

A model for predicting invasive weed and grass dynamics. II. Accuracy evaluation^{1,2}

Matthew J. Rinella

Corresponding author. U.S. Department of
Agriculture–Agricultural Research Service, 243 Fort
Keogh Road, Miles City, MT 59301;
mrinella@larrl.ars.usda.gov

Roger L. Sheley

U.S. Department of Agriculture–Agricultural
Research Service, 67826-A Highway 205, Burns,
OR 97720

The impact of invasive weed management on plant community composition is highly dependent on location-specific factors. Therefore, treatment means from experiments conducted at a given set of locations will not reliably predict community response to weed management elsewhere. We developed a model that rescales treatment means to better match local conditions. The goal of this paper was to determine if this rescaling improves predictions. We used our model to predict leafy spurge stem length density and grass biomass data from field experiments. The experiments consisted of herbicide-treated plots, untreated controls, and, in some cases, grass seeding treatments. When herbicides suppressed leafy spurge, the model explained 21 to 48% more variation in grass response than did mean grass response to the same or similar herbicide treatments applied at other sites. When herbicides killed grass, the model explained 53% more variation in leafy spurge response than did mean leafy spurge response to the same herbicide treatment applied at other sites. We regressed model predictions against observed data and tested the null hypothesis that resulting slope terms were equal to 1.0. Because the null hypothesis was rejected in two of four tests, the model may systematically over- or underpredict in some situations. However, measurement error in the observed data, unintended herbicide injury, or an inaccurate allometric relationship may account for a major proportion of the systematic deviations, and these factors would not cause prediction error in some management applications. Because the model tends to be better than the means from experiments at predicting plant community composition, we conclude that the model could advance managers' ability to predict plant community responses to invasive weed management.

Nomenclature: Leafy spurge, *Euphorbia esula* L. EPHES.

Key words: Competition model, meta-analysis, population dynamics, validation.

Demographic models have provided a detailed understanding of the population biology of some invasive weeds and have highlighted potentially viable control strategies (Parker 2000; Shea and Kelly 2004; Werner and Caswell 1977). To date, however, invasive weed models have not explicitly considered the demographics of desired plant groups growing in association with the weeds. Therefore, the models are ill-equipped for predicting plant community response to weed management actions. This is especially true when, as is typical, management only partially suppresses the weed. Under conditions of only partial weed suppression, plant communities cannot be expected to fully revert to their preinvasion composition.

Some plant population models do consider more than one species, but these models describe annual weeds growing with annual crops, as opposed to perennial weeds growing with naturally occurring perennial plants (e.g., Cousens 1985; Firbank and Watkinson 1986). The development and testing of crop–weed models has illustrated that, while intra-

and interspecific competitive relationships can be quite consistent from place to place and year to year (Freckleton and Watkinson 1998), weed seed emergence and mortality (i.e., factors driving population growth) are notoriously variable (Cousens 1995; Freckleton and Watkinson 1998; Kropff 1988). Because seed-related processes are so variable, models have not consistently predicted the impact of management on weed population sizes in croplands.

Millions of hectares of grassland are codominated by perennial invasive weeds and perennial grasses and forbs (Sheley and Petroff 1999). Seed dynamics are important for long-distance dispersal in grassland ecosystems, but beyond colonization, processes such as ramet production and adult plant survival often dominate dynamics (Eriksson 1989; Parker 2000). Therefore, lessons learned from phenomenological population models of annually tilled croplands do little to establish our expectations of these same kinds of models in invaded grasslands. In this article, we hope to refine our expectations by testing the predictive capability of a grassland weed model against data not used in developing the model. Cousens and Mortimer (1995) emphasize the importance of such tests for evaluating whether or not models are predictive outside the locations and years where and when they are developed.

Development of the following model is described in Rinella and Sheley (2005a):

¹ Experiments were conducted while the authors were at the Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717.

² Mention of a proprietary product does not constitute a guarantee or warranty of the product by the USDA, the Montana AES, or the authors and does not imply its approval to the exclusion of other products that may also be suitable. The USDA-ARS, Northern Plains Area, is an equal opportunity/affirmative action employer. All agency services are available without discrimination.

$$w_{t+1} = w_t \exp \left\{ r_w \left[1 - \frac{w_t(1 + \alpha g_{t+1})}{w_{\max}} \right] \right\} \quad [1]$$

$$g_{t+1} = g_t \exp \left\{ r_g \left[1 - \frac{g_t(1 + \beta w_t)}{g_{\max}} \right] \right\} \quad [2]$$

This model combines properties of the Ricker (1954) equation with properties of a plant competition model developed by Watkinson (1981). We call it the Watkinson–Ricker model. Independent and dependent variables are leafy spurge (*Euphorbia esula*) (w = weed) stem length density (units are centimeters per square meter) and grass (g) biomass (grams per square meter) at peak standing crop of year t and $t + 1$. Parameters are leafy spurge (r_w) and grass (r_g) population growth rates, leafy spurge (w_{\max}) and grass (g_{\max}) carrying capacities, the competitive effect of grasses on leafy spurge population growth (α), and the competitive effect of leafy spurge on grass population growth (β). Parameters of this model were estimated from two field experiments in which density matrices of leafy spurge, Kentucky bluegrass (*Poa pratensis*), and western wheatgrass (*Pascopyrum smithii*) were established.

We have outlined seven extrapolation problems that can prevent off-site experiments from predicting on-site invasive weed management outcomes. This article assesses the ability of the model (i.e., Equations 1 and 2) to overcome three of these problems. One of the extrapolation problems is caused by nonlinear competitive relationships. There is strong evidence that competitive relationships between leafy spurge and grasses are nonlinear (Rinella and Sheley 2005a). Thus, reducing leafy spurge density by a given amount at a research site and by the same amount within a management unit will cause a similar increase in grass production at both locations only when the preremoval leafy spurge densities at the two sites are similar. The model depicted by Equations 1 and 2 may alleviate the nonlinearity problem because it predicts nonlinear competitive relationships.

The second extrapolation problem involves varying plant productivities. Leafy spurge and grass carrying capacities vary spatially, which makes it risky to rely on results from an experiment without first rescaling them to match productivity attributes of the management unit (Rinella and Sheley 2005a). In theory, our model could enable managers to easily estimate local carrying capacities. This would be accomplished by measuring equilibrium grass and leafy spurge abundances in small quadrats and then inputting the measurements into equilibrium versions (i.e., zero-growth isoclines) of Equations 1 and 2.

The third extrapolation problem occurs because one invasive species can invade a variety of habitats and coexist with a multitude of grass species (Table 1), but experiments evaluate management strategies in areas containing only subsets of the possible grasses. There is accumulating evidence that per-unit-biomass competitive effects among coexisting species are often similar (Aguiar et al. 2001; Gaudet and Keddy 1988; Goldberg 1987; Mitchell et al. 1999; Peltzer and Kochy 2001). Our model scales competitive effects in terms of grass biomass and a measure that is highly correlated with leafy spurge biomass (i.e., the summed lengths of leafy spurge stems per square meter). Our model should alleviate the species problem if between-species variation in

competitive effects is due to between-species patterns in plant weight or size.

