting establishment and for providing quantifiable evidence concerning the value of Hycrest as an important species for revegetation of degraded semiarid lands of the Intermountain West.



local  
fritted clay?

## MATERIALS AND METHODS

This study was conducted in a controlled, glasshouse environment. Large fiber pots (33-cm upper diameter x 30-cm lower diameter x 36-cm depth) were used for each experimental unit. Ground fritted clay was used as the growth medium because it has excellent water-holding capacity and nutrient content, and is easy to wash from the roots (van Bavel et al. 1978). Each fritted clay-filled pot was rinsed with water to flush out any impurities and establish available water content for imbibion.

Hycrest seed lots were harvested in 1987 from U.S. Department of Agriculture, Agriculture Research Service (ARS) plots located in Logan, Utah, U.S.A. (41° 48' N, 111° 51' W), while Nordan seeds were purchased from a local seed company in the same year. 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). All crested wheatgrass seeds were hand sown in a 2-cm deep furrow with the furrow running north-south to minimize shading from adjacent plants. These furrows extended across the diameter of the pot's soil surface, and the seed was distributed evenly across the furrow and covered with fritted clay to simulate seed drilling. Cheatgrass seeds were hand sown randomly across the surface, including the area of the furrow where the crested wheatgrass seeds were sown. Cheatgrass seeds were covered with approximately 1 cm of fritted clay to insure adequate contact with the fritted clay and available water for the imbibing process. Seeding took place 11-15 October 1989. Each pot was seeded on the same day with all

Sowing  
Crested  
wheatgrass

Seeding  
of  
cheat

respective species. A pre-experiment germination study of all three species was conducted to establish seeding rates to achieve the desired seedling densities. Although prescribed, thinning was not necessary to maintain appropriate densities since distinct differences in actual densities were naturally maintained throughout the duration of the experiment and were used in developing multiple regression equations. Thus, with X representing the recommended seeding rate of approximately 260 seeds/m<sup>2</sup> (Asay et al. 1985a), four approximate densities were established for all species, 0.5X, 1X, 1.5X, and 2X, or 12, 24, 36, and 48 PLS/species/pot, depending on desired treatment (Fig. 1).

The experimental design for this study was a randomized, complete block using 4 blocks (replication) with 44 pots (treatments) per block, yielding a total of 176 pots. Each treatment represented a particular monoculture or mixture of Hycrest or Nordan and cheatgrass densities and was replicated four times (Fig. 1). Within each block or replication, each pot or treatment was randomly assigned to a stationary position within one of four rows comprised of 11 pots per row. Block length extended from north-south and included a 61 cm buffer zone from all walls and other blocks in the glasshouse.

Glasshouse temperatures were maintained at 24/7 °C for day/night temperatures, respectively. These were monitored with maximum/minimum thermometers placed at the soil surface in the center, and approximately 3 pots from the north and south end of the block. Naturally occurring photoperiods were used and growth extended from 11 October 1989 to 4 April 1990.

	48	X	X	X	X	X
HYCREST						
OR	36	X	X	X	X	X
NORDAN						
DENSITY	24	X	X	X	X	X
PER POT						
	12	X	X	X	X	X
	0		X	X	X	X
		0	12	24	36	48
		CHEATGRASS DENSITY PER POT				

**Fig. 1. Seeding rate design incorporating both monocultures and mixtures where each X represents one pot per treatment. Each mixture treatment was sown with the intersection density for each species.**

Water in the pots 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/L of water, yielding  $0.5 \times 10^{-3}$  g/m<sup>3</sup> of N, P, and K. Fertilizer solution (.95 L) was applied to each pot three times during the experiment: 16 days, 38 days, and 70 days from the date of seeding. In February, 1990, one application of Ortho Malathion™ was applied to plants in all pots to control aphids. Seedling germination was monitored to insure densities were maintained.

Pots were harvested in April and May of 1990 in the same order they were seeded. The aboveground biomass of each plant within each treatment was harvested and stored in envelopes. Additionally, tiller counts for each plant were recorded. Due to the variation in phenology of seed production for cheatgrass, seeds were not counted, but were included in aboveground biomass. Below-ground root biomass was collected for each treatment, but was not analyzed because of difficulties in separating roots of individual plants. All biomass was oven-dried at 70° C for 48 hrs. Individual plant aboveground biomass was recorded to the nearest 0.1 mg.

Aboveground biomass and tiller counts exhibited a skewed distribution for each species. A series of transformations, including log and square root transformations, were unable to transform the data to a normal distribution. Thus, median values for aboveground biomass and tiller counts for each species were used as a measure of central tendency (see Appendix).

## STATISTICAL ANALYSIS

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 Mallows'  $C_p$  statistic (Daniel and Wood 1980). Additionally, the ability to explain, biologically, the parameters of each model was crucial in the selection process.

Based on the selected model for each variable, several competition indices were calculated to evaluate the effects of species interactions and densities. The first, Relative Resource Total (RRT), was calculated for each species using:

$$RRT = d_1/d_{1,0} + d_2/d_{2,0} = p_1 + p_2, \quad (1)$$

where  $d_1$  and  $d_2$  are the densities of species 1 and 2 in a mixture that would yield  $w_1$  and  $w_2$  (aboveground biomass or tiller number production), while  $d_{1,0}$  and  $d_{2,0}$  are the pure stand densities of species 1 and 2 yielding the same  $w_1$  and  $w_2$  as the mixture. Thus,  $p_i$  represents the proportion,  $d_i/d_{i,0}$ . An RRT of 1 means that the yield of the species in mixture will equal that of the pure stand, while an  $RRT > 1$  implies that the mixture is either capturing more resources or using the same resources more effectively to produce a greater yield. An  $RRT < 1$  implies antagonism or reduced effectiveness in resource use in the mixtures where yields are lower than in monocultures. When species do not interfere at all, the RRT takes a value of 2. Values of RRT for all densities and



Table 1. Models tested for two-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
$1/Y_i = B_0 + B_1X_i + B_2X_j + B_3(X_i * X_j)$	Firbank & Watkinson 1985; Menchaca & Connolly 1990; Spitters 1982; Wright 1981
$Y_i = X_iW_i/(1 + C_iX_i + C_iA_{ij}X_j)$	Law & Watkinson 1987
$Y_i = X_iW_i/(1 + (X_i + A_{ij}X_j)^{D_i})$	Law & Watkinson 1987
$Y_i = X_iW_i/(1 + X_i + A_{ij}X_j)^{D_i}$	Law & Watkinson 1987
$Y_i = X_iW_i/(1 + C_iX_i + C_iA_{ij}X_j)^{D_i}$	Law & Watkinson 1987
$Y_i = X_iW_i/(1 + X_i^{D_{ii}} + X_j^{D_{ij}})$	Law & Watkinson 1987

mixture ratios were graphed and evaluated for trends.

Two additional indices of competition were substitution rates (S) and perceived densities (PD). The substitution rate measures the influence of one individual within a species in a mixture on individuals of the other species relative to individuals of its own species. At mixed density ( $d_1, d_2$ ), the substitution rates  $S_1$  and  $S_2$ , are:

$$S_1 = (\delta f_1 / \delta d_2) / (\delta f_1 / \delta d_1)$$

and (2)

$$S_2 = (\delta f_2 / \delta d_1) / (\delta f_2 / \delta d_2),$$

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. Perceived densities (PD) were derived as:

$$PD_1 = d_1 + S_1 d_2$$

and (3)

$$PD_2 = d_2 + S_2 d_1.$$

Each of these indices was calculated if allowable for selected models and graphed to evaluate their trend with changing densities. All of these indices are

competition coefficients, sensu Firbank and Watkinson (1985), and were not interpreted in a fitness sense.



## RESULTS

An inverse linear model best described biomass of all species for each of the two mixture experiments (Table 2). 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. The greatest amount of variation normally occurred in the lowest densities (see Appendix).

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. However, cheatgrass biomass was explained by changes in intraspecific density alone when grown in mixtures with Nordan.

Nonlinear models were used for three of the four tiller count variables because of their ability to describe the variability in competition coefficients as densities change. Although slightly lower in their explained variation ( $R^2$  value) than several linear models, the nonlinear models'  $C_p$  value equaled those of their linear counterparts. These models state that the numbers of tillers of both species in a mixture are reduced when densities are increased regardless of the species. Lastly, a linear model best described the tiller count data for cheatgrass in the Nordan and cheatgrass mixtures, indicating that tiller production is explained by changes in intraspecific density alone.

Both Hycrest and cheatgrass densities influenced the biomass of Hycrest

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	Model Type	Best-fit Model	No. of Parameters	R <sup>2</sup>	C <sub>p</sub>
<b>Hycrest x cheatgrass</b>						
Hycrest	Biomass	Inverse Linear	$1/Y_i = -0.22 + 0.2D_i + 0.12D_j - 0.002D_i^2$	3	0.72	2.5
Cheatgrass	Biomass	Inverse Linear	$1/Y_j = 0.35 + 0.01D_j + 0.007D_i + 0.0002D_j^2$	3	0.70	3.5
Hycrest	Tiller number	Nonlinear	$Y_i = D_i 22.61 / (1 + D_i^{1.52} + D_j^{1.16})$	3	0.67	2.9
Cheatgrass	Tiller number	Nonlinear	$Y_j = D_j 68.64 / (1 + D_j^{1.56} + D_i^{0.59})$	3	0.50	2.9
<b>Nordan x cheatgrass</b>						
Nordan	Biomass	Inverse Linear	$1/Y_i = 5.37 + 0.14D_i + 0.64D_j$	2	0.67	1.3
Cheatgrass	Biomass	Inverse Linear	$1/Y_j = 0.2 + 0.03D_j - 0.0002D_j^2$	2	0.59	2.0
Nordan	Tiller number	Nonlinear	$Y_i = D_i 51.15 / (1 + D_i^{1.8} + D_j^{1.59})$	3	0.84	2.9
Cheatgrass	Tiller number	Linear	$Y_j = 21.28 - 0.43D_j + 0.004D_j^2$	2	0.58	0.4

(Fig. 2A) and cheatgrass (Fig. 2B) on a per plant basis. Hycrest biomass was the highest at the lowest monoculture and mixture densities (Fig. 2A) and cheatgrass biomass exhibited the same trend (Fig. 2B). Examination of biomass production on a per area basis exhibited opposite trends for both species with the greatest production per area occurring at the highest density (Fig. 3A,B). Tiller numbers of Hycrest (Fig. 4A) and cheatgrass (Fig. 4B) 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. 4A). 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) appeared where, for those ranges of densities of both species, tiller numbers were maximized. In contrast, changes in Hycrest densities had smaller effects on cheatgrass tiller numbers (Fig. 4B).

