J. Range Manage.
48:392–397 September 1995

Interference between cheatgrass and yellow starthistle at 3 soil depths

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Abstract

Cheatgrass (*Bromus tectorum* L.) and yellow starthistle (*Centaurea solstitialis* L.) have invaded over 250 thousand hectares throughout the Pacific Northwest. Future management of rangelands dominated by these species will require an understanding of the plant-plant interactions which contribute to the regulation of community dynamics and the establishment of desirable plants. Addition series experiments, with total stand densities ranging from 20–20,000 plants m^{-2}, were used to quantify the interference between cheatgrass and yellow starthistle in unrestricted soil depths on 12-day intervals throughout the growing season and in soil depths restricted to 0.2- and 0.5-m. Intraspecific interference was nearly twice as important as interspecific interference when plants were grown in unrestricted soil. Resource partitioning by cheatgrass and yellow starthistle was associated with rooting depth. When restricted to a 0.5-m depth, resource partitioning did not occur and intra- and interspecific interference were similar for both species. Restriction to a 0.2-m depth resulted in cheatgrass density being twice as important as yellow starthistle density for predicting yellow starthistle shoot weight. Yellow starthistle density was not important for predicting cheatgrass shoot weight. Cheatgrass appeared to have a competitive advantage over yellow starthistle in shallow soils, but the rooting depth and seed production capacity of yellow starthistle was greater than cheatgrass in deep soil.

Key Words: *Centaurea solstitialis, Bromus tectorum*, addition series, community dynamics, competition, rangeland weeds.

Yellow starthistle (*Centaurea solstitialis* L.) is a noxious weed that has been spreading in the steppe regions of the Pacific Northwest since about 1920 (Maddox and Mayfield 1985, Talbott 1987, Sheley et al. 1993). Much of the rangeland under invasion by yellow starthistle is dominated by cheatgrass (*Bromus tectorum* L.), an undesirable, yet forage yielding annual grass (Talbott 1987, Mack 1989, Hironaka 1989). Currently, yellow starthistle and annual grasses co-dominate over 250 thousand hectares in the Pacific Northwest, and yellow starthistle is estimated to be advancing at a rate of 7,800 and 2,800 ha year^{-1} in Washington and Idaho, respectively (Maddox and Mayfield 1985, Talbott 1987, Prather and Callihan 1991).

Developing control and rehabilitation methods for these rangelands is limited by our knowledge of the plant-plant interactions affecting cheatgrass and yellow starthistle community dynamics. In companion studies, we compared the life-histories of cheatgrass and yellow starthistle and the growth and interference between cheatgrass and yellow starthistle seedlings (Sheley and Larson 1994a, 1994b). In this study we used addition series methodology to: 1) quantify the effects of interference between cheatgrass and yellow starthistle on shoot weight and seed output, and 2) determine the effect of soil depth on the interference between these 2 species.

Materials and Methods

Field studies were conducted during 1992 in southeastern Washington (NW 1/4, SE 1/4, sec. 32, T. 6 N., R. 35 E.) to evaluate the interference between cheatgrass and yellow starthistle at various harvest dates and soil depths. The study site lies within the bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith=*Pseudoroegneria spicata* (Pursh) Scribn. & Smith)–Idaho fescue (*Festuca idahoensis* Elmer) habitat type (Daubenmire 1970). The soil is a Walla Walla silt loam (coarse-silty, mixed, mesic Typic Haploxeroll). The elevation of the site is about 320 m. Temperatures for the study area range from 45 to -34°C, with an average frost-free season of 170 days. Normal annual precipitation is about 380 mm with a bimodal distribution pattern with peaks during the winter and spring.

Temperature, precipitation, and evaporation were monitored daily from October 1991 through June 1992. Environmental data collected prior to the initiation of the study (October–February) are summarized monthly. Data collected during the study (March–June) are summarized on 12-day intervals corresponding with experimental harvest dates.

