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Abstract approved:______________________

Larry L. Larson

In many areas of the Western U.S., diffuse knapweed (*Centaurea diffusa* Lam.) has invaded into plant communities dominated by bluebunch wheatgrass (*Pseudoroegnaria spicata* [Pursh] A. Löve). The objectives of this study were to compare growth response of both species when grown under altered moisture and temperature regimes while in the seedling stage and to further elucidate the competitive ability of diffuse knapweed compared to bluebunch wheatgrass. Isolated individuals were grown in four different environmental chamber conditions (12 hr day length, 10 and 16C and -0.01 MPa and -0.03 MPa soil moisture). Diffuse knapweed penetrated quicker than bluebunch wheatgrass starting on day 20, regardless of temperature and moisture and knapweed penetration was greatest under warm and wet soil conditions. Bluebunch wheatgrass developed more root length initially under warmer and drier conditions, but those differences diminished after thirty days growth. Warmer and wetter soil conditions favored diffuse knapweed leaf area production in later stages of seedling growth. Diffuse knapweed had more rapid root penetration than bluebunch wheatgrass under the

conditions studied. Diffuse knapweed maximized shoot production, indicative of a relatively fast growing species, while bluebunch wheatgrass maximized root production, characteristic of a relatively slow growing species. Diffuse knapweed seedlings grew best under warmer and wetter conditions. Comparing plant efficiency (indices of plant efficiency based on the measurement of a plant attribute divided by the total biomass of the plant), diffuse knapweed was apparently more efficient than bluebunch wheatgrass at producing the competitive attributes of root penetration, leaf area and root length.

Comparative Seedling Growth of Diffuse Knapweed and Bluebunch Wheatgrass Under Altered Moisture and Temperature Regimes

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Arnold A. Grammon, Author

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Introduction

Extensive exotic weed encroachment began in North American grasslands with the introduction of several annual grass species (i.e. cheatgrass [*Bromus tectorum* L.], medusahead wildrye [*Elymus caput-medusae* L.] and six-weeks fescue [*Festuca bromoides* L.]) in the late 1800's (Holechek et al 1989). Grasslands dominated by perennial bunchgrasses such as bluebunch wheatgrass (*Pseudoroegnaria spicata* [Pursh] A. Löve) in the Pacific Northwest were particularly vulnerable to both disturbance and invasion (Callihan and Evans 1991). Natural and man-caused disturbance during this time period served to reduce native plant vigor, increase the interstitial space inherent in perennial bunchgrass communities, and thereby accelerate the process of annual grass invasion. (Harris 1967, Harris and Wilson 1970, Daubenmire 1975, Nolan and Upadhyaya 1988). This initial shift toward exotic annual grasses reduced the resource value on Northwest rangelands. However, these same annual grasses provided crucial spring forage and management programs were developed to utilize this forage base.

Exotic plant impacts on Pacific Northwest rangelands did not end with annual grass invasion. Dicot weeds such as the *Centaurea* complex began invading these grasslands in the early 1900's. Consistent with other invasive weeds, they have the potential to invade both disturbed and undisturbed rangelands (Schirman 1981, Myers and Berube 1983, Roche et al. 1986, Lacey et al. 1990, Callihan and Evans 1991, Sheley and Larson 1994a, Sheley et al. 1997). However, in this case resource decline has been more evident because large herbivores generally avoid the dicot weeds in favor of more desirable grasses (Callihan and Evans 1991).

The purpose of this study is to investigate the role of seedling growth in the process of diffuse knapweed invasion., specifically to determine diffuse knapweed (*Centaurea diffusa* Lam.) and bluebunch wheatgrass seedling growth reponse to altered moisture and temperature regimes.

Review of the Literature

The purpose of this literature review is to summarize research of native bluebunch wheatgrass and the exotic dicot diffuse knapweed. The following review provides a comparative overview of the ecology of both species. Seedlings of diffuse knapweed differ from bluebunch wheatgrass in the production of a basal rosette of leaves vs. erect tillers and a taproot vs. a fibrous root system. In addition, diffuse knapweed is a semelparous (produces seed once) perennial forb while bluebunch wheatgrass is a somewhat long-lived perennial grass, reproducing by seed intermittently as well as vegetatively through tillering. The bluebunch wheatgrass cultivar 'Goldar' was used in the experimentation described in this thesis, and information specific to this cultivar has been included in the review.

Ecology of Bluebunch Wheatgrass

A. Bluebunch Wheatgrass Distribution

Bluebunch wheatgrass is a wide-spread native perennial that is found from northern Michigan to Alaska, south to western South Dakota, New Mexico, and California, and throughout the Great Basin (Hitchcock 1950). Millions of acres of bluebunch wheatgrass rangelands have been replaced by annuals such as cheatgrass, medusahead wildrye, and six-weeks fescue (Range Plant Handbook 1937). Bluebunch wheatgrass is generally found on deep well-drained loamy soils, but is adapted to coarser textured, calcareous hardpans as shallow as 20 cm (Heady 1950). Precipitation range is from 180 to 760 mm annually (Daubenmire 1970).

Depuit and Caldwell (1975) mentioned 7 phenological stages for bluebunch wheatgrass: (1)Winter dormancy; (2) Growth initiation (late April-early May); (3) 2-3 leaf stage and spikelet emergence (mid-late May); (4) 4-5 leaf stage and spikelet fully formed (June); (5) leaf dieback and summer dormancy initiated (July); (6) hard seed (August) and (7) seed scatter (September - early October).

B. Bluebunch Wheatgrass Germination

Kitchen and Monsen (1994) found that bluebunch wheatgrass seed contains 176 to 437 seeds per gram. The "Goldar" used in this research yielded 200 seeds per gram. The seed is cylindrical and 7 to 11 mm long.

Germination can begin in the fall with an increase in soil moisture and temperature moderation (Miller et al. 1986). Bluebunch wheatgrass germinates best at 20 to 22C, but has the potential to germinate over a wide range (1 to 35C) of temperature regimes. (Young et al. 1981, Kitchen and Monsen 1994).

Goebel et al. (1988) compared 'Secar' bluebunch wheatgrass with medusahead wildrye (an annual). They found that medusahead germinated quicker, was less inhibited by cold temperatures, and seedlings grew significantly faster than bluebunch wheatgrass. Kitchen and Monsen (1994) tested germination rate and emergence success of bluebunch wheatgrass (47 ascensions and one cultivar). The cultivar 'Goldar' had a higher germination rate then all 47 ascensions, and was among the heaviest seed tested. 'Goldar', originally from a native plant collected near Asotin, Washington in 1934, was released by the Plant Materials Center in Aberdeen, Idaho in 1989 (Plant Materials Center, NRCS, Aberdeen, Id). Kitchen and Monsen (1994) concluded that bluebunch wheatgrass increased seedling vigor and establishment success was associated with greater seed weight and size.

C. Bluebunch Wheatgrass as Seedlings

Successful establishment (i.e. an individual plant that is not reliant on seed reserves [Ries and Svejcar, 1991]) of seeded bunchgrasses is related to the rate of root penetration (Nelson et al. 1970). Bluebunch seedlings normally have a root penetration of less than 7 inches by spring, with the most active period of root growth being initiated in late spring (Harris 1967). Rapid root growth is initiated when soil temperatures average 8 to 10C. (Miller et al. 1986). Harris (1967) showed that bluebunch wheatgrass seedling roots grew very slowly at temperatures below 8C while cheatgrass seedling roots grew well at temperatures as low as 3C. Harris and Wilson (1970) found that cheatgrass and medusahead seedling roots had greater root penetration than bluebunch wheatgrass seedlings. They (Harris and Wilson 1970, Harris 1977) speculated that deeper root penetration by annual grass seedlings could exhaust soil moisture supplies ahead of bluebunch seedlings in drought years.

