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A model for predicting invasive weed and grass dynamics. I. Model development[1,2]

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Invasive weed managers are presented with a complicated and ever-enlarging set of management alternatives. Identifying the optimal weed management strategy for a given set of conditions requires predicting how candidate strategies will affect plant community composition. Although field experiments have advanced our ability to predict postmanagement composition, extrapolation problems limit the prediction accuracy achieved by interpreting treatment means as predictions. Examples of extrapolation problems include nonlinear relationships between competing plants, site-to-site variation in plant population growth rates, and the carrying capacities of desired species and weeds. Our objective was to develop a model that improves predictions of weed management outcomes by overcoming a subset of these problems. To develop the model, we used data from two field experiments in which four Kentucky bluegrass, six western wheatgrass, and six invasive plant (i.e., leafy spurge) densities were combined in field plots. Graphs of our model's predictions vs. observed field experiment data indicate that the model predicted the data accurately. Our model may improve predictions of plant community response to invasive weed management actions.

Nomenclature: Leafy spurge, *Euphorbia esula* L. EPHES; spotted knapweed, *Centaurea maculosa* Lam. CENMA; Kentucky bluegrass, *Poa pratensis* L. POAPR; western wheatgrass, *Pascopyrum smithii* Rydb.

Key words: Competition model, population dynamics, demography.

Competition by nonnative dicotyledonous weeds such as spotted knapweed (*Centaurea maculosa* Lam.) and leafy spurge (*Euphorbia esula* L.) has depleted grass populations on millions of hectares of grasslands in North America and elsewhere (DiTomaso 2000; Kroon et al. 1987; Lym and Tober 1997; Sheley et al. 2000). Federal agencies, ranchers, and other land managers are currently attempting to restore grasses by removing weeds with introduced biological control agents, grass seeding, herbicides, sheep and goat grazing, and other strategies (Ferrell et al. 1998; Kirby et al. 2000; Lym 2000; Lym et al. 1997; Sheley et al. 2001). Questions often arise as to which strategies to use, when and how to use them, and how grasses and invasive plants will respond to their use.

To answer these questions, managers interpret treatment responses from experiments as predictions of how the real-world grasslands under their care will respond to the same treatments (Ferrell et al. 1998; Kirby et al. 2000; Lym et al. 1997; Rinella et al. 2001). Seven extrapolation problems can render these predictions tenuous:

1. *Nonlinearity:* Plant competitive relationships are very often nonlinear (Buchanan et al. 1980; Coble and Ritter 1978; Gaudet and Keddy 1988; Goldberg 1987; Moolani et al. 1964). If relationships between weeds and desired species are nonlinear, reducing weed density by a given amount at a research site and a management unit will result in a similar increase in grass production at both locations only when preremoval densities are similar. If competitive relationships are highly nonlinear, linear corrections for preremoval differences in weed densities will provide very misleading predictions.
2. *Carrying Capacity:* Equilibrium grass and invasive weed biomass production vary dramatically from site to site, so experiments will provide erroneous predictions unless experiment results are somehow rescaled to match productivity attributes within management units (Figure 1).
3. *Species:* One invasive species can invade a variety of habitats and coexist with a multitude of grass species (Fay et al. 1991; Sheley et al. 2000), but experiments evaluate management strategies in areas containing only a subset of the possible grasses.
4. *Efficacy:* The impact of herbicides, biological controls, and other strategies on invasive weed populations varies by site and year, as does the impact of grass seeding on grass populations (Call and Roundy 1991; Clark et al. 2001; Kirby et al. 2000; Kronberg and Walker 1999; Lym and Messersmith 1985; Lym and Tober 1997; Robocker et al. 1965; Velagala et al. 1997).
5. *Competition:* The intensity of plant competition can vary from site to site and year to year, which makes it difficult to predict how invasive weeds will respond to grass seeding and how grasses will respond to weed removal (Briones et al. 1998; Grime 2001; Keddy et al. 2000; Moloney 1990).
6. *Growth Rate:* Growth rates of individual plants and plant

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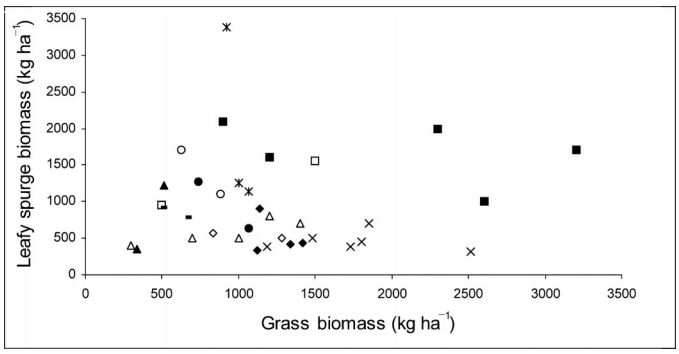

FIGURE 1. Leafy spurge and grass biomasses in the northwestern United States (Hein 1988; Kirby et al. 2000; Lym and Kirby 1987; Maxwell 1984; K. K. Sedivec, unpublished data). Unique symbol types denote sites, and individual symbols of a given type represent data from different years. Data from herbicide-treated plots and grazed plots are excluded.

populations vary temporally and spatially, which complicates attempts to predict dynamics that occur after a management strategy is applied but before a community equilibrates to the management-induced disturbance (Grime and Hunt 1975). Predicting these transient dynamics is important because some forms of management (e.g., herbicides) are reapplied whenever weeds recover from previous applications. The transient dynamics determine how often management will need to be applied.