Interference Without Rooting Depth Restriction

Mixtures of cheatgrass and yellow starthistle were grown to assess the interaction between the 2 species under unlimited root-

Research was funded by the National Park Service Grant CA 9000800006-13.
Published as Oregon Agr. Exp. Tech. Paper No. 10296
Manuscript accepted 29 Dec. 1994.

ing depth conditions. Cheatgrass and yellow starthistle densities were arranged to provide an addition series (Spitters 1983, Radosevich 1987). The cheatgrass:yellow starthistle densities were 10:10, 10:100, 10:1,000, 10:10,000, 100:10, 100:100, 100:1,000, 100:10,000, 1,000:10, 1,000:100, 1,000:1,000, 1,000:10,000, 10,000:10, 10,000:100, 10,000:1,000, 10,000:10,000 plants m^{-2}. Seeds of cheatgrass and yellow starthistle were collected from the study site during August and September 1991. Seeds were sown in 0.5 m^2 circular plots on 29 February and 1 March 1992 to avoid winter seedling mortality. Seeds were randomly broadcast, then manually separated to achieve a uniform distance between seeds. Seeds were lightly (<2 mm) covered with soil. Plants were thinned to the proper densities 1 week after emergence. The lowest density was thinned over time to provide samples for each harvest date. Plots with densities of 10,000 plants m^{-2} did not require thinning. Treatments were replicated 4 times in a randomized-complete-block design (16 densities). An individual shoot of each species was harvested from each plot on 12-day intervals beginning 24 days after planting. Six individual shoots (1 at lowest density) of each species were harvested from each plot at the final harvest, which was 96 and 120 days after planting for cheatgrass and yellow starthistle, respectively. Total seed production per plant was counted. Harvested shoots were dried to a constant weight (48 hours, 60°C) and weighed (g).

Interference With Rooting Depth Restriction

In 2 experiments, monocultures and mixtures of cheatgrass and yellow starthistle were grown to assess the effects of soil depth on each species and the interaction between the 2 species. Monoculture densities were 10, 100, 1,000, and 10,000 plants m^{-2} for each species. Cheatgrass and yellow starthistle mixtures of 100:100, 100:1,000, 100:10,000, 1,000:100, 1,000:1,000, 1,000:10,000, 10,000:100, 10,000:1,000, 10,000:10,000 plants m^{-2} were arranged to provide an addition series (Spitters 1983, Radosevich 1987). Monocultures and mixtures were established with the rooting depth restricted to 0.2-m and 0.5-m by placing an 8 mil impermeable plastic liner (9 × 0.7 m) below the soil surface. All monoculture densities and addition series were replicated 4 times in a split-plot design with soil depth as whole plots and plant density as subplots (monocultures: 2 species, 2 depths, 4 densities; mixtures: 2 depths, 9 densities). Seeds were collected, broadcast, and plants were thinned as described above. Samples of 6 individual shoots (4 at lowest density) of each species were harvested from each subplot 72 days after planting. These shoots were dried to a constant weight (48 hours, 60°C) and weighed (g).

Plant Moisture Stress

Predawn xylem water potential (MPa) was measured on a representative plant from each plot in each experiment. Measurements were collected between 0100 and 0400 on 14 and 15 May 1992 using a pressure chamber (PMS Inc., Corvallis, Ore.). All cheatgrass individuals were in the 2–4 leaf stage, and all yellow starthistle individuals were rosettes. An equipment malfunction while collecting data in block 1 resulted in unreliable data. Data from blocks 2–4 were analyzed and presented.

Analysis

Addition series data were incorporated into multiple linear models using stepwise regression procedures (SPSS., Chicago, Ill.) of the form:

In monocultures:
$$W_c = B_{co} + B_{cc} \log N_c + B_{cd} D$$
$$W_y = B_{yo} + B_{yy} \log N_y + B_{yd} D, \text{ and}$$
In mixtures:
$$W_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y + B_{cd} D$$
$$W_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c + B_{yd} D$$

where W_c and W_y were the average shoot weight or seed number per plant for cheatgrass and yellow starthistle, respectively, N_c and N_y were cheatgrass and yellow starthistle density, and D was the soil depth. Scatterplots of the residual vs. the standardized predicted values were used to determine the homogeneity of variances and degree of model fit. T-tests ($p \leq 0.05$) were used to determine significance of the regression coefficients.