Our model's ability, or inability, to predict data collected across a large region over a span of many years will provide information about the relative importance of the seven extrapolation problems described by Rinella and Sheley (2005a). If our model accurately predicts data presented in this article, we will conclude that the problems addressed by the model (i.e., nonlinearity, carrying capacity, and species problems) are the critical problems. If, on the other hand, the prediction error is extensive, we will conclude that the model may not adequately address these problems or, alternatively, that unaddressed extrapolation problems are major sources of error. The unaddressed extrapolation problems are caused by variable population growth rates, variable competition intensities, variable management effects, and random error.

Materials and Methods

Selective Plant Removal Experiments

Study Sites

Selective plant removal experiments (SPREs) were conducted at five locations within 249 km of Bozeman, MT (Table 1). Equations 1 and 2 were developed using data from field experiments conducted near Bozeman. Plant productivity appeared to vary spatially at four of the five locations, so more than one SPRE was conducted at these four locations to test the model under a variety of conditions. We conducted 20 SPREs. All SPRE sites within a location were <2 km apart.

Experimental Design

SPREs were composed of four 1- by 1-m plots that were fenced, where necessary, to exclude ungulate grazing. One plot was selected randomly, while the other three plots were selected systematically to be within 10 m of, and have vegetation characteristics similar to, the randomly selected plot. This plot selection procedure helped minimize error caused by small-scale variations in plant productivity. Treatments were randomly assigned to the four plots. Two plots were not treated, while herbicides that selectively kill either grasses or forbs were applied to the other two plots. Selective herbicides have proven useful for studying plant competition (Peltzer and Kochy 2001). Grasses were killed within one plot by applying the monocot-specific herbicide sethoxydim and crop oil concentrate at rates of 0.086 kg ai ha⁻¹ and 382 ml ha⁻¹, respectively. Leafy spurge was killed within one plot by applying the dicot-specific herbicide picloram at a rate of 0.56 kg ai ha⁻¹. Picloram was also applied to a 1-m-wide border strip surrounding this plot to prevent re-invasion from plot borders and to limit possible border effects. All herbicide treatments were applied mid-May 2001.

Data Collection

Plant data were collected in early August 2002. Grasses and forbs (other than leafy spurge) were measured by clipping plants within the inner 85- by 85-cm area of plots at ground level, separating forbs from grasses, drying to a constant weight at 50 C, and weighing. Leafy spurge was mea-

sured by totaling stem heights (hereafter referred to as stem length density with units: centimeters per square meter) within the inner 85- by 85-cm plot area.

Analysis

We used a few different forms of Equations 1 and 2 to predict the SPRE data. Leafy spurge stem length density in monocot herbicide-treated plots was predicted with a version of Equation 1, while grass biomass in dicot herbicide-treated plots was predicted with two versions of Equation 2.

For all accuracy assessments, biomass produced by species other than leafy spurge or grasses was grouped with grasses when predicting leafy spurge stem length density and was grouped with leafy spurge when predicting grass biomass. We also evaluated the reverse grouping procedure (i.e., grouping other-species biomass with grass when predicting grass and with leafy spurge when predicting leafy spurge), and it did not substantially affect our results. When grouping other-species biomass with leafy spurge, a linear regression relationship was used to convert biomass to equivalents of leafy spurge stem length density ($n = 51$, $R^2 = 0.62$). Data for the regression came from untreated SPRE plots and plots used for developing Equations 1 and 2 (Rinella and Sheley 2005a).

Zero-growth isoclines of Equations 1 and 2 are given by Equations 3 and 4, respectively:

$$w = w_{\max}(1 + \alpha g)^{-1} \quad [3]$$

$$g = g_{\max}(1 + \beta w)^{-1} \quad [4]$$

These equations describe the relationship between leafy spurge and grass abundances at carrying capacity. Competition parameters were estimated from two field experiments ($\alpha = 0.00055$, $\beta = 0.0088$) (Rinella and Sheley 2005a). Site-specific estimates of w_{\max} and g_{\max} were used for all accuracy assessments. These parameters were estimated by assuming untreated SPRE plots were at equilibrium and then solving zero-growth isoclines for the carrying capacity terms:

$$w_{\max,i} = \overline{w_{\text{untreat},i}}(1 + \alpha \overline{g_{\text{untreat},i}}) \quad [5]$$

$$g_{\max,i} = \overline{g_{\text{untreat},i}}(1 + \beta \overline{w_{\text{untreat},i}}) \quad [6]$$

The untreat subscripts denote untreated plots, the bars indicate means over untreated plots, and the i 's are experiments.

Approximately 1.5 growing seasons transpired between herbicide application (i.e., plant removals) and grass and leafy spurge measurement. Therefore, we projected plant abundances for 1.5 growing seasons with equations analogous to Equations 1 and 2:

$$\ln(w_{s,i}) = \ln \left[\overline{w_{\text{untreat},i}} \exp \left\{ r_w \left[1 - \frac{\overline{w_{\text{untreat},i}}(1 + \alpha \overline{g_{s,i}})}{w_{\max,i}} \right] \right\} \right] \quad [7]$$

$$\ln(g_{p,i}) = \ln \left[\overline{g_{\text{untreat},i}} \exp \left\{ r_g \left[1 - \frac{\overline{g_{\text{untreat},i}}(1 + \beta \overline{w_{p,i}})}{g_{\max,i}} \right] \right\} \right] \quad [8]$$

We worked with the natural logs of both sides of the equations because we assumed error variances to be log-normally distributed (Rinella and Sheley 2005a). Growth rate parameters were estimated from two field experiments ($r_w = 1.5$, $r_g = 0.8$) (Rinella and Sheley 2005a). The p and s subscripts

denote picloram- and sethoxydim-treated plots, respectively, at the end of SPRE i . Sethoxydim reduced grass biomass production halfway through the growing season (i.e., at $t = 0.5$), and leafy spurge was then allowed to equilibrate to grass removal for the next 1.5 growing seasons; therefore, $w_{s,i} \approx w_{t+2,i}$. We assumed untreated plots were at competitive equilibrium and used the approximations $w_{\text{untreat},i} \approx w_{t,i} \approx w_{t+1,i} \approx w_{t+2,i}$ in assessing the predictive ability of Equation 7. Grass biomass was measured at $t + 2$ but not at $t + 1$. Sethoxydim dramatically reduced grass production throughout the experiments, which allowed us to reasonably assume the following: $g_{s,i} \approx g_{t+1,i} \approx g_{t+2,i}$. The same logic was used for estimating dependent and independent variables of Equation 8: $g_{p,i} \approx g_{t+2,p}$, $g_{\text{untreat},i} \approx g_{t,i} \approx g_{t+1,i} \approx g_{t+2,p}$, $w_{p,i} \approx w_{t+1,i} \approx w_{t+2,i}$.

