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Influence of density on intermediate wheatgrass and spotted knapweed interference

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Abstract

Establishing competitive plants is essential for restoring spotted knapweed infested grasslands. Revegetation attempts typically fail because of weed competition during the initial stages of establishment. We hypothesized that competitive interactions can be shifted from spotted knapweed to intermediate wheatgrass by increasing wheatgrass seedling density over 1,000 plants m^{-2}. Spotted knapweed and intermediate wheatgrass were grown in addition series mixtures to assess their interference at low (0 to 1,000 plants m^{-2}) versus high (1,000 to 10,000 plants m^{-2}) densities. In the spring of 1995, 7 densities (0, 100, 500, 1,000, 3,000, 6,000, and 10,000 plants m^{-2}) of each species were seeded in a factorial arrangement (49 density combinations) in a randomized-complete-block design and replicated 3 times at 2 sites in Montana. Plants were grown in pots (2,250 mm^2 × 380 mm deep) for 60 days before harvesting. Regressions predicting shoot weight, root weight, total weight, leaf area, and root length were calculated using 1) low knapweed:low wheatgrass, 2) low knapweed:high wheatgrass, 3) high knapweed:low wheatgrass, and 4) high knapweed:high wheatgrass densities. Regression coefficients indicated intraspecific interference was most important in predicting intermediate wheatgrass weight at both sites. At the wet site (457 mm, annually), interspecific interference only occurred at high spotted knapweed densities. At the dry site (305 mm, annually), interspecific interference occurred at low densities. Increasing intermediate wheatgrass from low to high densities removed the effect of spotted knapweed on intermediate wheatgrass where interspecific interference occurred.

Key Words: *Centaurea maculosa*, *Elytriga intermedia*, competitive shift, seeding rates, revegetation

Resúmen

El establecimiento de plantas competitivas es esencial a la restauración de las tierras de pastos plagadas de *Centaurea maculosa* Lam. Normalmente fracasan los esfuerzos de revegetación durante las etapas iniciales de establecimiento debido a competición de la mala hierba. Propusimos la hipótesis de que las interacciones competitivas pueden desplazarse de la *C. maculosa* al *Elytriga intermedia* (Host) Nevski al aumentar la densidad de plantones de *E. intermedia* a más de 1,000 plantas m^{-2}. *C. maculosa* y *E. intermedia* fueron cultivados en mezclas hechas de series de aumentación para evaluar su intromisión en las densidades bajas (0 a 1,000 plantas m^{-2}) en comparación con las densidades altas (1,000 a 10,000 plantas m^{-2}). En la primavera de 1995, 7 densidades (0, 100, 500, 1,000, 3,000, 6,000, y 10,000 plantas m^{-2}) de cada especie fueron sembradas en orden factorial (49 combinaciones de densidades) en un diseño de bloque completo al azar y reproducidas 3 veces en 2 sitios en Montana. Se cultivaron las plantas en potes (2,250 mm^2 × 380 mm de fondo) por 60 días antes de cosecharlas. Se calcularon las regresiones prediciendo el peso de los retoños y las raíces, el peso total, el área de las hojas, y la longitud de las raíces empleando las siguientes densidades: 1) baja de *C. maculosa*: baja de *E. intermedia*, 2) baja de *C. maculosa*: alta de *E. intermedia*, 3) alta de *C. maculosa*: baja de *E. intermedia*, y 4) alta de *E. intermedia*. Los coeficientes de regresión indicaron que la intromisión intraespecífica fue de mayor importancia a la predicción del peso *E. intermedia* de los dos sitios. En el sitio mojado, (457 mm, anualmente), la intromisión interespecífica ocurrió solamente en las densidades altas de *C. maculosa*. En el sitio seco (305 mm, anualmente), la intromisión interespecífica ocurrió en las densidades bajas. Al aumentar las densidades bajas de *E. intermedia* a densidades altas, se eliminó el efecto de la *C. maculosa* en el *E. intermedia* donde ocurrió la intromisión interespecífica.

Spotted knapweed (*Centaurea maculosa* Lam.) is a deeply taprooted perennial Eurasian weed rapidly invading rangeland throughout the northwestern United States and Canada (Watson and Renney 1974, Strang et al. 1979, Harris and Cranston 1979). Spotted knapweed has been spreading at about 27% per year and infests about 2.2 million hectares of grassland in Montana alone (Chicoine et al. 1985, Lacey et al. 1989). Knapweed infestations have been associated with reductions in forage production (Watson and Renney 1974, Harris and Cranston 1979), plant species diversity (Tyser and Key 1988) and wildlife habitat (Bedunah and Carpenter 1989) as well as increases in bareground (Tyser and Key 1988), surface water runoff, and stream sedimentation (Lacey et al. 1989).