7. *Random Error:* The intensity and frequency of factors that are not explicitly studied in invasive weed experiments (e.g., grasshopper herbivory, hailstorms) vary spatially and temporally. Therefore, estimates of random error (i.e., prediction confidence) at one site may not accurately depict prediction confidence at other sites.

We present a model that describes interactions between perennial grasses and an invasive forb (i.e., leafy spurge). Our primary objective in developing this model was to diminish prediction error caused by the described nonlinearity, carrying capacity, and species problems. These problems are probably the least data-intensive to solve and could be important sources of prediction error.

A secondary objective was to quantify prediction uncertainty caused by the extrapolation problems and random error. Thus, we represent the extrapolation problems and random error as features of our model. Future research could quantify how the model parameters vary, which would estimate prediction uncertainty. We present asymptotic standard errors of the parameters, and these error terms provide some insight into the magnitude of spatial and temporal parameter variation.

Leafy spurge was used for this research because of its ecological and economic importance and because there are extensive data on this species. Leafy spurge is a rhizomatous perennial weed that infests approximately 1.2 million ha in the United States (Lajeunesse et al. 1999). Western wheatgrass (*Pascopyrun smithii* Rydb.) and Kentucky bluegrass (*Poa pratensis* L.) were used for this study because they commonly grow in association with leafy spurge (Nowierski and Harvey 1988). Western wheatgrass and Kentucky bluegrass are rhizomatous perennial grasses that occur in rangeland ecosystems of the western United States and Canada (Taylor and Lacey 1994).

Materials and Methods

Study Site

Two experiments were conducted 6.5 km west of Bozeman, MT, at the Montana State University Arthur H. Post Research Farm (45°41′N, 111°9′W). The elevation at the site is 1,463 m, the average annual precipitation is 457 mm, and the soil is an Amsterdam silt loam (fine-silty, mixed, frigid Typic Haplustolls). Because the site was previously used for agronomic research, it was tilled each year for many years prior to the initiation of our study.

Experimental Design

In Experiment 1, four Kentucky bluegrass and six western wheatgrass seeding rates and six leafy spurge seedling densities were combined in 1- by 1-m plots in every possible density combination ($4 \times 6 \times 6 = 144$ plots). This design is typically referred to as an addition series (Spitters 1983). Immediately prior to grass seeding, strips of grass sod (1 m wide) were laid around the plots to eliminate unrealistic growing conditions that would result from leaving plot borders bare. To better approximate target Kentucky bluegrass (0, 156, 1,250, and 10,000 plants m^{-2}) and western wheatgrass (0, 156, 312, 1,250, 5,000, and 10,000 plants m^{-2}) densities, seeding rates were adjusted using seedling emergence ratios that were estimated in a greenhouse. Grass seeding treatments were randomly assigned, and seeds were uniformly spread over plots and covered with approximately 2 mm of soil in early June 1998. Plots were periodically irrigated until grasses became established.

Leafy spurge seeds were collected near Bozeman, MT, in August 1999. Seedlings were established and thinned to one seedling per container (3 cm diam by 15 cm) in a greenhouse in September 1999. Leafy spurge seedlings were approximately 10 cm tall by spring 2000. Six densities of leafy spurge (0, 4, 9, 16, 25, and 36 seedlings m^{-2}) were planted in plots a few days after glyphosate was applied as described below. Glyphosate was applied at 1.6 kg ae ha^{-1} to kill grasses and thereby enhance survival of leafy spurge seedlings. Grasses were killed within 36 evenly spaced circular areas (diam = 6.35 cm) in each plot in May 2000. Seedlings were evenly spaced within the center of areas that had received glyphosate application. A pointed steel rod was used to make holes to accommodate seedlings, and soil was packed around seedlings by hand.

Experiment 2 was located about 50 m away from Experiment 1, and leafy spurge was established prior to grasses in this experiment. Experiment 2 was conducted because of concerns that leafy spurge might invade the dense grass stands of Experiment 1 very slowly, which would have prevented us from studying the leafy spurge densities typically found in naturally occurring infestations. Leafy spurge seedlings were planted with uniform spacing at densities of 0, 4, 9, 16, 49, and 64 seedlings m^{-2} in May 2000. Grasses were established in August 2000 using the methods and seeding rates of Experiment 1.

