

INFLUENCE OF SOIL WATER AVAILABILITY ON COMPETITION AMONG LEAFY SPURGE (*EUPHORBIA ESULA*) AND GRASSES

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ABSTRACT.—Some perturbations differentially influence invasive plant and grass production. For example, growth regulator herbicides and biological control agents can dramatically reduce leafy spurge production while having little or no influence on grass production, and overgrazing can reduce grass production while not substantially influencing leafy spurge production because cattle typically ingest little or no leafy spurge. To predict how grass production will respond to a perturbation that influences only leafy spurge and to predict how leafy spurge production will respond to a perturbation that affects only grasses, competitive relationships must be understood. Seeding mixtures of leafy spurge and 2 grasses were planted in experiments and grown for 127 days to determine whether different water application regimes influenced competition among these 3 species. Competition became less intense as the number of water applications increased. If this finding holds true under field conditions, then it indicates that competition is less intense in years and locations with numerous precipitation events. Competitive interactions (i.e., competition coefficients) were less variable when water was applied more frequently, but the ability of models to account for variation in plant weight (i.e., r^2) was not influenced by the frequency of water application. This suggests that models will predict invasive plant and grass biomass with equal accuracy in years with few or many precipitation events. Competitive effects were similar regardless of grass species, which suggests that grasses might be considered collectively in predicting response to perturbations in the field.

Key words: competition, invasive plants, soil water, rangeland.

Competitive relationships between invasive plants and grasses partially regulate plant community response to invasive plant management. For example, the change in grass biomass production that results from invasive plant control and the change in invasive plant biomass that results from grass seeding partially depend on competition intensity. Therefore, incomplete understanding of competitive relationships will result in imprecise predictions of management-induced shifts in invasive plant and grass abundances.

Developing a more complete understanding of competitive relationships between invasive plants and grasses requires knowing if these relationships vary temporally and/or spatially. If competitive relationships between invasive plants and grasses do vary temporally and spatially, a substantial portion of this variation is likely related to temporal and spatial variation in plant productivity, which can be attributed to variation in environmental conditions such as nutrient and water availability (Grime 2001).

While it has been shown that some aspects of plant competition do vary with environmental

conditions (Moloney 1990, Briones et al. 1998, Keddy et al. 2000), the relationship between competition intensity and plant productivity has been a point of contention between ecologists (Grime 1973, Newman 1973, Reader et al. 1994). Grime (2001) believes the preponderance of evidence indicates a positive relationship between competition intensity and plant productivity. However, at least one elaborate study suggests that wide productivity gradients are necessary to detect changes in competition intensity, and therefore variation in plant productivity might not strongly influence competition intensity within the productivity range that a single invasive plant species occupies (Reader et al. 1994).

Water availability often governs plant productivity in the semiarid regions where many invasive plants occur, and water availability varies with precipitation and soil water-holding characteristics (e.g., very coarse soils maintain less plant-available water; Bailey 1979). The ability of soil to hold water is regulated by soil type, landscape position, and soil management practices, among other factors (Afyumi et

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al. 1993, Gomez et al. 2002). If plant productivity (i.e., water availability) influences competition intensity between grasses and invasive plants in semiarid regions, per-unit-biomass competitive relationships will vary temporally and spatially with plant-available soil water.

Per-unit-biomass competitive relationships can also vary by species, and a single invasive plant species can grow in association with different grasses within each of several habitat types it infests. For example, spotted knapweed (*Centaurea maculata*) grows in association with western wheatgrass (*Agropyron smithii*), Kentucky bluegrass (*Poa pratensis*), needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), crested wheatgrass (*Agropyron cristatum*), rough fescue (*Festuca scabrella*), bluebunch wheatgrass (*Pseudoroegneria spicata*), prairie junegrass (*Koeleria cristata*), Idaho fescue (*Festuca idahoensis*), and other grasses (Fay et al. 1991, Sheley et al. 2000). Studying competitive relationships between spotted knapweed and each of these grasses would require resource-intensive experiments. The number of by-species competitive relationships that need to be estimated will further increase if per-unit-biomass competitive effects vary considerably by species because some regions harbor many invasive plant species. Using a small number of grasses to study the magnitude of variation in by-species competitive effects will elucidate the quantity of species-specific inquiries needed to understand competition between an invasive plant species and all grasses with which the invasive plant commonly coexists.