Spotted knapweed is well-adapted to a wide range of climatic and environmental conditions (Watson and Renney 1974, Chicoine et al. 1985). This weed is a strong competitor and relatively drought tolerant (Berube and Myers 1982). It has high seed output and longevity, which enables regeneration after herbicidal control (Watson and Renney 1974, Schirman 1981, Davis et al. 1993, Kalisz and McPeek 1993). Early germination and rapid

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growth rates enable knapweeds (*Centaurea* spp.) to capture resources before their competitors (Sheley et al. 1993). Knapweeds display germination and emergence polymorphism, which allows them to avoid intraspecific competition and occupy all available safe-sites by developing an hierarchy of age classes within the population (Sheley and Larson 1996).

In areas where residual plant species are absent, herbicides (Davis et al. 1993, Griffith and Lacey 1991), natural enemies (Story et al. 1991, Cuda et al. 1989), or sheep grazing (Olson et al. 1997) do not provide long-term control of spotted knapweed because desirable species are not available to occupy niches opened by the control procedure. In these areas, establishing competitive plants is essential for successional management of spotted knapweed and the restoration of desirable plant communities (Sheley et al. 1996). Revegetation with aggressive species has been shown to inhibit re-invasion by knapweeds (Hubbard 1975, Larson and McInnis 1989).

Typically, revegetation of spotted knapweed-infested rangeland involves late-fall discing and application of a non-selective herbicide, such as glyphosate (n-phosphomethyl glycine), after weeds emerge. Desirable grasses are immediately seeded. Grass and knapweed germination and emergence occurs the following spring. As long as there is adequate spring precipitation, both grass and knapweed seedlings survive. If grass seedlings survive until mid-summer, a reduced rate of 2,4-D (2,4-diclorophenoxy acetic acid) or mowing is usually applied to weaken spotted knapweed. Rehabilitation with desirable vegetation typically fails because of weed competition during these initial stages of establishment (Borman et al. 1991).

It is widely accepted that rangeland weeds are more competitive than perennial grass seedlings (Harris 1967, Prather and Callihan 1991). For example, Prather and Callihan (1991) found that yellow starthistle (*Centaurea solstitialis* L.) was more competitive than pubescent wheatgrass [*Thinopyrum intermedium* spp. *barbulatum* (Schur) Barkw. & D. R. Dewey] at densities up to 390 plants m^{-2}. They also found the aggressiveness of pubescent wheatgrass increased with increasing wheatgrass densities. In a growth chamber, Jacobs et al. (1996) found that bluebunch wheatgrass was 4 times more competitive than spotted knapweed seedlings at densities considered high for seedings (1,000–5,000 plants m^{-2}). Although crop-weed interactions at agronomic planting densities have been widely studied, very little is known about interference at extremely high densities (Zimdall 1980).

The overall objective of this study was to determine the potential of using plant density as a tool to facilitate the establishment of desirable grasses in spotted knapweed infested rangeland. Specific objectives were to 1) quantify the interference between intermediate wheatgrass (*Elytriga intermedia* (Host) Nevski) and spotted knapweed, and 2) compare the change in interference between these species at low versus high densities. We hypothesized that competitive interactions can be shifted from spotted knapweed to intermediate wheatgrass by increasing wheatgrass seedling density over 1,000 plants m^{-2}.

Materials and Methods

Study Sites

The study was conducted at 2 Montana State University research sites that occur within the Idaho fescue (*Festuca idahoensis* Elmer)-bluebunch wheatgrass habitat type (Daubenmire 1970). One site was at the Red Bluff Research Ranch (45° 34' N, 111° 40' W) located 8 km east of Norris, Mont. Elevation at the site is 1,500 m. Average annual precipitation is 305 mm. Site 2 was at the Arthur Post Research Farm (45° 41' N, 111° 9' W). This farm is located 6.5 km west of Bozeman, Mont. Elevation at this site is 1,463 m with an average annual precipitation of 457 mm. Precipitation and temperature were monitored within 4 miles of each site during the study period (Table 1).

Table 1. Precipitation and temperature at study sites.

Site	Period (1995)	Total precipitation	Mean temperature Min	Max
		(mm)	---- (°C)	----
Red Bluff	15 Jun. to 1 Jul.	13	12.5	14.2
	2 Jul. to 13 Jul.	23	16.1	18.0
	14 Jul. to 25 Jul.	6	16.2	18.5
	26 Jul. to 6 Aug.	13	18.7	20.9
	7 Aug. to 18 Aug.	27	14.6	16.5
	19 Aug. to 30 Aug.	25	16.6	18.8
Post Farm	20 Jun. to 5 Jul.	23	14.2	22.1
	6 Jul. to 17 Jul.	21	9.7	26.5
	18 Jul. to 29 Jul.	20	9.9	28.6
	30 Jul. to 10 Aug.	65	8.5	26.4
	11 Aug. to 22 Aug.	3	6.6	26.4
	23 Aug. to 3 Sep.	12	7.8	28.5

Environmental conditions were monitored daily. Twelve day values are presented during the study to correspond with harvest dates. Precipitation amounts are 12 day cumulative values.
Maximum and minimum temperatures are means for the designated time period.