Plant Measurements

Plant data were collected when repeated height measurements over time indicated that summer growth had ceased. Leafy spurge was measured in early September 2000, and

grasses and leafy spurge were measured in late August 2001 and 2002. Grasses were measured by clipping at ground level, separating by species, drying to a constant weight at 50 C, and weighing. Two 15- by 15-cm quadrats were permanently marked (one in the center of the southwest quarter of plots and the other in the center of the northeast quarter) at the beginning of the experiments, and grasses in these quadrats were measured in 2001 and 2002. (An analysis that is not presented indicated that grass clipping in 2001 did not influence 2002 grass production.) Grass biomass outside the 15- by 15-cm quadrats was also measured in 2002 (except for the peripheral 15 cm, because of possible edge effects). It was prohibitively time-consuming to separate all grass biomass by species in plots containing large quantities of both western wheatgrass and Kentucky bluegrass. Therefore, in 2002, grasses from 49% of the plots in Experiment 1 and 36% of the plots in Experiment 2 were thoroughly hand mixed, and three samples (dry weight = ≈15 g per sample) were sorted and used to estimate grass biomass by species. Summed lengths of leafy spurge stems per square meter (hereafter referred to as stem length density) were used to quantify leafy spurge abundances, as opposed to biomass, because clipping alters the subsequent growth of this species (Kirby et al. 1997).

Analysis

We evaluated models that predict leafy spurge stem length density and grass biomass. The models have the following terms:

$$w_{t+1} = f(w_t, g_{t+1}, \alpha, r_w, w_{\max}, k_t, \sigma_{\varepsilon,w}) \quad [1]$$

$$g_{t+1} = f(g_t, w_t, \beta, r_g, g_{\max}, \sigma_{\varepsilon,g}) \quad [2]$$

The predictor and response variables are leafy spurge stem length density (w = weed) and grass biomass (g) at the cessation of plant growth in years t and $t + 1$. The parameters are leafy spurge (r_w) and grass (r_g) population growth rates, leafy spurge (w_{max}) and grass (g_{max}) carrying capacities, the impact of grass on leafy spurge population growth (α), the impact of leafy spurge on grass population growth (β), the impact of leafy spurge management on leafy spurge population growth (k), and random error variances ($\sigma_{\epsilon,w}$ and $\sigma_{\epsilon,g}$).

Using grass at $t + 1$ to predict leafy spurge at $t + 1$ permitted data from an additional time step to be used in estimating parameters of the leafy spurge equation. The usefulness of the models is not affected by modeling in terms of future plant abundances because, after simulating g_{t+1}, the simulated grass value can be used to simulate w_{t+1}.

The models deal with the carrying capacity problem by acknowledging that $w_{\max}$ and $g_{\max}$ vary temporally and spatially. By measuring small quadrats in sites that are at equilibrium, managers can site-specifically estimate these parameters and thereby partially overcome the carrying capacity problem.

Our model will address the species problem if the per-unit-biomass impacts of grasses on leafy spurge (α) and the per-unit-stem length density impacts of leafy spurge on grasses (β) are similar for all perennial grass species that coexist with leafy spurge. Several studies support the assertion that per-unit-abundance competitive effects are similar among coexisting species (Aguiar et al. 2001; Gaudet and Keddy 1988; Goldberg 1987; Mitchell et al. 1999; Peltzer and Kochy 2001), and a greenhouse study supports this assertion specifically for leafy spurge and perennial grasses (Rinella and Sheley 2005a). Species-specific grass terms were evaluated in leafy spurge equations to determine if prediction accuracy was compromised by combining grasses (i.e., g = western wheatgrass biomass plus Kentucky bluegrass biomass).

The competition problem can be managed by the model by defining α and β as random variables, as opposed to fixed parameters, and the same is true of the growth rate r's and random error σ_ε's problems. Nonlinear models that follow Equations 1 and 2 were tested so that the nonlinearity problem would be addressed if it proved salient in this system.

The k_t parameter represents the reduction in leafy spurge stem length density caused by a management action during year t. The efficacy problem is dealt with by defining k_t as a random variable. Some management strategies, such as environmentally persistent herbicides, will reduce leafy spurge abundances beyond the year of application (Lym and Messersmith 1994). In these cases, k_{t+1}, $k_{t+2} \ldots k_{t+n}$ could be included. Other strategies, such as biological control or repeated sheep grazing, quasi-permanently reduce leafy spurge stem length densities, in which case management can be modeled as a decrease in $w_{\max}$ (Kirby et al. 2000; Landgraf et al. 1984; Olson and Wallander 1998). Seeding can cause long-term increases in grass production, which could be handled by manipulating $g_{\max}$ (Lym and Tober 1997; Masters and Nissen 1998).

