



Forecasting the response of invasive plant-infested communities to management
by Matthew James Rinella

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Abstract:

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Mixtures of leafy spurge, Kentucky bluegrass and western wheatgrass were combined in two field experiments. Deterministic models describing competition among these species were selected and parameters were estimated by minimizing the sum of squared errors. Models that combined grass species biomasses predicted competition experiment plant abundances as accurately as models with separate terms for each grass. Predictive ability of models was further evaluated using data from herbicide, selective plant removal and grass seeding experiments. In most cases, predicted lines were centered on observed values, suggesting that there are no systematic differences between experiments used to develop the models and the naturally occurring plant communities used to evaluate the models.

Bayesian parameter estimation techniques were used to develop stochastic versions of the deterministic predictive models. These models formulate predictions of management-induced shifts in grass and leafy spurge abundances as probability distributions. Prior probability distributions for competition coefficients were developed from herbicide, grass seeding and selective plant removal experiments. These prior distributions and non-informative prior distributions describing other parameters were updated with data from competition experiments using likelihood functions. By using available data and quantifying remaining uncertainty, output from the stochastic models characterizes our current ability to predict management-induced shifts in leafy spurge and grass abundances.

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APPROVAL

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This dissertation has been read by each member of the dissertation committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Grass and invasive plant abundances shift in response to management. The magnitudes of these shifts are major factors that determine if an invasive plant management action is warranted. I developed models that predict the leafy spurge (*Euphorbia esula*) and perennial grass abundances that result from management actions. Model variables are plant abundances and parameters describe competitive relationships, intrinsic rates of population increase, random error, and within-management unit plant productivities.

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CHAPTER 1

USING RESEARCH RESULTS TO FORECAST INVASIVE PLANT AND GRASS
RESPONSE TO INVASIVE PLANT MANAGEMENTSummary

This chapter develops methods that quantify and reduce prediction error that results from using invasive plant experiments to predict plant biomass response to herbicide, biological control, seeding, and grazing in management settings. This development ignores native forbs, shrubs and other plants and focuses on perennial grasses and dicotyledonous invasive plants of grasslands. Ignoring plant groups causes major limitations, but additional levels of complexity (i.e. other groups of plants) can be incorporated into the framework developed in this chapter. It is logical to structure this chapter around a grass-dicotyledonous plant divide because many invasive plant management strategies differentially target these taxonomic groups. For example, herbicides that selectively kill dicotyledonous plants (both invasive and native) in grasslands are widely used to control invasive plants. Likewise, seeding of invaded communities has focused primarily on establishing grasses, while classes of livestock differentially target forbs (sheep), shrubs (goats) and grasses (cattle).

Introduction

Unintentionally introduced nonnative perennial dicotyledonous plants currently exist on millions of hectares of grasslands in North America and other continents and are

referred to as invasive plants when they become dominate constituents of plant communities (Sheley and Petroff 1999). In North America examples of these plants include leafy spurge (*Euphorbia esula*) and spotted knapweed (*Centaurea maculosa*).

Globally, managers rely extensively on herbicide, biological control, seeding, and grazing strategies to manage invasive plants. To optimize natural resource values, managers must predict how biomass per unit area (hereafter biomass) of invasive plants and plant species that grow in association with invasive plants will respond to these invasive plant management strategies.

Eight problems that hinder land managers attempts to use results from herbicide, biological control, seeding and grazing experiments to predict invasive plant and grass biomass in management units are described in the following sections. These problems cause prediction error when results from research are used to predict how grass and invasive plant biomass will respond to invasive plant management strategies. This chapter proposes methods that both quantify and reduce this prediction error. These methods rely on existing and future invasive plant research, sampling of management units and modeling techniques.