Interference

Monocultures and mixtures of spotted knapweed and intermediate wheatgrass were grown to assess their interference using addition series methodology. Density series were 0:0, 0:100, 0:500, 0:1,000, 0:3,000, 0:6,000, 0:10,000, 100:0, 100:100, 100:500, 100:1,000, 100:3,000, 100:6,000, 100:10,000, 500:0, 500:100, 500:500, 500:1,000, 500:3,000, 500:6,000, 500:10,000, 1,000:0, 1,000:100, 1,000:500, 1,000:1,000, 1,000:3,000, 1,000:6,000, 1,000:10,000, 3,000:0, 3,000:100, 3,000:500, 3,000:1,000, 3,000:3,000, 3,000:6,000, 3,000:10,000, 6,000:0, 6,000:100, 6,000:500, 6,000:1,000, 6,000:3,000, 6,000:6,000, 6,000:10,000, 10,000:0, 10,000:100, 10,000:500, 10,000:1,000, 10,000:3,000, 10,000:6,000, 10,000:10,000 plants m^{-2} for spotted knapweed and intermediate wheatgrass, respectively. Density matrices were arranged in a randomized-complete-block design with 3 blocks (replications) at each site.

Seeds of spotted knapweed were collected from Deer Lodge County, Mont. in August 1989. 'Oahe' intermediate wheatgrass seeds were purchased from Circle S Seeds Inc., Three Forks, Mont. in March 1994. Seeds of intermediate wheatgrass and spotted knapweed were sown in plastic pots, each with 2,250 mm^2 soil surface area and 380 mm deep. Pots provided minimal rooting restriction to knapweed plants grown for a similar duration (Sheley and Larson 1994). Pots were filled with pasteurized soil mixture consisting of 2/3 Farland silt loam (fine silt, mixed Typic Agriboroll), and 1/3 sand. The soil was saturated with water and allowed to equilibrate to column capacity in the greenhouse and then transferred to each site.

Pots were placed underground with the soil surface in pots level to that of the surrounding area. Seeds were broadcast on the soil surface of each pot during 10 June through 14 June 1995 at

Red Bluff and 16 through 20 June 1995 at the Post Farm. Based on a preliminary emergence test, seeding densities were 2 times that of the desired plant densities. Seeds were manually arranged until a uniform distribution was achieved. Less than 2 mm depth of dry soil was used to cover seeds. Initially, pots were lightly watered and covered with clear plastic to ensure uniform seedling emergence. There was no additional watering. Plants were allowed to grow for 60 days.

Initial densities of spotted knapweed and intermediate wheatgrass were counted 1 week after emergence. Final harvesting involved manually shaking the dry soil from the roots, separating the species, and counting the number of plants of each species in each pot. Roots were cut from shoots, measured for total length (m) using a root length scanner (Comair Corp., Melbourne, Australia), dried to constant weight (48 hours, 600° C) and weighed (mg). Shoots and leaf material were scanned for surface area (cm^2) (Licor-3100 with conveyor belt, LI-COR, Inc. Lincoln, Neb.) and then dried to a constant weight and weighed (mg).

Addition series data were divided into low (0–1,000 plants m^{-2}) and high (1,000–10,000 plants m^{-2}) density matrices for each species. Data were transformed to their inverse and incorporated into multiple linear regression models (Spitters 1983). Coefficients of determination, sums of squares, and residuals were evaluated to determine the most suitable model. Regressions were calculated using 1) low knapweed:low wheatgrass, 2) low knapweed:high wheatgrass, 3) high knapweed:low wheatgrass, and 4) high knapweed:high wheatgrass densities.

Regressions predicted shoot weight, root weight, total weight, leaf area, and root length using harvest densities of spotted knapweed and intermediate wheatgrass as independent variables. Models were of the form:

$$w_s^{-1} = ß_{0s} + ß_{ss}N_s + ß_{si}N_i,$$
$$w_i^{-1} = ß_{0i} + ß_{ii}N_i + ß_{is}N_s,$$

where w_s and w_i were the average per plant growth response for spotted knapweed and intermediate wheatgrass, respectively, and N_s and N_i were their density. Regression coefficients $ß_{0s}$ and $ß_{0i}$ represent the inverse of the maximum response of each variable for an isolated individual for spotted knapweed and intermediate wheatgrass, respectively. Regression coefficients $ß_{ss}$ and $ß_{ii}$ and $ß_{si}$ and $ß_{is}$ represent intraspecific and interspecific competitive coefficient for spotted knapweed and intermediate wheatgrass, respectively.

