

Comparative growth and interference between cheatgrass and yellow starthistle seedlings

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Abstract

Annual grasslands in the Pacific Northwest are being invaded by Eurasian weeds, such as yellow starthistle (*Centaurea solstitialis* L.). Plant-plant interactions influence community dynamics and plant establishment. The objectives of this study were to quantify the effects of interference between seedlings of cheatgrass (*Bromus tectorum* L.) and yellow starthistle and to compare growth of isolated individuals of these species. Isolated individuals and addition series mixtures with total stand densities ranging from 20-20,000 plants m⁻² were grown in an environmental chamber (10° C, 12-hour daylength). Individuals were harvested on 4-day intervals between 10 and 46 days, and mixtures were harvested 37 days after planting. Shoot weight, root weight, leaf area, and total root length of isolated individuals were similar. Yellow starthistle roots penetrated deeper into the soil than did cheatgrass roots 22 days after planting. Intraspecific interference was greater than interspecific interference for both species, and resource partitioning via rooting depth was evident. The yellow starthistle root:shoot ratio and the cheatgrass lower (below 200 mm); upper (above 200 mm) root ratio increased with increasing densities. Yellow starthistle and cheatgrass minimize interspecific interference as seedlings through differential growth and rooting depth. Invasion of cheatgrass rangelands by yellow starthistle increase resource partitioning and reduce our ability to revegetate rangelands by conventional means.

Key words: *Centaurea solstitialis*, *Bromus tectorum*, alien winter annuals, resource allocation and partitioning.

The loss of native perennial vegetation on North American rangelands has been accompanied by invasions of aggressive alien annual weeds. The grassland steppe of the Pacific Northwest, once dominated by native perennial grasses (e.g. bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Scribn and Smith)), now contain extensive areas dominated by annual grasses (e.g. cheatgrass (*Bromus tectorum* L.)) (Mack 1981).

Cheatgrass, a winter annual that matures early in the growing season, arrived from Eurasia well adapted to arid and semi-arid habitats, and expanded its range to include most grasslands in the Intermountain West (Mack 1981, Morrow and Stahlman 1984).

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Much of the success of cheatgrass has been attributed to rapid germination and growth (Hulbert 1955, Harris 1967, Svejcar 1990, Aguirre and Johnson 1991) at low soil temperatures and rather low water availability (Harris 1967, Aguirre and Johnson 1991, Johnson and Aguirre 1991).

Ecologists are concerned that these annual grass communities are in jeopardy of site occupation by noxious Eurasian weeds, such as yellow starthistle (*Centaurea solstitialis* L.) (Roché and Roché 1988, Callihan et al. 1989, Harris 1989, Hironaka 1989). Currently yellow starthistle is spreading onto grasslands in Washington and Idaho at an estimated 7,800 and 2,800 hectares per year, respectively (Talbot 1987, Callihan et al. 1989). Hironaka (1989) proposed that the sequence of species replacement among winter annuals in the Pacific Northwest would be from early maturing species to later maturing ones. In this scenario, cheatgrass would be replaced by the later maturing medusahead (*Taeniatherum asperum* Nevski) or yellow starthistle.

Knowledge that improves the management of plant community dynamics will improve our ability to revegetate degraded rangelands (Rosenberg and Freedman 1984, Lukan 1990). Investigations aimed at plant-plant interactions and the relationships which affect dominance, community dynamics, and plant establishment are critical to the development of these successional management systems (MacMahon 1987, Allen 1988, Call and Roundy 1991, Pyke and Archer 1991).

This study was conducted to develop an initial understanding of cheatgrass-yellow starthistle interactions. We used addition series methodology to quantify the effects of interference between cheatgrass and yellow starthistle seedlings, and compare the growth of isolated individuals of these species.

Materials and Methods

Interference

Monocultures and mixtures of cheatgrass and yellow starthistle seedlings were grown to assess interaction between the 2 species. Densities of cheatgrass and yellow starthistle 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 sown in 1,824 mm² (surface area) x 400 mm (depth) polyvinyl chloride tubes (split vertically and taped to a facilitate root removal). Tubes were filled with sterilized Walla Walla silt loam (coarse-silty, mixed, mesic Typic

Haploxeroll; A horizon) soil. Moisture was added to the soil and allowed to equilibrate to field capacity. No additional watering took place during the study. Seeds were broadcast then manually arranged until a uniform seed distribution was achieved. A small amount (<2 mm depth) of dry soil was used to cover the seeds. Tubes were arranged in a randomized-complete-block design with 4 replications and 16 tubes per block in an environmental chamber (10°C, 12-hour daylength, 500 uE m² sec⁻¹ spectral light). Plants were harvested 37 days after planting.