Johnson and Aguirre (1991) studied the effect of water on the root morphology of bluebunch wheatgrass and two other grasses. They found that root branching decreased with less water application, and that longer external links increased the likelihood of seedling survival during periods of drought. They concluded that rooting characteristics are important for competitive effectiveness in range plants. Root development is particularly critical when the initial stages of growth coincide with limited water in late spring or early summer (Hassenyar and Wilson 1978). Aguirre and Johnson (1991) compared 'Whitmar' bluebunch wheatgrass with cheatgrass, and found that cheatgrass exhibited greater root length than bluebunch wheatgrass, and greater root length was associated with more rapid leaf and tiller development and greater leaf area. These findings concur with a study by Harris (1967) which showed that cheatgrass had greater root and leaf growth than 'Whitmar' bluebunch wheatgrass.

D. Bluebunch Wheatgrass as Adults

Perennial bunchgrasses such as bluebunch wheatgrass generally expend greater amounts of energy on root and phytomass production, and less on the production of seeds. They also tend to have relatively low seedling vigor and their seeds are short-lived in the seedbank (Callihan and Evans 1991).

Rapid leaf and shoot production of bluebunch wheatgrass generally commences during late April and continues into early June with maximum photosynthesis occurring between 20 and 25 C (Depuit and Caldwell 1975). This pattern of growth typically results in seasonal lows in carbohydrate root reserves and flower/seed production that is extremely variable (Quinton et al. 1982, Daubenmire 1978).

Eissenstat and Caldwell (1988), observed that crested wheatgrass had greater competitive ability than bluebunch wheatgrass on Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis)* sites. Soil moisture measurements showed that crested wheatgrass stands extract water more rapidly from the soil profile than bluebunch wheatgrass. Eissenstat and Caldwell (1987) found that the competitive ability of crested wheatgrass over bluebunch wheatgrass could not be attributed to differences in potential growth rates. Dibble and Spomer (1987) suggested that acclimation, rather than ecotypic differences, explained the distribution of bluebunch wheatgrass to a wide variety of moisture conditions.

Ndawula-Senyimba et al. (1971) observed more rapid water infiltration beneath bunches of wheatgrass than under bare ground. They speculated that this may be due to a funneling effect by aerial parts, and that the plant canopy may direct moisture from light summer rains into the rooting zone of individual plants. They hypothesized that the ability of bluebunch wheatgrass to intercept and redistribute limited summer rains may have a bearing on the capability of the species to withstand interspecific competition. Mueggler (1975) found that a partial reduction in competition more than doubled total herbage and tripled the number of flower stalks produced the following year by bluebunch wheatgrass.

Schlatterer and Hironaka (1972) observed that pre-conditioning of bluebunch wheatgrass plants to 3 temperature [14 hours at 29.4 and 10 hours at 12.8 C (greenhouse averages), 14 hours at 18.3 C and 10 hours at 1.7 C, and 14 hours at 32.3 C and 10 hours at 1.7 C] and 2 watering regimes (water applied every 5 days to achieve soil saturation, and water applied every 10 days to achieve soil saturation) affected their tolerance to moisture stress. They found that deviations from greenhouse conditions induced resistance to moisture stress.

The reproductive phase ends with leaf senescence and seed ripening, typically in mid-July (Miller et al. 1986, Harris and Goebel 1976). Pechanec et al. (1937) observed that drought conditions advanced the phenological stage approximately 1 month. However, Caldwell et al. (1981) observed that roots can continue growth into fall at shoot xylem potentials below -2.5 MPa. Depuit and Caldwell (1975) measured gas exchange in 'Whitmar' bluebunch wheatgrass, and determined that plants become photosynthetically dormant during periods of drought and higher temperatures in late summer.

Busso et al. (1990) suggested that bluebunch wheatgrass plants exposed to prolonged periods of drought or drought plus defoliation may result in rapid initial regrowth (following the removal of the stress) due to accumulation of total nonstructural carbohydrates in storage organs.

Willms, et al. (1980) studied the rate of tiller elongation of bluebunch following clipping or burning. They found that the rate of tiller elongation was not affected by clipping. By contrast, burning resulted in a more rapid rate of elongation at cool temperatures and a slower rate at warm temperatures.

Lacey et al. (1990) reported the successful invasion of diffuse knapweed onto a Western Montana bluebunch wheatgrass site in the absence of recent livestock grazing. This site, previously ungrazed for at least 20 years, was used by the Soil Conservation Service (currently the NRCS) as a relict site to evaluate ecological succession. It was bordered by established diffuse knapweed on the south edge of the site. In 1982, the area was disturbed by a severe hailstorm. Once established, diffuse knapweed persisted in the bluebunch wheatgrass community for the rest of the study.

Ecology of Diffuse Knapweed

E. Diffuse Knapweed Distribution

Diffuse knapweed may have the widest ecological amplitude of the knapweeds (Roche and Roche 1991). Originally from the Eurasian area, it currently occupies at least 1.2 million ha in the Western United States and extends into the Canadian provinces of British Columbia and Alberta (Watson and Renney 1974). According to Roche (1994), this weed has the potential to invade over 4.8 million ha of range by the year 2007 in Washington alone. It is found on various soils and habitats ranging from shallow scab sage sites and deep loamy sands to silt clay loam soils (Watson and Renney 1974, Talbott 1987). Watson and Renney (1974) listed the climatic ranges of diffuse knapweed in southern interior British Columbia as 7.2 to 9.4C annual mean temperature, 24.1 to 41.7 cm annual ppt. (precipitation), with April to August ppt. averaging 10.4 to 18.3 cm. Diffuse knapweed is likely most competitive in the bitterbrush/bluebunch wheatgrass community types (Talbott 1987).

F. Diffuse Knapweed Germination

Diffuse knapweed achenes are oblong, 2.3 to 3.6 mm long, 840 seeds per gram, tan to dark brown with the inner achenes of the involucre bract having a white scalely pappus less than 1 mm long.

Nolan and Upadhyaya (1988) found 3 types of germination in diffuse and spotted knapweed seed. Two were associated with light sensitivity toward red and far red light and one was light-insensitive. They concluded that the bare interspace areas found on bunchgrass rangeland provided a variety of light conditions that favored knapweed germination over time. Spears et al. (1980) found that diffuse knapweed germinates equally well at a range from 0 to 100% canopy cover, emerges best on the soil surface, and that emergence rate decreased with increasing depth.

Kiemnec and Larson (1991) studied the effects of water and salt stresses on germination and initial root growth. Diffuse knapweed germination was highest at 0.0 and -0.5 MPa of osmotic potential, which compares favorably with values of -0.03 MPa by Eddleman and Romo (1988) on spotted knapweed. They also showed germination was most rapid between 2 to 4 d and 4 to 6 d respectively, with initial root growth sensitivity to -0.5 MPa with diffuse knapweed.

On a bluebunch wheatgrass/needle-and-thread habitat type (Daubenmire 1970) ungrazed for 20 years, defoliation of bluebunch wheatgrass greater than 60% enhanced diffuse knapweed establishment, while moderate grazing of less than 60% did not appear to accelerate knapweed invasion (Sheley et al.1997). Diffuse knapweed seeding rates of up to 6000 seeds per m^2 had no effect on the density of diffuse knapweed in a bluebunch wheatgrass/needle-and -thread plant community.

Diffuse knapweed will establish on disturbed rangeland from very sparsely scattered seed (Roze et al. 1984). Schirman (1981) noted that survival of only about 0.1

percent of the seed produced is required to maintain stands of knapweed at current levels and still have the potential to invade adjoining noninfested land.

Sheley and Larson (1996) detected substantial resource partitioning between seedlings having different emergence dates. They proposed that continuous seedling emergence may allow diffuse knapweed to minimize intraspecific interference, and therefore maximizing safe site occupation, resulting in the monotypic stands of knapweed commonly found on Western rangelands.