Trends in biomass (both on a per plant and per area basis) and tiller numbers (per plant) for mixtures of Nordan and cheatgrass showed similar response figures to mixtures of Hycrest and cheatgrass, yet they differed in magnitude (Figs. 2, 3, and 4). On a per plant basis, Nordan generally produced lower biomass than Hycrest as cheatgrass densities increased (Fig. 2A,C). Cheatgrass biomass was not influenced by increasing Nordan densities

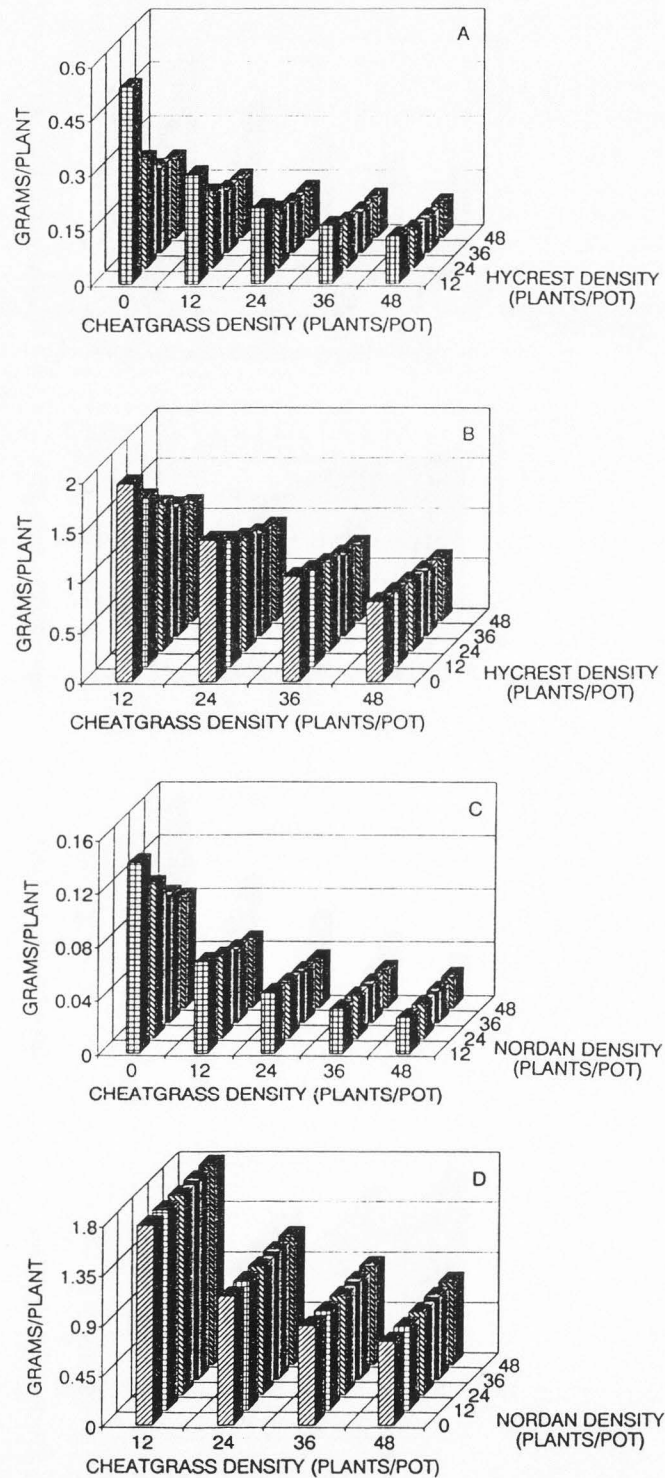
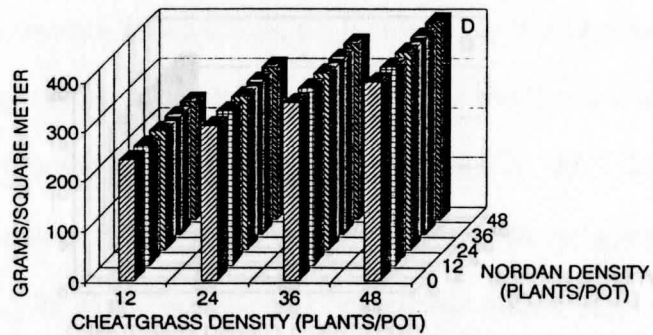
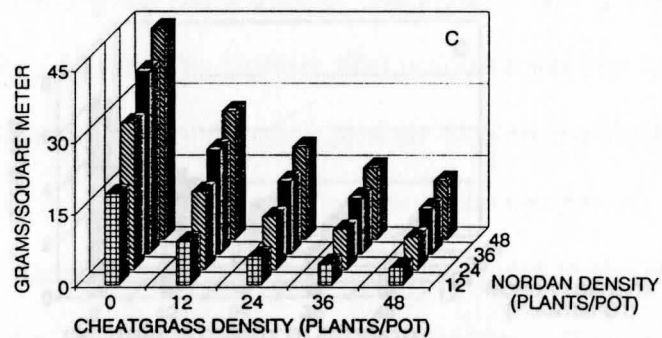
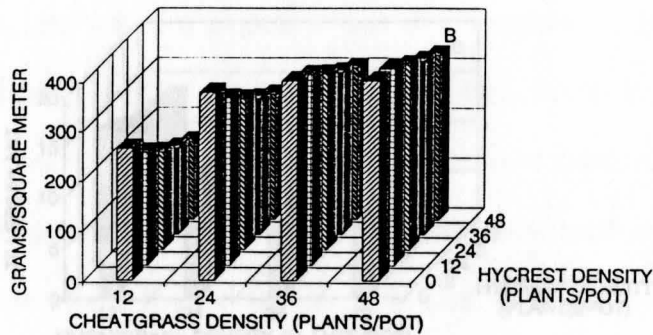
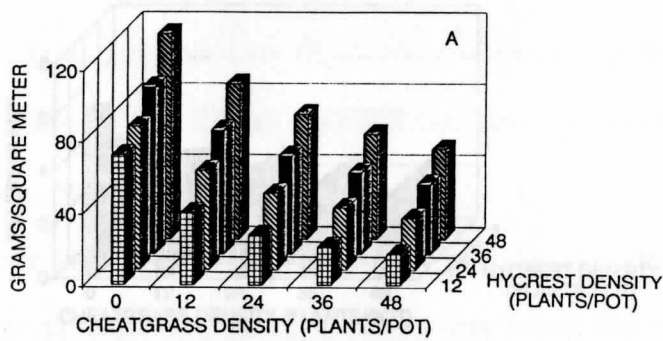


Fig. 2 (A-D). Modeled biomass per plant for Hycrest (A), Nordan (C) and cheatgrass (B and D) in two-species mixtures of Hycrest or Nordan with cheatgrass.



**Fig. 3 (A-D).** Modeled biomass on a per area basis for Hycrest (A), Nordan (C) and cheatgrass (B and D) in two-species mixtures of Hycrest or Nordan with cheatgrass.



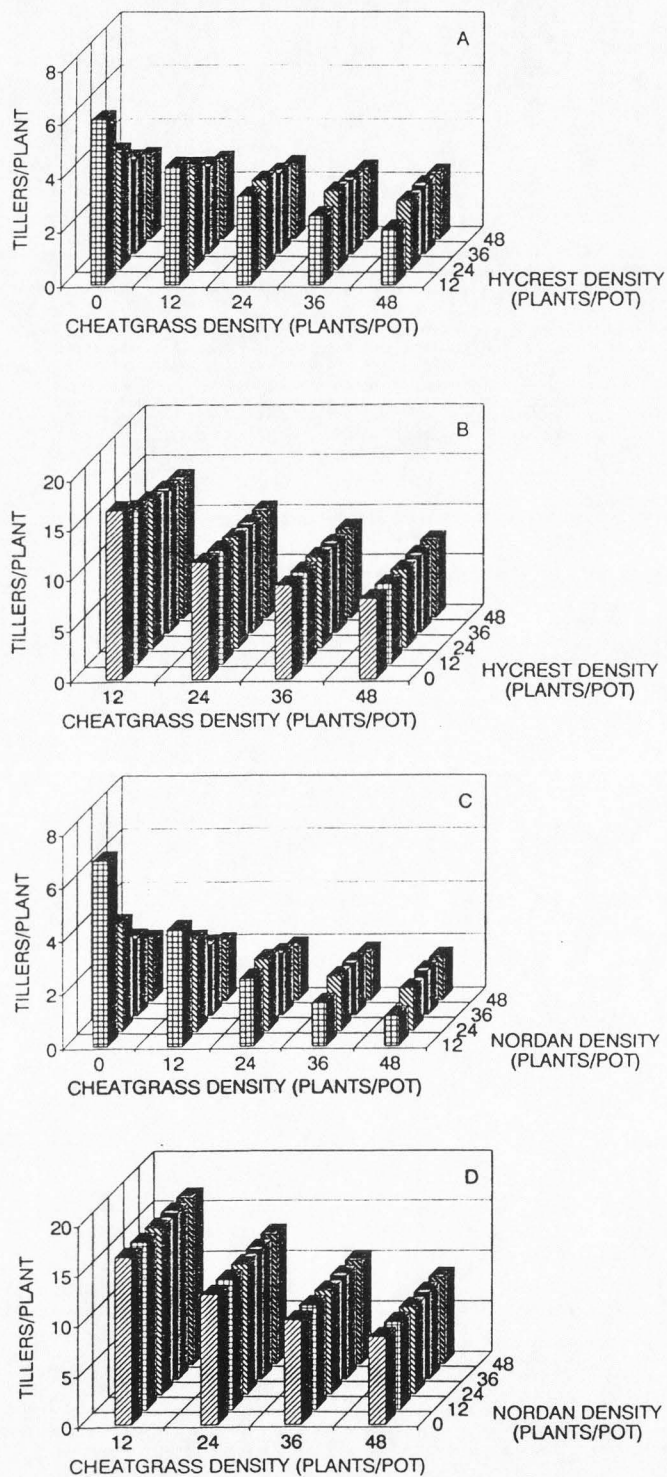


Fig. 4 (A-D). Modeled tiller production per plant for Hycrest (A), Nordan (C) and cheatgrass (B and D) in two-species mixtures of Hycrest or Nordan with cheatgrass.

(Fig. 2D), whereas increasing Hycrest densities reduced cheatgrass biomass when cheatgrass densities were low (Fig. 2B). As cheatgrass densities increased, cheatgrass yielded similar biomass regardless which cultivar of crested wheatgrass it was grown with.

Tiller counts for Hycrest and Nordan were similar at lower densities (6.1 vs. 6.9 per plant), but Hycrest produced more tillers at the higher densities (2.4 vs. 1.6 per plant), indicating a greater effect of cheatgrass on Nordan at higher densities than on Hycrest (Fig. 4A,C). Response figures for cheatgrass tiller numbers were similar in shape to those for Hycrest and Nordan, and differed only slightly in magnitude (Fig. 4B,D). Cheatgrass tiller production was slightly lower in Hycrest mixtures than in Nordan mixtures, but, more importantly, intraspecific competition played a greater role in determining tiller production for cheatgrass (Fig. 4B,D). The highest tiller numbers per plant for cheatgrass occurred at the lowest density for each species in both the Hycrest and Nordan subexperiments (values 16.7 and 16.6 per plant, respectively). Minimum cheatgrass tiller production ranged from 7.7 tillers/plant in the Hycrest experiment to 8.6 tillers/plant in the Nordan experiment (Fig. 4B,D).

Relative resource totals based on biomass for the Hycrest and cheatgrass mixtures ranged from 1.0 to 1.8, with the highest occurring in mixtures of 48 Hycrest and 48 cheatgrass per pot (Fig. 5A). It appeared that at the low densities of Hycrest and cheatgrass, interference was the greatest for both species. As both Hycrest and cheatgrass densities increased, relative resource totals increased, indicating a decreased antagonism between the two species. For the Nordan and cheatgrass mixtures, however, relative resource

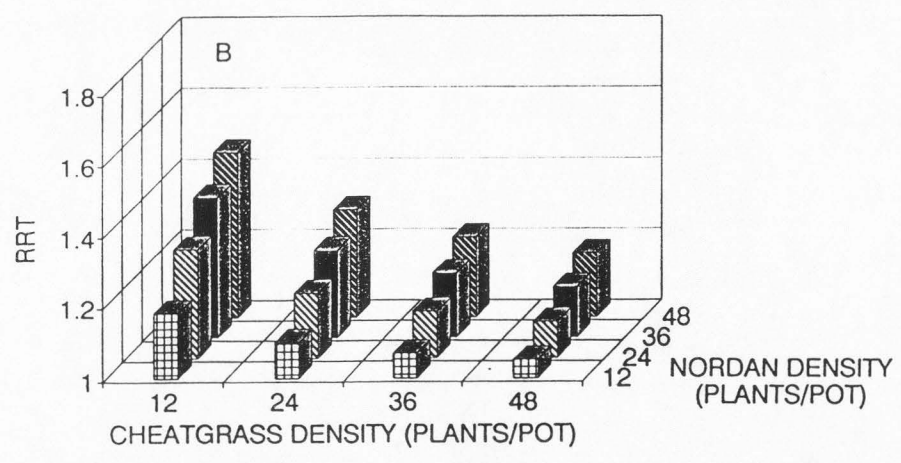
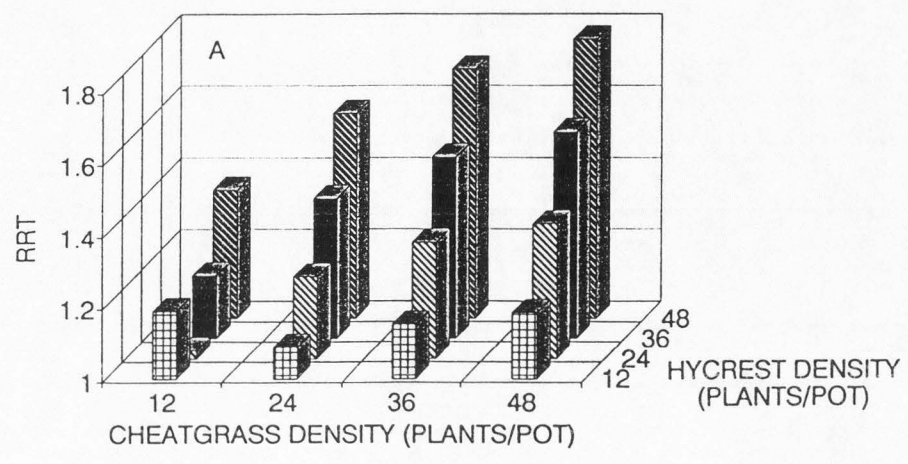


Fig. 5 (A-B). Biomass relative resource totals (RRT) for two-species mixtures of Hycrest (A) and Nordan (B) with cheatgrass.



totals tended to increase with increasing Nordan densities and decreasing cheatgrass densities (Fig. 5B), indicating that interference was the greatest from cheatgrass. This index is questionable as to its validity in mixtures having both desirable and undesirable plant species and will be considered in the discussion.