The regression coefficients B_{co} and B_{yo} estimate maximum shoot weight or seed output of an isolated individual. Regression coefficients B_{cc} and B_{yy} estimate intraspecific interaction, B_{cy} and B_{yc} estimate interspecific interaction, and B_{cd} and B_{yd} estimate importance of soil depth on the prediction of shoot weight. The model of interference without soil depth restriction did not include B_d regression coefficients. The coefficient ratios of $B_{cc}:B_{cy}$ and $B_{yy}:B_{yc}$ were used to determine the relative influence of a species on shoot weight. For example, a $B_{cc}:B_{cy}$ ratio of 2 indicated that cheatgrass had twice the impact upon itself in determining weight or seed output than yellow starthistle. A depth coefficient ratio was calculated by dividing B_d by the regression coefficient corresponding to intra- and interspecific interference for each equation.

The double ratio $[B_{cc}/B_{cy}:B_{yc}/B_{yy}]$ was used to assess the partitioning of resources between the 2 species (Spitters 1983, Connolly 1986, Joliffe 1988). The further the double ratio deviated from unity, the greater the degree of resource partitioning. The coefficient of determination (R^2) values were calculated to indicate the proportion of variability associated with W_c and W_y, which could be accounted for by N_c, N_y, and D.

Results

Environmental Conditions

Environmental conditions (temperature, precipitation, and evaporation) were monitored daily prior to and during the study (Table 1). About 195 mm of precipitation fell during the 5 months preceding the study, and 63 mm of precipitation was received during the 4 months of the study. By comparison, the 59-year average precipitation for the 4 month study period is 218 mm. Below average spring precipitation is expected to occur 4 times in a 10-year period, and the precipitation during the months of March, April, May, and June is predicted to be less than 15, 10, 10, and 5 mm respectively, once in 10 years. Months with the lowest and highest maximum mean temperatures were December (4.5°C) and June (34.7°C), respectively. There were several unusually warm (>19°C) days during March 1992. December and February minimum mean temperatures were below freezing.

Interference Without Rooting Depth Restriction

Intraspecific interference was about twice as important as interspecific interference for the prediction of shoot weight for both species when grown without rooting depth restriction (Tables 2 and 3). An inverse association began between plant density and cheatgrass shoot weight 48 days after planting (Table 2).

Table 1. Environmental conditions at the study site.[1]

Time period	Total precipitation	Total evaporation	Mean temperature max.	min.
	(mm)		(°C)	
Oct. 1991	50.5	_[2]	20.0	0.6
Nov.	79.8	_	8.4	1.1
Dec.	16.3	_	4.5	-0.6
Jan. 1992	18.8	_	8.1	0.2
Feb.	28.5	_	10.6	-0.2
12 Mar.	5.0	_	13.3	0.8
24 Mar.	3.6	_	18.0	1.2
5 Apr.	0.0	_	18.9	1.9
17 Apr.	22.4	27.2	17.1	5.2
29 Apr.	0.0	56.9	24.1	6.4
11 May	11.2	72.1	24.7	6.0
23 May	0.5	76.5	24.6	4.9
4 Jun.	6.4	87.9	29.4	14.4
16 Jun.	14.7	77.7	26.1	9.4
28 Jun.	1.7	114.6	34.7	15.9

[1]Environmental conditions were monitored daily. Monthly values are presented for the 5 months preceding the study. Twelve day values are presented during the study to correspond with harvest dates. Precipitation and evaporation amounts are cumulative values. Maximum and minimum temperatures are means for the designated time period.
[2]Evaporation data were not collected during months with a potential for freezing.

Cheatgrass growth ceased 96 days after planting with the predicted maximum weight of an isolated cheatgrass individual being 1.8 g. At that time, a 10-fold increase in cheatgrass and yellow starthistle density reduced the predicted cheatgrass shoot weight 0.32 g and 0.19 g, respectively.