The above SPRE-based assessment of Equation 8 relied on observed leafy spurge measurements. These fairly precise leafy spurge observations were critical for testing Equation 8 because large observation variances would mask inadequate features of the equation. Observed leafy spurge data cannot, however, be used to test the equation's predictions of grass response to herbicide use. When predicting grass response to herbicide use, leafy spurge mortality has to be predicted (i.e., it is unobservable prior to herbicide application). We used the following version of Equation 8 to assess how accurately our model predicted grass response to a widely used leafy spurge herbicide (i.e., picloram):

$$\begin{aligned} & \ln(g_{p,i}) \\ &= \ln \left[\overline{g_{\text{untreat},i}} \exp \left\{ r_g \left[1 - \frac{\overline{g_{\text{untreat},i}}(1 + \beta \overline{w_{\text{untreat},i} \bar{k}})}{g_{\max,i}} \right] \right\} \right] \quad [9] \end{aligned}$$

The parameter $\bar{k} = w_{p,i} / \overline{w_{\text{untreat},i}}$ describes leafy spurge mortality caused by picloram. Specifically, \bar{k} is the proportional reduction in leafy spurge stem length density production averaged over all i 's (except for grass biomass for the i being predicted). This method formulates grass biomass predictions solely in terms of quantities observable prior to herbicide application.

Herbicide Experiments

Several experiments have evaluated the efficacy of leafy spurge herbicides (Gylling and Arnold 1985; Hein 1988; Lym 2000; Lym and Messersmith 1985, 1994; Markle and Lym 2001; Maxwell 1984; Vore 1984). Equations analogous to Equation 2 were evaluated using data from these experiments. Each herbicide experiment consisted of untreated plots and plots treated with dicot-specific herbicides (Table 1). Data came from 14 sites, and many sites were measured during multiple years. Individual predictions were formulated for each year's data (i.e., data were not averaged across years).

Some herbicide experiments reported data on leafy spurge and grasses only (Table 1). In other cases, other-species data were also reported, and these data were grouped with leafy spurge data. Other-species biomass data were converted to equivalents of leafy spurge stem length density using the previously described linear regression relation. This relationship was also used for converting leafy spurge biomass to units of stem length density.

Insufficient information on the timing of herbicide applications prevented us from testing the population growth

TABLE 1. Site locations, grass species naturally present at sites, treatment descriptions, and plant abundances (leafy spurge stem length density, grass biomass, and biomass of all other plant species) for leafy spurge experiments.

Citations	Approximate locations	Treatments		Naturally occurring grasses	Plant abundance means and (standard deviations)					
		Herbicide ^a			Untreated control		Treated			
		Grass	Leafy Spurge seeding		Leafy spurge (cm m ⁻²)	Grass (g m ⁻²)	Other (g m ⁻²)	Leafy spurge (cm m ⁻²)	Grass (g m ⁻²)	Other (g m ⁻²)
1 ^b	Big Timber, MT	Y ^c	N	n, p, w ^d	5,265 (1,467)	80 (19)	11 (7)	6,767, e,f 0	12, e 141	1, e 0
1	Deer Lodge, MT	Y	N	n, p, w	4,012 (155)	38 (16)	0	7,602, 51	0, 85	0, 0
1	Deer Lodge, MT	Y	N	p	2,276 (162)	50 (16)	2	3,234, 0	0, 109	0, 0
1	Deer Lodge, MT	Y	N	p	5,897 (2,399)	195 (29)	3 (3)	10,556, 23	3, 303	1, 5
1	Deer Lodge, MT	Y	N	p, w	6,056 (f)	223 (f)	6 (f)	9,659, 33	16, 185	18, 0
1	Florence, MT	Y	N	p, w	2,896 (752)	103 (16)	19 (2)	1,978, 0	0, 216	0, 0
1	Florence, MT	N	N	p, w	5,471 (4,245)	146 (37)	30 (8)	m, g 0	m, 356	m, 0
1	Florence, MT	Y	N	j, p, w	4,350 (360)	176 (15)	26 (1)	4,465, 0	0, 327	0, 0
1	Florence, MT	Y	N	p, w	4,931 (485)	112 (35)	17 (20)	5,405, 0	0, 323	0, 0
1	Florence, MT	Y	N	j, p, w	1,256 (186)	43 (46)	54 (0.4)	1,925, 0	0, 149	0, 0
1	Florence, MT	Y	N	p	16,840 (1,790)	43 (11)	0	14,150, 0	7, 186	0, 0
1	Florence, MT	Y	N	p	10,823 (1,920)	82 (9)	0	14,220, 0	13, 168	0, 0
1	S of Bozeman, MT	Y	N	p	8,899 (1,436)	45 (9)	18 (5)	5,502, 105	2, 111	16, 8
1	S of Bozeman, MT	Y	N	b	4,830 (690)	27 (2)	21 (5)	7,084, 27	2, 32	1, 2
1	S of Bozeman, MT	Y	N	p, w	7,022 (f)	12 (f)	34 (f)	7,673, 209	9, 103	6, 7
1	SE of Bozeman, MT	Y	N	p, w	4,865 (3,747)	106 (33)	25 (6)	6,152, 0	0, 201	4, 0
1	SE of Bozeman, MT	Y	N	j, p	7,075 (f)	87 (f)	0	15,135, 0	0, 172	0, 0
1	SE of Bozeman, MT	Y	N	p	9,527 (2,797)	32 (45)	47 (58)	12,955, 20	0, 149	5, 0
1	SE of Bozeman, MT	Y	N	p	10,428 (1,846)	33 (11)	9 (4)	8,622, 0	0, 112	0, 0
1	SE of Bozeman, MT	Y	N	b, p	8,969 (106)	58 (7)	22 (31)	21,972, 0	0, 153	0, 0
2	Crook CO, WY	N	N	a, g, j, p, w	5,492 (936)	67 (22)	nr ^h	1,619 (1,366)	114 (36)	nr
2	Johnson CO, WY	N	N	a, g, i, n, t, w	3,150 (401)	171 (12)	nr	1,286 (909)	355 (29)	nr
3	Grass Range, MT	N	N	c, d, i, n, o, p, v, w, x	1,662 (1,570)	138 (35)	9 (7)	269 (527)	166 (36)	0.1 (0.4)
4	Woonsocket, SD	N	N	e, l, m, p, s, t	3,637 (nr)	140 (nr)	nr	1,262 (2,014)	234 (65)	nr
5	McLeod, ND	N	N	d, e, p, s, w	2,783 (644)	42 (9)	nr	524 (720)	60 (22)	nr
5	Valley City, ND	N	N	d, e, p, s, w	1,104 (588)	56 (43)	nr	165 (170)	81 (36)	nr
5	Valley City, ND	N	N	d, e, p, s, w	2,919 (1,337)	26 (22)	nr	546 (445)	47 (25)	nr
6	Grass Range, MT	N	N	b, f, h, i, l, p	2,703 (203)	66 (16)	nr	1,435 (1,224)	148 (31)	nr
7	Chaffee, ND	N	N	p, w	1,438 (784)	159 (45)	1 (3)	896 (689)	173 (43)	3 (9)
7	Valley City, ND	N	N	d, e, s, w	4,948 (1,185)	141 (70)	7 (6)	1,564 (1,020)	230 (72)	4 (7)
8	Fargo, ND	N	Y	nr	2,602 (1,428)	69 (19)	nr	1,323 (1,419)	221 (136)	nr
8	Jamestown, ND	N	Y	nr	1,490 (602)	180 (155)	nr	747 (508)	222 (118)	nr
9	Fort Ransom, ND	N	N	s, w	3,089 (1,031)	215 (63)	nr	219 (141)	314 (78)	nr
9	Jamestown, ND	N	Y	p	3,114 (2,018)	234 (81)	nr	290 (181)	265 (54)	nr
9	Walcott, ND	N	Y	s, w	3,215 (2,338)	159 (70)	nr	228 (182)	269 (125)	nr
10	ND ⁱ	N	N	d, e, g, p, s, w	3,988 (nr)	191 (nr)	nr	917 (856)	245 (20)	nr