Substitution rates for Hycrest based on biomass increased with increases in the Hycrest density from 0.8 to 21.6 (Fig. 6A). For cheatgrass, substitution rates decreased with increases in the cheatgrass density from 0.5 to 0.3 (Fig. 6B). Using these rates, perceived densities for Hycrest ranged from 22 to 1086 (due to the high substitution rate) and for cheatgrass from 18 to 61 (Fig. 7A,B).

Substitution rates for Nordan remained constant at 4.6 because of the linear model, with resulting perceived densities ranging from 67 to 269 (Fig. 7C). These indices could not be calculated for cheatgrass in this mixture with Nordan because density terms for Nordan were not present in the model for cheatgrass biomass.

Values of RRT based on tiller counts for both mixture experiments exhibited similar trends with increasing densities to those associated with biomass (Figure 8A,B). The RRT values for the Hycrest and cheatgrass mixtures ranged from 1.1 to 1.7 (Fig. 8A), while values for the Nordan and cheatgrass mixtures ranged from 1.1 to 1.9 (Fig. 8B). In both mixture experiments, the RRT for tiller counts increased as crested wheatgrass densities increased, but decreased with increasing cheatgrass densities.

Substitution rates for tiller production provided valuable insights into the

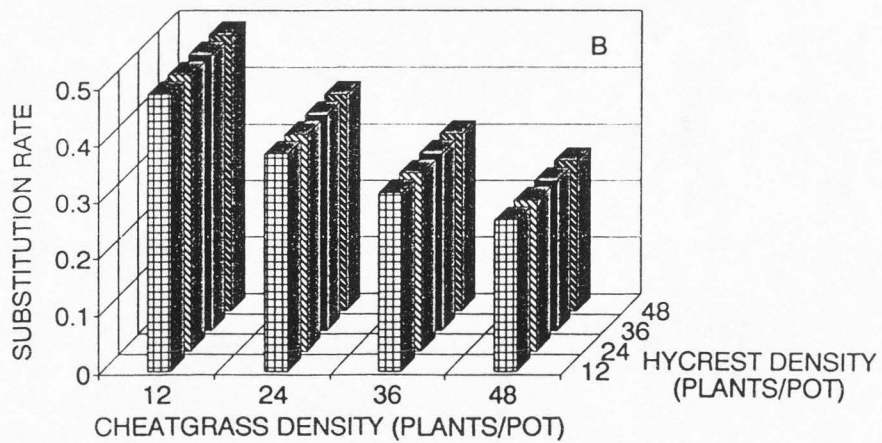
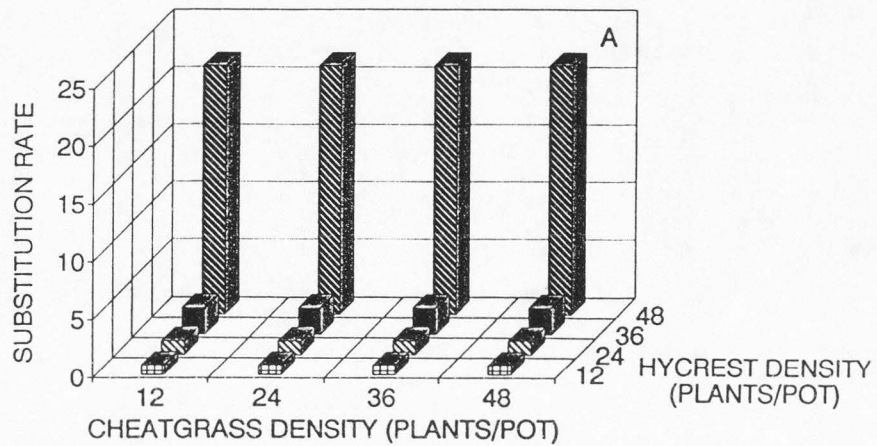


Fig. 6 (A-B). Biomass substitution rates for Hycrest (A) and cheatgrass (B) for the Hycrest and cheatgrass mixture.

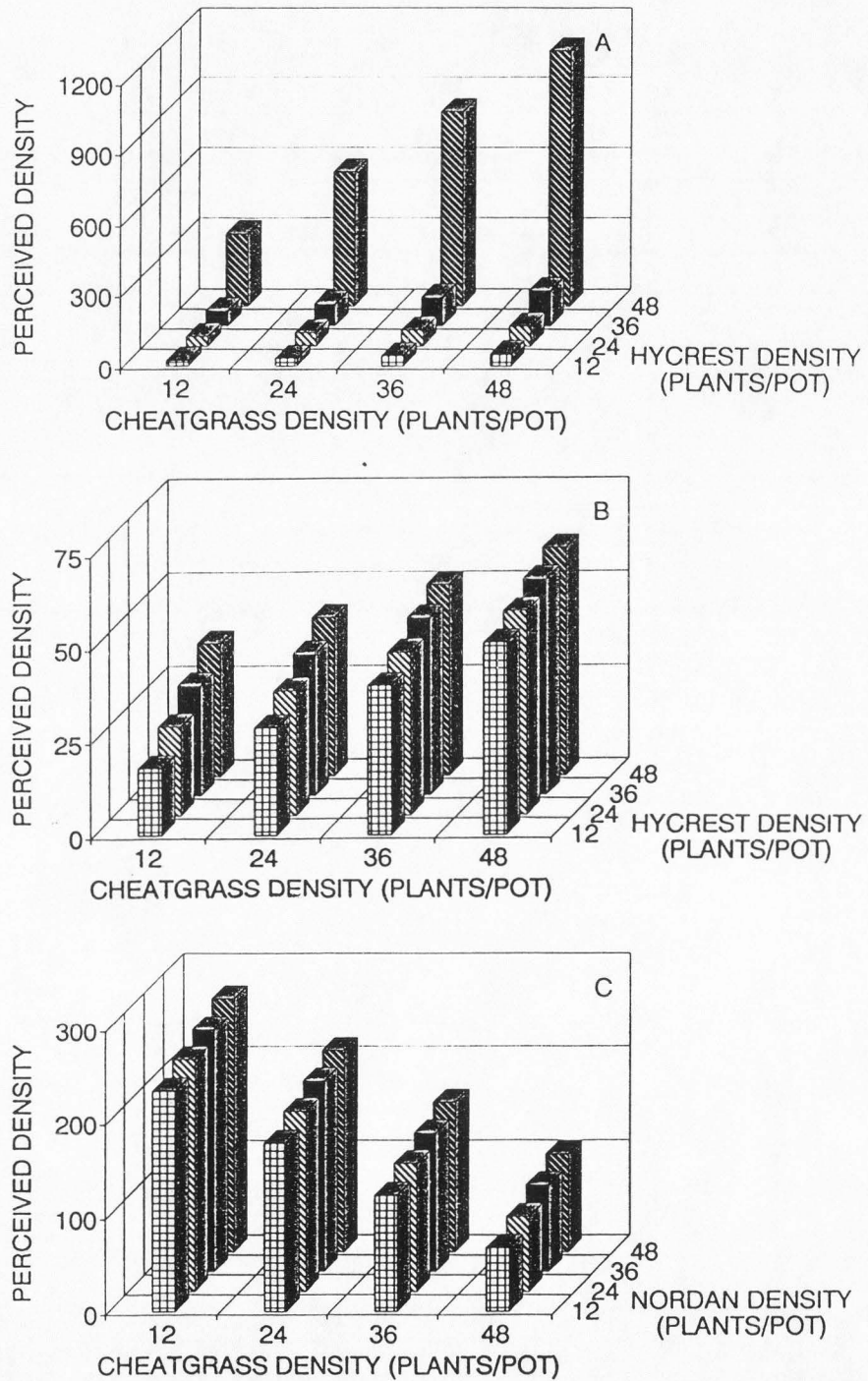


Fig. 7 (A-C). Biomass perceived density (plants per pot) for Hycrest (A) and cheatgrass (B) for the Hycrest and cheatgrass mixture, and for Nordan (C) in the Nordan and cheatgrass mixture.