The extra sums of squares procedure was used to compare slopes generated using each density matrix (Snedecor and Cochran 1980). For example, slopes generated from low spotted knapweed and intermediate wheatgrass densities were compared to slopes from low spotted knapweed and high wheatgrass densities. Coefficient of determination (R^2) values were calculated to indicate the proportion of the variability associated with the dependent variables that were accounted for by plant density.

Growth Analysis

Isolated plants of spotted knapweed and intermediate wheatgrass were grown in a randomized-complete block design (2 species, 5 harvest dates, 3 blocks). The study was initiated by broadcasting 15 seeds on the soils surface of each individual pot (15 × 15 cm; 38 cm deep). Seeds were sown, similar to that described above, on 15 June (Red Bluff) and 20 June 1995 (Post Farm). Plants were lightly watered and covered with plastic to facilitate seedling emergence and then thinned to a single individ-

Table 2. Regression coefficients predicting intermediate wheatgrass weight (mg) using harvest densities[1].

Density matrices	Dependent variable (W)	Post Farm				Red Bluff			
		$ß_{0i}$	$ß_{ii}$	$ß_{is}$	R_i^2	$ß_{0i}$	$ß_{ii}$	$ß_{is}$	R_i^2
Low_s	Total weight	0	60.0	0	0.78	308.5	60.8	10.7	0.81
Low_i		(NS)	(6.8)	(NS)		(74.7)	(4.8)	(4.3)	
	Shoot weight	0	91.6	0	0.71	412.8	98.5	19.9	0.73
		(NS)	(12.6)	(NS)		(150.7)	(9.8)	(8.7)	
	Root weight	0	190.0	0	0.49	1262.0	162.2	0	0.53
		(NS)	(39.2)	(NS)		(378.4)	(24.7)	(NS)	
Low_s	Total weight	0	49.8	0	0.75	0	63.9	0	0.98
$High_i$		(NS)	(7.8)	(NS)		(NS)	(3.7)	(NS)	
	Shoot weight	0	74.2	0	0.76	0	109.5	0	0.93
		(NS)	(12.0)	(NS)		(NS)	(10.7)	(NS)	
	Root weight	0	149.0	0	0.52	0	151.3	0	0.93
		(NS)	(33.1)	(NS)		(NS)	(14.5)	(NS)	
$High_s$	Total weight	427.1	50.7	3.4	0.67	0	0	0	0.87
Low_i		(139.5)	(9.7)	(0.9)		(NS)	(NS)	(NS)	
	Shoot weight	0	83.0	7.3	0.69	0	0	0	0.85
		(NS)	(15.6)	(1.5)		(NS)	(NS)	(NS)	
	Root weight	2710.0	108.0	0	0.24	0	0	0	0.89
		(640.0)	(44.5)	(NS)		(NS)	(NS)	(NS)	
$High_s$	Total weight	0	74.4	0	0.93	0	0	0	NS
$High_i$		(NS)	(7.0)	(NS)		(NS)	(NS)	(NS)	
	Shoot weight	0	102.7	0	0.78	0	0	0	NS
		(NS)	(16.4)	(NS)		(NS)	(NS)	(NS)	
	Root weight	0	253.9	0	0.82	0	0	0	NS
		(NS)	(43.9)	(NS)		(NS)	(NS)	(NS)	

[1]The model used was: $w_i^{-1} = ß_{0i} + ß_{ii}N_i + ß_{is}N_s$. Where w_i is the average per plant growth response for intermediate wheatgrass, and N_i is its density. Regression coefficients $ß_{0i}$, $ß_{ii}$ and $ß_{is}$ represent the inverse of the maximum response of each variable for an isolated individual, intraspecific competitive coefficient and the interspecific competition coefficient for intermediate wheatgrass, respectively.

Table 3. Extra sums of squares[1] comparing intermediate wheatgrass regression slopes generated for each density range.