Jackknife cross-validation was used to characterize the predictive capabilities of several models (Efron and Tibshirani 1993; Hjorth 1994). The jackknife procedure entailed deleting one plot's data and then using a regression routine to minimize the sum of squared errors; we used the International Mathematical and Statistical Library subroutine DRNLIN (Visual Numerics 1997). Models and deleted predictor data were then used to predict deleted response data, and the squared residuals were calculated. The procedure was automated using FORTRAN 6.6.a (Compaq Computer Corporation 2000) and was repeated for each plot's data. To calculate the jackknife mean-square error (JMSE), the sum of squared residuals was divided by the number of data points.

Models can be highly unrealistic and still have low JMSEs (i.e., they can still accurately predict the range of data used in model development). But, when models are unrealistic (e.g., have biologically implausible parameter estimates), they can inaccurately predict data not used in model development. Scatter plots, isocline plots, and least-squares parameter estimates were used to characterize the realism of models, and models were dropped from consideration if they had unrealistic isoclines or parameter estimates.

Results and Discussion

We assumed error variances to be log-normally distributed in estimating parameters, calculating JMSEs, and evaluating models because scatter plots indicate that means and standard deviations of plant abundances are positively related (Figure 2) (Hilborn and Mangel 1997). We first evaluated the two-species Ricker equation (Ricker 1954) and the two-species logistic equation (Pearl and Reed 1920) (Table

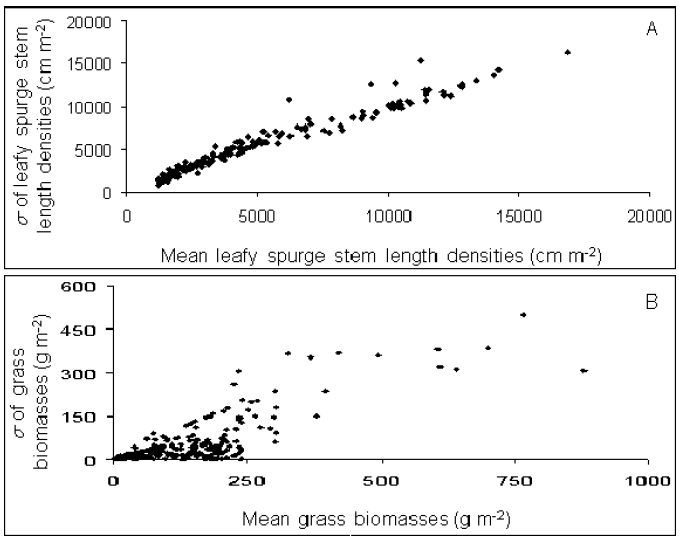

FIGURE 2. Means and standard deviations of leafy spurge (A) and grass (B) abundances from individual field plots that were measured annually. Leafy spurge data were collected in 2000, 2001, and 2002, while grass biomass data were collected in 2001 and 2002. The positive relationships between means and standard deviations justify the assumption that error variances are log-normally distributed.

1), two widely used discrete-time population dynamics equations. Experiment 2 plots produced substantially more leafy spurge stem length and grass biomass than did Experiment 1 plots (Figure 3), which prompted us to evaluate experiment-specific growth rate, competition, and carrying capacity parameters. Site-specific terms were included in the Ricker equation, for example, as follows (see Haining 1990):

$$w_{t+1} = w_t \exp\left[(r_w + r_{w,s}s)\cdot\left(1 - \frac{w_t + \alpha g_{t+1} + \alpha_s s g_{t+1}}{w_{\max} + w_{\max,s}s}\right)\right] \quad [3]$$

$$g_{t+1} = g_t \exp\left[(r_g + r_{g,s}s)\cdot\left(1 - \frac{g_t + \beta w_t + \beta_s s w_t}{g_{\max} + g_{\max,s}s}\right)\right] \quad [4]$$

The s term is a dummy variable that takes on the values 0 and 1 for Experiments 1 and 2, respectively. Therefore, the parameters $r_{w,s}$, $r_{g,s}$, β_s, α_s, $w_{\max,s}$, and $g_{\max,s}$ adjust r_w, r_g, β, α, $w_{\max}$, and $g_{\max}$, if necessary, to better reflect parameter values for Experiment 2. Adding experiment-specific carrying capacity parameters (i.e., $g_{\max,s}$ and $w_{\max,s}$) reduced JMSEs, but adding other experiment-specific terms did not. The parameter estimates and fit statistics of Table 1 were derived after including $g_{\max,s}$ and $w_{\max,s}$ in all equations. The least-squares estimates of $g_{\max,s}$ and $w_{\max,s}$ are listed in Table 1, but for ease of explanation, these terms are not depicted in the equations of Table 1 or in any of the equations that follow.