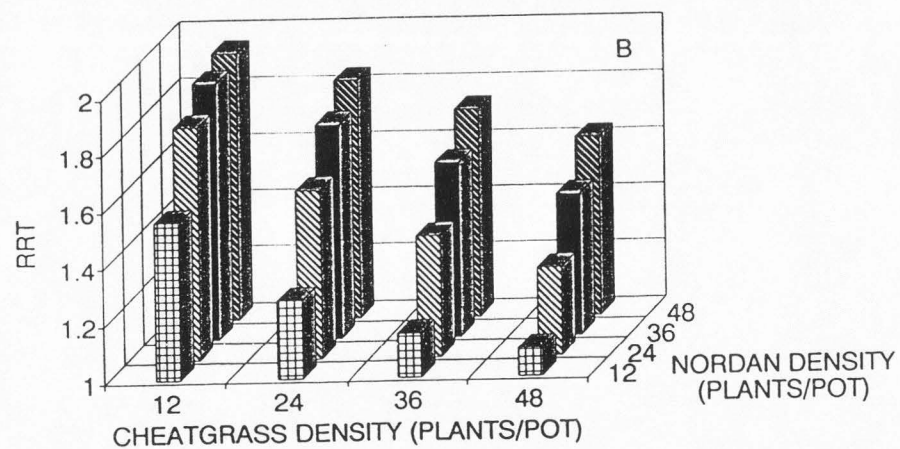
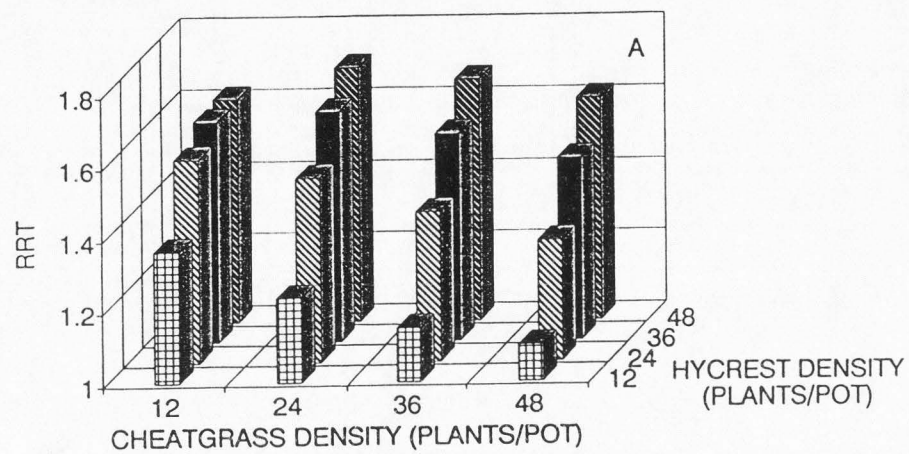
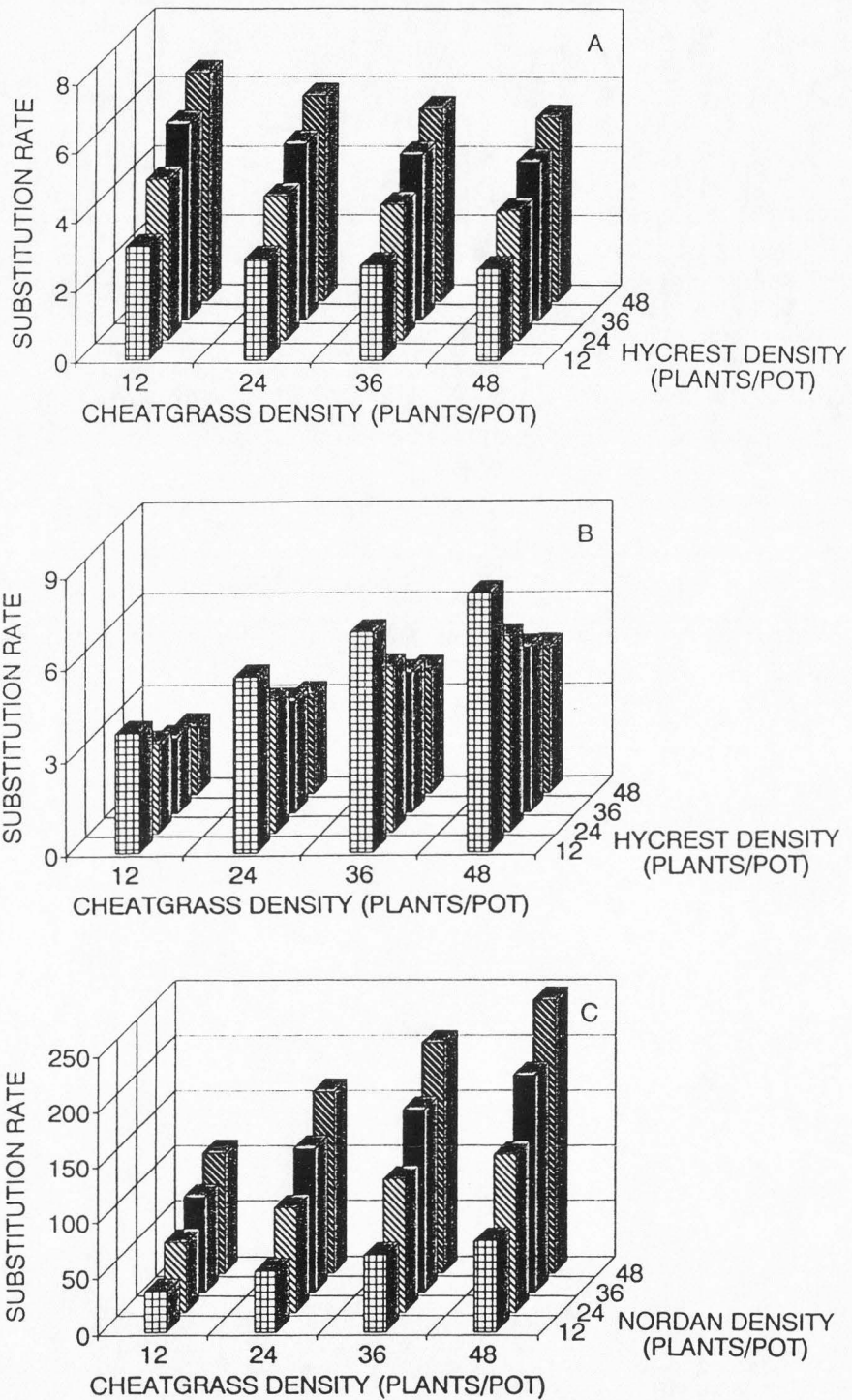


Fig. 8 (A-B). Tiller number relative resource totals (RRT) for Hycrest (A) and Nordan (B) in two-species mixtures with cheatgrass.



dynamics of these mixtures. Substitution rates ranged from 2.5 to 6.6 for Hycrest and from 2.1 to 8.3 for cheatgrass, with the lowest rates for Hycrest and cheatgrass occurring at the 12 Hycrest and 48 cheatgrass per pot, and at the 48 Hycrest and 12 cheatgrass mixtures, respectively (Fig. 9A,B). For both Hycrest and cheatgrass, as intraspecific densities increased, substitution rates increased. Conversely, as interspecific densities increased, substitution rates decreased (Fig. 9A,B). Intraspecific competition apparently reduced tiller production more than interspecific competition. Correspondingly, both Hycrest and cheatgrass are perceiving the mixtures as having higher total densities than actually exist (Fig. 10A,B).

In the Nordan and cheatgrass mixtures, substitution rates for tiller production could only be calculated for Nordan due to model constraints. Nordan substitution rates ranged from 35.8 to 246.1 (Fig. 9C), clearly indicating the cheatgrass density effect. Likewise, perceived densities by Nordan were high when compared to actual densities (Fig. 10C).



**Fig. 9 (A-C).** Tiller number substitution rates for Hycrest (A) and cheatgrass (B) in the Hycrest and cheatgrass mixture, and for Nordan (C) in the Nordan and cheatgrass mixture.

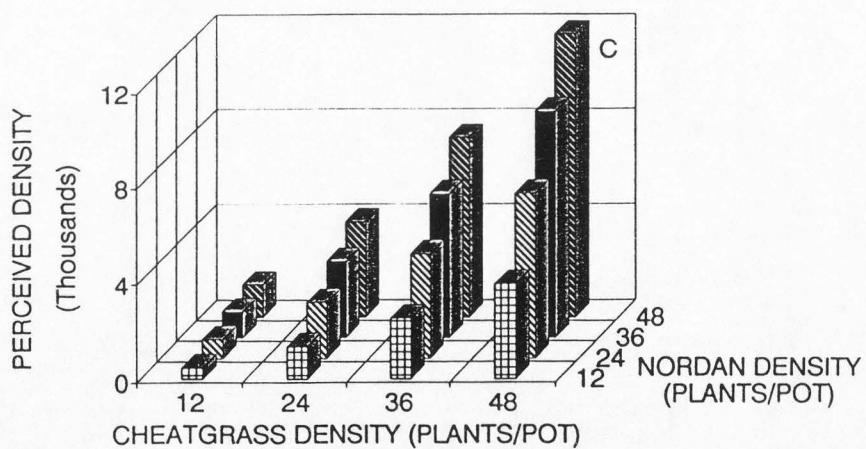
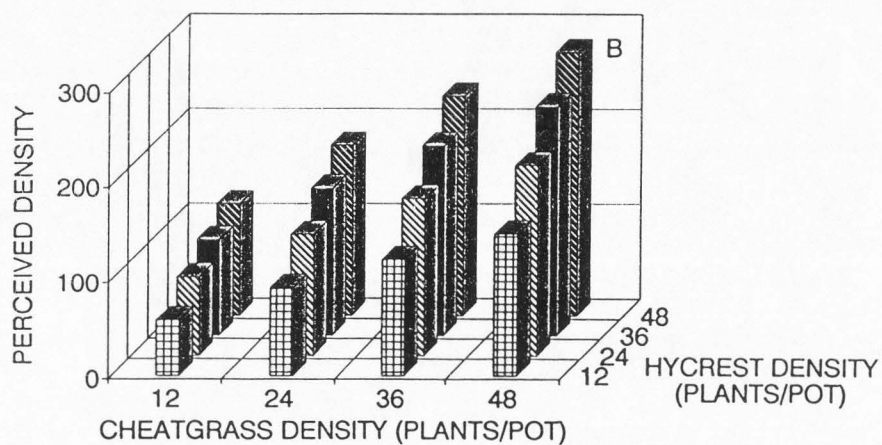
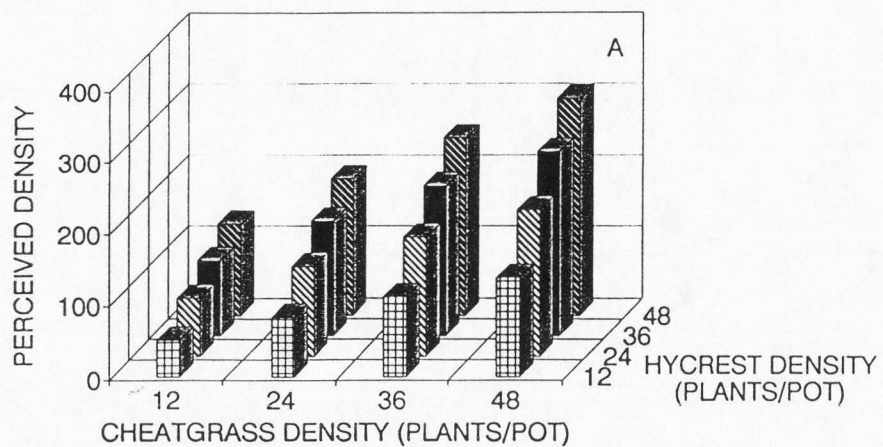


Fig. 10 (A-C). Tiller number perceived density (plants per pot) for Hycrest (A) and cheatgrass (B) in the Hycrest and cheatgrass mixture, and for Nordan (C) in the Nordan and cheatgrass mixture.

## DISCUSSION

Previous work evaluating competition between these species has shown varied results with most citing cheatgrass as the more 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 population densities and mixture ratios, and a more realistic evaluation across a range of population densities and mixture ratios is required (Call and Roundy 1991, Pyke and Archer 1991). In this study, a range of mixed densities and mixtures ratios provided a broader evaluation of the dynamics of these species interactions. Results from this study indicated that comparisons of maximum biomass and tiller production as measured on a per individual and per area basis demonstrated opposite trends. This indicates that the number of individuals in higher density mixtures compensates for lower individual biomass producing more total biomass at the higher mixtures. While significant from a production standpoint, it is unknown how many of these small individuals of Hycrest will survive after the first year. Thus, responses of individuals are likely to be more important to the final establishment.

Models used to describe cheatgrass biomass and tiller counts for the Nordan and cheatgrass mixture lacked a Nordan density term, indicating that Nordan as a species had little or no effect on cheatgrass. Thus, for this mixture, intraspecific competition had the greatest impact on regulating yields



of cheatgrass. Because neither Hycrest nor Nordan appears to effectively suppress cheatgrass at any of the examined densities, recommendations for appropriate seeding rates may require studies that are field oriented and extend beyond one year. However, recognizing this limitation, the results of this experiment do provide an adequate view of the role of intra- and interspecific competition on first-year growth of these crested wheatgrasses. As such, comparison of the two crested wheatgrasses clearly demonstrated that Hycrest was more competitive than Nordan when grown with cheatgrass.

Cheatgrass has morphological and physiological advantages over crested wheatgrass species when they are competing for resources, 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 (Aguirre and Johnson 1991a); 3) greater total root length and root dry weight at higher cumulative growing degree days (Aguirre and Johnson 1991a); 4) faster leaf and tiller development (Aguirre and Johnson 1991a); 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). Results from this study indicate that Hycrest and Nordan have a greater chance for exploiting resources in less crowded populations. Recognizing that these results are limited to a controlled setting, field research is needed to verify the application of these results.

Establishment of a seedling 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. Inherently important to this process is the season of sowing. This experiment used a fall-winter-spring growing season rather than the normal spring growing season for crested wheatgrass. Recognizing that cheatgrass may germinate in the fall, most of these seedlings would be killed due to the seeding process (e.g., seedbed preparation and seed drilling). This ultimately means that interacting individuals of cheatgrass and crested wheatgrass are likely to germinate in the same season (e.g., late winter). Given this, results of this study indicate that when cheatgrass densities are below 260 plants/m<sup>2</sup>, crested wheatgrass may be sown at densities below the recommended levels (260 plants/m<sup>2</sup>) to maximize both biomass and tiller numbers. Yet, when cheatgrass densities are above 260 plants/m<sup>2</sup>, then crested wheatgrass tiller numbers are maximized when sown at recommended levels. Realizing that all three species maximized biomass production on a per area basis at the highest mixtures, this outcome should be carefully evaluated. 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. Thus, the important relationship to establish and understand is the plant-to-plant. Together, these results emphasize the need for knowledge of the cheatgrass seed pool size to predict cheatgrass densities as well as the survivability of the perennial species in succeeding years. With this knowledge, seeding rates can be more accurately calculated to insure establishment and growth in subsequent years.