Sampling involved manually rinsing soil from roots and measuring primary root penetration. Five individual root systems for each species (2 root systems at lowest density) were extracted from each tube, separated from shoots, divided into upper (0-200 mm) and lower (>200 mm) portions, measured for total length (cm) using a root length scanner (Comair Corp., Melbourne, Australia), and then dried to a constant weight (48 hours, 60° C) and weighted (mg). Leaf material was scanned for surface area (cm²) (Licor-3100 with conveyor belt, LI-COR, Inc., Lincoln, Neb.), dried to a constant weight (48 hours, 60°C) and weighted (mg).

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

$$V_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$$

$$V_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$$

where V_c and V_y were the average per plant growth response for cheatgrass and starthistle, respectively, and N_c and N_y were their density. Regression coefficients B_{co} and B_{yo} estimate the maximum response of each variable for an isolated individual. Negative and/or nonsignificant intercepts are reported. They are considered to be estimates of values outside the range of the regression plane (Spitters 1983, Rejmanek et al. 1989), or random errors (Pantone and Baker 1991).

The regression coefficients B_{cc} and B_{yy} estimate intraspecific interaction, and B_{cy} and B_{yc} estimate interspecific interaction. The ratios $B_{cc}:B_{cy}$ and $B_{yy}:B_{yc}$ determine the relative influence of each species on the variable response. For example, a $B_{cc}:B_{cy}$ ratio of 2 suggests that cheatgrass has twice the influence upon itself in determining the variable response when compared to yellow starthistle. Zero was used for all non-significant coefficients in the regression model, and a constant of 0.0001 was used for ratio calculations (Roush 1988).

The $[B_{cc}/B_{cy}:B_{yy}/B_{yc}]$ double ratio was used to determine the partitioning of resources between species (Spitters 1983, Connolly 1986, Joliffe 1988). Deviations from unity indicate increased resource partitioning (niche separation). The coefficient of determination (R^2) values were calculated to indicate the proportion of the variability associated with the dependent variable (V_c or V_y) that was accounted for by plant density (N_c and N_y).

Scatterplots of the residuals vs. standardized predicted values were used to determine the homogeneity of variances and the degree of model fit. The t-tests ($P \leq 0.05$) were used to determine significance of regression coefficients.

Individual Growth of Isolated Plants

Seeds of cheatgrass and yellow starthistle were pregerminated and 4 seedlings were transplanted into polyvinyl chloride tubes for each of 10 harvest dates (46 days duration, 4 days harvest interval initiated on day 10). Tube surface area was increased with harvest date to insure minimal restriction of root growth (Table 1). Tube length was a constant 800 mm. Tubes were prepared following procedures described in the interference study. Tubes were arranged in a randomized-complete-block design with 5 replications and 10 tubes of

Table 1. Surface area of PVC tubes¹ at each harvest.

Time from planting Days	Tube surface area ---(mm) ² ---
10	50.6
14	50.6
18	202.7
22	202.7
26	456.0
30	810.7
34	1,266.7
38	1,824.1
42	1,824.1
46	1,824.1

¹Tube length was 800mm.

each species per block, and placed into an environmental chamber (10°C, 12-hours daylength, 500 uE m² sec⁻¹ spectral light). Plants were transplanted on day 1 of the experiment and thinned to a single individual on day 5. Sampling procedures followed those described for the interference study, with the exception that upper and lower root portions were not separated. Data were analyzed using ANOVA (SPSS., Chicago, Ill.); Fisher's protected L.S.D. ($P \leq 0.05$) mean comparisons are presented (Peterson 1985).