Our objective was to determine the influence of soil water on competition among leafy spurge, Kentucky bluegrass, and western wheatgrass in a greenhouse. Leafy spurge is a cool-season, nonnative, perennial invasive plant that infests close to 1.2 million ha in 29 states in the USA (Lajeunesse et al. 1999). Kentucky bluegrass is a cool-season, nonnative, perennial grass that occurs throughout much of the United States. Western wheatgrass is a native, cool-season, rhizomatous, perennial grass that occurs in many rangeland ecosystems of the western United States and Canada (Taylor and Lacey 1994). These grasses often grow in association with leafy spurge.

It was hypothesized that per-unit-plant-abundance competitive relationships would not vary (1) by grass species and (2) with the

number of water applications (i.e., plant productivity). Because the factors that limit plant growth are different at varying levels of water availability, we hypothesized that (3) the magnitude of variation in competitive relationships would change with water availability. If observed, this change would reflect different magnitudes of variation in the underlying factors that limit plant growth (e.g., soil nutrient availability) at different levels of soil water.

MATERIALS AND METHODS

Procedures

Plastic pots (7.6-L) were filled with a pasteurized soil mixture containing equal parts of a silt loam soil (classification unknown), washed concrete sand, and Canadian sphagnum peat moss. The wetting agent AquaGro® 2000 G was added at $0.5 \text{ kg} \cdot \text{m}^{-3}$, and the mixture was steam pasteurized at 80°C .

Percent germination of leafy spurge, Kentucky bluegrass, and western wheatgrass was estimated by sowing 30 seeds of each species in 1-L pots in a greenhouse (1 pot per species). Seeds were covered with approximately 2 mm of soil, and the soil was misted with water every other day for 20 days. We then calculated the following ratio for each type of seed: seedlings emerged:seeds planted. These ratios were used to adjust seeding rates and achieve target plant densities.

Target densities were 0, 670, 1340, and 2010 plants $\cdot \text{m}^{-2}$ for each species. Three addition series matrices consisting of all possible seed density combinations were established (4 Kentucky bluegrass densities \times 4 western wheatgrass densities \times 4 leafy spurge densities = 64 pots per density matrix \times 3 density matrices = 192 pots per experiment) in the 7.6-L pots (Spitters 1983). These density matrices also contained between 2 and 8 isolated plants of each species (depending on survival).

Density matrices were arranged in a completely randomized design in a greenhouse. Pots were periodically rearranged to average the influence of environmental gradients across all plants. Greenhouse photoperiod was extended to 14 hours with 1000-W metal halide bulbs, and temperature was maintained at approximately 22°C during the light period and 18°C during the dark period. Seeds were uniformly scattered over the soil surface and covered with about 2 mm of soil. To encourage

germination, we misted the soil surface with water every other day for 27 days. After the misting period (28 days after planting), all pots were watered to capacity. Pots in 2 density matrices were watered to capacity 61 days after planting, and 1 of these matrices was watered to capacity a 3rd time 94 days after planting. Hereafter, pots watered once, twice, or 3 times will be said to have received dry, intermediate, or wet treatments, respectively. After receiving final water applications, plants in the pots were harvested by clipping at the soil surface upon showing signs of severe water stress, or 127 days after planting, whichever occurred first. All plants were then dried to a constant weight at 50°C. The experiment was conducted during the winter of 1999 (run 1) and was repeated during the winter of 2000 (run 2).

Soil Water Sampling

To determine gravimetric water content, pots were weighed the day before each watering, and pots that were watered were reweighed the day after watering. Pots were weighed after harvest, and soil was removed and thoroughly mixed. We took a uniform sample from each pot, each of which was weighed, dried to a constant weight at 50°C, and reweighed to determine soil dry weight (soil dry weight = post-harvest soil weight × sample dry weight / sample wet weight - pot weight). Two soil samples were submitted to the Montana State University Soil Testing Laboratory where pressure plate analysis was used to determine gravimetric water content at matric pressures of 0.01, 0.03, 0.1, 0.5, and 1.5 MPa.