Efficacy Problem: Direct Effects of Management Strategies Vary

Vegetation response to experimental treatments varies temporally and spatially, which makes it difficult for managers to use research results to predict efficacy within management units. For example, the level of invasive plant control provided by herbicides is variable. Picloram (4-amino-3, 5, 6-trichloropicolinic acid), one of the most effective herbicides for managing leafy spurge, provided less than 5% control two

months after treatment in one experiment and 74% control 33 months after treatment in another experiment (Lym and Messersmith 1985b). Also, seeding of grass species can result in good, poor or no grass establishment in invasive plant-infested sites, depending on environmental conditions (Robocker et al. 1965, Call and Roundy 1991, Lym and Tober 1997, Velagala et al. 1997). Similarly, biological control agents can establish and reduce invasive plant populations considerably at some sites and fail to establish at other sites (Kirby et al. 2000, Clark et al. 2001). It has also been shown that the same species of grazing animal can consume different quantities of invasive plant biomass at different sites (Kronberg and Walker 1999). Temporal and spatial variation in efficacy of invasive plant management strategies causes uncertainty when results from invasive plant research are used to predict grass and invasive plant biomass within management units.

Nonlinearity Problem: Competitive Relationships are Nonlinear

The effect of the biomass or density per unit area of one plant species on the biomass of a competing plant species is rarely if ever linear, which makes it difficult to use experiment results to predict invasive plant and grass biomass within management units (Moolani et al. 1964, Coble and Ritter 1978, Buchanan et al. 1980, Goldberg 1987, Gaudet and Keddy 1988). For example, if the same nonlinear relationship describes competition at an experiment site and within a management unit, but invasive plant biomass within the two sites is different, removing 1000 kg ha⁻¹ of invasive plant biomass from the experiment site and the management unit will not cause the same change in grass biomass. In many situations competitive relationships must be quantified to successfully apply invasive plant research results to management units.

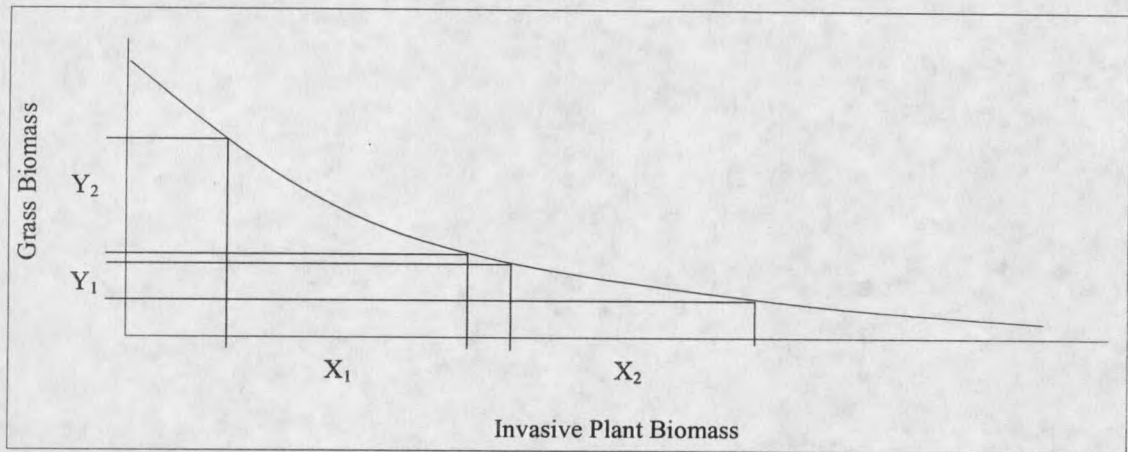


Figure 1.1. Hypothetical nonlinear relationship between invasive plant and grass biomass. The change in grass biomass (Y) resulting from a change in invasive plant biomass (X) depends upon the initial invasive plant biomass. In this example $X_1 = X_2$ but $Y_1 > Y_2$. Nonlinear relationships will complicate attempts to extrapolate results from an invasive plant experiment site to a management unit unless invasive plant biomass is the same in both places.

Sampling Problem: Management Unit Plant Biomasses Vary

Because it is impractical to measure plant biomass in large areas, biomass of invasive plants and grasses must be estimated from small representative areas of fixed size (i.e. samples) within management units (Sheley et al. 1997). Each sample provides an imperfect estimate of the true plant biomasses of the entire management unit. Imperfect knowledge of management unit biomasses will impede attempts to select optimal invasive plant management strategies. For example, estimates of changes in grass production resulting from invasive plant removal are subject to error because invasive plant biomass within management units is unknown. Livestock producers must accurately predict increases in forage production resulting from herbicide use to determine if herbicide use is cost effective (Griffith and Lacey 1991, Bangsund et al. 1996).