Results

Interference

Intraspecific interference was more important than interspecific interference for the prediction of plant weight (Tables 2 and 3). The influence of cheatgrass density on total cheatgrass weight was 2 times greater than the influence of yellow starthistle density. Similarly, yellow starthistle density was twice as important as cheatgrass density in the prediction of total yellow starthistle weight. Shoot weight and leaf area (data not shown) had a similar interference pattern (Tables 2 and 3). In both cases, cheatgrass density was about 1.5 times more important than yellow starthistle density in the prediction of cheatgrass response, and yellow starthistle density was

Table 2. Multiple regression analysis¹ for the prediction of cheatgrass total plant weight (mg), shoot weight, and root weight using plant densities.²

Dependent variable	B_{co}	B_{cc}	B_{cy}	B_{cc}/B_{cy}	R^2
Total plant weight (mg)	41.82 (3.01)	-6.26 (0.82)	-3.07 (0.60)	2.04	0.69
Shoot weight (mg)	28.49 (2.60)	-4.07 (0.72)	-2.90 (0.52)	1.40	0.58
Root weight (mg)	12.96 (0.89)	-2.19 (0.28)	0 (NS)	∞	0.56
Upper root weight (mg) (0-200 mm)	12.73 (0.80)	-2.24 (0.22)	-0.44 (0.16)	5.08	0.71
Lower root weight (mg) (>200 mm)	No significant variables				

$$^1 V_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$$

²The intercept B_{co} estimated the weight of an isolated cheatgrass seedling. Intraspecific interference for cheatgrass is measured by the regression coefficient B_{cc} , and interspecific interference with yellow starthistle by B_{cy} . Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 3. Multiple regression analysis¹ for the prediction of yellow starthistle total plant weight (mg), shoot weight, and root weight using plant densities.²

Dependent variable	B _{yo}	B _{yy}	B _{yc}	B _{yy} /B _{yc}	R ²
Total plant weight (mg)	34.56 (2.69)	-5.30 (0.75)	-2.69 (0.55)	1.97	0.62
Shoot weight (mg)	25.45 (2.33)	-4.27 (0.65)	-2.00 (0.47)	2.14	0.58
Root weight (mg)	9.11 (0.67)	-1.03 (0.19)	-0.69 (1.37)	1.49	0.55
Upper root weight (mg) (0-200 mm)	7.29 (0.60)	-0.89 (0.17)	-0.65 (0.12)	1.37	0.56
Lower root weight (mg) (>200 mm)	No Significant Variables				

¹ $V_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$
² The intercept B_{yo} estimated the weight of an isolated yellow starthistle seedling. Intraspecific interference for yellow starthistle is measured by B_{yy} and interspecific interference with cheatgrass by B_{yc}. Numbers in parentheses are standard errors for coefficients significantly different from zero.

about twice as important as cheatgrass density in predicting yellow starthistle response.

Increasing plant densities were associated with decreasing root weight for both species in the upper portion of the soil profile (Tables 2 and 3). Cheatgrass density had 5 times the influence of yellow starthistle density on cheatgrass root weight (0-200 mm). In contrast, yellow starthistle density was 1.37 times greater than cheatgrass density in influencing yellow starthistle root weight (0-200 mm). At soil depths below 200 mm, root weight was not associated with plant density for either species.

The prediction of cheatgrass root length suggests that intraspecific interference was greatest in the upper rooting zone (3.97) (Table 4).

Table 4. Multiple regression analysis¹ for the prediction of cheatgrass and yellow starthistle on the total root length (cm), upper root length, and lower root length using plant densities.²

Dependent variable	B _{co}	B _{cc}	B _{cy}	B _{cc} /B _{cy}	R ²
Cheatgrass					
Total root length (cm)	502.24 (44.47)	-47.27 (12.42)	-53.92 (9.00)	0.88	0.53
Upper root length (cm) (0-200 mm)	507.30 (41.45)	-89.34 (11.53)	-22.52 (8.40)	3.97	0.60
Lower root length (cm) (>200 mm)	0 (NS)	8.58 (3.55)	7.80 (2.63)	1.10	0.24
Yellow starthistle					
Total root length (cm)	509.02 (55.92)	-89.67 (18.02)	0 (NS)	∞	0.35
Upper root length (cm) (0-200 mm)	45.42 (55.29)	-72.02 (15.34)	-28.27 (11.19)	2.54	0.39
Lower root length (cm) (>200 mm)	12.45 (21.27)	-17.82 (6.87)	0 (NS)	∞	0.13

¹ Cheatgrass $V_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$
 Yellow starthistle $V_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$
² The intercepts B_{co} and B_{yo} estimated the root length of an isolated individual. Intraspecific interactions for cheatgrass and yellow starthistle are measured by the B_{cc} and B_{yy} regression coefficients, and the interspecific interactions by the B_{cy} and B_{yc} regression coefficients, respectively. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 5. Multiple regression analysis¹ for the prediction of cheatgrass and yellow starthistle root:shoot (mg mg⁻¹), root length:leaf surface area (cm cm⁻²), and lower:upper root length ratios (cm cm⁻³) using plant densities.²