While the modeled data provided important insight and evidence for seeding Hycrest and Nordan at lower densities for increased competitive ability, the additional indices of relative resource totals, substitution rates, and perceived densities provided the means to evaluate the competitive interactions as densities and mixtures ratios changed. Evaluation of relative resource total trends for all mixtures suggested that higher densities of crested wheatgrass species (especially Hycrest) would be more effective or efficient in using the resources. However, through further examination of the substitution rates and perceived densities, it becomes very clear that the latter indices strongly indicate that lower densities of crested wheatgrass species can better compete with cheatgrass. In all cases, lower densities of Hycrest and Nordan allow the species to "view" cheatgrass as less of a competitor. However, as crested wheatgrass and cheatgrass densities increase, Hycrest and Nordan's view of cheatgrass becomes more antagonistic.

The unexpected trends for relative resource totals can be explained by examination of the values derived for biomass and tiller numbers for each of these species. While values within either experiment for the crested wheatgrass species remain similar throughout the mixtures (excluding the low densities), cheatgrass values changed in magnitude as mixtures changed. The plateau effect of the crested wheatgrass species, coupled with larger value changes for cheatgrass, dictates the relative resource total outcome. Even so, it can still be seen that Nordan is less competitive with cheatgrass than Hycrest as demonstrated by the reduced RRT values with increased cheatgrass density.

While important in mixtures of two or more desirable plant species

because overall biomass can be maximized by coexisting species, the RRT index is not as applicable in mixtures of desirable and undesirable species. Its main function is to provide a comparison between yields in monocultures versus mixtures of various species. As such, it would be a more important index to use in situations where companion species are desired. When the objective is a description of the competitive relationship between desirable and undesirable, then the best index is the substitution rate.

Comparative results for Hycrest or Nordan competition from other work is very limited and hard to apply because most studies did not allow for variations in densities and mixture ratios or did not examine these variables. The results of the current study are consistent with field studies by Rummal (1946) and Hull (1963), who found that as cheatgrass density increased, crested wheatgrass (pre-Hycrest era) shoot weight decreased. The results are also consistent with greenhouse results of Aguirre and Johnson (1991a,b), who found young cheatgrass 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. Because of these results, some have suggested that lower densities of aggressive perennials may enable these species to better compete with invasive annuals such as cheatgrass (Buman et al. 1988, Pyke and Archer 1991). Pyke and Archer (1991) suggested that when formulating seed mixtures, information on overlap in plant resource requirements and acquisition strategies may help determine: 1) which species are likely in direct competition and therefore 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. Ideally, in a desirable vs. undesirable mixture, the goal for revegetation efforts would be to create a situation where the undesirable species is detecting a reduction in resources similar to a larger population.

In this study, Hycrest proved to be a better competitor with cheatgrass than Nordan and competed better with cheatgrass at recommended and lower densities. Nordan was severely affected by cheatgrass regardless of species density, and overall biomass and tiller production were lower than for Hycrest. To achieve optimum Hycrest growth in the first year, it would seem more advantageous to prescribe Hycrest seeding rates at or below recommended densities (approximately 260 seeds/m<sup>2</sup>) 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. However, field tests are needed to verify this recommendation and to determine if the competitive advantage of Hycrest is maintained in subsequent years.

While revegetation technology apparently has progressed more rapidly than revegetation science over the past decades (Call and Roundy 1991), steps are being taken to reestablish the science involved in the revegetation process. The goal for future work should involve determining the requirements and positive characteristics of different species (Aber 1987, Call and Roundy 1991,



Pyke and Archer 1991), while at the same time 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 the interactions can provide the information needed to produce stable and diverse plant communities for the future.

## LITERATURE CITED

- ✓ Aber, J. D. 1987. Restored forests and the identification of critical factors in species-site interactions. Pages 241-250 in W. R. Jordan III, M. E. Gilpin, and J. D. Aber, editors. Restoration ecology: A synthetic approach to ecological research. Cambridge University Press, New York, New York, USA.
- Aguirre, L., and D. A. Johnson. 1991a. Root morphological development in relation to shoot growth in seedlings of four range grasses. *Journal of Range Management* 44:341-346.
- ✓ Aguirre, L., and D. A. Johnson. 1991b. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. *Journal of Range Management* 44:347-354.
- Asay, K. H., D. R. Dewey, F. B. Gomm, D. A. Johnson, and J. R. Carlson. 1985a. Registration of Hycrest crested wheatgrass. *Crop Science* 25:368-369.
- ✓ Asay, K. H., W. H. Horton, and W. T. Hanson. 1985b. New grasses for Intermountain rangelands. *Utah Science* 46:119-123.
- ✓ Buman, R. D., S. B. Monson, and R. H. Abernathy. 1988. Seedling competition between mountain rye, "Hycrest" crested wheatgrass and downy brome. *Journal of Range Management* 41:30-34.
- Call, C. A., and B. A. Roundy. 1991. Perspectives and processes in revegetation of arid and semiarid rangelands. *Journal of Range Management* 44:543-549.

- Connolly, J. 1986a. On difficulties with replacement series methodology in mixture experiments. *Journal of Applied Ecology* 23:125-137.
- \_\_\_\_\_. 1986b. Importance and measurement of mixture effects in grazing systems. Pages 323-333 *in* Gudmundsson, O., editor. Proceedings of grazing research at northern latitudes. Hvanneyri, Iceland.
- \_\_\_\_\_. 1987. On the use of response models in mixture experiments. *Oecologia* 72:95-103.
- Connolly, J., and T. Nolan. 1976. Design and analysis of mixed grazing experiments. *Animal Production* 23:63-71.
- Connolly J., P. Wayne, and R. Murray. 1990. Time course of plant-plant interactions in experimental mixtures of annuals : density, frequency, and nutrient effects. *Oecologia* 82:513-526.
- Daniel, C., and F. Wood. 1980. Fitting equations to data, revised edition. John Wiley & Sons, New York, New York, USA.
- Evans, R. D. 1961. Effects of different densities of downy brome (Bromus tectorum) on growth and survival of crested wheatgrass (Agropyron desertorum) in the greenhouse. *Weeds* 9:216-223.
- Firbank, L. G., and A. R. Watkinson. 1985. On the analysis of competition within two-species mixtures of plants. *Journal of Applied Ecology* 22:503-517.
- ✓ Harper, J. L. 1977. Population biology of plants. Academic Press, New York, New York, USA.
- ✓ Harris, G. A. 1967. Some competitive relationships between Agropyron spicatum and Bromus tectorum. *Ecological Monographs* 37:89-111.

- \_\_\_\_\_. 1977. Root phenology as a factor of competition among grass seedlings. *Journal of Range Management* 30:172-177.
- Hulbert, L. C. 1955. Ecological studies of Bromus tectorum and other annual brome grasses. *Ecological Monographs* 25:181-213.
- Hull, A. C., Jr. 1963. Competition and water requirements of cheatgrass and wheatgrasses in the greenhouse. *Journal of Range Management* 16:199-203.
- Inouye, R. S., and W. M. Schaffer. 1981. On the ecological meaning of ratio (de Wit) diagrams in plant ecology. *Ecology* 62:1679-1681.
- Joliffe, P. A., A. N. Minjas, and V. C. Runeckles. 1984. A reinterpretation of yield relationships in replacement series experiments. *Journal of Applied Ecology* 21:227-243.
- ✓ Klemmedson, J. O., and J. G. Smith. 1964. Cheatgrass (Bromus tectorum). *Botanical Review* 30:226-262.
- Law, R., and A. R. Watkinson. 1987. Response-surface analysis of two-species competition : an experiment on Phleum arenarium and Vulpia fasciculata. *Journal of Ecology* 75:871-886.
- ✓ Mack, R. N. 1981. Invasion of Bromus tectorum L. into western North America : an ecological chronicle. *Agro-Ecosystems* 7:145-165.
- Maynard Smith, J. 1974. *Model in ecology*. Cambridge University Press, New York, New York, USA.
- Mead, R. 1979. Competition experiments. *Biometrics* 35:41-54.

- Melgoza, G., and R. S. Nowak. 1991. Competition between cheatgrass and two native species after fire : Implications from observations and measurements of root distribution. *Journal of Range Management* 44:27-33.
- Menchaca, L., and J. Connolly. 1990. Species interference in white clover-ryegrass mixtures. *Journal of Ecology* 78:223-232.
- Pyke, D. A. 1987. Demographic responses of Bromus tectorum and seedlings of Agropyron spicatum to grazing by small mammals : the influence of grazing frequency and plant age. *Journal of Ecology* 75:825-835.
- Pyke, D. A., and A. Archer. 1991. Plant-plant interactions affecting plant establishment and persistence on revegetated rangeland. *Journal of Range Management* 44:550-557.
- Roush, M. L., S. R. Radosevich, R. G. Wagner, B. D. Maxwell, and T. D. Peterson. 1989. A comparison of methods for measuring effects of density and proportion in plant competition experiments. *Weed Science* 37:268-275.
- Rummel, R. S. 1946. Some effects of competition from cheatgrass brome on crested wheatgrass and bluestem wheatgrass. *Ecology* 27:159-167.
- Silvertown, J. 1987. *Introduction to plant population ecology*, 2nd edition. Longman Scientific, Harlow, UK.
- Spitters, C. J. T. 1983. An alternative approach to the analysis of mixed cropping experiments. I. Estimation of competition effects. *Journal of Agriculture Science (Netherlands)* 31:1-11.



- Suehiro, K., and H. Ogawa. 1980. Competition between two annual herbs, Atriplex gmelini CA May and Chenopodium album L., in mixed cultures irrigated with seawater of various concentrations. *Oecologia* (Berlin) 45:167-177.
- Svejcar, T. 1990. Root length, leaf area, and biomass of crested wheatgrass and cheatgrass seedlings. *Journal of Range Management* 43:446-448.
- van Bavel, C. H. M., R. Lascano, and D. R. Wilson. 1978. Water relations of fritted clay. *Soil Science Society of America Journal* 42:657-659.
- Wright, A. J. 1981. The analysis of yield-density relationships in binary mixtures using inverse polynomials. *Journal of Agriculture Science* (Cambridge) 96:561-567.
- Young, J. A., and R. D. Evans. 1985. Demography of Bromus tectorum in Artemisia communities. Pages 489-502 in J. White, editor. *The population structure of vegetation*. Dr. W. Junk Publishers, LaJolla, California, USA.