Competition Problem: Competition Intensity Varies

Competitive relationships partially determine how biomass production of particular species responds to removal or augmentation of biomass of other species. If competition at research sites is more or less intense than competition within management units, of grass biomass response to invasive plant removal in experiments will not accurately predict response to invasive plant removal within management units. Likewise, if competition intensity varies invasive plant biomass response to grass seeding experiments will not accurately predict invasive plant response to seeding in management units. Research indicates that some competitive relationships vary temporally and spatially (Moloney 1990, Briones et al. 1998, Keddy et al. 2000). The influence of plant productivity gradients on competition intensity (i.e. competitive effect per unit biomass) has received extensive study because of disagreement over whether or not competition stays similar (Newman 1973, Wilson 1991) or intensifies (Grime 1973, Keddy 1989) with increasing plant productivity.

Growth Rate Problem: Population Growth Rates Vary

Repeated application of management strategies is often necessary because currently available management tactics do not kill all invasive plant propagules at invasive plant-infested sites (James et al. 1991). For example, livestock managers often repeatedly use herbicides to control invasive plants in rangelands with the goal of increasing grass forage production (Lym and Messersmith 1994, Sheley et al. 2000). Herbicides often kill large proportions of invasive plant propagules, but invasive plant populations usually re-attain pre-application population sizes within a few years of herbicide application unless

herbicides are re-applied (Lym and Messersmith 1985b, Fay et al. 1991). The length of time between herbicide application and recovery of invasive plant populations to their equilibrium biomass is partially determined by intrinsic invasive plant population growth rates. Intrinsic population growth rates also partially determine changes in grass forage production that occur during periods when herbicides have suppressed invasive plants. Because intrinsic plant population growth rates vary with environment (i.e. mineral nutrient, water and light availability), herbicide experiments will not always accurately predict the change in grass forage production resulting from a given level of invasive plant removal within management units (Grime and Hunt 1975).

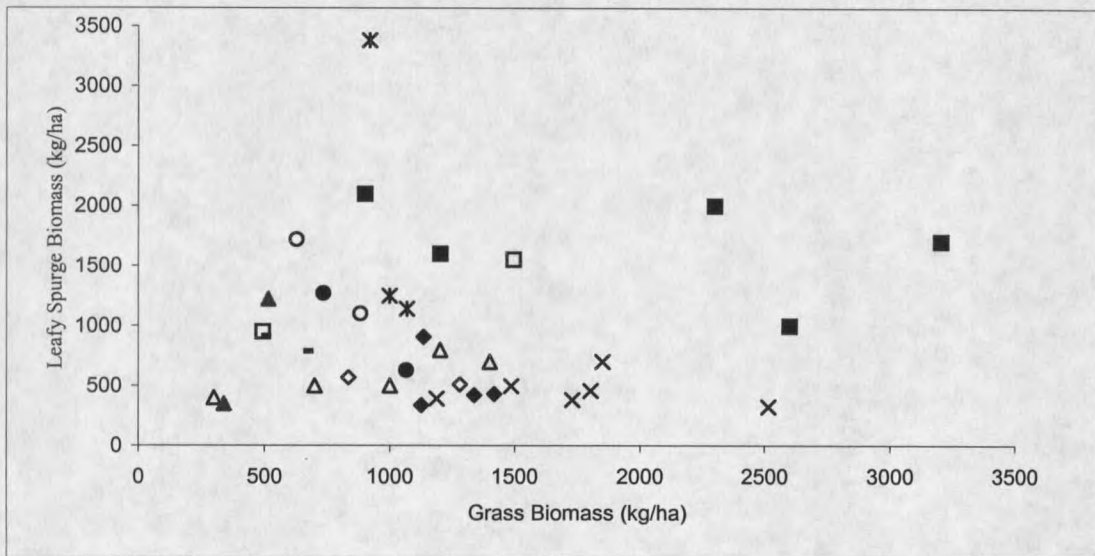


Figure 1.2. Leafy spurge and grass production at various sites throughout the northwestern United States that were not subjected to grazing or invasive plant management. Each site is denoted by its own symbol type, and each individual symbol represents data from a different year. Variation within a symbol type represents intra-site temporal variation, and variation between groups of symbols represents spatial variation. Data comes from several researchers ((Maxwell 1984, Lym and Kirby 1987, Hein 1988, Kirby et al. 2000), Sedivec unpublished data).