Grass species-specific terms were added to leafy spurge equations to assess how grouping western wheatgrass and Kentucky bluegrass affected prediction accuracy. Species-specific terms were added to the Ricker equation, for example, as follows:

$$w_{t+1} = w_t \exp\left[r_w\left(1 - \frac{w_t + \alpha_1 g_{1,t+1} + \alpha_2 g_{2,t+1}}{w_{\max}}\right)\right] \quad [5]$$

Competition parameters (α) and grass terms (g) subscripted with the number 1 represent western wheatgrass, and those

TABLE 1. Jackknife mean-square errors (JMSE), R^2, and least-square parameter estimates and standard errors of growth rate (r), competition (α, β), and carrying capacity ($w_{\max}$, $g_{\max}$, $w_{\max,s}$, and $g_{\max,s}$) parameters of equations that predict leafy spurge stem length density (w_{t+1}) and grass biomass (g_{t+1}). Experiment 1 carrying capacities for leafy spurge stem length density (cm m^{-2}) and grass biomass (g m^{-2}) are given by $w_{\max}$ and $g_{\max}$, respectively, while carrying capacities for Experiment 2 are given by $w_{\max} + w_{\max,s}$ and $g_{\max} + g_{\max,s}$.

				Least-squares estimates					Standard errors				
Equation name	Equation	JMSE	R^2	r_w or r_g	α or β	$w_{\max}$ or $g_{\max}$	$w_{\max,s}$ or $g_{\max,s}$	r_w or r_g	α or β	$w_{\max}$ or $g_{\max}$	$w_{\max,s}$ or $g_{\max,s}$
Logistic	$w_{t+1E} = w_t + r_w w_t(1 - s(w_t + \alpha g_{5+1})/w_{\max})$	0.48	0.85	3.0	12.0	7,691	18,859	0.1	2.4	938	1,215
Ricker	$w_{t+1} = w_t \exp[r_w(1 - (w_t + \alpha g_{t+1})/w_{\max})]$	0.18	0.88	1.7	11.1	7,254	11,971	0.04	1.5	647	915
ln-Ricker	$w_{t+1} = w_t \exp[r_w(1 - (\ln(w_t) + \alpha g_{t+1})/\ln(w_{\max}))]$	0.19	0.88	3.9	0.005	19,604	118,759	0.1	0.0006	4,744	26,805
Watkinson–Ricker	$w_{t+1} = w_t \exp[r_w(1 - w_t(1 + \alpha g_{t+1})/w_{\max})]$	0.19	0.88	1.5	0.01	7,614	18,857	0.03	0.00055	743	1,539
Logistic	$g_{t+1} = g_t + r_g g_t(1 - (g_t + \beta w_t)/g_{\max})$	0.49	0.66	0.9	0.07	298	6,881	0.1	0.02	26	10,448
Ricker	$g_{t+1} = g_t \exp[r_g(1 - (g_t + \beta w_t)/g_{\max})]$	0.28	0.73	1.1	0.04	213	935	0.1	0.009	13	262
ln-Ricker	$g_{t+1} = g_t \exp[r_g(1 - (\ln(g_t + \beta w_t)/\ln(g_{\max}))]$	0.21	0.80	2.9	0.0002	172	1,654	0.2	0.00002	14	795
Watkinson–Ricker	$g_{t+1} = g_t \exp[r_g(1 - g_t(1 + \beta w_t)/g_{\max})]$	0.31	0.70	0.8	0.001	259	1,035	0.1	0.0088	35	643

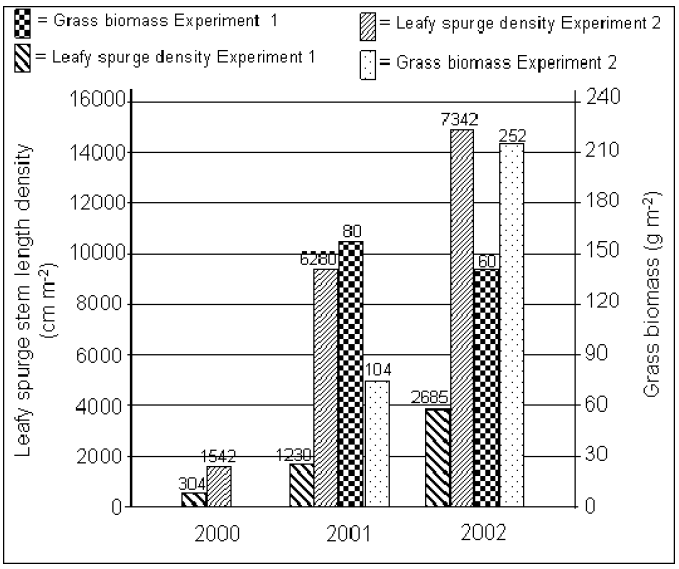

FIGURE 3. Means (bars) and standard deviations (numbers above bars) of grass biomasses and leafy spurge stem length densities from Post Farm experiments. Grasses, though present in 2000, were not measured.

subscripted with the number 2 represent Kentucky bluegrass. Leafy spurge equations with species-specific grass terms had slightly larger JMSEs than equations in which grass biomasses were grouped and multiplied by a single competition parameter. It appears that western wheatgrass and Kentucky bluegrass compete similarly with leafy spurge on a per-unit-biomass basis, and including species-specific parameters caused "overfitting." However, because some per-species grass weights were estimated from subsamples, as opposed to being directly measured, measurement error may have unduly inflated the JMSEs of grass species–specific equations.