**APPENDIXES**

**APPENDIX A. BIOMASS**

**Table 3. Median weight (grams) per plant and total weight for species per treatment of Hycrest (HMW and HTW, respectively) and cheatgrass (BMW and BTW, respectively) at each treatment density (TRMT). Hycrest (DH) and cheatgrass (DB) densities are given for each replication (REP).**

TRMT	REP	DH	DB	HMW	BMW	HTW	BTW
1	1	0	12	0	1.9687	0	28.4849
1	2	0	11	0	2.6779	0	31.3383
1	3	0	15	0	1.9944	0	31.8918
1	4	0	14	0	1.4615	0	22.5144
2	1	0	34	0	0.94335	0	31.1529
2	2	0	30	0	1.0771	0	39.7335
2	3	0	27	0	1.0298	0	30.1332
2	4	0	26	0	1.462	0	42.8242
3	1	0	47	0	0.6595	0	32.1363
3	2	0	46	0	0.972	0	43.3603
3	3	0	46	0	0.99855	0	52.7146
3	4	0	45	0	0.8868	0	40.9164
4	1	0	71	0	0.5659	0	41.9272
4	2	0	60	0	0.61775	0	41.6279
4	3	0	52	0	1.0883	0	60.8089
4	4	0	50	0	0.76025	0	40.6058
100	1	15	0	0.3862	0	5.626	0
100	2	15	0	0.1859	0	4.1453	0
100	3	15	0	0.4242	0	6.414	0
100	4	14	0	0.46875	0	6.8717	0
101	1	9	18	0.2466	1.4001	2.5174	26.7959
101	2	15	18	0.1586	1.66355	2.3808	25.4429
101	3	15	17	0.2926	1.0993	5.0409	21.5364
101	4	16	15	0.2178	1.5613	3.7852	26.6393
102	1	13	29	0.1867	1.0433	2.2922	33.261
102	2	14	30	0.1435	1.06975	2.0384	33.6396
102	3	15	27	0.2012	1.268	2.7596	36.4738
102	4	15	32	0.1232	0.8919	2.0277	33.4198
103	1	15	48	0.2204	0.5338	3.1292	27.9916
103	2	13	42	0.1269	0.9193	1.5722	40.5771
103	3	13	47	0.2715	1.3587	3.3458	61.3875
103	4	13	47	0.0864	0.6319	1.6302	29.9342
104	1	13	64	0.0818	0.50025	1.2191	35.2965
104	2	16	54	0.12395	0.6001	1.876	37.2048
104	3	16	66	0.1452	0.5127	2.3954	35.317
104	4	13	56	0.1001	0.70395	1.5383	49.8776
200	1	28	0	0.32165	0	11.1365	0



TRMT	REP	DH	DB	HMW	BMW	HTW	BTW
200	2	24	0	0.4361	0	11.7781	0
200	3	32	0	0.24725	0	9.7418	0
200	4	25	0	0.707	0	16.0206	0
201	1	27	13	0.172	1.3335	5.0573	21.2527
201	2	25	15	0.1801	1.0978	4.771	21.3566
201	3	27	21	0.235	1.1466	7.1425	35.0515
201	4	28	16	0.2362	2.28285	7.9837	41.2953
202	1	27	32	0.1049	0.81435	3.3727	25.8155
202	2	28	32	0.1204	0.82145	3.561	37.1378
202	3	27	27	0.1847	0.9312	5.4523	27.0183
202	4	28	30	0.15285	1.71005	5.7767	54.8739
203	1	26	40	0.1167	0.74035	3.4275	32.5693
203	2	21	44	0.1131	0.6891	2.7292	32.5837
203	3	25	45	0.1242	0.774	3.3472	35.1278
203	4	28	45	0.1542	0.9981	4.498	51.2412
204	1	31	58	0.1061	0.46735	3.5145	31.1982
204	2	26	58	0.07455	0.60825	2.3237	37.8423
204	3	31	62	0.0792	0.5941	2.8582	39.5844
204	4	25	59	0.0885	0.4432	2.3982	29.7595
300	1	41	0	0.2439	0	11.6559	0
300	2	44	0	0.28315	0	11.9191	0
300	3	44	0	0.21455	0	10.4457	0
300	4	40	0	0.19885	0	7.9587	0
301	1	42	16	0.2067	0.96865	8.7385	16.5081
301	2	42	17	0.1528	1.1494	7.3047	22.9016
301	3	38	15	0.2186	2.4582	8.9774	34.3107
301	4	36	18	0.09635	0.54655	4.1349	13.3728
302	1	41	32	0.0817	0.7571	4.5359	25.5218
302	2	40	32	0.1164	1.103	4.8201	34.7069
302	3	39	28	0.1096	1.13735	4.6249	32.7822
302	4	36	28	0.15495	1.2508	6.2714	33.1457
303	1	39	51	0.079	0.5301	3.6325	28.3786
303	2	42	45	0.1246	0.6142	5.0609	30.0651
303	3	39	43	0.0971	0.7092	4.0229	34.8483
303	4	39	48	0.1125	1.2507	5.0939	59.8234
304	1	32	56	0.1062	0.48905	3.6918	31.685
304	2	41	63	0.0675	0.5877	3.4709	40.8647

TRMT	REP	DH	DB	HMW	BMW	HTW	BTW
304	3	35	58	0.0842	0.59385	2.906	36.2525
304	4	37	56	0.0781	0.55775	3.4776	31.9861
400	1	56	0	0.2121	0	13.323	0
400	2	54	0	0.22855	0	12.2636	0
400	3	55	0	0.2241	0	12.7551	0
400	4	56	0	0.3149	0	22.0543	0
401	1	56	9	0.1517	1.3202	9.149	11.2133
401	2	48	15	0.13715	1.0107	7.375	16.4461
401	3	50	16	0.15905	1.7274	9.1534	30.2515
401	4	45	18	0.1401	0.9006	7.328	16.3246
402	1	53	34	0.0883	0.76805	5.4372	24.266
402	2	58	28	0.11045	0.79865	7.1065	26.5461
402	3	51	26	0.1338	1.60405	7.2281	45.9679
402	4	44	29	0.104	0.6984	5.4106	20.0177
403	1	54	40	0.118	0.6261	6.8859	29.8145
403	2	57	48	0.1071	0.642	6.8808	34.4963
403	3	57	45	0.1121	0.6781	6.634	32.7842
403	4	50	47	0.07395	0.6934	4.4838	35.6968
404	1	52	50	0.1337	0.4885	7.412	31.3294
404	2	52	60	0.09615	0.4315	5.4197	29.5235
404	3	57	58	0.0872	0.6084	5.8385	37.1627
404	4	49	55	0.0705	0.4235	4.0681	28.274

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**Table 4. Median weight (grams) per plant and total weight for species per treatment of Nordan (NMW and NTW, respectively) and cheatgrass (BMW and BMT, respectively) at each treatment density (TRMT). Nordan (DN) and cheatgrass (DB) densities are given for each replication (REP).**

TRMT	REP	DN	DB	NMW	BMW	NTW	BTW
1	1	0	12	0	1.9687	0	28.4849
1	2	0	11	0	2.6779	0	31.3383
1	3	0	15	0	1.9944	0	31.8918
1	4	0	14	0	1.4615	0	22.5144
2	1	0	34	0	0.94335	0	31.1529
2	2	0	30	0	1.0771	0	39.7335
2	3	0	27	0	1.0298	0	30.1332
2	4	0	26	0	1.462	0	42.8242
3	1	0	47	0	0.6595	0	32.1363
3	2	0	46	0	0.972	0	43.3603
3	3	0	46	0	0.99855	0	52.714
3	4	0	45	0	0.8868	0	40.9164
4	1	0	71	0	0.5659	0	41.9272
4	2	0	60	0	0.61775	0	41.6279
4	3	0	52	0	1.0883	0	60.8089
4	4	0	50	0	0.76025	0	40.6058
10	1	7	0	0.2166	0	1.9818	0
10	2	12	0	0.1047	0	2.4535	0
10	3	7	0	0.6713	0	6.2736	0
10	4	4	0	1.1871	0	4.8736	0
11	1	4	17	0.0548	2.1855	0.2466	32.6215
11	2	6	19	0.07215	1.1351	0.4584	24.0423
11	3	7	14	0.0649	2.2779	0.4277	35.9063
11	4	7	15	0.0521	1.2423	0.9876	20.9405
12	1	6	29	0.03825	0.8721	0.2617	26.7171
12	2	10	26	0.0602	1.14075	0.6301	37.1061
12	3	8	36	0.0431	0.89385	0.4112	33.3453
12	4	3	30	0.0628	1.04275	0.1657	31.92
13	1	11	44	0.0233	0.758	0.3817	33.6511
13	2	11	46	0.02266	0.63725	0.292	30.6641
13	3	7	45	0.0286	0.6843	0.1966	35.6348
13	4	4	42	0.02505	0.6471	0.0991	25.5768
14	2	5	52	0.0202	0.7776	0.1239	42.7951
14	3	8	55	0.01605	0.4689	0.1624	27.6757
14	4	5	57	0.0548	0.8964	0.2231	58.09
20	1	16	0	0.29565	0	5.3182	0
20	2	18	0	0.1804	0	3.444	0

TRMT	REP	DN	DB	NMW	BMW	NTW	BTW
20	3	20	0	0.2218	0	4.6571	0
20	4	13	0	0.2008	0	3.3328	0
21	1	10	20	0.05475	0.97375	0.5747	23.6436
21	2	19	15	0.0448	1.7898	1.0555	33.076
21	3	17	14	0.0548	1.395	0.9069	22.5784
21	4	15	14	0.0648	4.1004	1.9883	62.2517
22	1	17	39	0.0349	0.8706	0.5954	36.3957
22	2	25	31	0.039	1.1608	1.0684	37.1286
22	3	12	25	0.02155	1.2788	0.3048	34.874
22	4	17	31	0.0488	1.0447	0.8529	41.0156
23	1	18	41	0.03535	0.8568	0.7572	38.1619
23	2	18	43	0.0439	0.6907	0.8179	34.2396
23	3	25	43	0.0271	0.7003	0.8353	33.725
23	4	12	42	0.07825	1.02215	0.3301	53.0855
24	1	18	56	0.0359	0.70005	0.7703	40.1638
24	2	5	59	0.0218	0.6982	0.1179	44.9415
24	3	16	56	0.01525	0.65455	0.2971	41.0965
30	1	18	0	0.14825	0	3.0122	0
30	2	24	0	0.12045	0	4.9043	0
30	3	28	0	0.14575	0	4.4951	0
30	4	31	0	0.3036	0	9.707	0
31	1	19	20	0.0683	1.5704	1.2777	32.0309
31	2	22	15	0.0247	0.9836	0.6913	16.803
31	3	35	14	0.0321	1.57005	1.3915	23.7418
31	4	18	14	0.0406	1.11025	0.9672	16.896
32	1	10	32	0.02075	1.1015	0.2481	32.3172
32	2	39	32	0.0247	0.7939	1.1792	27.449
32	3	32	58	0.0194	0.9348	0.8528	61.6137
32	4	11	26	0.0432	1.3522	0.5448	30.7264
33	1	30	42	0.0278	0.9498	1.0586	41.9296
33	2	28	49	0.0246	0.7948	0.878	40.127
33	3	11	42	0.0407	0.6727	0.4485	32.2873
33	4	26	47	0.02895	0.7042	0.8531	37.3619
34	1	20	58	0.0272	0.6742	0.6314	42.0321
34	2	22	57	0.01525	0.7249	0.4831	41.4673
34	3	23	31	0.0322	1.267	0.9174	47.0298
34	4	21	56	0.0219	0.77315	0.4913	46.1332



TRMT	REP	DN	DB	NMW	BMW	NTW	BTW
40	1	25	0	0.1036	0	4.6241	0
40	2	46	0	0.1247	0	7.4457	0
40	3	51	0	0.1438	0	8.7047	0
40	4	37	0	0.2294	0	11.1874	0
41	1	3	43	0.0295	0.4252	0.0914	22.5879
41	2	38	25	0.0425	1.1396	1.5426	32.47
41	3	47	15	0.0292	0.9985	1.73	17.8029
41	4	22	16	0.0332	1.3732	0.9464	25.8734
42	1	29	43	0.0283	0.6392	0.9694	30.4182
42	2	46	30	0.0281	1.2176	1.7073	38.7309
42	3	20	33	0.0271	0.9045	0.7206	31.4586
42	4	27	28	0.042	1.8957	1.4635	60.4562
43	1	29	44	0.0311	0.84595	0.9208	37.0919
43	2	45	47	0.0257	0.5518	1.2406	39.6962
43	3	44	45	0.0277	0.8424	1.2388	42.7423
43	4	26	40	0.03185	1.09505	1.347	47.9673
44	1	48	55	0.02255	0.6297	1.2769	39.6241
44	2	39	53	0.0191	0.714	0.8774	40.1231
44	3	39	51	0.0327	0.989	1.2977	51.8214
44	4	25	57	0.0244	0.836	0.8794	50.4119