rate parameter of Equation 2 (r_g). Therefore, our approach was to test the zero-growth isocline of this equation (i.e., Equation 4). A fair test of Equation 4 requires data from grass populations that are at equilibrium. Highly suppressed grass populations may sometimes require more than one growing season to fully equilibrate to leafy spurge removal. Therefore, to better ensure that Equation 4 was tested against equilibrium data, grass data from the year of herbicide application were omitted from the accuracy evaluation.

Site-specific grass carrying capacities were estimated with data from a randomly selected herbicide treatment by solving Equation 4 for g_{\max} :

$$\ln(g_{\max,i,t}) = \frac{1}{n_k} \sum_{k=1}^{n_k} \ln[g_{i,k,t}(1 + \beta w_{i,k,t})] \quad [10]$$

The i 's are sites, the t 's are years, and n_k is the number of replications. Data used for estimating $\ln(g_{\max,i,t})$ were omitted from the accuracy evaluation. Including these data would have overestimated prediction accuracy, because independent and dependent variable values would then be calculated from the same data points.

Site-specific $\ln(g_{\max,i,t})$ values were estimated exclusively from data collected during the year after herbicide application. Therefore, when data collection occurred beyond the year after herbicide application, we predicted future grass biomass using only predictor data that were available during the present year (i.e., $g_{t=x} = f(g_{\max,t<x})$).

Predicted values were calculated for treated plots

$$\ln(g_{\text{treat},i,t=1 \text{ or } t>1}) = \frac{1}{n_{\text{treat}}} \frac{1}{n_k} \sum_{j=1}^{n_{\text{treat}}} \sum_{k=1}^{n_k} \ln\left(\frac{g_{\max,i,j,k,t=1}}{1 + \beta w_{\text{treat},i,j,k,t=1 \text{ or } t>1}}\right) \quad [11]$$

and untreated plots

$$\ln(g_{\text{untreat},i,t=1 \text{ or } t>1}) = \frac{1}{n_k} \sum_{k=1}^{n_k} \ln\left(\frac{g_{\max,i,k,t=1}}{1 + \beta w_{\text{untreat},i,k,t=1 \text{ or } t>1}}\right) \quad [12]$$

The total number of herbicide treatments minus the treatment used for estimating $\ln(g_{\max,i,t})$ is denoted by n_{treat} . Predictions were averaged across replications and, in the case of herbicide-treated plots, across treatments. Mean predictions were compared to mean observed values. Means were used because g_{\max} varies dramatically from plot to plot (Table 1). By averaging over small-scale variation in g_{\max} , we more accurately assessed the ability of Equation 4 to predict

mean grass biomass across management units. In our opinion, basing management decisions on average management unit responses is more logical than basing decisions on the response of some number of small plots within management units.

A second accuracy assessment was also based on herbicide experiment data. We exclusively used past-year untreated plot data to predict current-year herbicide-treated grass biomass:

$$\ln(g_{\text{treat},i,t>1}) = \frac{1}{n_k} \sum_{k=1}^{n_k} \ln\left(\frac{g_{\max,i,k,t=1}}{1 + \beta w_{\text{untreat},i,k,t=1} \bar{k}}\right) \quad [13]$$

Grass carrying capacity was estimated from untreated plot data using Equation 10. The \bar{k} term denotes mean proportional leafy spurge mortality over all herbicide-treated plots with the exception of data from Experiment i . This accuracy assessment is analogous to how we envision managers might use Equation 4 to predict grass response to herbicides.

Grass Seeding Experiments

We tested a version of Equation 1 using data from two experiments that combined 2,4-D and glyphosate applications with tillage and grass seeding or no grass seeding (Lym and Tober 1997) (Table 1). These experiments did not report leafy spurge stem length density. We converted leafy spurge biomass to units of stem length density using the previously described regression relationship. Leafy spurge carrying capacity was estimated from not-seeded plot data by solving Equation 3 for $\ln(w_{\max,i,t})$:

$$\ln(w_{\max,i,t}) = \frac{1}{n_k} \sum_{k=1}^{n_k} \ln[w_{\text{unseeded},i,k,t}(1 + \alpha g_{\text{unseeded},i,k,t})] \quad [14]$$

Data for estimating $\ln(w_{\max,i,t})$ were collected 2 and 3 yr after the application of 2,4-D and glyphosate. Leafy spurge populations typically recover from exposure to these herbicides within 2 yr of application (Chow 1984; Ferrell et al. 1989; Lym and Messersmith 1985).

Predicted leafy spurge values were calculated for each seeded grass species (i.e., each j) as follows:

$$\ln(w_{i,j,t+1}) = \ln\left[\frac{1}{n_k} \sum_{k=1}^{n_k} w_{i,j,k,t} \exp\left\{r w \left[1 - \frac{w_{i,j,k,t}(1 + \alpha g_{i,j,k,t+1})}{w_{\max,i,t+1}}\right]\right\}\right] \quad [15]$$

←

^a These columns indicate the species targeted by the herbicide.

^b 1 = Selective Plant Removal Experiment (see text), 2 = Vore 1984, 3 = Maxwell 1984, 4 = Gylling and Arnold 1985, 5 = Lym and Messersmith 1985, 6 = Hein 1988, 7 = Lym and Messersmith 1994, 8 = Lym and Tober 1997, 9 = Lym 2000, 10 = Markle and Lym 2001.

^c Y indicates that a treatment type was used, and N indicates that it was not.

^d a = downy brome (*Bromus tectorum*), b = bluebunch wheatgrass (*Pseudoroegneria spicata*), c = *Carex* spp., d = crested wheatgrass (*Agropyron cristatum*), e = big bluestem (*Andropogon gerardii*), f = desert wheatgrass (*Agropyron desertorum*), g = blue grama (*Bouteloua gracilis*), h = needle and thread (*Hesperostipa comata*), i = prairie junegrass (*Koeleria macrantha*), j = Japanese brome (*Bromus japonicus*), l = slender wheatgrass (*Elymus trachycaulus*), m = little bluestem (*Schizachyrium scoparium*), n = green needlegrass (*Nassella viridula*), o = orchardgrass (*Dactylis glomerata*), p = *Poa* spp., r = Canada wildrye (*Elymus canadensis*), s = smooth brome (*Bromus inermis*), t = switchgrass (*Panicum virgatum*), v = plains reedgrass (*Calamagrostis montanensis*), w = western wheatgrass (*Pascopyrum smithii*), x = timothy (*Phleum pratense*).