Plant Sampling

Number of plants per pot of each species was counted at harvest. Aboveground biomass of each species was determined after plants were dried to a constant weight at 50°C.

Soil Data Analysis

The van Genuchten (1980) water retention relationship was fit to pressure plate analysis data by minimizing the sum of squared errors ($r^2 = 0.98$) to estimate the relationship between matric pressure and gravimetric water content. An index of overall matric pressure was calculated by computing the average of matric pressure measurements. Measurements

from each measurement period were included until a pot received its final water application and pot matric pressure reached 1.5 MPa (permanent wilting point). If pots did not reach 1.5 MPa by the end of the experiment, then all matric pressure measurements were included in the average.

Plant Data Analysis

Plant data were fit to the following inverse yield models by minimizing the sum of squared errors (Spitters 1983).

$$1/pw_{ls} = B + B_{ls,den} * den_{ls} + B_{kb,bio} * bio_{kb} + B_{ww,bio} * bio_{ww} \quad (1)$$

$$1/pw_{kb} = B + B_{kb,den} * den_{kb} + B_{ls,bio} * bio_{ls} + B_{ww,bio} * bio_{ww} \quad (2)$$

$$1/pw_{ww} = B + B_{ww,den} * den_{ww} + B_{ls,bio} * bio_{ls} + B_{kb,bio} * bio_{kb} \quad (3)$$

Inverse plant weight was used to linearize relationships. The subscripts ls, kb, and ww denote leafy spurge, Kentucky bluegrass, and western wheatgrass, respectively. The response variable 1/pw is the inverse of average individual plant weight per pot. Regression coefficients without subscripts (Bs) are intercept terms and Bs subscripted with den and bio are competition coefficients that describe the influence of plant density and biomass, respectively. Density was used to describe intraspecific competition instead of biomass because of the complex relationship between pw and bio. Models were independently fit to data from the dry, intermediate, and wet treatments to yield a total of 9 models (9 models = 3 water treatments × 3 species).

Regression coefficients of 1, 2, and 3 were compared to test the null hypothesis that per-unit-plant-abundance competitive effects do not vary with the number of water applications and also to test the null hypothesis that per-unit-plant-abundance competitive effects do not vary by species. Density coefficients were compared within a species across water treatments, and biomass coefficients were compared across species when comparing within a water treatment and within a species when comparing across water treatments. Standard deviations of regression coefficients were evaluated to test the null hypothesis that the magnitude of variation in competitive relationships would change with water availability.

The following model:

$$\text{amp}_{\text{sp}} = B + B_{\text{ls, bio}} * \text{bio}_{\text{ls}} + B_{\text{kb, bio}} * \text{bio}_{\text{kb}} + B_{\text{ww, bio}} * \text{bio}_{\text{ww}} \quad (4)$$

in which amp is an index of average matric pressure, was used to assess whether or not the 3 species used the same amount of water in producing a unit of biomass. This model was fit to data from each water treatment to yield a total of 3 models.

A bootstrap algorithm was used to compare regression coefficients (Efron and Tibshirani 1993, Hjorth 1994). Cases from data sets were randomly selected with replacement and inserted into a bootstrap sample until the number of cases was equal to the number of cases in the original data set, and the model of interest was then fit to the bootstrap sample to generate least-squares estimates of X and Y. For this example, the variables X and Y are regression coefficients that are being compared, and the least-squares estimate of X is greater than that of Y. These steps were repeated 1000 times to generate vectors (x and y) of bootstrap regression coefficient estimates with 1000 elements. The number of cases in which $x_i > y_j$ was evaluated for $i = 1, 2, \dots, 1000$ and $j = 1, 2, \dots, 1000$. This resulted in $x * y = 1,000,000$ comparisons. The quantity $(1 - (\text{number of cases where } x_i > y_j) / 1,000,000) * 2$ is a 2-tailed hypothesis test of $H_0: (X = Y)$. When regression coefficients were compared to 0, a similar approach was used with each observation in the vector of bootstrap regression coefficient estimates compared to 0. P -values were calculated independently for each comparison and were not adjusted to provide "tablewise" or "experimentwise" error protection.