An inverse association between yellow starthistle shoot weight and plant density was detected 36 days after planting (Table 3). Yellow starthistle growth ceased after 120 days with the predicted maximum size of an isolated individual being 17.2 g. At 120 days, a 10-fold increase in yellow starthistle and cheatgrass density reduced the predicted yellow starthistle shoot weight 3.6 and 1.5 g, respectively. The B_{yy}:B_{yc} ratio at the 108 and 120 days after planting, indicate that intraspecific interference by yellow starthistle continued after cheatgrass growth ceased.

Table 2. Multiple regression analysis[1] for the prediction of cheatgrass (W_c) shoot weight (g) using plant densities without soil depth restriction.[2]

Days after planting	B_{co}	B_{cc}	B_{cy}	B_{cc}/B_{cy}	R^2
24	No significant variables				
36	No significant variables				
48	0.3 (0.05)	-0.05 (0.01)	-0.03 (0.01)	1.96	0.29
60	0.7 (0.07)	-0.14 (0.02)	-0.05 (0.01)	2.50	0.55
72	0.9 (0.08)	-0.15 (0.02)	-0.09 (0.01)	1.55	0.62
84	1.6 (0.17)	-0.31 (0.05)	-0.14 (0.03)	2.16	0.55
96	1.8 (0.19)	-0.32 (0.05)	-0.19 (0.04)	1.68	0.56

[1]$W_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$
[2]The intercept B_{co} estimated the shoot weight of an isolated cheatgrass plant. Intraspecific interference for cheatgrass is measured by the regression coefficient B_{cc} and interspecific interference by B_{cy}. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 3. Multiple regression analysis[1] for the prediction of yellow starthistle (W_y) shoot weight (g) using plant densities without soil depth restriction.[2]

Days after planting	B_{yo}	B_{yy}	B_{yc}	B_{yy}/B_{yc}	R^2
24	No significant variables				
36	0.01 (0)	-0.01 (0)	-0.01 (0)	1.50	0.22
48	0.4 (0.10)	-0.09 (0.03)	— —	—	0.15
60	0.6 (0.08)	-0.10 (0.02)	-0.06 (0.02)	1.63	0.42
72	1.9 (0.33)	-0.38 (0.09)	-0.17 (0.07)	2.18	0.35
84	4.6 (0.67)	-0.94 (0.19)	-0.43 (0.14)	2.21	0.44
96	5.5 (0.74)	-1.05 (0.20)	-0.56 (0.15)	1.88	0.47
108	7.4 (1.45)	-1.56 (0.40)	-0.56 (0.29)[3]	2.77	0.29
120	17.2 (2.52)	-3.57 (0.70)	-1.46 (0.51)	2.44	0.43

[1] $W_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$
[2] The intercept B_{yo} estimated the shoot weight of an isolated yellow starthistle plant. Intraspecific interference for yellow starthistle is measured by the regression coefficient B_{yy} and interspecific interference by B_{yc}. Numbers in parentheses are standard errors for coefficients significantly different from zero.
[3] $p = 0.06$

Intraspecific interference influenced seed output (Table 4). The maximum predicted output of an isolated cheatgrass and yellow starthistle plant was about 22 and 1,446 seeds per individual, respectively. The regression model predicts a reduction of about 100 and 300 yellow starthistle seeds per individual with 10-fold increases in cheatgrass and yellow starthistle density, respectively. The same increase in cheatgrass and yellow starthistle density reduced cheatgrass seed production 4 and 2 seeds per individual, respectively.

The double ratio [B_{cc}/B_{cy}:B_{yc}/B_{yy}] ranged from 2.9 to 4.8 with respect to shoot weight and was 5.4 based on seed output (Table 5). These results indicate that resource partitioning between

Table 4. Multiple regression analysis[1] for the prediction of cheatgrass (SP_c) and yellow starthistle (SP_y) seed production using plant densities, without soil depth restriction.[2]

Dependent variable	B_{co}	B_{cc}	B_{cy}	B_{cc}/B_{cy}	R^2
SP_c	22 (4)	-4 (1)	-2 (1)	1.7	0.35
SP_y	1,446 (216)	-312 (60)	-99 (44)	3.1	0.42

[1] $SP_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$
$SP_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$
[2] The intercept B_{co} and B_{yo} estimated the seed production of an isolated plant. Intraspecific interference is measured by the regression coefficient B_{cc} and B_{yy} and interspecific interference by B_{cy} and B_{yc}. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 5. Double ratio $[B_{cc}/B_{cy}:B_{yc}/B_{yy}]$ assessing the resource partitioning[1] between cheatgrass and yellow starthistle based on shoot weight (g) and seed production when grown without soil depth restriction.