^e First number within column refers to sethoxydim-treated plots; second number refers to picloram-treated plots.

^f Standard deviation not calculable because mean reflects one observation.

^g Missing data.

^h Not reported.

ⁱ Combined data from Walcott and Valley City, ND.

Measures of Model Performance

Model Accuracy

We used two classes of tests for assessing the model. The first type of test evaluated whether the model was realistic. Do curves generated with the model match the data? Are the parameter estimates realistic? When conducting these kinds of tests, it is best to use data with minimal measurement error, even if it means conducting tests with slightly abstract interpretations (e.g., using data from a given year and site to predict other data gathered during the same year and at the same site). It is much more difficult to identify unrealistic features of models when the accuracy assessment data are imprecise because measurement error and temporal and spatial variation tend to mask problems with the model.

We graphed model predictions vs. observed data to assess whether the model was realistic. Because current-year data were often the most accurate data available, we sometimes relied on data from a given year and site to formulate predictions of plant abundances for that same year and site. As such, the graphs are designed for identifying realistic and unrealistic features of the model, and they only indirectly assess the model's ability to predict future weed management outcomes.

If the model structure or parameter estimates are unrealistic, slopes of predicted vs. observed relationships might differ significantly from 1.0. We used a bootstrap procedure to test the null hypothesis that predicted vs. observed slopes are equal to 1.0 (Efron and Tibshirani 1993; Hjorth 1994). Cases were randomly sampled with replacement (i.e., each case could be selected multiple times) to construct bootstrap samples with n equal to the original number of data points. A linear regression relationship was fitted to 10,000 of these bootstrap samples, and the resulting empirical histogram of slope coefficients was compared to 1.0. If the least-squares estimate of the slope term was <1.0 , then the following quantity was interpreted as the P value of the null hypothesis: $2 \times ((\text{number of bootstrap samples} > 1.0)/10,000)$. If the slope estimate was >1.0 , then $2 \times (1.0 - (\text{number of bootstrap samples} > 1.0)/10,000)$ was interpreted as the P value.

Model Predictive Capability

Even if our model is quite realistic, it may still be inferior to off-site experiments at predicting grass and leafy spurge responses to management. The model formulates predictions from on-site data. If these data have large observation variances or are biased, then prediction accuracy could be very poor even if the model is good. Also, if management units are similar to sites where the experiments take place, then experiments might predict management unit responses quite accurately. In this case, slight imperfections in the model or measurement error might cause model-based predictions to be inferior to predictions based on off-site experiments. If off-site experiments predict grass and leafy spurge abundances more accurately than the model does, then the previously outlined extrapolation problems are not severe enough to warrant use of the model, and predictions based on off-site experiments would be preferred.

A second class of test was used to compare model-based predictions to predictions based on off-site experiments. Model predictions were formulated with Equations 7, 9, and

13. Equations 8, 11, 12, and 15 were useful for evaluating model accuracy, but predictions based on these equations were not tested against predictions based on off-site experiments. A test of Equation 8 would be highly redundant with a test of Equation 9, and a test of Equation 11 would be redundant with a test of Equation 13. A test of Equation 12 would compare experiment- and model-based predictions of grass biomass production in untreated control plots. Such a test would be of little relevance to managers that are trying to predict grass response to leafy spurge control efforts. Using Equation 15 to predict how grass seeding will affect leafy spurge production requires an estimate of how seeding will affect grass production at the site of interest. Because grass response to grass seeding is unknown before grasses are seeded, it is unclear how Equation 15 could be used to formulate future predictions of leafy spurge response to grass seeding. Equation 15 is used to predict leafy spurge response to several seeded grass species. Therefore, the Equation 15 test is well-suited for determining if spatial and temporal variation in grass species compositions affects our model's predictive capability.

We used an index similar to the coefficient of determination (R^2) to compare model predictions with predictions based on off-site experiments:

$$V = 1 - \frac{\frac{1}{n} \sum_{i=1}^n (Y_i^* - Y_{\text{obs},i})^2}{\frac{1}{n} \sum_{i=1}^n (\bar{Y}_i - Y_{\text{obs},i})^2} \quad [16]$$

Predicted values (Y^*) were formulated with our model, Y_{obs} 's are "predictee" values, and \bar{Y} is the mean over plots receiving the same or similar treatments as Y_{obs} but at other sites. The mean-square error that results from predicting plant abundances at a given site from experiments conducted elsewhere is given by the denominator of Equation 16, and the mean-square error that results from using the model is given by the numerator. The index V describes variation explained by the model that is not explained by experiments conducted at other sites. If the value of V is positive, the model has probably addressed one or more of the extrapolation problems.

For the accuracy assessment involving Equation 7, Y_i^* is predicted leafy spurge stem length density for the monocot herbicide-treated plot of SPRE i , and $Y_{\text{obs},i}$ is the corresponding observed value. The term \bar{Y} denotes mean leafy spurge stem length density over all monocot herbicide-treated plots (except for the monocot herbicide-treated plot at SPRE i), and n is the total number of SPREs. The calculation of V for Equation 9 was the same as that for Equation 7, except that Y^* , Y_{obs} , and \bar{Y} were predicted and observed grass biomasses in dicot herbicide-treated plots. For the V calculation involving Equation 13, \bar{Y} was grass biomass data averaged across all herbicide-treated plots, except for the plots being predicted.

Results and Discussion

Using Grass Data to Evaluate the Model

Model Evaluation Using Grass Data from SPRE

Picloram-treated plots produced more grass biomass than did untreated plots in all but one SPRE (Table 1). Lower