RESULTS

Regression coefficients in tables will be referenced without the letter B, the comma (,) will be replaced by a hyphen (-), and the coefficients will not be subscripted. For example, $B_{\text{ls, bio}} = \text{ls-bio}$ and $B_{\text{ls, den}} = \text{ls-den}$. Because the dependent variable is inverse plant weight, the magnitude of competition coefficients and competition intensity is positively related.

In interpreting results it is important to remember that matric pressure is negatively related to soil water content. Therefore, as water availability decreases, matric pressure increases.

Influence of Competition on Leafy Spurge Individual Plant Weight

Leafy spurge density became less negatively related to leafy spurge individual plant weight as the number of water applications increased in run 1 (Table 1), while the intensity of this intraspecific competition was unrelated to water treatment in run 2. Kentucky bluegrass and western wheatgrass biomass negatively affected leafy spurge plant weight in the dry and intermediate treatments but did not negatively affect plant weight in the wet treatment in run 1. The competitive effect of grasses on leafy spurge did not vary significantly with water treatments in run 2, and per-unit-biomass effects of Kentucky bluegrass and western wheatgrass on leafy spurge were similar to one another in both runs.

Influence of Competition on Kentucky Bluegrass Individual Plant Weight

Kentucky bluegrass density had a similar negative effect on Kentucky bluegrass individual plant weight in the dry and intermediate treatments but had little or no effect in the wet treatment in run 1 (Table 2). Kentucky bluegrass density had a negative effect on Kentucky bluegrass plant weight in run 2, but the relationship was independent of water treatment. The effect of western wheatgrass and leafy spurge biomass on Kentucky bluegrass plant weight diminished as the number of water applications increased in both runs. Western wheatgrass was more competitive with Kentucky bluegrass than was leafy spurge in both runs.

Influence of Competition on Western Wheatgrass Individual Plant Weight

Western wheatgrass density had a greater negative effect on western wheatgrass individual plant weight in the dry and intermediate treatments than in the wet treatment in both runs (Table 3). Similarly, Kentucky bluegrass and leafy spurge became less competitive with western wheatgrass as the number of water applications increased in both runs. Kentucky bluegrass was less competitive with western wheatgrass than was leafy spurge in the dry and intermediate treatments in both runs, and

TABLE 1. Competition coefficient estimates, r^2 , standard deviations (s) of coefficient estimates, and comparisons of coefficients at the 5% level of confidence. The coefficients are from a multiple linear regression model fit to data from a greenhouse study with inverse of leafy spurge individual plant weight as the dependent variable and leafy spurge plant density and western wheatgrass and Kentucky bluegrass plant biomass as the independent variables.

Run	Water treatment	r^2	Competition coefficients	Coefficient estimates	s	Comparisons of regression coefficients		
1	Dry	0.18	ls-den	0.38	0.16	$=ls_{intermediate}$	$\neq ls_{wet}$	
	Dry		kb-bio	11.79	5.11	$=ww_{dry}$	$=kb_{intermediate}$	$\neq kb_{wet}$
	Dry		ww-bio	5.82	4.74	$=ww_{intermediate}$	$\neq ww_{wet}$	
	Intermediate	0.45	ls-den	0.26	0.17	$\neq ls_{wet}$		
	Intermediate		kb-bio	6.24	2.14	$=ww_{intermediate}$	$=kb_{wet}$	
	Intermediate		ww-bio	8.15	2.15	$=ww_{wet}$		
	Wet	0.34	ls-den	-0.13	0.02			
	Wet		kb-bio	-0.23	0.23	$=ww_{wet}$		
	Wet		ww-bio	-0.12	0.24			
2	Dry	0.38	ls-den	0.56	0.21	$=ls_{intermediate}$	$=ls_{wet}$	
	Dry		kb-bio	9.74	5.06	$=ww_{dry}$	$=kb_{intermediate}$	$=kb_{wet}$
	Dry		ww-bio	22.00	5.62	$=ww_{intermediate}$	$=ww_{wet}$	
	Intermediate	0.53	ls-den	0.71	0.18	$\neq ls_{wet}$		
	Intermediate		kb-bio	9.30	2.63	$=ww_{intermediate}$	$=kb_{wet}$	
	Intermediate		ww-bio	14.64	2.40	$=ww_{wet}$		
	Wet	0.54	ls-den	0.25	0.26			
	Wet		kb-bio	1.64	1.78	$=ww_{wet}$		
	Wet		ww-bio	1.86	1.90			