Days after planting	Resource partitioning ratio
24 (weight)	—
36 (weight)	—
48 (weight)	2.9
60 (weight)	4.1
72 (weight)	3.4
84 (weight)	4.8
96 (weight)	3.2
108 (weight)	_[2]
120 (weight)	_[2]
120 (seed production)	5.4

[1]Resource partitioning were only calculated when B coefficients were significant. Ratios other than unity indicate the occurrence of resource partitioning.
[2]Growth of yellow starthistle after cheatgrass matured.

cheatgrass and yellow starthistle occur throughout the growing season. The coefficient of determination (R^2) was 0.56 and 0.43 for cheatgrass and yellow starthistle, respectively at their final harvest dates (Tables 2 and 3).

Interference With Rooting Depth Restriction

Monocultures

Regression analysis for both species indicate that soil depth was nearly 5 times more important than intraspecific interference in the prediction of shoot weight 72 days after planting (Table 6). Increased density reduced predicted shoot weight, whereas additional soil depth increased shoot weight. About 70% of the variation in yellow starthistle shoot weight was accounted for by soil depth and density variables.

Mixtures

Regression models ($W_c = 0.570 - 0.122 \log N_c - 0.095 \log N_y + 0.612D$, $R^2 = 0.44$; $W_y = 0.456 - 0.091 \log N_y - 0.102 \log N_c + 0.778D$, $R^2 = 0.38$) incorporating cheatgrass density, yellow starthistle density and soil depth indicate that cheatgrass density was more important than yellow starthistle density in predicting shoot weight. Soil depth had 5 and 7 times the effect of density on predicting cheatgrass and yellow starthistle shoot weight, respectively.

Table 6. Multiple regression analysis[1] for the prediction of cheatgrass (W_c) and yellow starthistle (W_y) shoot weight (g) using monoculture plant densities and soil depth restriction.[2]

Dependent variable	B_{co}	B_{cc}	B_{cd}	B_{cd}/B_{cc}	R^2
W_c =	0.6	-0.3	1.4	4.7	0.35
	(3.8)	(1.0)	(0.8)		
	B_{yo}	B_{yy}	B_{yd}	B_{yd}/B_{yy}	R^2
W_y =	0.9	-0.4	2.0	5.1	0.72
	(3.8)	(1.0)	(0.8)		

[1]$W_c = B_{co} + B_{cc} \log N_c + B_{cd} D$
$W_y = B_{yo} + B_{yy} \log N_y + B_{yd} D$
[2]The intercepts B_{co} and B_{yo} estimate the shoot weight of an isolated individual. Intraspecific interference for cheatgrass and yellow starthistle are measured by the B_{cc} and B_{yy} coefficients. The impact of soil depth is expressed by the B_{cd} and B_{yd} coefficients. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 7. Multiple regression analysis[1] for the prediction of cheatgrass (W_c) shoot weight (g) using cheatgrass and yellow starthistle densities and soil depth restriction.[2]

Independent variable held constant	B_{co}	B_{cc}	B_{cy}	B_{cd}	Coefficient ratio	R^2
Depth (0.2 m)	0.1	-0.02	—	—	—	0.38
	(0.02)	(0.01)	—			
Depth (0.5 m)	1.4	-0.22	-0.18	—	1.2	0.58
	(0.18)	(0.04)	(0.04)			
Cheatgrass 100 plants m^{-2}	0.3	—	-0.17	1.35	7.7	0.59
	(0.15)	—	(0.04)	(0.24)		
Cheatgrass 1,000 plants m^{-2}	0.1	—	-0.02	0.47	20.4	0.87
	(0.02)	—	(0.01)	(0.03)		
Cheatgrass 10,000 plants m^{-2}	0.1	—	—	0.02	—	0.16
	(0.01)	—	—	(0.01)		
Starthistle 100 plants m^{-2}	0.4	-0.19	—	1.26	6.7	0.57
	(0.16)	(0.04)	—	(0.25)		
Starthistle 1,000 plants m^{-2}	0.2	-0.08	—	0.45	5.3	0.75
	(0.05)	(0.01)	—	(0.08)		
Starthistle 10,000 plants m^{-2}	0.1	—	—	0.12	—	0.20
	(0.01)	—	—	(0.05)		