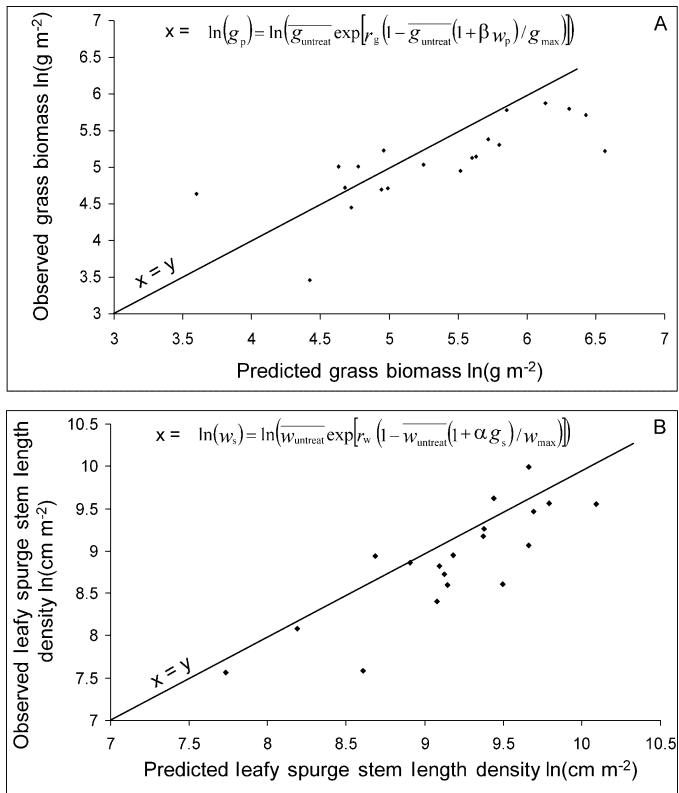


FIGURE 1. Predicted vs. observed data from selective plant removal experiments. Each data point within a graph is from a different experiment. (A) Grass biomass in plots treated with a dicot-specific herbicide (g_p , p denotes picloram) is modeled as a function of grass population growth rate (r_g), a leafy spurge competition parameter (β), grass biomass in untreated plots (g_{untreat}), leafy spurge stem length density in dicot herbicide-treated plots (w_p), and grass carrying capacity estimated from untreated plots (g_{max}). (B) Leafy spurge stem length density in plots treated with a monocot-specific herbicide (w_s , s denotes sethoxydim) is modeled as a function of the leafy spurge population growth rate (r_w), a grass competition parameter (α), leafy spurge stem length density in untreated plots (w_{untreat}), grass biomass in monocot herbicide-treated plots (g_s), and leafy spurge carrying capacity estimated from untreated plots (w_{max}).

grass production in the one SPRE was likely due to picloram injury of grasses, plot-to-plot variation in grass carrying capacities, absence of leafy spurge competition with grasses, or mutualism between leafy spurge and grasses. A plot of predicted vs. observed grass data shows that Equation 8 tended to overpredict the data (Figure 1A). The hypothesis test of the predicted vs. the observed slope being equal to 1.0 confirms this assessment; we rejected this hypothesis ($P = 0.02$).

Many factors could have caused the overpredictions. Perhaps competition at most SPRE sites was more intense than was competition at the site where the model was developed. Or, maybe the structure of the model that gives rise to the data varies spatially. If either of these explanations caused the overpredictions, then the model will probably tend to slightly overpredict grass biomass production. Another possibility is that the population growth rate at most SPRE sites is greater than at the site where the model was developed. If this is true, the model will tend to overpredict grass biomass production in the first few growing seasons following severe leafy spurge mortality events, but the predictions will become more accurate as grasses fully equilibrate to leafy spurge removal.

Other plausible explanations for lack of fit have nothing

to do with parameter variation. Vore (1984) found that leafy spurge roots often survived exposure to picloram, even when aboveground biomass production was completely suppressed. If leafy spurge roots survived, they may have continued to compete with grasses for soil resources after picloram was applied. Picloram sometimes injures grasses, and this, too, could explain the overpredictions.

Although the model tended to overpredict SPRE grass data (Figure 1A), it still predicted SPRE grass biomass more accurately than did off-site experiments. Because the value of V for Equation 9 is 0.21, the model explains 21% of the variation in grass biomass production that is left unexplained by off-site SPREs.

All data for calculating V for Equation 9 were measured during the same year, so error owing to temporal variation was ignored. Factoring out temporal variation may have caused the mean-square errors to be underestimated. Temporal variation would likely have a similar effect on mean-square errors resulting from model-based predictions and experiment-based predictions. Therefore, temporal variation would probably not dramatically affect V , which is the ratio of the mean-square errors.

Model Evaluation Using Grass Data from Herbicide Experiments

Leafy spurge herbicides increased grass production at all herbicide experiment sites (Table 1). On the basis of Figure 2, the model did not systematically over- or underpredict grass biomass production at herbicide experiment sites. Because we failed to reject the null hypothesis that the slope is equal to 1.0 ($P = 0.47$), we believe that the model was an unbiased predictor of grass biomass at these sites.

The model tended to outperform off-site experiments in predicting grass biomass at herbicide experiment sites. The model explained $V = 48\%$ of the variation in grass biomass that could not be explained by the off-site herbicide experiments. The V estimate for Equation 11 constitutes a very realistic test of the model because future predictions were formulated exclusively from presently available data.

Using Leafy Spurge Data to Evaluate the Model

Model Evaluation Using Leafy Spurge Data from SPRE

Plots treated with sethoxydim produced more leafy spurge than did untreated plots in all but four SPREs (Table 1). Reduced leafy spurge production in the four SPREs was probably due to sethoxydim injury of leafy spurge, plot-to-plot variation in leafy spurge carrying capacities, absence of grass competition with leafy spurge, or mutualism between grasses and leafy spurge.

The model appeared to slightly overpredict the leafy spurge data (Figure 1B). We concluded that the overpredictions were not statistically significant because the null hypothesis that the predicted vs. observed slope is equal to 1.0 was not rejected ($P = 0.73$).

Average off-site leafy spurge data did not predict leafy spurge stem length density as accurately as did Equation 7 ($V = 0.53$). Like the Equation 9 V estimate, the Equation 7 V estimate relied on predicted and observed data that were measured during the same growing season. An additional abstraction in calculating V for Equation 7 was that the grass

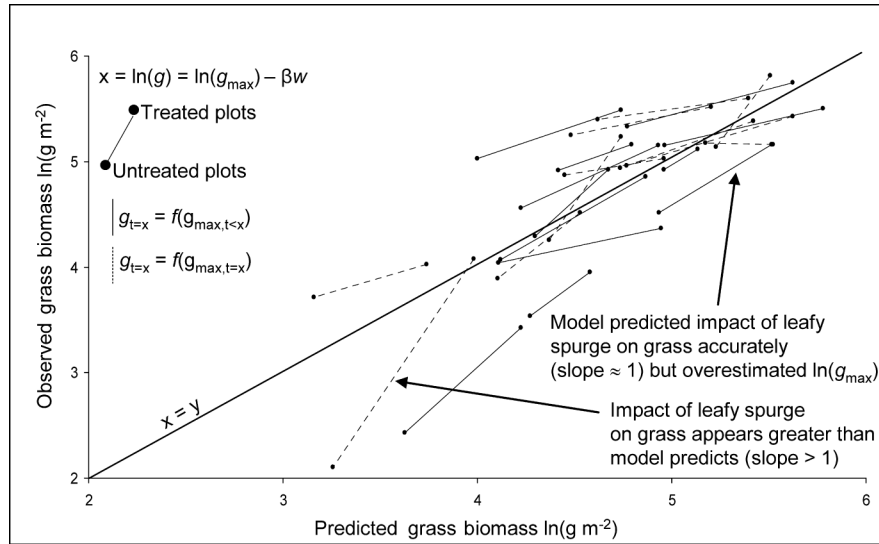


FIGURE 2. Predicted vs. observed grass biomass data from herbicide experiments. Each set of connected points is from a unique combination of site and year. Grass biomass (g) is modeled as a function of leafy spurge stem length density (w), a leafy spurge competition parameter (β), and site-specifically estimated grass carrying capacity (g_{max}).

mortality data were observed in contrast to being predicted from other sites. We chose a test of model accuracy, as opposed to a more realistic test of the model's predictive capability, because it is highly unlikely that managers would use the model to predict leafy spurge response to intentional grass removal with herbicides.