Intermediate wheatgrass	Dependent variable	Low_s Low_i vs Low_s $High_i$		Low_s Low_i vs $High_s$ Low_i		Low_s Low_i vs $High_s$ $High_i$		Low_s $High_i$ vs $High_s$ Low_i		Low_s $High_i$ vs $High_s$ $High_i$		$High_s$ Low_i vs $High_s$ $High_i$	
		F cal	Fstat	F cal	Fstat	F cal	Fstat	F cal	Fstat	F cal	Fstat	F cal	Fstat
Post Farm	Total weight	42.7	4.08	1.49	3.21	1.84	1.78	4.13	1.74	0.39	3.01	11.0	2.95
	Shoot weight	42.6	4.08	1.34	3.21	2.19	1.77	3.65	1.73	0.26	3.01	12.8	2.93
	Root weight	42.1	4.08	-1.36	3.21	1.32	1.78	5.38	1.74	0.21	3.01	10.7	2.95
	Leaf area	32.5	4.08	11.50	3.21	2.74	1.77	2.31	1.73	-0.02	3.01	11.8	2.93
	Root length	43.4	4.08	2.75	3.21	3.07	1.78	2.38	1.74	-0.24	3.01	10.3	2.95
Red Bluff	Total weight	25.4	3.21	-0.03	3.23	NS	NS	0.29	2.65	NS	NS	NS	NS
	Shoot weight	21.3	3.21	-0.10	3.23	NS	NS	0.24	2.65	NS	NS	NS	NS
	Root weight	34.4	3.21	-0.80	3.23	NS	NS	0.39	2.65	NS	NS	NS	NS
	Leaf area	30.0	3.21	0.92	3.23	NS	NS	0.35	2.65	NS	NS	NS	NS
	Root length	390.0	2.21	-1.77	3.23	NS	NS	5.62	2.65	NS	NS	NS	NS

[1]Slopes were compared at P = 0.05.

ual 10 days after emergence. Harvest dates occurred on 12-day intervals beginning 16 days after planting. Final harvest occurred on 30 August (Red Bluff) and 3 September (Post Farm), 1995. Data collection followed procedures described in interference experiments. Data were analyzed using simple linear regression using time as the independent variable.

Emergence and Survivorship

Initial densities were fitted into simple linear regression models using seeding density as the independent variable. Similarly, harvest densities were fitted into linear regression models using initial density as the independent variable.

Results

Interference

Intermediate Wheatgrass

Intraspecific interference was most important in predicting intermediate wheatgrass weight at all densities at the Post Farm (Tables 2 and 3). Based on plant weight, regressions indicate that no interspecific interference occurred between spotted knapweed and intermediate wheatgrass at low spotted knapweed densities at this site. At high spotted knapweed and low wheatgrass densities, spotted knapweed reduced intermediate wheatgrass total and shoot weight. Effects of spotted knapweed were removed at high wheatgrass densities. At the Post Farm, regressions predicting intermediate wheatgrass leaf area and root length followed a similar pattern as that of weight (Tables 3 and 4).

Only models at low spotted knapweed densities were significant in predicting intermediate wheatgrass weight at Red Bluff (Tables 2 and 3). Intraspecific interference was most important at all densities, similar to that at the Post Farm. At low densities of both species, increasing spotted knapweed density reduced intermediate wheatgrass total and shoot weight. At high wheatgrass densities, the effects of spotted knapweed were removed on this site.

At low densities of both species, only intraspecific interference was associated with intermediate wheatgrass leaf area and root length at Red Bluff (Tables 3 and 4). At low spotted knapweed and high intermediate wheatgrass densities, spotted knapweed was most important in predicting intermediate wheatgrass leaf area. Density was not associated with root length at these densities at this site.

Table 4. Regression coefficients predicting intermediate wheatgrass leaf area (mm^2) and root length (cm) using harvest densities[1].

Density matrices	Dependent variable (W)	Post Farm $ß_{0i}$	Post Farm $ß_{ii}$	Post Farm $ß_{is}$	Post Farm R_i^2	Red Bluff $ß_{0i}$	Red Bluff $ß_{ii}$	Red Bluff $ß_{is}$	Red Bluff R_i^2
Low_s	Leaf area	0	0.01	0	0.73	0.97	0.13	0	0.54
Low_i		(NS)	(0.001)	(NS)		(0.31)	(0.02)	(NS)	
	Root length	0	0.38	0	0.69	2.64	0.33	0	0.31
		(NS)	(0.05)	(NS)		(1.25)	(0.08)	(NS)	
Low_s	Leaf area	0	0.13	0	0.65	2.23	0.09	0.14	0.97
$High_i$		(NS)	(0.02)	(NS)		(0.73)	(0.005)	(0.05)	
	Root length	0	0.31	0	0.37	28.55	0	0	0.07
		(NS)	(0.11)	(NS)		(9.07)	(NS)	(NS)	
$High_s$	Leaf area	0	0.01	0.01	0.64	0	0	0	0.53
Low_i		(NS)	(0.02)	(0.002)	(NS)	(NS)	(NS)		
	Root length	0	0.66	0	0.34	0	0	0	0.25
		(NS)	(0.24)	(NS)	(NS)	(NS)	(NS)		
$High_s$	Leaf area	0	0.12	0	0.52	0	0	0	NS
$High_i$		(NS)	(0.04)	(NS)	(NS)	(NS)	(NS)		
	Root length	0	0	0	0.33	0	0	0	NS
		(NS)	(NS)	(NS)	(NS)	(NS)	(NS)		

[1]The model used was: $V_i^{-1} = ß_{0i} + ß_{ii}N_i + ß_{is}N_s$; where V_i is the average per plant growth response for intermediate wheatgrass, and N_i is its density. Regression coefficients $ß_{0i}$, $ß_{ii}$ and $ß_{is}$ represent the inverse of the maximum response of each variable for an isolated individual, intraspecific competitive coefficient and the interspecific competition coefficient for intermediate wheatgrass, respectively.