Diffuse Knapweed as Seedlings

Sheley and Larson (1996) found that co-emerging knapweed seedlings influence their own shoot weight more than knapweed seedlings emerging either earlier or later. They speculated that diffuse knapweed may avoid intraspecific interference by the continuous recruitment of seedlings. This process of continuous emergence may be an important mechanism for providing temporal resource partitioning, allowing diffuse knapweed to occupy all available safe sites as they become available.

Watson and Renney (1974) found that densities of diffuse knapweed were correlated with increased disturbance. They observed maximum seedling densities up to 545 plants per square meter and found that the density of knapweed was related to the age of the infestation.

Berube and Myers (1982) studied the effectiveness of crested wheatgrass in suppressing the invasion of diffuse knapweed on established plots of crested wheatgrass and Russian wild rye in British Columbia. Their experiments indicated that a lack of soil moisture resulted in high knapweed seedling mortality and prevented knapweed invasion into crested wheatgrass plots. Berube and Myers (1982) also found diffuse knapweed seedlings are influenced by chance events, particularly those related to moisture availability. They concluded that the seedling-to-rosette stage as being the period most sensitive to water deficit.

Larson and McInnis (1989) tested the survivability of diffuse knapweed and yellow starthistle when subjected to grass seedling interference. Their findings as well as those of Huston et al. (1984) suggest that grass seedlings will be competitive when moisture and other nutrients are removed from the rooting zone of knapweeds and their period of growth also overlap the active growth period of the knapweed species.

Myers and Berube (1983) studied the influence of diffuse knapweed on grass biomass and growth. They found that in spring dry weight comparisons, 1 g of knapweed reduced grass biomass 1.5 g, and in fall comparisons 1 g of knapweed reduced grass biomass by approximately 0.33 g. Grass growth was lowest on the control plots, while 2,4-D treated plots increased grass growth by about 1.5 times. Growth response appeared very quickly on chemically treated plots.

H. Diffuse Knapweed as Adults

Thompson and Stout (1991) found that diffuse knapweed can demonstrate a variety of life cycles. In this study, diffuse knapweed plants were observed to have an annual, biennial, pseudotriennial, and triennial life cycle. They also found that the bolting threshhold and the commencement of the adult period appears to be associated with the development of a 13 leaf rosette. This type of elasticity suggests an ability to tolerate sub-optimal conditions until sufficient resources have been sequestered to complete the life cycle. Silvertown (1984) suggests that this variation is more accurately termed a "semelparous perennial". Roze et al. (1984) found that diffuse knapweed typically remained in rosette stage for two years before bolting. This type of life cycle displays characteristics found in many invasive weeds.

These characteristics also include the ability to produce thousands of seeds per m^2 in combination with the ability of the plant to produce both short and long-lived seed which germinate over a variety of conditions and time periods (Watson and Renney 1974). Schirman (1981) compared diffuse knapweed response in a wet year with a dry year and found that above-normal precipitation resulted in greater seed production than below-normal precipitation years. By contrast, cheatgrass and other early growing annuals tend to have a competitive advantage over perennial grasses such as bluebunch wheatgrass during typical moisture years but are reletively poor competitors during periods of above average precipitation (Harris 1967, Miller et al. 1986).

Sauer and Uresk (1976) observed that several years of above-average rainfall should favor seasonally late growing species such as diffuse knapweed, while an extended period of dry years should favor early growing species such as cheatgrass. They contend that early growing species can tolerate periods when only the top soil layers are wetted, but are unable to take advantage of deep soil moisture during periods of above average rainfall.

Maxwell et al. (1992) studied a site in southern British Columbia and found that diffuse knapweed reestablishment was more rapid on sprayed-then-grazed treatment sites than on ungrazed treatment sites.

Materials and Methods

I. Introduction

Seedling growth parameters were measured at 10 day intervals through day 40, and included root penetration, root length, root biomass, leaf area, leaf biomass, leaf number, and root-to-shoot ratios. These growth parameters will be used for comparison in a future study to analyze interspecific and intraspecific interference of these 2 species when in the critical seedling stage.

J. Procedures

This study focuses on 40 days of diffuse knapweed and bluebunch wheatgrass seedling establishment in 4 different environments (Cool and Moist [10C and -0.01 MPa], Warm and Moist [16C and -0.01 MPa], Cool and Dry [10C and -0.03 MPa], and Warm and Dry [16C and -0.03 MPa]).

Individual plant growth was determined by growing plants in PVC tubes in controlled environmental conditions. PVC tubes, 800 mm depth, were split vertically and taped to facilitate root removal. Tube surface area and circumference was increased with harvest date (50 mm^2 on day 10, 203 mm^2 on day 20, 811 mm^2 on day 30, and 1824 mm^2 on day 40) to insure minimal restriction of root growth (Sheley and Larson 1994a).

Soil moisture levels were achieved by batch pre-mixing a Walla Walla silt loam (coarse-silty, mixed, mesic Typic Haploxeroll) with water and monitoring for a 24 hour period using tensiometers. Soil was added to the prepared tubes by filling a third, dropping the tube 3 to 5 cm on concrete each time filled to facilitate soil settling and repeat the process until the tube was filled. Additional tubes were prepared and monitored for soil moisture content with tensiometers for the duration of the study. Tubes were arranged in a randomized complete block design with 4 replications and 16 tubes per block in an environmental chamber (10C or 16C, 12 h daylength, 500 uE m^{-2} sec^{-1} spectral light).

Mature diffuse knapweed plants were collected during the 1995 growing season on a site near La Grande, Oregon. Plants were stored at room temperature for 3 months before the seed was harvested. The dried-on-plant seeds were removed by shattering the involucre bract, separating the seed using a mechanized seed cleaner and inspecting for unfilled seed. Foundation Goldar bluebunch wheatgrass seed was obtained from Grassland West in 1995. Seeds of both species were rinsed in a 5% sodium hypochlorite solution for 30 seconds followed by 3 distilled water rinses.

Five seeds of diffuse knapweed and bluebunch wheatgrass were sown into the tubes for each of 4 harvest dates (40 d duration, 10 d harvest interval initiated on day 10) to assess individual plant growth. Planting was staggered (bluebunch wheatgrass was planted 3 days prior to diffuse knapweed) to facilitate synchronized germination. After each tube was planted, 2 ml of water were added to the tube to initiate germination. No other water was added to the tubes for the duration of the experiment. Tubes were covered with plastic for the first 48 hours to minimize moisture loss. Plants were thinned to two individuals on day 5 of the experiment. Growth parameter data was taken from the remaining individuals. Tubes were observed daily to monitor environmental conditions.

Seedling growth was measured using root penetration, root length, root biomass, leaf area, leaf biomass, leaf number, and root-to-shoot ratio. In addition, leaf area ratios, (Poorter and Remkes 1990; Radosevich et al. 1997) and efficiency indices (Svejcar 1990; Aguirre and Johnson 1991) were calculated to estimate the competitive abilities of each species in the seedling stage. Data reported in the study reflect the response of individual plants to specific environments and do not necessarily reflect the growth of plants grown at different densities or species combinations. Sampling involved manually rinsing soil from roots and measuring primary root penetration.

Roots were separated from shoots and measured for total root length using a root length scanner (CI-203RL, CID, Inc., Vancouver, Wa.), dried to a constant weight (48 hours, 60°C) and weighed (mg). Leaf area was measured using a leaf scanner (CI-203RL, CID, Inc., Vancouver, Wa.), dried to a constant weight (48 hours, 60°C) and then weighed (mg).

K. Analysis

Significant differences ($p \leq 0.05$) in individual plant growth were determined by analysis of variance procedures (Statgraphics Plus for Windows, ver. 3). Mean separation was determined by least significant difference ($p \leq 0.05$).