[1] $W_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y + B_{cd} D$
[2] The intercept B_{co} estimates the weight of an isolated individual. Intraspecific interference by cheatgrass was measured by B_{cc} and interspecific interference by yellow starthistle by B_{cy}. The impact of soil depth restriction was estimated by B_{cd}. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Analysis of variance comparisons (data not shown) of shoot weight indicate a significant 3-way interaction (depth × cheatgrass density × yellow starthistle density) for both species at 72 days after planting. Intraspecific and interspecific interference were about equal in their importance for the prediction of cheatgrass and yellow starthistle shoot weight at the 0.5-m soil depth (Tables 7 and 8).

At 0.2-m soil depth, the maximum predicted shoot weight of isolated cheatgrass and yellow starthistle individuals were 0.1 g (Tables 7 and 8). An increase in cheatgrass density from 100 to 1,000 plants m^{-2} reduced the predicted cheatgrass and yellow starthistle shoot weight by 0.02 g. The same increase in yellow starthistle density reduced the predicted starthistle shoot weight by 0.01 g. Yellow starthistle density was not associated with cheatgrass shoot weight.

At all density combinations, the importance of soil depth for the prediction of shoot weight for either species was greater than that of plant density (Tables 7 and 8). In general, as the density of cheatgrass increased, the relative importance of soil depth increased.

When yellow starthistle density was held constant at 100 plants m^{-2}, the importance of soil depth was about 6 times greater than the effects of interference in predicting shoot weight (W_c and W_y) for both species (Tables 7 and 8). The importance of soil depth was about 5 times the effects of interference in predicting shoot weight of both species when yellow starthistle density was held at a constant 1,000 plants m^{-2}. At either a constant cheatgrass or yellow starthistle density of 10,000 plants m^{-2}, soil depth was more important than interference for predicting cheatgrass or yellow starthistle shoot weight.

Table 8. Multiple regression analysis[1] for the prediction of yellow starthistle (W_y) shoot weight (g) using plant densities and soil depth restriction.[2]

Independent variable held constant	B_{yo}	B_{yy}	B_{yc}	B_{yd}	Coefficient ratio	R^2
Depth (0.2 m)	0.1	-0.01	-0.02	—	0.5	0.48
	(0.02)	(0.01)	(0.01)	—		
Depth (0.5 m)	1.8	-0.25	-0.25	—	1.0	0.54
	(0.25)	(0.06)	(0.06)	—		
Starthistle 100 plants m^{-2}	0.5	—	-0.29	1.89	6.6	0.56
	(NS)	—	(0.08)	(0.46)		
Starthistle 1,000 plants m^{-2}	0.2	—	-0.09	0.52	5.9	0.66
	(0.07)	—	(0.02)	(0.11)		
Starthistle 10,000 plants m^{-2}	0.1	—	-0.02	0.12	7.3	0.60
	(0.02)	—	(0.01)	(0.03)		
Cheatgrass 100 plants m^{-2}	0.6	-0.30	—	1.59	5.3	0.54
	(0.31)	(0.08)	—	(0.46)		
Cheatgrass 1,000 plants m^{-2}	0.1	-0.09	—	0.67	7.7	0.75
	(0.07)	(0.02)	—	(0.10)		
Cheatgrass 10,000 plants m^{-2}	—	—	—	0.07	—	0.62
	—	—	—	(0.01)		

[1] $W_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c + B_{yd} D$
[2] The intercept B_{yo} estimates the weight of an isolated individual. Intraspecific interference by yellow starthistle was measured by B_{yy} and interspecific interference by cheatgrass by B_{yc}. The impact of soil depth restriction was estimated by B_{yd}. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Plant Moisture Stress