Table 5. Regression coefficients predicting spotted knapweed weight (mg) using harvest densities[1].

Density matrices	Dependent variable (W)	Post Farm β_{0s}	Post Farm β_{ss}	Post Farm β_{si}	Post Farm R_s^2	Red Bluff β_{0s}	Red Bluff β_{ss}	Red Bluff β_{is}	Red Bluff R_s^2
Low_s	Total weight	29130.0	0	0	0.11	139740.0	0	0	0.07
Low_i		(15630.0)	(NS)	(NS)		(40370.0)	(NS)	(NS)	
	Shoot weight	0	0	0	0.11	147240.0	0	0	0.09
		(NS)	(NS)	(NS)		(47990.0)	(NS)	(NS)	
	Root weight	0	0	0	0.07	591510.0	0	0	0.04
		(NS)	(NS)	(NS)		(17994.0)	(NS)	(NS)	
Low_s	Total weight	0	0	0	0.07	204850.0	-4013.0	0	0.64
$High_i$		(NS)	(NS)	(NS)		(27990.0)	(1223.0)	(NS)	
	Shoot weight	0	0	0	0.05	238140.0	-6130.0	0	0.59
		(NS)	(NS)	(NS)		(36360.0)	(2080.0)	(NS)	
	Root weight	0	0	0	0.12	0	0	0	0.46
		(NS)	(NS)	(NS)		(NS)	(NS)	(NS)	
$High_s$	Total weight	0	51.9	0	0.27	0	0	0	0.04
Low_i		(NS)	(23.4)	(NS)		(NS)	(NS)	(NS)	
	Shoot weight	0	67.2	0	0.29	0	0	0	0.02
		(NS)	(27.1)	(NS)		(NS)	(NS)	(NS)	
	Root weight	0	0	0	0.08	0	0	0	0.31
		(NS)	(NS)	(NS)		(NS)	(NS)	(NS)	
$High_s$	Total weight	0	0	703.8	0.67	0	0	0	NS
$High_i$		(NS)	(NS)	(183.9)		(NS)	(NS)	(NS)	
	Shoot weight	0	0	805.1	0.68	0	0	0	NS
		(NS)	(NS)	(205.0)		(NS)	(NS)	(NS)	
	Root weight	0	0	5624.0	0.64	0	0	0	NS
		(NS)	(NS)	(1695.0)		(NS)	(NS)	(NS)	

[a]The model used was: $w_s^{-1} = \beta_{0s} + \beta_{ss}N_s + \beta_{si}N_i$; where ws is the average per plant growth response for spotted knapweed, and Ns is its density. Regression coefficients β_{0s}, β_{ss} and β_{si} represent the inverse of the maximum response of each variable for an isolated individual, intraspecific competitive coefficient and the interspecific competition coefficient for spotted knapweed, respectively.

Spotted Knapweed

At low spotted knapweed densities, models predicting spotted knapweed weight, leaf area, or root length were either non-significant or had a poor fit at the Post Farm (Tables 5, 6 and 7). At high spotted knapweed and low wheatgrass densities, only intraspecific interference was associated with spotted knapweed total and shoot weight. Intraspecific and interspecific interference was associated with spotted knapweed leaf area at these densities. At high densities of both species, wheatgrass density was most important in predicting spotted knapweed weight and leaf area at this site.

Regression models indicate that at low spotted knapweed densities and high wheatgrass densities, spotted knapweed increased its own weight at Red Bluff (Table 5 and 6). At these same densities, only wheatgrass density was associated with spotted knapweed leaf area (Table 6 and 7). All other regressions were either non-significant or poor fitting models.

Growth Analysis

Regressions predicting total plant weight over time indicate that intermediate wheatgrass grew 4 and 14 times faster than spotted knapweed at the Post Farm and Red Bluff, respectively (Table 8). Intermediate wheatgrass and spotted knapweed grew 2 and 7 times faster at the Post Farm than at Red Bluff. Other parameters followed a similar pattern to total weight.

Table 6. Extra sums of squares[1] comparing spotted knapweed regression slopes generated for each density range.