Results and Discussion

I. Root Growth : Species

Main Effects

Diffuse knapweed penetrated deeper into the soil profile than bluebunch wheatgrass beginning on day 20 (Table 1) and remained 20 - 40% greater than bluebunch wheatgrass for the duration of the study, regardless of moisture and temperature.

Bluebunch wheatgrass produced more root biomass than diffuse knapweed on day 10, 20 ($p \leq 0.10$) and 30 (Table 2), and developed higher root to shoot ratios on day 30 and 40 (Table 3). In addition, bluebunch wheatgrass root length exceeded diffuse knapweed on day 10 and 30, but were similar at the end of the study (Table 4).

Species × Moisture Interactions

Species and moisture treatments affected root penetration (Table 5). Species differences were most evident at -0.01 MPa, where diffuse knapweed penetration exceeded bluebunch by more than 40% (sample dates 20 through 40).

By contrast, bluebunch wheatgrass had greater root to shoot ratios than diffuse knapweed on days 20 through 40 (Table 6) when grown at -0.01 MPa. However, this difference was not evident when both species were grown under drier conditions.

Soil moisture also affected root length (Table 7). Bluebunch wheatgrass also produced more initial root length than diffuse knapweed (day 10, $p \leq 0.10$; day 30, $p \leq 0.05$) when grown under dry conditions. However, by day 40 both species had similar root length regardless of soil moisture conditions.

Table 1. Soil depth penetration as affected by species, moisture and temperature (main effects).

	Species		Moisture		Temperature		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	-0.01 MPa	-0.03 MPa	10C	16C	LSD[1] (.05)
				cm			
10	19.30	17.1	16.9	19.5	14.7	21.6	4.30
20	39.3	27.3	27.2	39.4	27.6	39	6.40
30	56.4	46.1	50.4	52.1	41.2	61.3	7.80
40	74.80	57.80	66.30	66.30	56.10	76.50	6.40

[1] Mean comparisons may be made along rows.

Table 2. Root biomass as affected by species, moisture, and temperature (main effects)

	Species		Moisture		Temperature		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	-0.01 MPA	-0.03 MPA	10C	16C	LSD[1] (.05)
	-----	-----	-----	-----mg-----	-----	-----	-----
10	1.7	3.5	2.1	3.1	1.8	3.4	1.0
20	11.6	16.8	11.6	16.8	7.4	21.0	5.6
30	65.6	111.1	66.4	110.3	29.6	147.1	32.0
40	133.2	216.4	228.5	121.2	53.4	296.2	103.1

[1] Mean comparisons may be made along rows.

Table 3. Root to shoot ratios as affected by species, moisture, and temperature (main effects).

	Species		Moisture		Temperature		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	-0.01 MPA	-0.03 MPA	10C	16C	LSD[1] (.05)
	---mg mg^{-1}---						
10	.56	.95	.60	.91	.77	.74	.42
20	.81	.84	.62	1.03	.84	.81	.20
30	.90	1.65	.93	1.64	.91	1.66	.29
40	.74	1.08	.88	.94	.85	.96	.30

[1] Mean comparisons may be made along rows.

Table 4. Root length as affected by species, moisture, and temperature (main effects)

	Species		Moisture		Temperature		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	-0.01 MPa	-0.03 MPa	10C	16C	LSD[1] (.05)
	--cm--						
10	22.9	32.6	27.4	28.1	18.7	36.7	7.7
20	136.6	152.9	124.7	164.7	59.4	230	57.4
30	504.9	823.1	492.7	835.3	137.2	1190.9	239
40	1032.5	1071.7	1116.5	987.7	281.6	1822.6	424.4

[1] Mean comparisons may be made along rows.

Table 5 . Soil depth penetration for diffuse knapweed and bluebunch wheatgrass as affected by moisture differences (interactions).

	-0.01 MPa		-0.03 MPa		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	----------	----------	cm	----------	----------
10	18.6	15.1	19.9	19.1	6.1
20	32.2	22.3	46.4	32.4	9.1
30	59.5	41.4	53.4	50.8	11.1
40	79	53.5	70.6	62.1	9.1

[1] Mean comparisons may be made along rows.

Table 6. Root to shoot ratios for diffuse knapweed and bluebunch wheatgrass as affected by moisture differences (interactions).

	-0.01 MPa		-0.03 MPa		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	mg mg^{-1}				
10	.51	.69	.59	1.22	.60
20	.46	.79	1.15	.90	.28
30	.62	1.23	1.19	2.08	.41
40	.56	1.20	.91	.95	.43

[1] Mean comparisons may be made along rows.

Table 7. Root length for diffuse knapweed and bluebunch wheatgrass as affected by moisture differences (interactions).

	-0.01 MPa		-0.03 MPa		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	cm				
10	23.1	31.7	22.7	33.5	10.9
20	133.0	116.5	140.2	189.3	81.1
30	431.7	553.7	578.1	1092.6	338.0
40	1209.6	1023.5	855.4	1120.0	600.2

[1] Mean comparisons may be made along rows.

Species × Temperature Interactions

Diffuse knapweed penetrated deeper than bluebunch wheatgrass at 10C on day 20 and 30 (Table 8) and at 16C on day 20 and 40.

Bluebunch wheatgrass produced more root length than knapweed on day 10 and 30 when grown at 16C (Table 9) and more root biomass on day 10, 20 ($p \leq 0.10$), and 30 when grown at 16C (Table 10).

These data suggest that diffuse knapweed seedlings will tend to have greater root penetration than bluebunch wheatgrass under the moisture and temperature conditions studied. Our results and others (Sheley and Larson, 1994) suggest that quick initial root penetration may play an integral role in the ability of knapweeds to occupy sites and exploit resources. Root penetration by diffuse knapweed should be greatest under warmer (16C) and wetter (-0.01 MPa) soil conditions. Knapweed is also capable of quicker root penetration than bluebunch wheatgrass when grown at 10C.

While it is apparent that bluebunch wheatgrass seedlings produce more initial root length under warmer and drier conditions than diffuse knapweed, root length differences between species diminished after 30 days of growth, regardless of the moisture and temperature regimes studied.

Table 8. Soil depth penetration for diffuse knapweed and bluebunch wheatgrass as affected by temperature differences (interactions).

	10C		16C		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	cm				
10	16.3	13.1	22.2	21.1	6.1
20	33.3	21.9	45.4	32.7	9.1
30	48.2	34.1	64.6	58	11.1
40	67.8	44.4	81.9	71.1	9.1

[1] Mean comparisons may be made along rows.

Table 9. Root length for diffuse knapweed and bluebunch wheatgrass as affected by temperature differences (interactions).

	10C		16C		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	----------	----------	cm	----------	----------
10	15.0	22.5	30.7	42.7	10.9
20	46.7	72.1	226.5	233.6	81.1
30	83.1	191.2	926.7	1455.0	338.0
40	198.9	364.4	1866.1	1779.1	600.2

[1] Mean comparisons may be made along rows.

Table 10. Root biomass for diffuse knapweed and bluebunch wheatgrass as affected by temperature differences (interactions).

	10C		16C		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	---mg---				
10	1.35	2.34	2.13	4.71	1.36
20	5.81	8.97	17.35	24.69	7.95
30	13.35	45.82	117.87	176.27	45.3
40	27.85	78.97	238.56	353.89	145.8

[1] Mean comparisons may be made along rows.

M. Shoot Growth: Species

Main Effects

Knapweed produced more leaf area than bluebunch wheatgrass on day 30 and 40 of the study (Table 11), regardless of temperature and moisture.

Diffuse knapweed produced more leaves than bluebunch wheatgrass beginning on day 10 and remained 10 - 50% greater than bluebunch through day 30, regardless of moisture and temperature (Table 12).