Carrying Capacity Problem: Plant Carrying Capacities Vary

Invasive plant abundance in the absence of grasses (invasive plant carrying capacity) and grass abundance in the absence of invasive plants (grass carrying capacity) vary temporally and spatially (Figure 1.2). If plant carrying capacity at an invasive plant experiment site is different than carrying capacity within a management unit, experiment results will not accurately predict grass and invasive plant biomass within the management unit.

Random Error Problem: Magnitude of Random Error Varies

Data from an experiment can be used to formulate a prediction of other data from the same experiment, but due to random error, this prediction will be imperfect. Random error results from factors (e.g. soil heterogeneity, spatially variable, insect herbivory) that are not completely controlled within the experiment site.

Consider the following case. Assume that random error in predicted grass biomass is normally distributed with a mean of zero and a fixed variance at an herbicide experiment site, and consider using results from the herbicide experiment to predict grass biomass within a management unit. Also assume that herbicide efficacy, intensity of plant species interactions, population growth rates, and plant carrying capacities at the herbicide experiment site and within the management unit are identical. In the same way that experiment data will not perfectly predict other data within the same experiment, experiment data will not perfectly predict grass biomass in the management unit. The error distribution that is estimated from the herbicide experiment will give an estimate of uncertainty in predictions of grass biomass at the experiment site. Even this uncertainty

estimate is suspect when it is used to formulate prediction uncertainty estimates within management units because the variance of the error distribution varies in concert with the frequency and intensity of factors that cause prediction uncertainty (e.g. hailstorms, plant disease, insect herbivory).

Species Problem: Species Compositions Vary

One invasive plant species can grow in association with different plant species within each of several habitats it infests. For example, spotted knapweed grows in association with western wheatgrass (*Agropyron simithii*), Kentucky bluegrass (*Poa pratensis*), needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), crested wheatgrass (*Agropyron cristatum*), rough fescue (*Festuca scabrella*), bluebunch wheatgrass (*Pseudoroegneria spicatum*), prairie junegrass (*Koeleria cristata*), Idaho fescue (*Festuca idahoensis*) and other grasses (Fay et al. 1991, Sheley et al. 2000). It is impractical to study interactions between spotted knapweed and each of these grasses because plant interaction experiments require extensive effort, and some regions harbor many invasive plant species, which further expands the effort required to estimate the by-species competitive relationships that are of relevance to managers.

Addressing the Problems

The eight problems that are outlined in the introduction can be represented with models. Parameters of these models must be defined as probability distributions (as opposed to point-estimates) to represent the seven problems that result from variable quantities. To represent the one remaining problem (i.e. the non-linearity problem),

model forms that capture nonlinear relationships between grass and invasive plant biomass must be used. Nonlinear models that contain the following terms will represent the eight problems:

$$gs_{t+1} = f(gs_t, ip_t, r_{gs}, \beta, j, K_{gs}, \epsilon_{gs}) \quad (1.1)$$

$$ip_{t+1} = f(ip_t, gs_t, r_{ip}, \alpha, j, K_{ip}, \epsilon_{ip}) \quad (1.2)$$