The logistic equation has a considerably larger JMSE than the Ricker equation, and the Experiment 2 estimate of $g_{\max}$ for the logistic equation is unrealistically large (Table 1). The Ricker equation predicts the data accurately (i.e., has a small JMSE), but scatter plots and plots of zero-growth isoclines suggest that both the Ricker and logistic equations are unsatisfactory. Both equations reduce to the following zero-growth isoclines at equilibrium (i.e., when $w_{t+1} = w_t$ or $g_{t+1} = g_t$):

$$w = w_{\max} - \alpha g \qquad [6]$$

$$g = g_{\max} - \beta w \qquad [7]$$

These isoclines predict that grasses and leafy spurge are linearly related (Figures 4A–D), while a scatter plot of grass vs. leafy spurge abundances clearly indicates a curvilinear relationship (Figure 5). Also, the parameter estimates of the Ricker and logistic equations for Experiment 1 meet the following conditions: $g_{\max} < w_{\max}/\alpha$ and $w_{\max} > g_{\max}/\beta$, which, as can be shown by plotting isoclines, predict that grass will become extinct. The prediction that leafy spurge causes local grass extinction is probably unrealistic because, in a meta-analysis of data from 60 leafy spurge–infested sites (data not shown), grasses were present at all sites. Furthermore, parameter estimates of the logistic equation for Experiment 2 predict that leafy spurge will become extinct. This prediction appears unrealistic because, in spite of extensive control efforts, leafy spurge coexists with Kentucky bluegrass and western wheatgrass at sites very similar to, and within 10 km of, our research sites.

The theta-Ricker equation is often used when linear zero-growth isoclines are unrealistic (Turchin 2003). The theta-Ricker structure of a grass equation, for example, is given by:

$$g_{t+1} = g_t \exp\left\{(r_g + r_{g,s}s)\cdot\left[1 - \frac{(g_t + \beta w_t + \beta_s s w_t)^{\theta}}{g_{\max} + g_{\max,s}s}\right]\right\} \qquad [8]$$

The shape parameter θ allows for curvature in the zero-growth isocline. Convergence problems and highly unrealistic parameter estimates resulted from attempts to fit the theta-Ricker equation to our data, which led us to believe that the data contained too much random variation and that the sample size was insufficient to accurately estimate the parameters of five-parameter equations (e.g., r_g, β, $g_{\max}$, $g_{\max,s}$, θ).

In an effort to develop accurate and realistic four-parameter equations with curvilinear isoclines, we evaluated two Ricker-like equations that reduce to published curvilinear plant competition models at equilibrium. We refer to these equations as ln-Ricker (natural log-Ricker) and Watkinson–Ricker equations (Table 1). The ln-Ricker equation reduces to the following leafy spurge and grass zero-growth isoclines at equilibrium (Figures 4A–D):

$$\ln(w) = \ln(w_{\max}) - \alpha g \qquad [9]$$

$$\ln(g) = \ln(g_{\max}) - \beta w \qquad [10]$$

Gaudet and Keddy (1988) used this form to model plant competition between wetland plants. The ln-Ricker equation was dropped from consideration because fitted $w_{\max}$ and $g_{\max}$ values were unrealistically large (Table 1).

The Watkinson–Ricker equation reduces to the following zero-growth isoclines (Figure 4):

$$w = w_{\max}(1 + \alpha g)^{-1} \qquad [11]$$

$$g = g_{\max}(1 + \beta w)^{-1} \qquad [12]$$

These isoclines have been used to predict individual plant weights (Goldberg 1987; Watkinson 1981). The JMSEs of the Watkinson–Ricker equation are similar to, or smaller than, the JMSEs of the other equations, and parameter estimates of this equation are realistic (Table 1). The zero-growth isoclines of the Watkinson–Ricker equations predict the equilibrium coexistence of grasses and leafy spurge in Experiments 1 and 2 (Figures 4E and F), and this prediction is consistent with our experiences with leafy spurge in grassland environments. However, whether or not equilibriums occur in nature, and the position of these equilibriums, depends on the intensity and frequency of factors that cause zero-growth isocline parameters to vary (e.g., variation in the physical environment and herbivory) (Huston 1979; Silvertown and Charlesworth 2001). We believe the Watkinson–Ricker equation is superior to the other equations we evaluated. Collectively, we refer to the Watkinson–Ricker equations for predicting grass and leafy spurge abundances as the Watkinson–Ricker model. Figure 6 depicts the fit of this model to our data.