Species × Moisture Interactions

At field capacity (-0.01 MPa), diffuse knapweed produced more leaf area than bluebunch wheatgrass on day 30 and 40 (Table 13).

Comparing species response to moisture, diffuse knapweed produced 33 and 48% more leaves on day 10 and 20, respectively, than bluebunch at -0.01 MPa. By contrast, diffuse knapweed produced 65 and 25% more leaves, respectively, than wheatgrass at -0.03 Mpa on day 10, 20 and 30 (Table 14).

Species × Temperature Interactions

Diffuse knapweed maintained a leaf area nearly 2 times that of bluebunch at 16C (day 30 and 40) (Table 15).

Warmer temperatures produced variable leaf biomass results. On day 10, bluebunch grown at 16C produced 57% more leaf biomass than diffuse (Table 16). By day 30, diffuse knapweed reversed this relationship and had 23% more leaf biomass than

Table 11. Leaf area as affected by species, moisture, and temperature (main effects)

	Species		Moisture		Temperature		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	-0.01 MPA	-0.03 MPA	10C	16C	LSD[1] (.05)
	-----	-----	-----	cm²	-----	-----	-----
10	1.7	1.8	1.9	1.6	0.7	2.8	0.6
20	5.1	4.7	5.7	4.1	1.4	8.4	1.7
30	24.4	14.7	24.2	14.9	2.6	36.5	4.6
40	48.5	29.8	55.0	22.3	8.9	68.4	24.6

[1] Mean comparisons may be made along rows.

Table 12. Leaf number as affected by species, moisture, and temperature (main effects)

	Species		Moisture		Temperature		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	-0.01 MPA	-0.03 MPA	10C	16C	LSD[1] (.05)
10	2.6	1.8	2.3	2.1	1.8	2.6	0.4
20	4.5	3.3	3.9	3.9	3.2	4.6	0.4
30	6.8	6.1	6.8	6.1	4.1	8.8	0.8
40	9.1	10.2	10.3	9.0	6.7	12.6	1.9

[1] Mean comparisons may be made along rows.

Table 13. Leaf Area for diffuse knapweed and bluebunch wheatgrass as affected by moisture differences (interactions).

	-0.01 MPa		-0.03 MPa		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	cm^2				
10	1.9	1.8	1.5	1.7	0.8
20	6.2	5.3	4.0	4.2	2.4
30	29.8	18.7	19.1	10.7	6.4
40	73.6	38.4	23.4	21.1	32.0

[1] Mean comparisons may be made along rows.

Table 14. Leaf number for diffuse knapweed and bluebunch wheatgrass as affected by moisture differences (interactions).

	-0.01 MPa		-0.03 MPa		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
10	2.8	1.8	2.5	1.8	0.5
20	4.6	3.1	4.4	3.5	0.5
30	6.8	6.9	6.8	5.4	1.1
40	9.9	10.8	8.4	9.6	2.7

[1] Mean comparisons may be made along rows.

Table 15. Leaf Area for diffuse knapweed and bluebunch wheatgrass as affected by temperature differences (interactions).

	10C		16C		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	cm^2				
10	0.8	0.6	2.6	3.0	0.8
20	1.4	1.4	8.8	8.0	2.4
30	2.3	2.9	46.5	26.5	6.4
40	8.1	9.7	89.0	49.8	34.8

[1] Mean comparisons may be made along rows.

Table 16. Leaf biomass for diffuse knapweed and bluebunch wheatgrass as affected by temperature differences (interactions).

	10C		16C		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	mg				
10	3.1	2.6	3.9	6.2	1.7
20	7.8	10.3	25.2	32.9	9.9
30	13.7	24.7	160.7	130.6	30.3
40	44.5	78.4	332.4	308.6	146.7

[1] Mean comparisons may be made along rows.

bluebunch grown at 16C ($p \leq 0.10$). Although not significant, this trend continued through day 40.

Diffuse knapweed produced more leaves at 10C than bluebunch wheatgrass on day 10 through 30. By contrast, knapweed grew more leaves at 16C on day 10, but by day 40, this relationship was reversed. By harvest day 40, bluebunch grew more leaves than diffuse at 16C (table 17).

These results suggest that diffuse knapweed is able to produce more leaf area and leaf biomass than bluebunch wheatgrass in the later stages of seedling growth under all the moisture and temperature conditions studied. Diffuse knapweed also produced a larger number of leaves than bluebunch wheatgrass during the initial stages of seedling growth.

Warmer and wetter soil conditions tend to favor diffuse knapweed leaf area production in the later stages of seedling growth. At that time, knapweed grown at 16C yielded more leaf biomass than bluebunch.

Table 17. Leaf number for diffuse knapweed and bluebunch wheatgrass as affected by temperature differences (interactions).

	10C		16C		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
10	2.0	1.5	3.3	2.0	0.5
20	3.8	2.6	5.3	4.0	0.5
30	4.8	3.5	8.8	8.8	1.1
40	7.3	6.1	11.0	14.3	2.7

[1] Mean comparisons may be made along rows.

N. Root and Shoot Growth: Temperature and Moisture

Plants of both species had greater root penetration (Table 1), consistently produced more root biomass (Table 2) and initial root length (Table 4) at 16C when compared to plants grown at 10C. Plants yielded more root biomass when grown under water limited conditions at 10, 20 ($p \leq -0.10$), and 30 days of growth (Table 2). However, by day 40, plants produced almost twice the root biomass when grown at field capacity as they did under water-limited conditions (Table 2).

Both species consistently produced more leaf area (day 10-40, day 20 $p \leq -0.10$) and biomass (day 30 and 40) when grown at field capacity than those produced under water limited conditions (Tables 11 and 18). In addition, plants yielded greater leaf area (Table 11), biomass (Table 18) and number (Table 12) when grown at 16C compared to 10C.

It is apparent from these data that root (penetration, root length and root biomass) and leaf characteristics (leaf area, leaf biomass and leaf count) increase with warmer soil temperature.

These data also suggest that both species will initially increase root biomass when subjected to water limited conditions. However, this difference (wet vs. dry) will decrease as root growth under moist conditions continues into the growing season (Tables 2 and 19).

Table 18. Leaf biomass as affected by species, moisture, and temperature (main effects)

	Species		Moisture		Temperature		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	-0.01 MPA	-0.03 MPA	10C	16C	LSD[1] (.05)
	mg						
10	3.5	4.4	4.1	3.8	2.8	5.1	1.2
20	16.5	21.6	21.8	16.3	9.1	29.0	7.0
30	87.2	77.6	97.7	67.2	19.2	145.6	21.4
40	188.4	193.5	253.9	128.0	61.4	320.5	103.8

[1] Mean comparisons may be made along rows.

Table 19. Root biomass for diffuse knapweed and bluebunch wheatgrass as affected by moisture differences (interactions).

	-0.01 MPa		-0.03 MPa		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	mg				
10	1.71	2.56	1.77	4.48	1.36
20	8.71	14.56	14.45	19.1	7.95
30	43.19	89.52	88.04	132.57	45.3
40	182.61	274.29	83.8	158.57	145.8

[1] Mean comparisons may be made along rows.

O. Supporting Indices

Poorter and Remkes (1990) demonstrated a high correlation with leaf area ratio (leaf area m^2 / total plant biomass) and relative growth rate. In reference to the work of Poorter and Remkes (1990), Radosevich et al. (1997) theorized that the more a plant "invested" in leaf area, the faster it could grow and produce new biomass. Svejcar (1990) and others (Aguirre and Johnson 1991) advanced a similar index of efficiency based on the measurement of an attribute divided by the total biomass of the plant.