TABLE 2. Competition coefficient estimates, r^2 , standard deviations (s) of coefficient estimates, and comparisons of coefficients at the 5% level of confidence. The coefficients are from a multiple linear regression model fit to data from a greenhouse study with inverse of Kentucky bluegrass individual plant weight as the dependent variable and Kentucky bluegrass plant density and western wheatgrass and leafy spurge biomass as the independent variables.

Run	Water treatment	r^2	Competition coefficients	Coefficient estimates	s	Comparisons of regression coefficients		
1	Dry	0.44	kb-den	0.62	0.23	$=kb_{intermediate}$	$\neq kb_{wet}$	
	Dry		ww-bio	11.58	3.87	$=ls_{dry}$	$\neq ww_{intermediate}$	$\neq ww_{wet}$
	Dry		ls-bio	24.50	6.64	$\neq ls_{intermediate}$	$\neq ls_{wet}$	
	Intermediate	0.83	kb-den	0.33	0.04	$\neq kb_{wet}$		
	Intermediate		ww-bio	3.58	0.61	$\neq ls_{intermediate}$	$=ww_{wet}$	
	Intermediate		ls-bio	7.93	1.59	$\neq ls_{wet}$		
	Wet	0.47	kb-den	0.15	0.05			
	Wet		ww-bio	1.93	0.59	$=ww_{wet}$		
	Wet		ls-bio	2.91	1.59			
2	Dry	0.60	kb-den	0.18	0.15	$=kb_{intermediate}$	$\neq kb_{wet}$	
	Dry		ww-bio	17.07	2.56	$\neq ls_{dry}$	$\neq ww_{intermediate}$	$\neq ww_{wet}$
	Dry		ls-bio	46.99	9.17	$\neq ls_{intermediate}$	$\neq ls_{wet}$	
	Intermediate	0.71	kb-den	0.20	0.05	$=kb_{wet}$		
	Intermediate		ww-bio	4.71	0.53	$\neq ls_{intermediate}$	$\neq ww_{wet}$	
	Intermediate		ls-bio	11.45	2.59	$\neq ls_{wet}$		
	Wet	0.41	kb-den	0.10	0.05			
	Wet		ww-bio	1.86	0.33	$\neq ww_{wet}$		
	Wet		ls-bio	3.36	1.89			

TABLE 3. Competition coefficient estimates, r^2 , standard deviations (s) of coefficient estimates, and comparisons of coefficients at the 5% level of confidence. The coefficients are from a multiple linear regression model fit to data from a greenhouse study with inverse of western wheatgrass individual plant weight as the dependent variable and western wheatgrass plant density and leafy spurge and Kentucky bluegrass plant biomass as independent variables.