Model Evaluation Using Leafy Spurge Data from Grass Seeding Experiments

Grass seeding decreased leafy spurge production (Table 1). Equation 15 appeared to systematically underpredict data from some site-year combinations and overpredict data from other site-year combinations (Figure 3). The null hypothesis that the predicted equaled observed slope was equal to 1.0 was rejected ($P = 0.0001$). Prediction error could have resulted from between-site differences in leafy spurge

population growth rates, between-site differences in competitive relationships, or error in the relationship we used to convert leafy spurge biomass to units of stem length density. Equation 15 appeared to predict leafy spurge response to all grass species with similar accuracy.

Summary

Our model is given by Equations 1 and 2. This model tends to outperform mean data from off-site experiments at predicting grass and leafy spurge abundances (i.e., $V > 0$). Therefore, we believe the model could improve on our current ability to predict weed management outcomes.

Several factors distort the view of model accuracy given by Figures 1–3, and these same factors affect V estimates. Predictor and response data were often measured during the same growing season or sometimes even in the same plots,

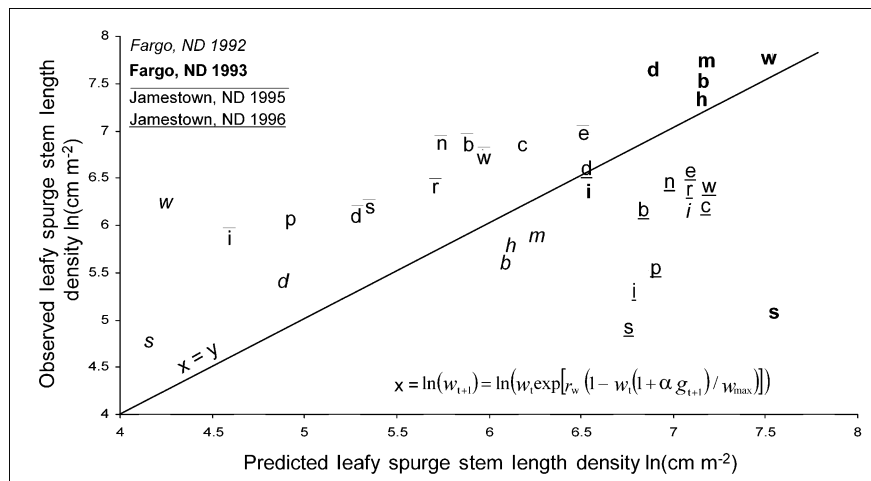


FIGURE 3. Predicted vs. observed leafy spurge data from grass seeding experiments. Each data point is from a unique combination of site, year, and grass species. Seeded grasses were commercial varieties of *Elymus* spp. (m, b, d, r), smooth brome (s), western wheatgrass (w), slender wheatgrass (e), green needlegrass (n), crested wheatgrass (c), and intermediate wheatgrass (i, p). Current-year leafy spurge stem length density in plots seeded with grasses (w_{t+1}) is modeled as a function of the leafy spurge population growth rate (r_w), a grass competition parameter (α), previous-year leafy spurge stem length density (w_t), current-year grass biomass (g_{t+1}), and leafy spurge carrying capacity estimated from unseeded plots (w_{max}).

so error owing to temporal and spatial variation is under-represented. An exception to this is the V value estimated from herbicide experiment data (see Equation 11). Also, because the model predicted spatially varying plot data, the figures illustrate error resulting from plot-to-plot variation in the response variable. In practical applications, the model would most likely be used to predict mean grass and leafy spurge abundances over entire management units (i.e., fixed response variables). Finally, measurement error, grass injury by dicot herbicides, leafy spurge injury by monocot herbicides, aboveground leafy spurge mortality that was not proportional to belowground mortality, and the imperfect regression relationship used to relate leafy spurge biomass to stem length density could have inflated prediction error. Imperfections in the accuracy assessment data sets, though a major source of annoyance in testing the model, would not always cause prediction error when using the model to predict weed management outcomes.

Our analysis did not conclusively identify the major sources of prediction error. Much of the error could have resulted from unaddressed or insufficiently addressed extrapolation problems or random error. Alternatively, the majority of the error could have resulted from imperfections of the accuracy assessment data sets. We can use properties of the accuracy assessments to speculate about which extrapolation problems may have caused substantial error. Without question, equilibrium plant abundances and carrying capacities vary temporally (Rinella and Sheley 2005a), but temporal variation could have manifested itself in a portion of only one accuracy assessment (Figure 2, solid lines, and V calculated from the herbicide experiment data). In all other accuracy assessments, the data for estimating carrying capacities (i.e., predictor data) were gathered during the same year as the observed data (i.e., predictee data). Temporally varying carrying capacities caused prediction error, but so did other sources of error.

On the basis of Figure 3, we strongly suggest that expressing competitive effects on a per-unit plant abundance basis circumnavigates the need to model grass species separately. No “by-species” patterns of over- or underprediction are evident in Figure 3. Other studies support the notion that a gram of plant biomass suppresses neighboring plants similarly, regardless of which species produces the gram (Aguiar et al. 2001; Goldberg 1987; Mitchell et al. 1999; Peltzer and Kochy 2001; Rinella and Sheley 2005b).

If the structure of the model is inaccurate or if an appropriate structure at one site is not necessarily an appropriate form elsewhere, systematic deviations about $x = y$ lines (Figures 1–3) would result. Systematic prediction error was not apparent in Figure 1B or Figure 2, but possible biases are depicted at the upper end of the X plane in Figure 1A and in the lower portion of the plane in Figure 3. However, because so many factors could have caused systematic errors, it is impossible to attribute these errors to any one cause. There is no strong evidence that the model structure is inaccurate, and therefore, we conclude that the model could at least partially alleviate the nonlinearity problem.

On the basis of the slopes of lines connecting untreated plot data to treated plot data, the competition problem may have been a significant source of prediction error (Figure 2). Depending on site and year, competition appeared to be more (slope > 1.0) or less (slope < 1.0) intense than the

model predicted. However, we cannot rule out the possibility that variation in slope resulted from between-plot variation in grass carrying capacity, unintended herbicide injury, measurement error, or other previously discussed factors, rather than variation in competition intensity.

If competition intensity does vary spatially or temporally, one covariate that could explain this variation might involve small-scale spatial structuring of leafy spurge and grass populations. Our model is based on the assumption that spatial structuring is invariant across sites and years or, if variable, that it does not affect competition intensity (Pacala 1997). A second covariate might be an overall plant productivity term. Whether competition intensity increases in magnitude (Grime 2001; Keddy 2001) or remains similar (Newman 1973; Wilson and Tilman 1991) as productivity increases is a point of contention among ecologists. We did not observe a pattern when we used the herbicide experiment data to plot competition intensity vs. plant productivity (data not shown). Therefore, we do not believe competition intensity varies widely over the productivity range that leafy spurge invades, or at least over the productivity range within which herbicides are tested.