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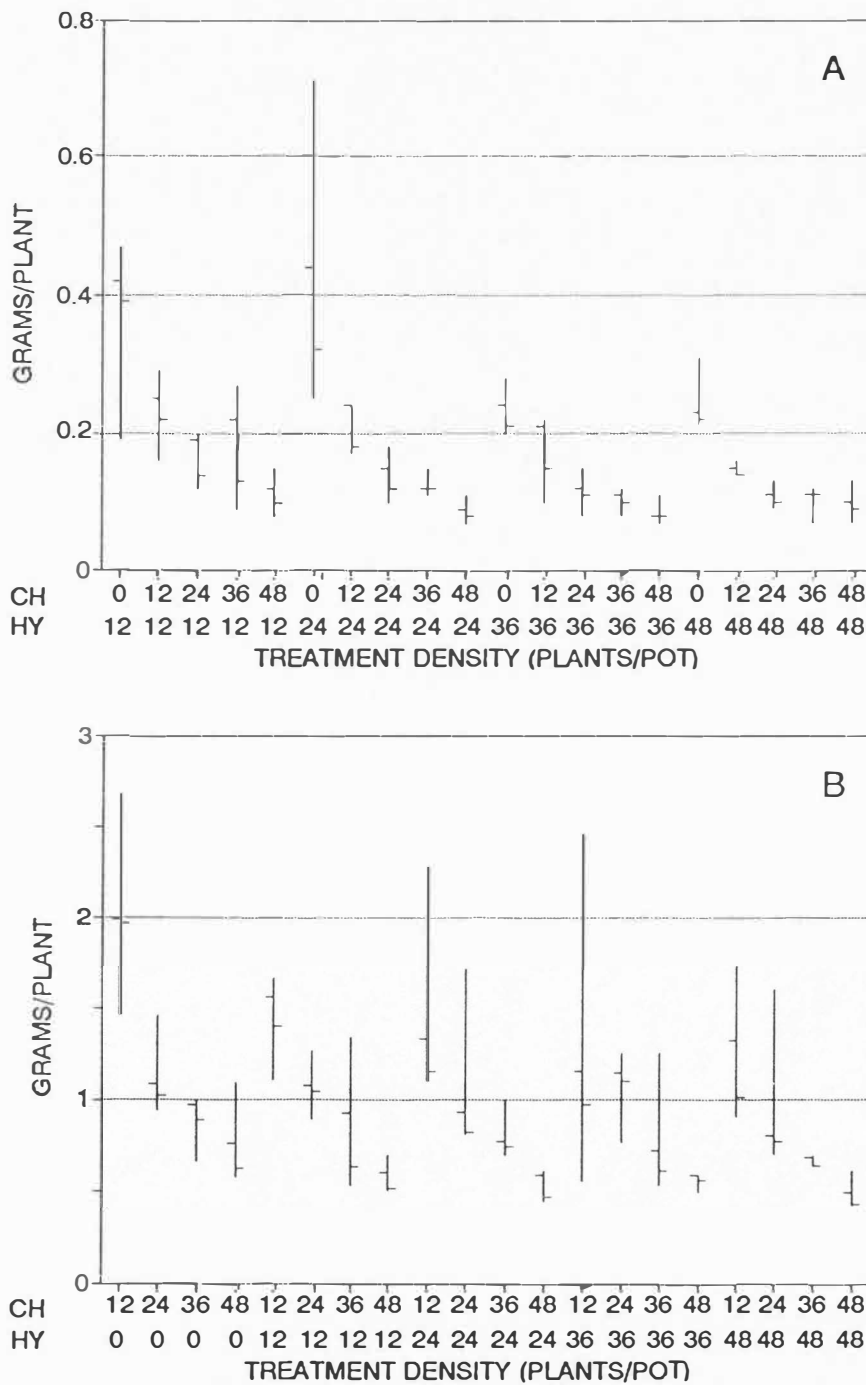


Fig. 11 (A-B). Median biomass per plant for Hycrest (A) and cheatgrass (B) at each treatment density. The end points and tick marks on each vertical line are the four replicates used to calculate the biomass-density model. The treatment density is a mixture of cheatgrass (CH) and of Hycrest (HY).

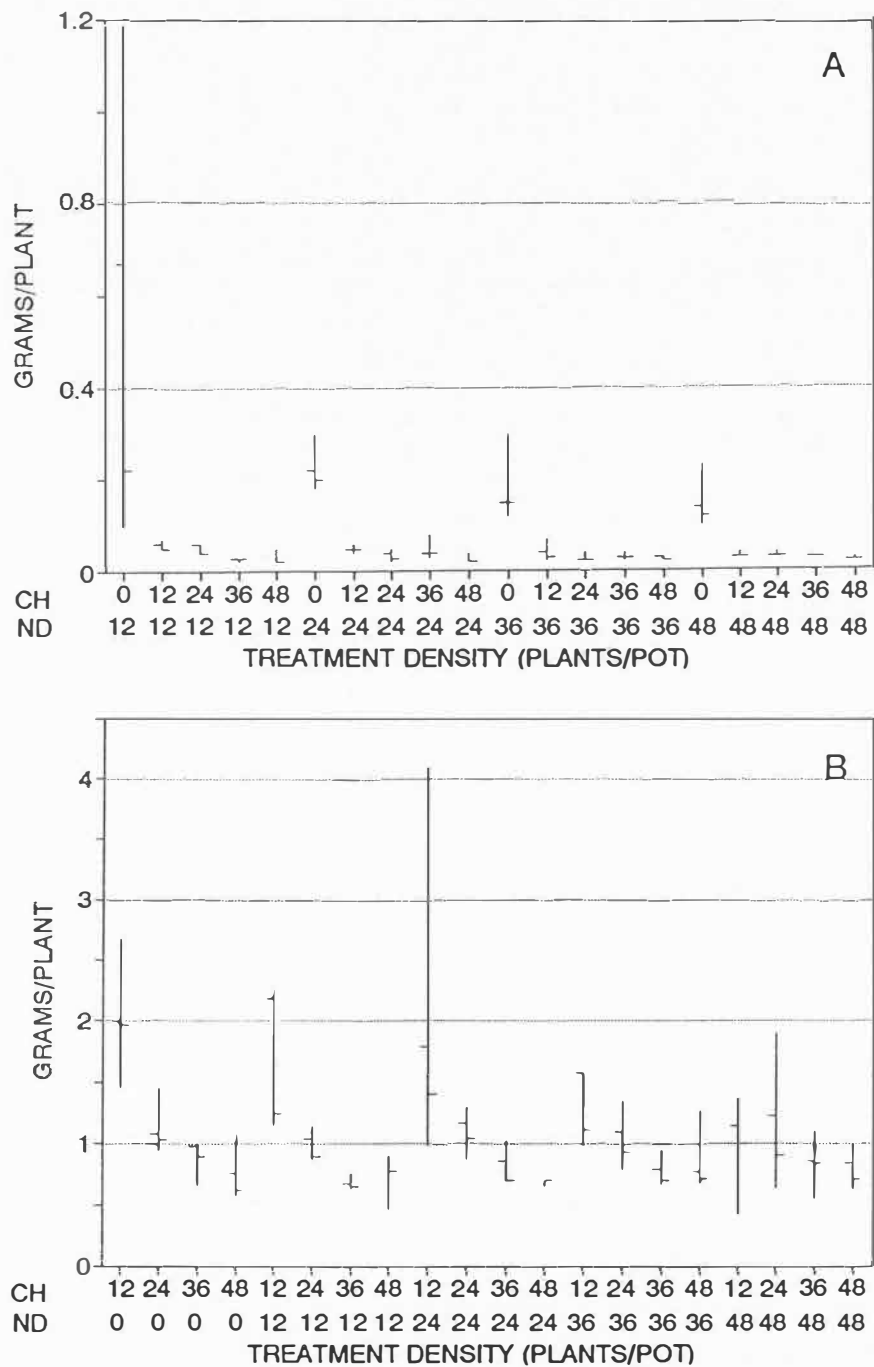


Fig. 12 (A-B). Median biomass per plant for Nordan (A) and cheatgrass (B) at each treatment density. The end points and tick marks on each vertical line are the four replicates used to calculate the biomass-density model. The treatment density is a mixture of cheatgrass (CH) and of Nordan (ND).

**APPENDIX B. TILLER NUMBER**

Table 5. Median tiller numbers per plant and total tiller numbers for species per treatment of Hycrest (HMT and HTT, respectively) and cheatgrass (BMT and BTT, respectively) at each treatment density (TRMT). Hycrest (DH) and cheatgrass (DB) densities are given for each replication (REP).



TRMT	REP	DH	DB	HMT	BMT	HTT	BTt
1	1	0	12	0	15	0	228
1	2	0	11	0	18	0	187
1	3	0	15	0	20	0	299
1	4	0	14	0	18.5	0	297
2	1	0	34	0	5	0	263
2	2	0	30	0	8.5	0	301
2	3	0	27	0	12	0	321
2	4	0	26	0	9.5	0	260
3	1	0	47	0	8	0	349
3	2	0	46	0	11	0	511
3	3	0	46	0	12	0	571
3	4	0	45	0	10	0	471
4	1	0	71	0	8	0	593
4	2	0	60	0	8	0	560
4	3	0	52	0	9	0	505
4	4	0	50	0	9	0	486
100	1	15	0	6	0	93	0
100	2	15	0	5	0	79	0
100	3	15	0	5	0	89	0
100	4	14	0	5.5	0	84	0
101	1	9	18	4	11	36	212
101	2	15	18	3	14.5	48	247
101	3	15	17	4	9	74	345
101	4	16	15	4	20	61	339
102	1	13	29	3	6	43	243
102	2	14	30	3	8.5	46	299
102	3	15	27	4	9	57	312
102	4	15	32	3	10	36	375
103	1	15	48	3	8	42	439
103	2	13	42	3	7	38	273
103	3	13	47	3	11	48	549
103	4	13	47	2	7	33	387
104	1	13	64	2	7.5	27	544
104	2	16	54	3	11	43	613
104	3	16	66	3	8	39	552
104	4	13	56	2	7	26	465
200	1	28	0	4	0	124	0

TRMT	REP	DH	DB	HMT	BMT	HTT	BTT
200	2	24	0	6	0	149	0
200	3	32	0	4	0	151	0
200	4	25	0	4	0	131	0
201	1	27	13	4	11	97	189
201	2	25	15	4	16	88	297
201	3	27	21	3	11	83	264
201	4	28	16	3	6.5	89	130
202	1	27	32	3	9	68	289
202	2	28	32	3	6.5	73	241
202	3	27	27	3	14	90	318
202	4	28	30	2	12	68	359
203	1	26	40	3	8	75	413
203	2	21	44	3	8	62	343
203	3	25	45	2	9	61	459
203	4	28	45	2	6	57	301
204	1	31	58	2	5	76	297
204	2	26	58	2	5.5	62	369
204	3	31	62	2	8	61	546
204	4	25	59	2	8	49	484
300	1	41	0	3	0	123	0
300	2	44	0	4	0	187	0
300	3	44	0	4	0	179	0
300	4	40	0	4	0	137	0
301	1	42	16	2	7	107	144
301	2	42	17	3	18	138	305
301	3	38	15	3	19	126	270
301	4	36	18	2	6.5	88	128
302	1	41	32	2	10	91	308
302	2	40	32	3	7	103	262
302	3	39	28	3	11	103	340
302	4	36	28	2	8.5	78	246
303	1	39	51	2	7	93	418
303	2	42	45	3	8	108	436
303	3	39	43	2	8	71	374
303	4	39	48	2	8.5	76	432
304	1	32	56	2	7	71	442
304	2	41	63	2	3	93	307

TRMT	REP	DH	DB	HMT	BMT	HTT	BTT
304	3	35	58	2	9	61	523
304	4	37	56	2	6	75	376
400	1	56	0	4	0	190	0
400	2	54	0	4	0	216	0
400	3	55	0	4	0	212	0
400	4	56	0	3	0	180	0
401	1	56	9	3	17	142	149
401	2	48	15	3	15	140	253
401	3	50	16	3	13.5	140	233
401	4	45	18	3	70	129	145
402	1	53	34	2	9.5	115	354
402	2	58	28	3	6.5	159	221
402	3	51	26	2	8	111	269
402	4	44	29	2.5	12	109	371
403	1	54	40	2	9	124	391
403	2	57	48	2	8	132	420
403	3	57	45	2	9	129	437
403	4	50	47	2	9	90	491
404	1	52	50	2	3	119	247
404	2	52	60	2	6	108	432
404	3	57	58	2	7.5	112	481
404	4	49	55	2	8	99	467

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**Table 6. Median tiller numbers per plant and total tiller numbers for species per treatment of Nordan (NMT and NTT, respectively) and cheatgrass (BMT and BTT, respectively) at each treatment density (TRMT). Nordan (DN) and cheatgrass (DB) densities are given for each replication (REP).**