Intermediate wheatgrass	Dependent variable	Low_s Low_i vs Low_s $High_i$ F cal	Fstat	Low_s Low_i vs $High_s$ Low_i F cal	Fstat	Low_s Low_i vs $High_s$ $High_i$ F cal	Fstat	Low_s $High_i$ vs $High_s$ Low_i F cal	Fstat	Low_s $High_i$ vs $High_s$ $High_i$ F cal	Fstat	$High_s$ Low_i vs $High_s$ $High_i$ F cal	Fstat
Post Farm	Total weight	167.06	4.08	-12.27	3.21	0.95	1.77	15.8	1.73	0.55	3.01	8.10	2.93
	Shoot weight	40.80	4.08	-11.8	3.21	1.55	1.77	1.45	1.73	-1.64	3.01	8.02	2.93
	Root weight	45.90	4.08	-21.2	3.21	1.09	1.77	0.87	1.73	-1.66	3.01	7.60	2.93
	Leaf area	165.90	4.08	-4.6	3.21	0.82	1.77	7.79	1.73	-0.14	3.01	6.09	2.93
	Root length	60.50	4.09	-8.57	3.21	1.53	1.78	1.90	1.74	0.96	3.03	5.32	2.93
Red Bluff	Total weight	-2.49	3.23	39.5	3.26	NS	NS	2.06	3.04	NS	NS	NS	NS
	Shoot weight	9.74	3.21	36.4	3.23	NS	NS	1.62	2.65	NS	NS	NS	NS
	Root weight	-3.45	2.87	-8.47	3.29	NS	NS	0.01	3.35	NS	NS	NS	NS
	Leaf area	5.46	3.21	45.1	3.23	NS	NS	0.09	2.65	NS	NS	NS	NS
	Root length	-16.65	3.23	3.08	3.26	NS	NS	0.21	3.04	NS	NS	NS	NS

[1]Slopes were compared at P = 0.05.

Table 7. Regression coefficients predicting spotted knapweed leaf area (mm^2) and root length (cm) using harvest densities[1].

Density matrices	Dependent variable (W)	Post Farm β_{0i}	Post Farm β_{ss}	Post Farm β_{is}	Post Farm R_s^2	Red Bluff β_{0s}	Red Bluff β_{ss}	Red Bluff β_{is}	Red Bluff R_s^2
Low_s	Leaf area	0	0	0	0.06	94.73	0	0	0.02
Low_i		(NS)	(NS)	(NS)		(32.16)	(NS)	(NS)	
	Root length	356.6	0	0	0.07	2640.0	0	0	0.05
		(120.5)	(NS)	(NS)		(1240.0)	(NS)	(NS)	
Low_s	Leaf area	0	0	0	0.09	84.96	0	0.41	0.51
$High_i$		(NS)	(NS)	(NS)		(24.50)	(NS)	(0.17)	
	Root length	0	0	0	0.11	0	0	0	0.36
		(NS)	(NS)	(NS)		(NS)	(NS)	(NS)	
$High_s$	Leaf area	0	0.07	0.68	0.52	0	0	0	(0.02)
Low_i		(NS)	0.02	(0.24)		(NS)	(NS)	(NS)	
	Root length	0	0	0	0.19	0	0	0	0.06
		(NS)	(NS)	(NS)		(NS)	(NS)	(NS)	
$High_s$	Leaf area	0	0	0.62	0.48	0	0	0	NS
$High_i$		(NS)	(NS)	(0.24)		(NS)	(NS)	(NS)	
	Root length	441.2	0	0	0.36	0	0	0	NS
		(174.5)	(NS)	(NS)		(NS)	(NS)	(NS)	

[1]The model used was: $V_{.S.}^{-1} = \beta_{0s} + \beta_{ss}N_s + \beta_{si}N_i$; where $V_{.S.}$ is the average per plant growth response for spotted knapweed, and Ns is its density. Regression coefficients β_{0s}, β_{ss} and β_{si} represent the inverse of the maximum response of each variable for an isolated individual, intraspecific competitive coefficient and the interspecific competition coefficient for spotted knapweed, respectively.

Emergence and Survivorship

Regressions predicting initial density based on seeding rate indicated that 29 and 18% of the seeds emerged for spotted knapweed and intermediate wheatgrass, respectively, at the Post Farm. Conversely, 19 and 36% of knapweed and wheatgrass, respectively, emerged at Red Bluff.

Regression models predicting harvest densities using initial densities as the independent variable shows 83% of spotted knapweed plants survived to the end of the experiment, while 86% of the wheatgrass plants survived that period at the Post Farm. Only 13% of the initial spotted knapweed seedlings survived to the end of the experiment at Red Bluff, whereas 91% of the initial wheatgrass seedlings survived.

Discussion

Our study suggests that density-independent and density-dependent factors interact to determine seedling survival and competitiveness of spotted knapweed and to a lesser extent, intermediate wheatgrass. Weldon and Slauson (1986) proposed that R^2 values generated from addition series regressions indicate the degree to which interference is important to the success of the target species. R^2 for spotted knapweed at all density ranges, except high densities of both species, were below 0.29 at the Post Farm. In this case, we believe that competition was minimized by the high precipitation (Table 1). Once densities became high, competition became more important.