Dependent variable	B _{co}	B _{cc}	B _{cy}	B _{cc} /B _{cy}	R ²
Cheatgrass					
Root:shoot	0 (NS)	0 (NS)	-0.26 (0.06)	0	0.32
Root length:leaf area	0 (NS)	49.29 (18.93)	0 (NS)	∞	0.13
Lower:upper	-0.47 (0.11)	0.22 (0.03)	0.06 (0.02)	3.81	0.55
Yellow starthistle					
Root:shoot	0 (NS)	0.19 (0.04)	0 (NS)	∞	0.31
Root length:leaf area	392.40 (207.33) ³	-109.48 (57.50) ³	178.29 (42.00)	-0.61	0.33
Lower:upper	No Significant Variables				

¹ Cheatgrass $V_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$
 Yellow starthistle $V_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$
² The intercepts B_{co} and B_{yo} estimated the root length of an isolated individual. Intraspecific interactions for cheatgrass and yellow starthistle are measured by the B_{cc} and B_{yy} regression coefficients, and the interspecific interactions by the B_{cy} and B_{yc} regression coefficients, respectively. Numbers in parentheses are standard errors for coefficients significantly different from zero.
³ P=0.06

Decreasing root length (total and upper) was associated with increased cheatgrass density. Intraspecific interference decreased yellow starthistle root length (Table 4). Cheatgrass density decreased yellow starthistle upper root length.

Increasing cheatgrass density was associated with increases in the cheatgrass root length:leaf area and lower:upper root length ratios (Table 5). However, increasing yellow starthistle density was associated with a decrease in cheatgrass root:shoot ratios. Mean comparisons (P<0.05) of cheatgrass root length:leaf area ratios showed that cheatgrass densities of 10,000 plants m⁻² were necessary to achieve a significant ratio increase (data not shown).

Yellow starthistle root length:leaf area ratio was influenced by intraspecific and interspecific interference (Table 5). Increases in yellow starthistle density decreased the root length:leaf area ratio of yellow starthistle. Whereas, increasing cheatgrass density increased the yellow starthistle root length:leaf area ratio. Lower:upper root length ratios for yellow starthistle were not associated with either yellow starthistle or cheatgrass density.

The increases in root:shoot and lower:upper root ratios described above were associated with detectable increases in soil depth penetration. The model fit for predicting soil depth penetration was poor. The effect of density on soil depth penetration by yellow starthistle suggests a trend of decreasing penetration with increasing yellow

Table 6. Double ratio (B_{cc}/B_{cy}:B_{yc}/B_{yy}) assessing the resource partitioning based on cheatgrass and yellow starthistle weight (mg).¹

Dependent variable	B _{cc} /B _{cy} :B _{yc} /B _{yy}
Total plant weight	4.86
Total shoot weight	3.10
Total root weight (0-400 mm)	∞
Upper root weight (0-200 mm)	6.98

¹ Ratio other unity indicate occurrence of resource partitioning.

Table 7. Mean shoot weight, root weight, leaf area, total root length, and root length/leaf area ratio for cheatgrass and yellow starthistle grown in isolation.

Days from planting	Shoot weight/plant ----(mg)----	Root weight/plant ----(mg)----	Leaf area/plant (cm ²)	Total root length/plant (cm)	Root length: leaf area ratio (cm cm ⁻²)
10	1.12	0.36	0.27	41	164
14	2.43	1.24	0.55	131	232
18	3.59	2.62	0.87	257	299
22	7.85	3.15	1.61	317	203
26	13.19	5.46	3.23	437	140
30	27.65	12.85	5.77	970	177
34	45.00	22.85	9.11	1,233	133
38	107.48	42.00	16.64	1,652	113
42	143.38	56.93	22.25	2,017	94
46	327.71	137.81	41.34	3,858	95
LSD(0.05)	53.36	13.22	4.51	363	*

starthistle density (Soil depth penetration by starthistle = $420.9 - 9.71 \log N_y$; $R^2 = 0.10$). In contrast, soil depth penetration by cheatgrass increased with density increases in either species (Soil depth penetration by cheatgrass = $219.53 + 23.51 \log N_c + 16.31 \log N_y$; $R_2 = 0.20$).