TRMT	REP	DN	DB	NMT	BMT	NTT	BTT
1	1	0	12	0	15	0	228
1	2	0	11	0	18	0	187
1	3	0	15	0	20	0	299
1	4	0	14	0	18.5	0	297
2	1	0	34	0	5	0	263
2	2	0	30	0	8.5	0	301
2	3	0	27	0	12	0	321
2	4	0	26	0	9.5	0	260
3	1	0	47	0	8	0	349
3	2	0	46	0	11	0	511
3	3	0	46	0	12	0	571
3	4	0	45	0	10	0	471
4	1	0	71	0	8	0	593
4	2	0	60	0	8	0	560
4	3	0	52	0	9	0	505
4	4	0	50	0	9	0	486
10	1	7	0	11	0	69	0
10	2	12	0	6.5	0	92	0
10	3	7	0	12	0	88	0
10	4	4	0	15.5	0	58	0
11	1	4	17	3.5	16	14	250
11	2	6	19	3.5	15	19	338
11	3	7	14	3	18.5	22	288
11	4	7	15	4	13	25	213
12	1	6	29	2	8	14	276
12	2	10	26	3	13.5	31	360
12	3	8	36	2	11	17	446
12	4	3	30	4	17	12	477
13	1	11	44	2	9	22	411
13	2	11	46	2	8	22	508
13	3	7	45	1	10	10	467
13	4	4	42	1	9	4	394
14	2	5	52	2	10	10	576
14	3	8	55	1	8	11	459
14	4	5	57	1	5	5	368
20	1	16	0	5.5	0	92	0
20	2	18	0	5	0	109	0

TRMT	REP	DN	DB	NMT	BMT	NTT	BTT
20	3	20	0	5	0	85	0
20	4	13	0	6	0	95	0
21	1	10	20	3	11.5	24	252
21	2	19	15	3	14	54	221
21	3	17	14	2	23.5	39	317
21	4	15	14	2	13	37	216
22	1	17	39	1	8	25	327
22	2	25	31	3	17	67	521
22	3	12	25	1	11	18	339
22	4	17	31	2	9	36	326
23	1	18	41	2	9	49	394
23	2	18	43	2	10	39	518
23	3	25	43	2	13	62	578
23	4	12	42	1	9	12	445
24	1	18	56	2.5	10	45	581
24	2	5	59	1	9	6	552
24	3	16	56	1	8.5	22	511
30	1	18	0	4	0	73	0
30	2	24	0	5	0	144	0
30	3	28	0	4	0	130	0
30	4	31	0	4	0	131	0
31	1	19	20	4	13.5	66	265
31	2	22	15	1	10	42	173
31	3	35	14	2	16.5	80	248
31	4	18	14	1	18	41	263
32	1	10	32	1	10	11	333
32	2	39	32	2	13	81	408
32	3	32	58	1	8.5	46	561
32	4	11	26	2	11.5	27	309
33	1	30	42	1	5.5	50	280
33	2	28	49	2	9	56	497
33	3	11	42	1	11	17	459
33	4	26	47	1	10	32	571
34	1	20	58	1	6	31	446
34	2	22	57	1	9	30	551
34	3	23	31	1	12	46	393
34	4	21	56	1	8	25	517



TRMT	REP	DN	DB	NMT	BMT	NTT	BTT
40	1	25	0	4	0	121	0
40	2	46	0	4	0	209	0
40	3	51	0	5	0	254	0
40	4	37	0	4	0	167	0
41	1	3	43	2	6	6	278
41	2	38	25	3	11	104	332
41	3	47	15	2	14	90	254
41	4	22	16	3	12.5	62	229
42	1	29	43	2	9	54	376
42	2	46	30	2	13	108	435
42	3	20	33	2	11	38	398
42	4	27	28	1	16	51	468
43	1	29	44	1	11	48	477
43	2	45	47	1	6	78	309
43	3	44	45	2	10	88	478
43	4	26	40	2	9	58	404
44	1	48	55	2	4	84	290
44	2	39	53	1	9	57	536
44	3	39	51	1	11	71	629
44	4	25	57	1	8	48	480

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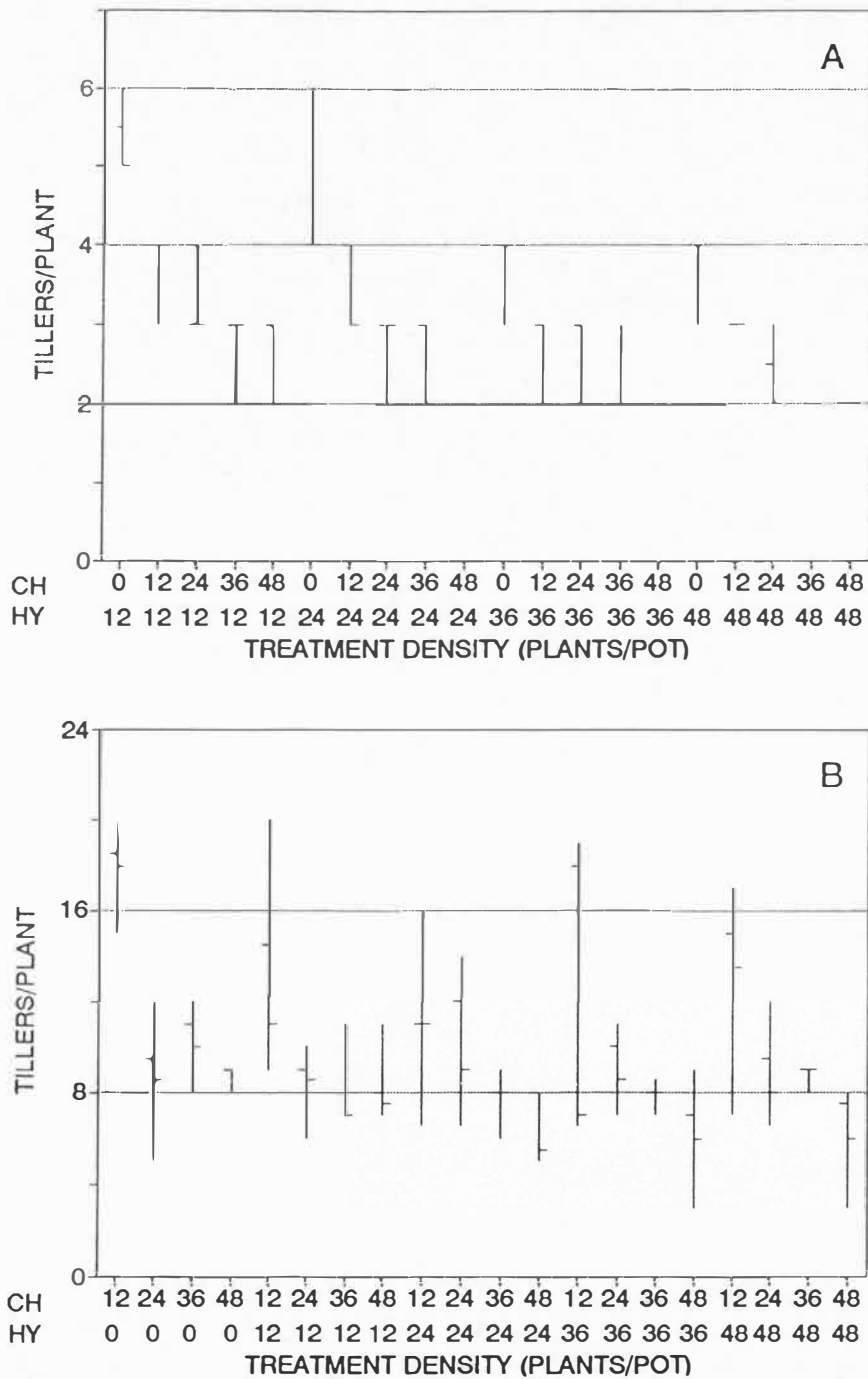


Fig. 13 (A-B). Median tiller numbers per plant for Hycrest (A) and cheatgrass (B) at each treatment density. The end points and tick marks on each vertical line are the four replicates used to calculate the tiller number-density model. The treatment density is a mixture of cheatgrass (CH) and of Hycrest (HY).

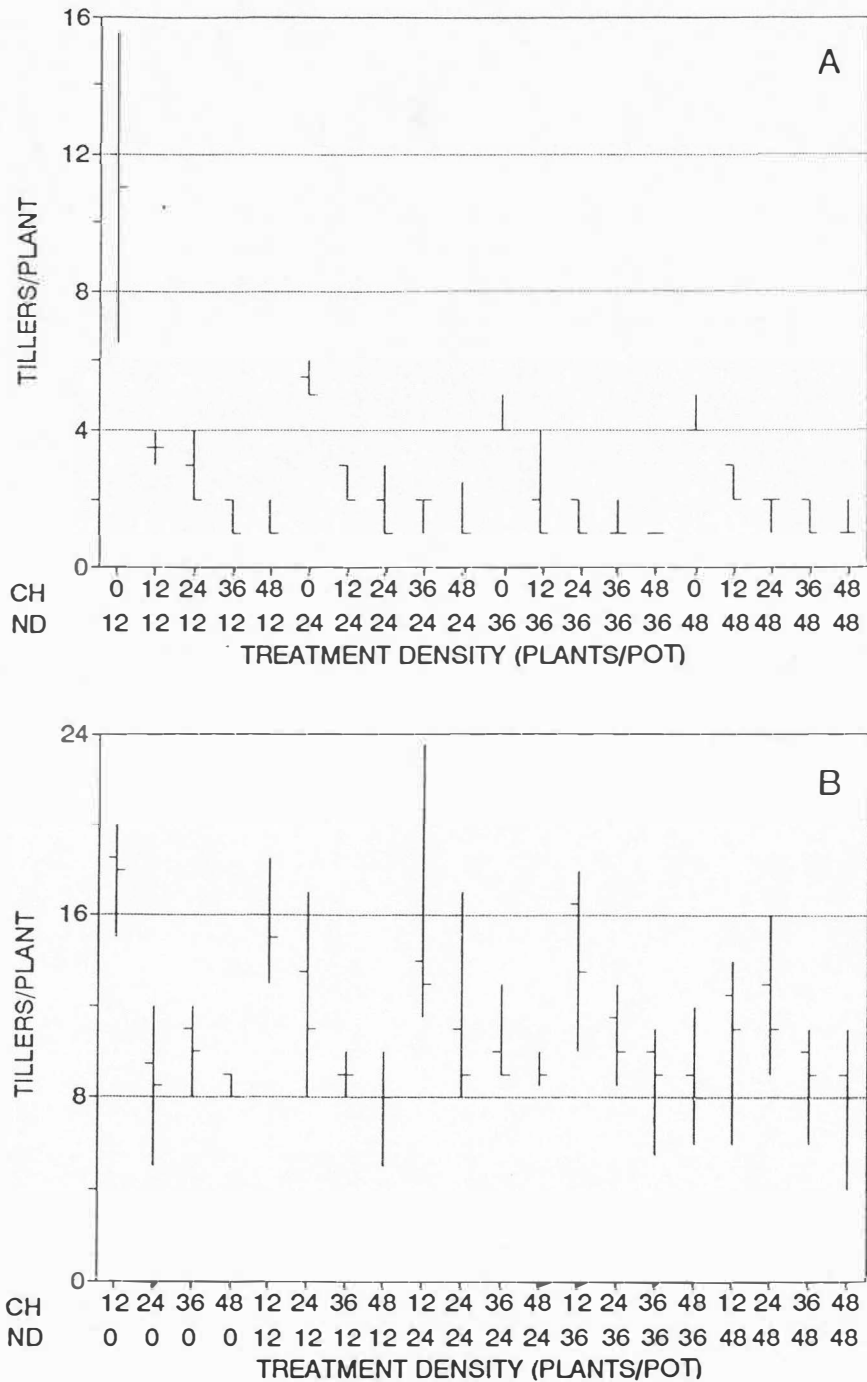


Fig. 14 (A-B). Median tiller numbers per plant for Nordan (A) and cheatgrass (B) at each treatment density. The end points and tick marks on each vertical line are the four replicates used to calculate the tiller number-density model. The treatment density is a mixture of cheatgrass (CH) and of Hycrest (HY).