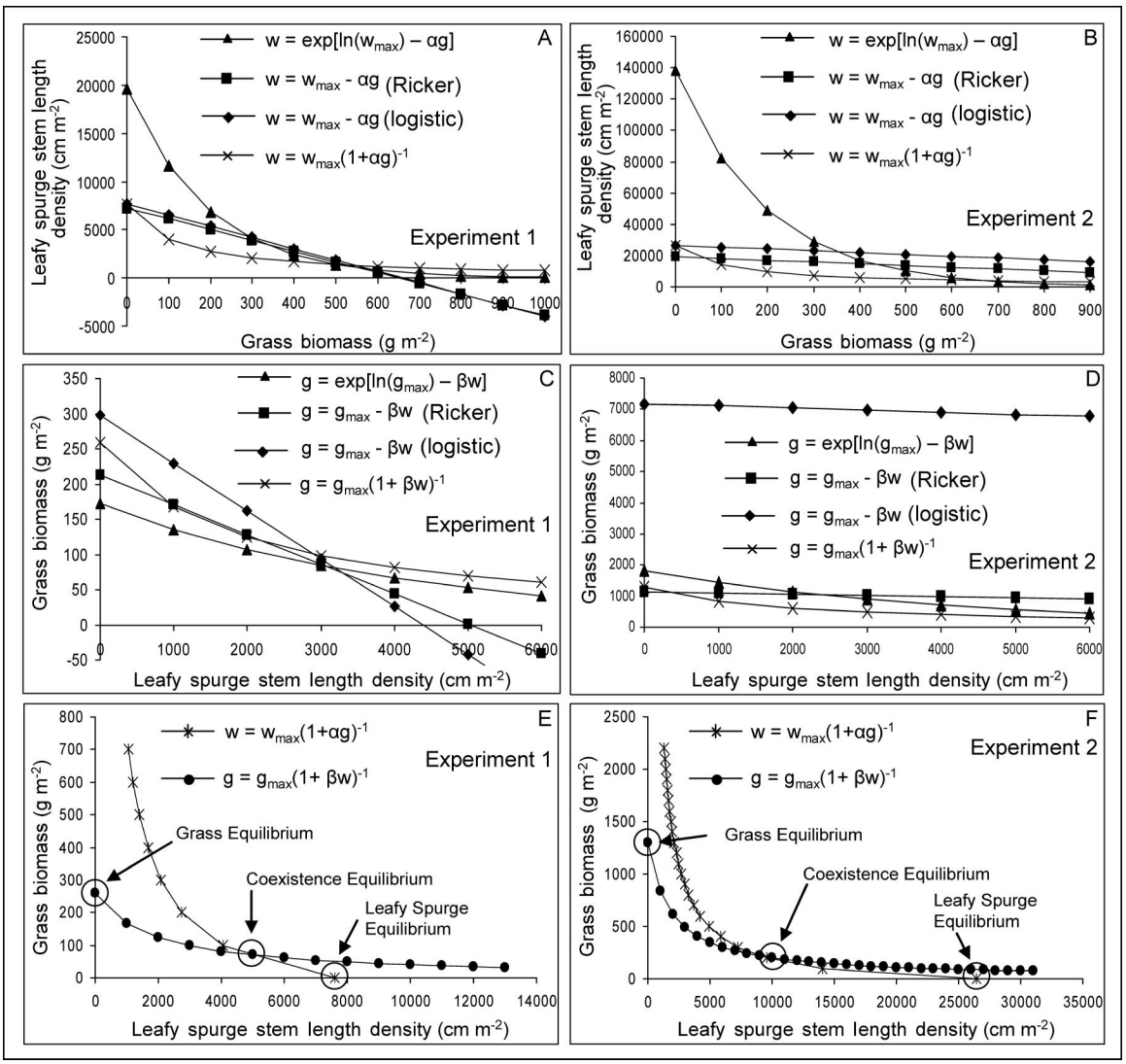

FIGURE 4. Zero-growth isoclines of equations that predict leafy spurge and grass abundances. Zero-growth isoclines of leafy spurge (A, B) and grass (C, D) equations for low (Post Farm Experiment 1) and high (Post Farm Experiment 2) productivity sites. Zero-growth isoclines of the Watkinson–Ricker model depicting equilibriums at low (Experiment 1) (E) and high (Experiment 2) (F) productivity sites.