Variation in population growth rates could be a substantial source of error in Figures 1 and 3 (Figure 2 does not assess the population growth rate parameter). Our model assumes that asymptotic approaches to carrying capacity are the same for all grass species and within all environments. The model is also based on the assumption that population growth is not influenced by plant stage class structuring (e.g., 1 cm of leafy spurge seedling height is equivalent to 1 cm of flowering stem height) or that the populations always have a stable stage class distribution. When modeling communities that are not near equilibrium, such as communities in which biological control or herbicides have recently induced massive leafy spurge mortality, these assumptions are less likely to be valid, and if invalid, could be important sources of error. Further testing and elaboration of our model would benefit from experiments specifically designed to measure grass and leafy spurge population growth rates at a variety of sites, for a variety of grass species, and over several dissimilar growing seasons.

The dynamics of crop–weed systems have been studied much more thoroughly than the dynamics of weed-invaded natural systems. Therefore, invasive weed ecologists will profit greatly from the ideas, advancements, and conclusions of agro-ecologists. However, because perennial grasslands are so different from annual cropping systems, we cannot expect opportunities, challenges, and accomplishments of invasive weed ecology to completely mirror those of agro-ecology. We believe our analysis illustrates that attempts to predict population trajectories in perennial weed–dominated ecosystems may not culminate in the same pessimism that has resulted from similar attempts in annual weed–dominated croplands (Cousens and Mortimer 1995).

Acknowledgments

We thank R. G. Lym for the extensive use of his data and the USDA-ARS for funding.

Literature Cited

Aguiar, M. R., W. K. Lauenroth, and D. P. Peters. 2001. Intensity of intra- and interspecific competition in coexisting shortgrass species. *J. Ecol.* 89:40–47.

- Chow, P.N.P. 1984. Control of leafy spurge in pastures using dicamba and 2,4-D. *J. Range Manage.* 37:159–162.
- Cousens, R. 1985. A simple model relating yield loss to weed density. *Ann. Appl. Biol.* 107:239–252.
- Cousens, R. 1995. Can we determine the intrinsic dynamics of real plant populations? *Funct. Ecol.* 9:15–20.
- Cousens, R. and A. M. Mortimer. 1995. *Dynamics of Weed Populations*. Cambridge, Great Britain: Cambridge University Press.
- Efron, B. and R. Tibshirani. 1993. *An Introduction to the Bootstrap*. New York: Chapman & Hall.
- Eriksson, O. 1989. Seedling dynamics and life histories in clonal plants. *Oikos* 55:231–238.
- Ferrell, M. A., T. D. Whitson, and H. P. Alley. 1989. Control of leafy spurge (*Euphorbia esula*) with growth regulator–herbicide combinations. *Weed Technol.* 3:479–484.
- Firbank, L. G. and A. R. Watkinson. 1986. Modelling the population dynamics of an arable weed and its effects upon crop yield. *J. Appl. Ecol.* 23:147–159.
- Freckleton, R. P. and A. R. Watkinson. 1998. Predicting the determinants of weed abundance: a model for the population dynamics of *Chenopodium album* in sugar beet. *J. Appl. Ecol.* 35:904–920.
- Gaudet, C. L. and P. A. Keddy. 1988. Predicting competitive ability from plant traits: a comparative approach. *Nature* 334:242–243.
- Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. *Ecology* 68:1211–1223.
- Grime, J. P. 2001. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. 2nd ed. West Sussex, Great Britain: J. Wiley.
- Gylling, S. R. and W. E. Arnold. 1985. Efficacy and economics of leafy spurge (*Euphorbia esula*) control in pasture. *Weed Sci.* 33:381–385.
- Hein, D. G. 1988. Single and Repetitive Picloram Treatments on Leafy Spurge and Resulting Changes in Shoot Density, Canopy Cover, Forage Production and Utilization by Cattle. Ph.D. dissertation. University of Wyoming, Laramie, WY.
- Hjorth, J.S.U. 1994. *Computer Intensive Statistical Methods*. London: Chapman & Hall.
- Keddy, P. 2001. *Competition*. Boston, MA: Kluwer.
- Kropff, M. J. 1988. Modelling the effects of weeds on crop production. *Weed Res.* 28:465–471.
- Lym, R. G. 2000. Leafy spurge (*Euphorbia esula*) control with glyphosate plus 2,4-D. *J. Range Manage.* 53:68–72.
- Lym, R. G. and C. G. Messersmith. 1994. Leafy spurge (*Euphorbia esula*) control, forage production, and economic return with fall-applied herbicides. *Weed Technol.* 8:824–829.
- Lym, R. G. and C. G. Messersmith. 1985. Leafy spurge control and improved forage production with herbicides. *J. Range Manage.* 5:386–391.
- Lym, R. G. and D. A. Tober. 1997. Competitive grasses for leafy spurge (*Euphorbia esula*) reduction. *Weed Technol.* 11:782–792.
- Markle, D. M. and R. G. Lym. 2001. Leafy spurge (*Euphorbia esula*) control and herbage production with Imazapic. *Weed Technol.* 15:474–480.
- Maxwell, B. D. 1984. Changes in an Infested Plant Community after an Application of Picloram, the Effect of Glyphosate on Bud Dormancy, the Effect of Pulling and the Fuel Potential of Leafy Spurge (*Euphorbia esula* L.). M.S. thesis. Montana State University, Bozeman, MT.
- Mitchell, R. J., B. R. Zutter, D. H. Gjerstad, G. R. Glover, and C. W. Wood. 1999. Competition among secondary-successional pine communities. A field study of effects and responses. *Ecology* 80:857–872.
- Newman, E. I. 1973. Competition and diversity in herbaceous vegetation. *Nature* 244:310–311.
- Pacala, S. W. 1997. Dynamics of plant communities. Pages 532–555 in M. J. Crawley, ed. *Plant Ecology*. Cambridge, Great Britain: Cambridge University Press.
- Parker, I. M. 2000. Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecol. Appl.* 10:726–743.
- Peltzer, D. A. and M. Koehy. 2001. Competitive effects of grasses and woody plants in mixed-grass prairie. *J. Ecol.* 89:519–527.
- Ricker, W. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* 11:559–623.
- Rinella, M. J. and R. L. Sheley. 2005a. A model for predicting invasive weed and grass dynamics: I. Model development. *Weed Sci.* 53:586–593.
- Rinella, M. J. and R. L. Sheley. 2005b. Influence of soil water availability on competition among leafy spurge (*Euphorbia esula*) and grasses. *West. North Am. Nat.* 65:233–241.
- Shea, K. and D. Kelly. 2004. Modeling for management of invasive species: musk thistle (*Carduus nutans*) in New Zealand. *Weed Technol.* 18:1338–1341.
- Sheley, R. L. and J. K. Petroff. 1999. *Biology and Management of Noxious Rangeland Weeds*. Corvallis, OR: Oregon State University Press.
- Vore, R. E. 1984. Effect of Herbicide Treatments on Leafy Spurge Shoot and Root Control, Forage Production and Herbicide Residue. Ph.D. dissertation. University of Wyoming, Laramie, WY.
- Watkinson, A. R. 1981. Interference in pure and mixed populations of *Agrostemma githago* L. *J. Appl. Ecol.* 18:967–976.
- Werner, P. A. and H. Caswell. 1977. Population growth rates and age versus stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). *Ecology* 58:1103–1111.
- Wilson, S. D. and D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72:1050–1065.

Received November 17, 2004, and approved April 29, 2005.