In addition to our analysis, we include leaf area ratios and efficiency indices (Poorter and Remkes, 1990; Svejcar, 1990; Aguirre and Johnson, 1991; Radosevich et al., 1997) as additional indicators of the apparent competitive advantage of diffuse knapweed in the seedling stage. Efficiencies are indices of plant efficiency based on the measurement of a plant attribute divided by the total biomass of the plant. In evaluation of these efficiency indices, we looked for trends and large visible differences.

Day 40 diffuse knapweed was apparently more efficient at root penetration than bluebunch wheatgrass when grown under cool conditions (Figure 1). Diffuse knapweed produced more leaf area for a given amount of plant biomass at all 4 moisture and temperature regimes (Figure 2). Diffuse knapweed was also more efficient than bluebunch wheatgrass at producing root length (Figure 3) under warm and dry conditions, which incidently, are the conditions associated with the onset of summer. In general, diffuse knapweed was more efficient than bluebunch wheatgrass seedlings at producing the competitive attributes of root penetration, leaf area and root length.

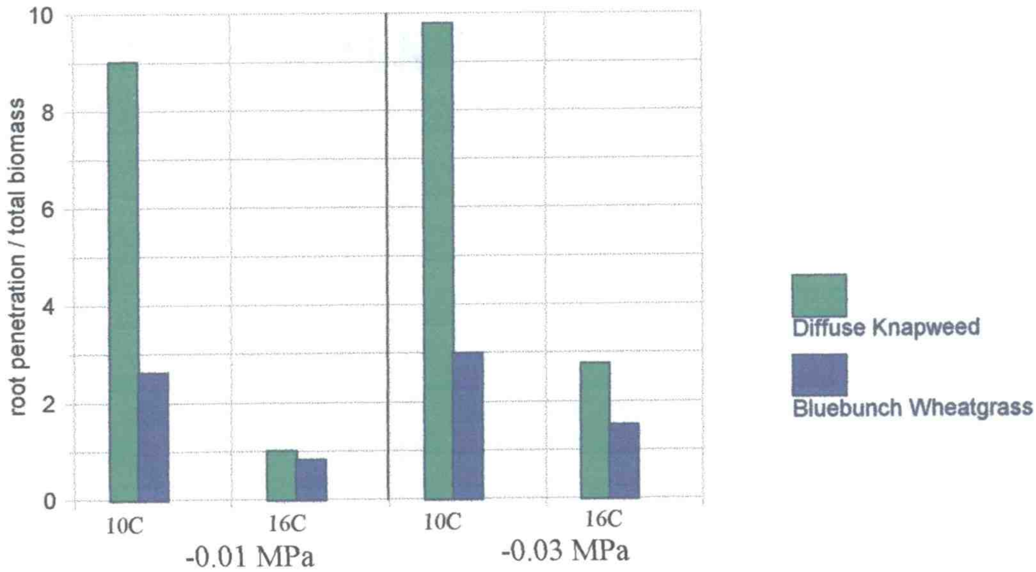

Figure 1. Efficiency of diffuse knapweed (DK) and bluebunch wheatgrass (BB) root penetration at 40 days.

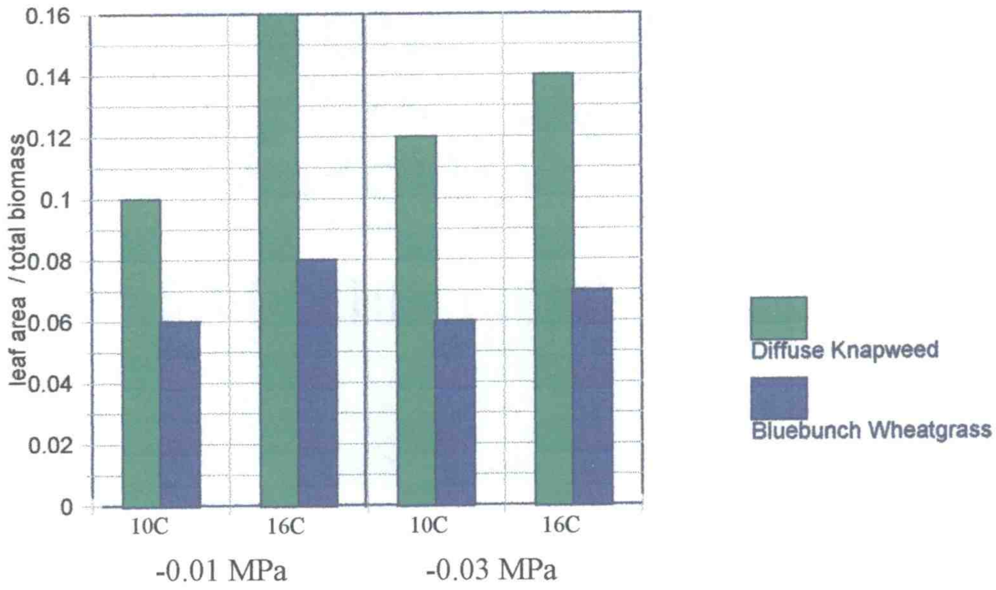

Figure 2. Efficiency of diffuse knapweed (DK) and bluebunch wheatgrass (BB) leaf area at 40 days.

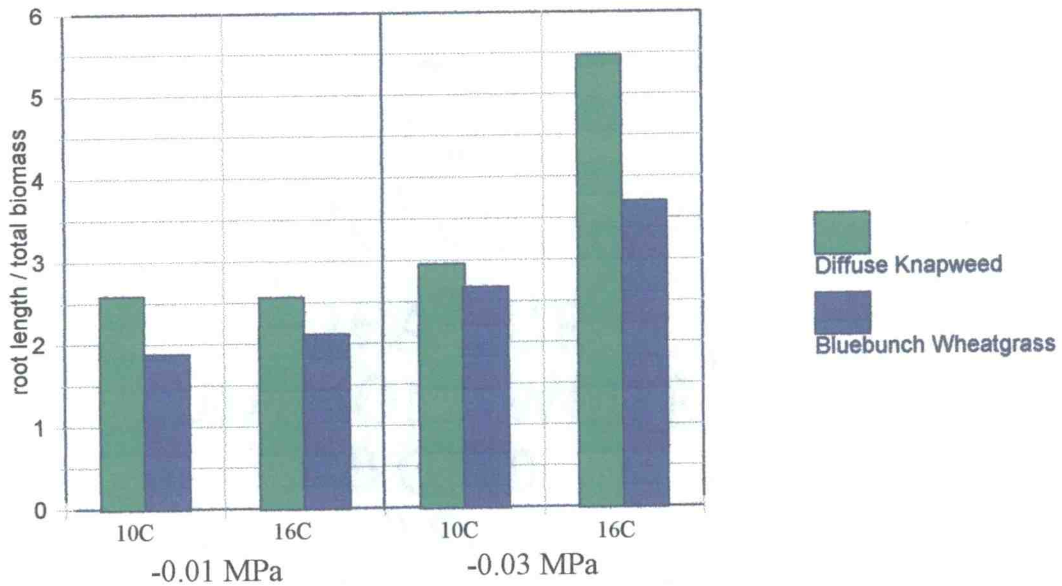

Figure 3. Efficiency of diffuse knapweed (DK) and bluebunch wheatgrass (BB) root length at 40 days.

Conclusions

Rooting characteristics influence the competitive effectiveness of range plants (Johnson and Aguirre 1991). In many situations, resource preemption is determined primarily by rapid germination and root growth (Harper, 1977). Results from this study indicate that root penetration plays an important role in the ability of diffuse knapweed seedlings to successfully compete with perennial bunchgrass seedlings. This result is due in part to the tap root growth habit of diffuse knapweed which resulted in deeper root penetration than bluebunch wheatgrass starting at day 20 when grown under moist soil conditions. Bluebunch wheatgrass seedlings, while exhibiting greater root length, root biomass and higher root to shoot ratios, were unable to penetrate the soil at the rate of diffuse knapweed.