Summary

Assessing management strategies is the goal of much invasive weed research. One of the main challenges in assessing management strategies has been that the impacts of strategies depend on the site. In part, this site-dependence is a consequence of spatially varying plant carrying capacities (Figure 1) and nonlinear competitive relationships (Figure 5). Our model may improve site-specific assessments (i.e., predictions) of weed management strategies because it corrects for nonlinear relationships and site-specific carrying capacities. At sites that are at equilibrium, managers could site-specifically estimate carrying capacities by measuring small quadrats and inserting the measured data into versions of Equations 11 and 12 that have been solved for w_{max} and g_{max}.

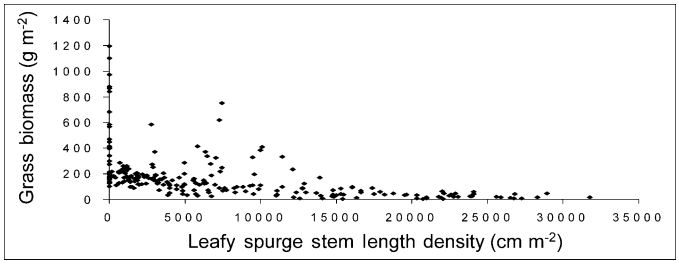

FIGURE 5. Leafy spurge and grass abundances in plots of two field experiments. All data were collected from Post Farm Experiments 1 and 2 during 2002.

Our model may sufficiently alleviate the species problem in leafy spurge–infested grasslands because it expresses grass population sizes in units of biomass and leafy spurge population sizes in units of stem length density, which is highly correlated with leafy spurge biomass. Accumulating evidence indicates that per-unit-biomass competitive effects are similar across species within a community (Aguiar et al. 2001; Goldberg 1987; Mitchell et al. 1999; Peltzer and Kochy 2001; Rinella and Sheley 2005a), and constructing separate terms for Kentucky bluegrass and western wheatgrass did not improve the predictive capabilities of the Watkinson–Ricker model. If between-species variation in competitive

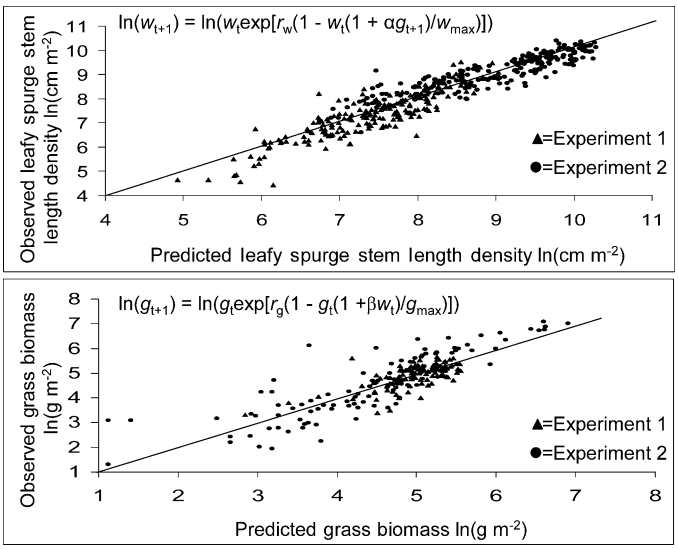

FIGURE 6. Predicted and observed leafy spurge and grass abundances. Leafy spurge stem length density (w) was measured in 2000, 2001, and 2002, and grass biomass (g) was measured in 2001 and 2002 in Post Farm Experiments 1 and 2. Parameters describe leafy spurge (r_w) and grass (r_g) intrinsic rates of increase, leafy spurge (w_{max}) and grass (g_{max}) carrying capacities, the impact of leafy spurge on grass production (β), and the impact of grass on leafy spurge production (α).

effects is due to between-species patterns in plant weight or size, our model will alleviate the species problem.

Some theorists believe the competition problem could be partially alleviated by expressing competition terms as increasing functions of habitat productivity (Grime 2001; Keddy 2001). Conflicting theories assert that these functions are unnecessary because competition intensity does not vary with productivity (Newman 1973; Wilson and Tilman 1991). Other than correcting for competition–productivity relationships, or maybe a few other easily quantifiable relationships, models are not likely to reduce the severity of the competition problem. Studying variables that cause competition to vary would require rigorous, and thus costly, experimentation, and a large number of variables may be responsible for temporal and spatial variation in competition intensity. Similar statements are true of the growth rate, random error, and efficacy problems. By representing these problems as model parameters, we have made progress toward quantifying prediction uncertainty, because quantifying temporal and spatial variation in model parameters will quantify prediction uncertainty. Invasive weed management decisions are based on predicted plant community dynamics. Models may improve our ability to predict dynamics, but regardless of how sophisticated the models become, prediction uncertainty will remain. Estimates of the magnitude of the prediction uncertainty will be important to sound decision making.

Conclusive tests of our model's ability to overcome extrapolation problems and predict weed management outcomes will require that our model be subjected to tests using independent data (i.e., data not used in model development). These tests are the focus of a companion paper (Rinella and Sheley 2005b).

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