Run	Water treatment	r^2	Competition coefficients	Coefficient estimates	s	Comparisons of regression coefficients		
1	Dry	0.60	ww-den	0.37	0.07	$\neq ww_{intermediate}$	$\neq ww_{wet}$	
	Dry		kb-bio	3.97	1.85	$\neq ls_{intermediate}$	$= kb_{intermediate}$	$= kb_{wet}$
	Dry		ls-bio	13.58	2.08	$\neq ls_{intermediate}$	$\neq ls_{wet}$	
	Intermediate	0.79	ww-den	0.21	0.02	$= ww_{wet}$		
	Intermediate		kb-bio	1.28	0.19	$\neq ls_{intermediate}$	$= kb_{wet}$	
	Intermediate		ls-bio	2.49	0.41	$= ls_{wet}$		
	Wet	0.57	ww-den	0.18	0.03			
	Wet		kb-bio	1.09	0.18	$\neq ls_{wet}$		
	Wet		ls-bio	-0.16	0.54			
2	Dry	0.75	ww-den	0.55	0.06	$\neq ww_{intermediate}$	$\neq ww_{wet}$	
	Dry		kb-bio	4.52	1.04	$\neq ls_{intermediate}$	$\neq kb_{intermediate}$	$\neq kb_{wet}$
	Dry		ls-bio	17.62	3.65	$\neq ls_{intermediate}$	$\neq ls_{wet}$	
	Intermediate	0.71	ww-den	0.32	0.03	$\neq ww_{wet}$		
	Intermediate		kb-bio	1.44	0.42	$\neq ls_{intermediate}$	$= kb_{wet}$	
	Intermediate		ls-bio	7.98	1.80	$\neq ls_{wet}$		
	Wet	0.69	ww-den	0.22	0.02			
	Wet		kb-bio	1.02	0.22	$= ls_{wet}$		
	Wet		ls-bio	2.70	1.11			

this relationship was reversed in the wet treatment in run 1. Kentucky bluegrass and leafy spurge had a similar competitive effect on western wheatgrass plant weight in the wet treatment in run 2.

Influence of Water Availability on Variation in Competition Intensity

With few exceptions, estimates of the standard deviation of competition coefficients decreased or stayed the same as the number of water applications increased. This indicates that there was less variation in competitive effects when water was applied more frequently. On the other hand, there was no clear relationship between r^2 of models and the number of water applications. Whereas the competitive interactions were less variable when water was applied more frequently, factors not included in models 1, 2, and 3 (e.g., plant diseases and genetics and nutrient availability) caused greater random error when water was applied more frequently.

Influence of Plant Biomass on Average Matric Pressure

Leafy spurge and grasses had a similar effect on average matric pressure in the dry treatment in run 1 (Table 4). In the dry treat-

ment in run 2, leafy spurge used more water in producing a unit of biomass than did the grasses, and western wheatgrass used more water in producing a unit of biomass than did Kentucky bluegrass. In the intermediate and wet treatments in run 1, leafy spurge used less water in producing a unit of biomass than did grasses, while the opposite was true for these 2 treatments in run 2.

DISCUSSION

There are 2 prevalent competing theories regarding the influence of plant productivity on competition. One theory contends that competition becomes more intense as plant productivity increases because plant biomass increases, which results in increased competition for light and space (Grime 1973, 2001, Keddy 1989). The other theory predicts that competition is similar in habitats with high and low productivity because belowground competition for nutrients is more intense in habitats with low standing crop (Newman 1973, Wilson and Tilman 1991). In this view, the intensity of above- and belowground competition is negatively related, so that net competition intensity remains similar along productivity gradients. Several field studies have relied on the response of a target plant to removal of

TABLE 4. Model r^2 and coefficient estimates for multiple linear regression model with average matric pressure as the dependent variable and plant biomasses as independent variables in a greenhouse study.

Run	Water treatment	r^2	Regression coefficients		
			kb-bio	ww-bio	ls-bio
1	Dry	0.37	-0.05a ^a	0.01a	-0.02a
	Intermediate	0.40	0.09a	0.04a	-0.03b
	Wet	0.37	0.09a	0.09a	-0.01b
2	Dry	0.41	0.05a	0.16b	0.44c
	Intermediate	0.24	0.05a	0.06a	0.18b
	Wet	0.44	0.08a	0.14a	0.55b

^aCoefficients within a row that are followed by the same letter are not significantly different at the 5% level of confidence.

surrounding vegetation as a measure of competition intensity along productivity gradients, and differences in competition intensity have (Del Moral 1983, Reader and Best 1989) and have not (Wilson and Tilman 1991, 1993) been detected.