Plummer (1943) suggested that the root length of bunchgrasses may play a role in their competitive ability while in the seedling stage. Bluebunch wheatgrass seedlings grew numerous thick, fleshy, adventitious roots in the upper soil profile under moist growing conditions, while a singular seminal root extended into the lower soil profile under dry soil conditions. However, regardless of this apparent change in root morphology, there were no general trends in root length associated with moisture treatment.

These apparent rooting differences may not benefit bluebunch wheatgrass when competing against diffuse knapweed on deep soils with uniform or increasing resource availability at depth. Data from this study would suggest that additional moisture and warmth in the spring will result in deeper penetration by diffuse knapweed in comparison with bluebunch wheatgrass, resulting in greater resource access on into the summer months. These conclusions are supported by Berube and Myers (1982) and Sheley et al. (1997), which state that above normal precipitation in early season will likely contribute to successful establishment of diffuse knapweed onto rangelands. Furthermore, our results support Sauer and Uresk's (1976) conclusion that several years of above average yearly rainfall should favor seasonally late growing *Centaurea* species, providing increased biomass response and subsequently greater seed production (Schirman 1981).

Research by Poorter and Remkes (1990) indicate that faster growing species, given ideal conditions, tend to maximize shoot functioning while slower growing species generally maximize root functioning. Diffuse knapweed consistently produced more leaf area and than bluebunch wheatgrass at field capacity on later harvest dates, likely resulting from potentially quicker resource acquisition and growth rates under these conditions. By comparison, bluebunch wheatgrass growth response to the temperature and moisture conditions studied was to develop more roots than shoots.

Schirman (1981) noted a four-fold increase in diffuse knapweed seed production observed with above-normal precipitation compared with below-normal precipitation. Furthermore, Sheley and Larson (1994b) observed a reduction in seed output with yellow starthistle during dry spring conditions while an increase was evident with moist spring conditions.

Our results indicate that diffuse knapweed would be able to reach the threshold number of leaves (i.e 13 leaves [Thompson and Stout 1990]) , and the subsequent termination of the juvenile growth stage quicker when grown in warm/wet conditions than when grown in cool/dry conditions.

Among other performance advantages of *Centaurea* species, Larson et al. (1997) listed the rate of growth, which resulted in increased sequestering of resources for knapweeds, while decreasing limited resources for other species. Resource preemption is often determined by the speed of germination as well as the rate of root growth (Harper 1977, Harris 1967). Diffuse knapweed germinates much quicker than bluebunch wheatgrass (under 30 hrs vs. over 72 hrs, pers. observ.).

In addition, we have supplied supportive evidence of resource preemption, expressed through efficiency indices. These indicate diffuse knapweed is apparently more efficient than bluebunch wheatgrass at producing the competitive attributes of root penetration, leaf area and root length.

Taken as a whole, growth attributes of diffuse knapweed appear to be more competitive than bluebunch wheatgrass under all moisture and temperature regimes. A possible exception may be the lack of significant differences between species at 40 days when grown under drier soil conditions, although efficiency indices do not necessarily support this association.

Bluebunch wheatgrass appears to be least competitive with diffuse knapweed when grown under cooler temperatures. Waiting until later into the spring when temperatures are optimal for bluebunch seedling germination and growth may increase success with rangeland revegetation projects, although it is imparitive for resource managers to note that warmer conditions also favor diffuse knapweed growth. Once again, this underscores the need for knapweed control prior to bunchgrass seeding onto rangelands.

Nelson et al. (1970) found that successful establishment of seeded bunchgrasses is related to the rate of root penetration into the soil profile. Our results and others (Sheley et al. 1993, Larson and McInnis 1989) indicate that rapid germination combined with rapid root penetration allows the preemption of moisture and other nutrients from the rooting zone of bluebunch wheatgrass, allowing the successful establishment of *Centaurea* species onto bluebunch wheatgrass sites.

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APPENDICES

Appendix A1. Root:shoot ratios for diffuse knapweed and bluebunch wheatgrass as affected by temperature differences (interactions).(no significant differences)

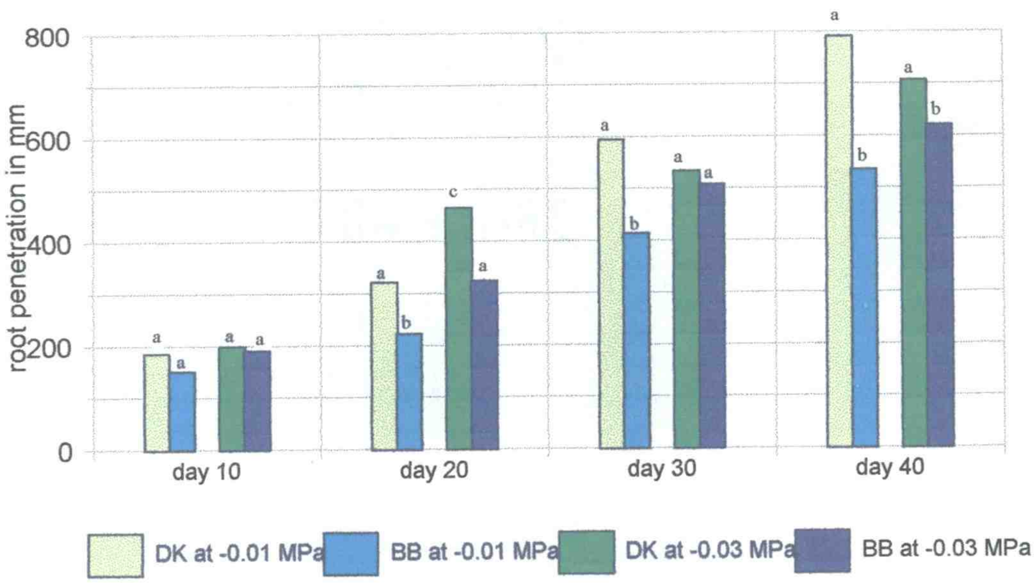
	10C		16C		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	----------mg mg^{-1}----------				
10	.49	1.04	.62	.87	.60
20	.78	.90	.84	.78	.28
30	.99	1.87	.82	1.45	.41
40	.68	1.02	.8	1.13	.43

[1] Mean comparisons may be made along rows.

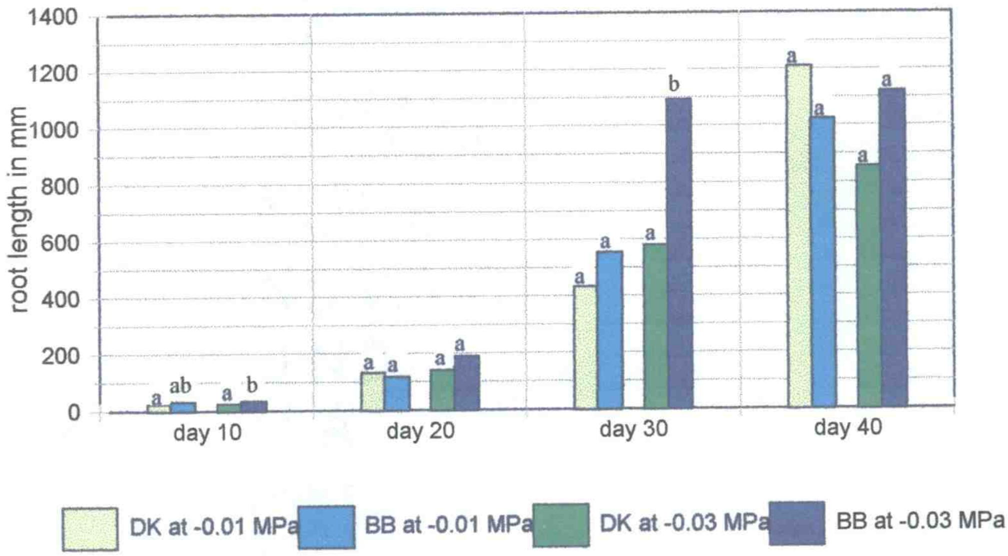
Appendix A2. Leaf biomass for diffuse knapweed and bluebunch wheatgrass as affected by moisture differences (interactions).(no significant differences)