Coefficient of determination (R^2) values ranged from 0.56 to 0.71 for each dependent variable involving weight (Tables 2 and 3). The double ratio [$B_{cc}/B_{cy}; B_{yc}/B_{yy}$] analysis indicates that resource partitioning occurred with respect to total plant, total shoot, total root, and upper root weight (Table 6). Ratio values ranged from 3.10 to infinity.

Individual Growth of Isolated Plants

Shoot weight, root weight, leaf area, and total root length were similar for both species (Table 7). At each harvest date t-test ($P \leq 0.05$) failed to show differences between species. After 34 days from planting, each parameter increased as days from planting increased, with the exception of the root length:leaf area ratio which tended to decline throughout the 46-day experiment.

Yellow starthistle had a lower initial root:shoot ratio (0.16) than did cheatgrass (0.55) (Table 8). Individual t-tests at other harvest dates failed to reveal significant differences. Yellow starthistle roots grew deeper into the soil than cheatgrass after 22 days, and penetrated almost twice as deep as cheatgrass by 46 days.

Discussion

Cheatgrass and yellow starthistle seedling populations are influenced primarily by intraspecific rather than interspecific interference. The ecological importance of intraspecific interference is associated with the process of self-thinning and being a strong competitor (Aarssen 1983, Pyke and Archer 1991). Palmald (1968) studied intraspecific density effects upon several weeds, including cheatgrass. He concluded that cheatgrass used the process of self-thinning along with plasticity to ensure a reliable seed source. The ability of cheatgrass seedlings to suppress perennial grass seedlings has been attributed to rapid growth rate and the development of a root system adapted to declining soil moisture profiles (Evans 1961, Harris 1967, Svejcar 1990, Aquirre and Johnson 1991, Johnson and Aquirre 1991). Similarly, yellow starthistle was found to be a stronger competitor than perennial pubescent wheatgrass (*Thinopyrum intermedium*

Table 8. Root:shoot ratios and soil depth penetration for cheatgrass and yellow starthistle grown in isolation.¹

Days from planting	Root:shoot ratio		Soil depth penetration	
	Cheatgrass	Starthistle	Cheatgrass	Starthistle
	----(mg mg ⁻¹)----		----(mm)----	
10	0.55	0.16	81	93
14	0.65	0.51	120	150
18	0.85	0.69	114	184
22	0.38	0.57	150	260
26	0.38	0.50	166	325
30	0.52	0.52	209	427
34	0.54	0.42	265	521
38	0.47	0.32	335	567
42	0.50	0.34	382	715
46	0.43	0.63	404	767
	LSD (0.05) = 0.22		LSD (0.05) = 88	

¹Mean comparisons may be made within columns or along rows.

um spp. *barbulatum* (Schur) Bark, W. & D. R. Dewey) (Prather and Callihan 1991). Yellow starthistle possesses seedling growth rates similar to cheatgrass in terms of root and shoot weight, leaf area, and root length.

Our results suggest that cheatgrass and yellow starthistle seedlings reduce interspecific interaction by partitioning resources, and that the mechanism for this partitioning is related to rooting depth (Table 8). Functional niche differentiation between plant populations and the ability of species coexistence based on rooting depth has a strong theoretical basis (Berendse 1979, Berendse 1981, Berendse 1982). Yellow starthistle roots grew to a greater soil depth than cheatgrass roots, suggesting vertical resources partitioning (e.g. soil moisture) between populations. Furthermore, yellow starthistle populations typically mature later than cheatgrass (Sheley et al. 1993, Sheley and Larson 1994). We believe that interspecific interference between cheatgrass and yellow starthistle is limited by vertical and temporal resource partitioning.

Density related plasticity was associated with increased root resource allocation. Yellow starthistle root:shoot ratio increased with increasing densities. Similar trends have been reported for other species (Berendse 1981) and for cheatgrass (Dakheel 1986). Increasing cheatgrass densities were also associated with increased cheatgrass and yellow starthistle root length:leaf area ratios. Resource allocation to lower root portions (>200 mm) increased in cheatgrass as densities increased. This characteristic should serve to stabilize populations and reduce the number of non-reproducing individuals during drought conditions.

Knowledge of resource partitioning can enhance efforts to revegetate degraded rangelands (Pyke and Archer 1991). Selection of plants having contrasting above and below ground allocation patterns, in particular at seedling and juvenile stages, augment resource partitioning, and the probability of niche separation. The invasion by yellow starthistle into cheatgrass dominated rangeland also represents resource partitioning. However, in this case, resource partitioning in conjunction with population plasticity will likely decrease our ability to revegetate rangelands by conventional means.

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