In this greenhouse study competition intensity stayed similar or decreased as the number of water applications (i.e., plant productivity) increased (Tables 1–3), and therefore the null hypothesis that competition would be unaffected by the frequency of water application is rejected. Competition staying similar is consistent with one of the prevalent theories that relates competition intensity to plant productivity (Newman 1973, Wilson and Tilman 1991), but an inverse relationship between competition intensity and frequency of water application is inconsistent with both theories. This finding is also inconsistent with studies in which interspecific competition among 3 desert plants and intraspecific competition of a desert annual intensified when water was added in the field (Kadmon 1995, Briones et al. 1998). All plants were still quite small (<25 cm in height) by the end of these greenhouse experiments, signifying that competition for light may not have offset competition for water in treatments that resulted in high water availability (i.e., treatments with low seeding densities and 3 water applications).

Competition intensity decreased when water supply was increased in a field experiment that studied competition between tree seedlings and herbaceous species (Davis et al. 1998), which is similar to the findings of these greenhouse experiments. One explanation for the inverse relationship between competition intensity and water availability found in both experiments is supplied by a theory predicting

that competition intensity will decrease when high supplies of new resources become available (Huston and DeAngelis 1994). If competition does become less intense as the number of precipitation events increases in the field, competition between grasses and leafy spurge is less intense in years and locations with both frequent and substantial precipitation events.

These greenhouse experiments contribute to our ultimate goal of developing models that predict invasive plant and grass biomass response to management strategies in the field. The fact that competition coefficient standard deviations tended to decrease as the number of water applications increased suggests that models will predict plant biomass more accurately in wet years (Tables 1–3). However, there was no clear relationship between the importance of competition (model r^2) and the number of water applications (Tables 1–3; Welden and Slauson 1986), which suggests that models will account for variation in plant biomass equally well in years with few and many precipitation events. It appears that the influence of competition became less variable when water was applied more frequently, but other factors that cause variation in plant weight (disease, genetics, nutrients) had a more pronounced effect when water was applied more frequently. The null hypothesis that variation in competition intensity is related to the number of water applications is not rejected.

The competitive influence of Kentucky bluegrass biomass on leafy spurge plant weight was similar to that of western wheatgrass biomass regardless of water treatment (Table 1). The null hypothesis that per-unit abundance competitive effects of the grasses are similar is not rejected. Biesboer et al. (1994) reported that 5 grasses did not affect leafy spurge shoot

weight in a greenhouse, but these grasses did decrease root weight with the magnitude of the effect depending on the grass species. Different grass species also affect leafy spurge aboveground biomass production differently in the field (Ferrell et al. 1992, Biesboer et al. 1994, Lym and Tober 1997). However, unlike the analysis reported in this manuscript, the effect of a grass species was confounded by the amount of biomass the species produced in these studies, and all of the grasses may have competed similarly if competitive effects were expressed on a per-unit-biomass basis. Several studies support the theory that per-unit-biomass competitive effects of many plant species are similar (Goldberg 1987, Mitchell et al. 1999, Aguiar et al. 2001, Peltzer and Kochy 2001). If our results hold true in the field, Kentucky bluegrass, western wheatgrass, and probably other grasses may be considered collectively in estimating the influence of grass production on leafy spurge production.

Results from this greenhouse study might improve our ability to predict the influence of environmental conditions on relationships between invasive plants and grasses if conclusions can be extrapolated to natural conditions. However, conclusions should be viewed very cautiously because there are substantial differences between greenhouse and field conditions. An even-aged, somewhat even-sized cohort of juvenile plants was used in this study, while most biomass is attributed to mature plants in the field. This resulted in a contrived partitioning of soil resources because leafy spurge was not capable of accumulating resources from substantially deeper depths than grasses, as is the case in the field (Bakke 1936). Grasses and leafy spurge attained similar heights in this study, while leafy spurge is usually taller than grasses in the field. Pots with high densities of leafy spurge may have misrepresented high-density patches of leafy spurge, because leafy spurge may be a better competitor for light under field conditions. Also, evidence suggests that shading can decrease plant water stress in dry soils, which indicates that competition for water may diminish with plant height (Salisbury and Chandler 1993). Results from this study provide some insight into the influence of water availability on competition between grasses and leafy spurge, but it will be necessary to compare results to field experiment results to substantiate the findings. If

field and greenhouse results are similar, results from future greenhouse studies might be viewed with more confidence.

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