	-0.01 MPa		-0.03 MPa		
Days from planting	Diffuse Knapweed	Bluebunch Wheatgrass	Diffuse Knapweed	Bluebunch Wheatgrass	LSD[1] (.05)
	---mg---				
10	3.69	4.58	3.31	4.25	1.67
20	20.76	22.76	12.21	20.37	9.92
30	106.06	89.23	68.29	66.04	30.3
40	288.91	218.88	87.90	168.06	146.72

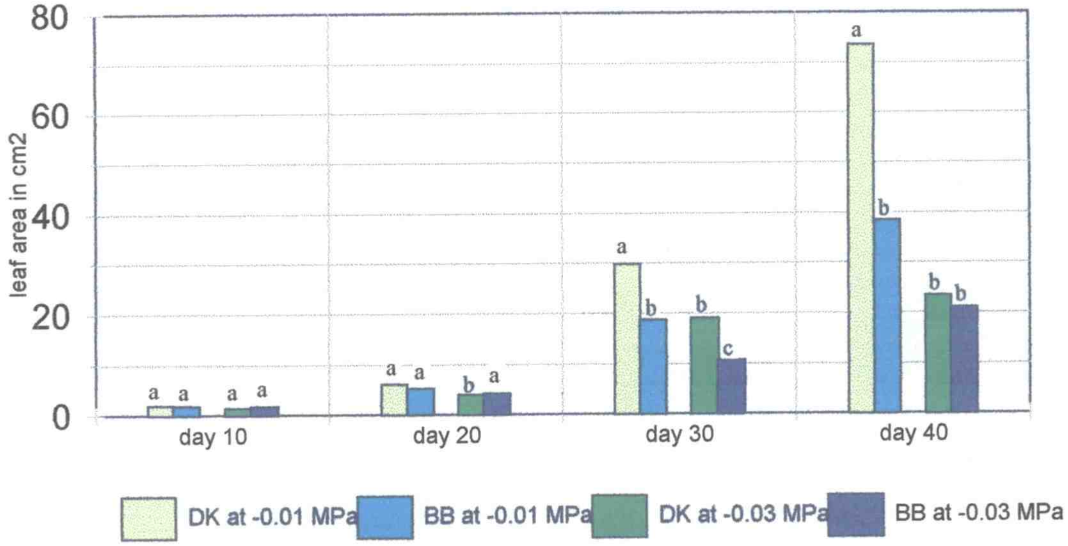
[1] Mean comparisons may be made along rows.



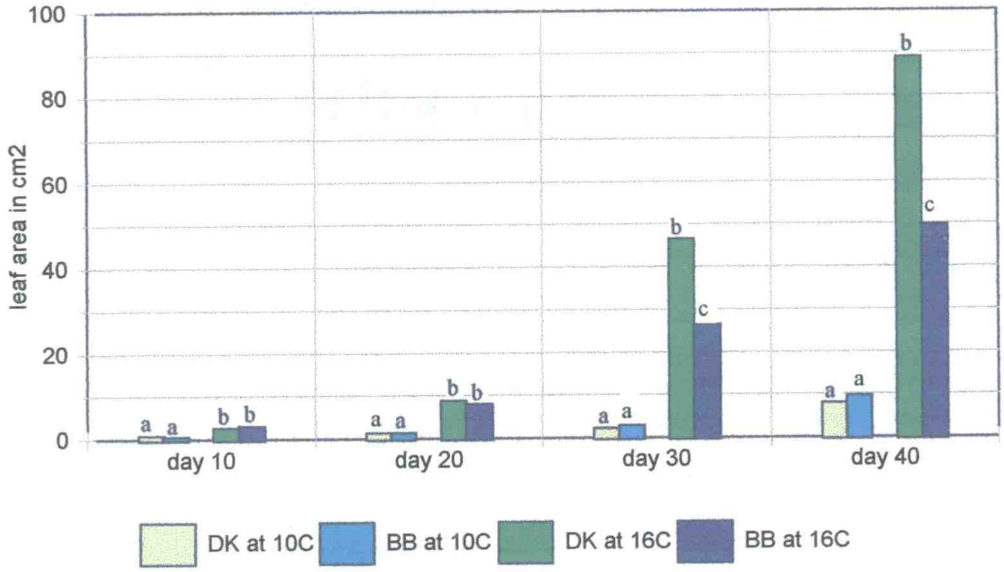
Appendix B1. Effects of moisture on diffuse knapweed (DK) and bluebunch wheatgrass (BB) root penetration. Different letters within harvest dates (day 10 - 40) are statistically significant ($p \leq 0.05$).



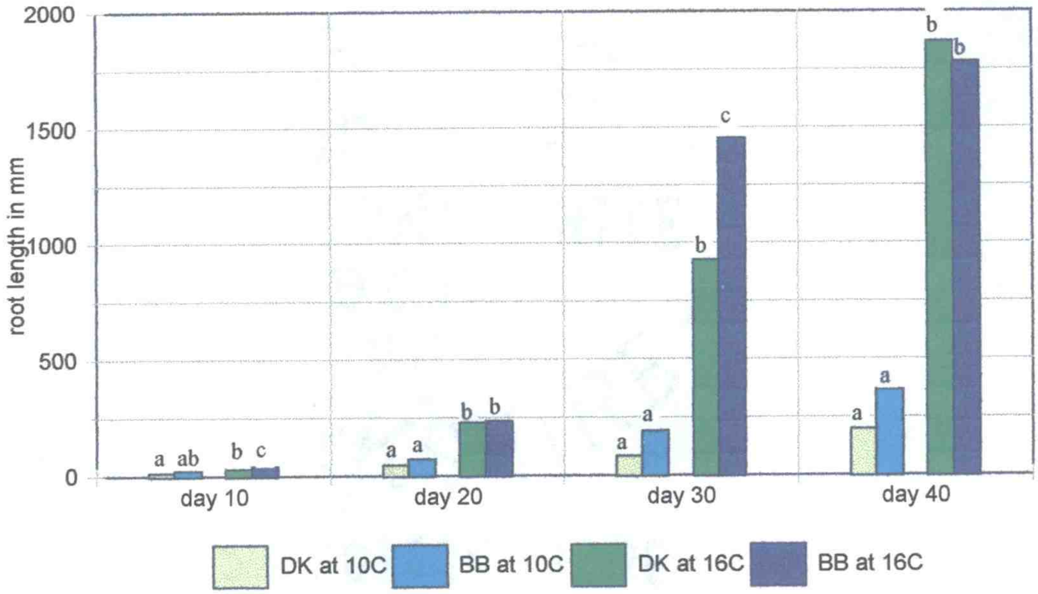
Appendix B2. Effects of moisture on diffuse knapweed (DK) and bluebunch wheatgrass (BB) root length. Different letters within harvest dates (day 10 - 40) are statistically significant ($p \leq 0.05$).



Appendix B3. Effects of moisture on diffuse knapweed (DK) and bluebunch wheatgrass (BB) leaf area. Different letters within harvest dates (day 10 - 40) are statistically significant ($p \leq 0.05$).



Appendix B4. Effects of temperature on diffuse knapweed (DK) and bluebunch wheatgrass (BB) leaf area. Different letters within harvest dates (day 10 - 40) are statistically significant ($p \leq 0.05$).



Appendix B5. Effects of temperature on diffuse knapweed (DK) and bluebunch wheatgrass (BB) root length. Different letters within harvest dates (day 10 - 40) are statistically significant (p≤0.05).