At the dryer site, Red Bluff, R^2 values ranged from 0.46 to 0.64 at low densities of spotted knapweed and high densities of intermediate wheatgrass. All other models had lower R^2. This suggests that enough soil moisture was available at lower densities to minimize interference. At higher densities of spotted knapweed, survivorship lines (Fig. 1) and R^2 values show that seedling mortality was high. Furthermore, growth rates of isolated spotted knapweed individuals were lower on this site than at the Post Farm.

Survivorship lines and R^2 values suggest that, in most situations, interference was important in determining the success of intermediate wheatgrass. In those cases, intraspecific competition accounted for most of the variation in the model. However, at high densities of both species under the dry conditions at Red Bluff, intermediate wheatgrass was influenced by other factors than density. A majority of intermediate wheatgrass individuals emerging survived to the end of the study.

Interference between species depends on their density, proportion, and spatial arrangement (Radosevich 1987). In a growth chamber study, Jacobs et al. (1996) found bluebunch wheatgrass to be more competitive than spotted knapweed at densities ranging from 1,000 to 5,000 plants m^{-2}. In our field study, increasing intermediate wheatgrass density removed the competitive influence of spotted knapweed under those condition where interspecific interference was significant. Our study suggests that the competitive balance between spotted knapweed and intermediate wheatgrass can be shifted from spotted knapweed by establishing high densities (> 1,000 plants m^{-2}) of wheatgrass under those conditions where interspecific interference occurs.

Table 8. Mean total weight, leaf area, shoot weight, root length, root weight per day for spotted knapweed and intermediate wheatgrass at Post Farm and Red Bluff.

Growth parameter	Post Farm Knapweed	Post Farm Wheatgrass	Red Bluff Knapweed	Red Bluff Wheatgrass
Plant weight (mgd^{-1})	40.5	162.5	5.8	81.6
	(11.66)	(22.33)	(2.08)	(11.66)
Leaf area (cm^2d^{-1})	2.73	7.68	0.44	4.37
	(0.53)	(0.98)	(0.17)	(0.53)
Shoot weight (mgd^{-1})	34.1	130.7	4.1	58.3
	(10.66)	(17.50)	(1.66)	(10.25)
Root length (md^{-1})	0.27	2.29	0.06	2.01
	(0.09)	(0.45)	(0.02)	(0.55)
Root weight (mgd^{-1})	6.0	31.6	1.6	22.5
	(1.66)	(6.66)	(0.75)	(5.33)

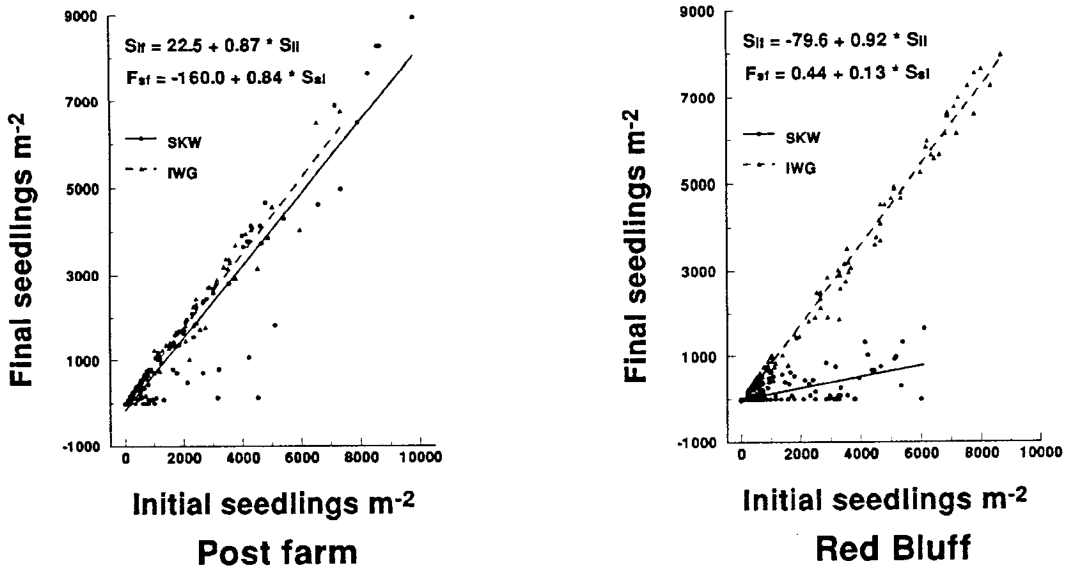

Fig. 1. Regression predicting spotted knapweed (SKW) and intermediate wheatgrass (IWG) survivorship.

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