The predawn xylem water potentials associated with unrestricted soil depth indicate that juvenile (2–4 leaf) cheatgrass plants were under greater (t-test; $p \leq 0.0001$) moisture stress than juvenile (rosette) yellow starthistle plants (–1.27 vs –0.71 MPa). Regression models for individual species indicate that intraspecific interference increased moisture stress in both cheatgrass and yellow starthistle ($-PP_c = -1.0 - 0.11 \log N_c$, $R^2 = 0.25$; $-PP_y = -0.52 - 0.1 \log N_y$, $R^2 = 0.43$).

Cheatgrass xylem water potential was lower (t-test; $p \leq 0.05$) than yellow starthistle when grown with a 0.5-m soil depth restriction at cheatgrass:starthistle densities of 10:10 (-2.6 vs -2.9 MPa) and 1,000:10 (–2.4 vs –3.3 MPa). Regression models for each species indicate that intra- and interspecific interference increased moisture stress ($-PP_c = -1.87 - 0.40 \log N_c - 0.54 \log N_y$, $R^2 = 0.56$; $-PP_y = -2.0 - 0.51 \log N_y - 0.36 \log N_c$, $R^2 = 0.54$) and that yellow starthistle density was most important in both cases. The predicted pressure potential for an isolated cheatgrass and yellow starthistle individual grown in moderately deep soil was about 2 and 4 times more negative than in unrestricted soil, respectively.

Cheatgrass and yellow starthistle xylem water potentials exceeded –5.0 MPa when the soil depth restriction was 0.2-m. The only exception to this observation occurred with cheatgrass at the lowest density combination (–3.0 MPa).

Discussion

Cheatgrass and yellow starthistle populations are influenced by intraspecific more than interspecific interference when edaphic conditions provide unrestricted rooting depth. These results are consistent with those reported by Sheley and Larson (1994b) for cheatgrass and yellow starthistle seedlings. Ecologically, intraspecific interference is associated with self-thinning and the ability to capture resources (Aarssen 1983, Pyke and Archer 1991).

Regression models of seed output (Table 4) indicate that a community dominated by 10,000 yellow starthistle and 100 cheatgrass individuals m^{-2} will produce about 5 seeds per individual of cheatgrass, and yellow starthistle seed output would approach zero. If the densities were reversed, yellow starthistle predicted seed output would be 424 per individual, and cheatgrass predicted seed output would approach zero. These results suggest that dominance within annual communities can be influenced by intraspecific interference. In the case of cheatgrass and yellow starthistle the shift will be toward the species with the lower plant density and will be buffered by the composition of the soil seed bank.

Dakheel (1986) found that the competitive relationship between cheatgrass and medusahead (*Elymus caput-medusae* L.) was dependent on nutrient and moisture availability. In our study, the relationship between cheatgrass and yellow starthistle was influenced by soil depth. On deep soils, intraspecific interference was 2 times greater than interspecific interference for both species. On soils restricted to 0.5-m, the intensity of intraspecific and interspecific interference were nearly equal for both species. On shallow soils, restricted to 0.2-m, cheatgrass interference was 2 times greater than intraspecific interference in determining yellow starthistle shoot weight. However, interference from yellow starthistle did not affect cheatgrass shoot weight.

These results support the hypothesis that differential rooting depth is the mechanism for vertical and temporal resource partitioning between cheatgrass and yellow starthistle (Sheley et al. 1993, Sheley and Larson 1994b). The relatively shallow and fibrous rooting system of cheatgrass appeared to be better suited for resource capture in shallow soil. Conversely, yellow starthistle had an advantage over cheatgrass in deep soils where taproot development enabled continued resource uptake (e.g. soil moisture) and increased seed output when adequate deep moisture was available (Sheley et al. 1993, Sheley and Larson 1994a, Sheley and Larson 1994b). This study was conducted in a relatively dry environment (below average precipitation) which may have intensified the effect of soil depth on cheatgrass-yellow starthistle interactions.

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