The response variables gs and ip represent perennial grass and dicotyledonous invasive plant biomass at peak standing crop of a growing season, respectively. The t and $t+1$ subscripts denote peak standing crop plant biomass of a given year and the following year, respectively. The sampling problem manifests itself in the models as variation in ip_t and gs_t (i.e. each sample from a management unit will provide a different estimate of these two predictor variables). The species problem is represented in the models if ip and/or gs represent more than one invasive plant and/or grass species. The intrinsic growth rate parameters are denoted by r_{gs} for grasses and r_{ip} for invasive plants. Defining these parameters as probability distributions represents the growth rate problem in the models. This is also the case for the carrying capacity problem (K_{gs} = grass biomass at peak standing crop of a given growing season in the absence of invasive plants (i.e. grass carrying capacity), K_{ip} = invasive plant biomass at peak standing crop of a given growing season in the absence of grasses (i.e. invasive plant carrying capacity)). The β competition coefficient describes the influence of invasive plant biomass on grass biomass, and the α competition coefficient describes the influence of grass biomass on invasive plant biomass. Defining these parameters as probability distributions, as opposed to point estimates, represents the competition problem in the models.

The parameter j denotes the proportional reduction in invasive plant biomass production caused by a control measure (i.e. the direct effect of management). The efficacy problem is represented in the models by defining this parameter as a probability distribution.

The error terms represent all of the influences that are not included in models (1.1) and (1.2), such as hailstorms, insect herbivory and plant diseases. The error distribution represents the intra-site random error problem. The inter-site random error problem is represented by defining the variance of the random error distribution (σ_e) as a probability distribution.

Addressing the Efficacy Problem

Several factors influence efficacy of invasive plant management strategies (i.e. j). The level of invasive plant mortality caused by herbicides, for example, varies with air temperature (Lym and Messersmith 1990), spray solution PH, relative humidity (Moxness and Lym 1989), and soil conditions (Krzyszowska et al. 1994, Lavy et al. 1996) and may also vary with population genetics (Ebke and McCarty 1983). Biological control establishment varies with many factors including soil type, number of insects released and invasive plant density at release sites (Kirby et al. 2000, Clark et al. 2001). Experiments that identify optimal methods for using invasive plant management strategies continue to be needed, but outlining these experiments is not one of the goals of this chapter. Simple within-management unit experiments might also provide insight into the site-specific efficacy of management strategies.

Addressing the Nonlinearity Problem

To quantify nonlinear competitive relationships, such as the one depicted in Figure 1.1, competing plant species must be studied along plant density gradients. Naturally occurring gradients cannot be used because these gradients often reflect gradients in plant carrying capacity. If invasive plant and grass carrying capacity increase along a naturally occurring gradient (e.g. a soil depth gradient), measuring plant biomasses along the gradient can suggest that grass and invasive plant biomass are positively related. However, removing grass at any point along the gradient and allowing the invasive plant to equilibrate to grass removal might result in an increase in invasive plant biomass, which would illustrate that the invasive plant and grass biomass are negatively related.

Experiments that establish plant density gradients, control variation in plant carrying capacity and estimate plant biomass over time can identify the correct forms of models that follow (1.1) and (1.2). A few experimental designs in which plant density gradients of both mixtures and monocultures of competitors are established from seeds or other propagules (addition series, replacement series, etc.) are used to characterize competitive relationships (see review in (Silvertown and Doust 1993). Competition has also been studied in naturally occurring plant communities by selectively removing some plants and measuring community response (Fowler and Antonovics 1981, Del Moral 1983, Wilson 1991). Spatial variation in plant carrying capacity can be somewhat controlled within these experiments by selecting sites with uniform vegetation characteristics.

The following models, which are similar to a model used for predicting individual plant weight, are presented for demonstrative purposes (Watkinson 1981, Goldberg 1987):

$$gs = (K_{gs}(1 + \alpha ip)^{-1}) \quad (1.3)$$

$$ip = (K_{ip}(1 + \beta gs)^{-1}) \quad (1.4)$$

Shapes similar to the one depicted in Figure 1.1 can be generated with these models.

Because these models do not contain population growth rate parameters, they best describe plant biomass at equilibrium and therefore, are zero-growth isoclines of models that contain population growth parameters. Zero-growth isoclines are models that predict plant biomass values that yield zero population growth. Population growth rates can be estimated from competition experiments (e.g. addition series or selective plant removal experiments) if plants are measured over time. The following widely used Lotka-

Volterra models contain population growth rate parameters:

$$gs_{t+1} = gs_t \exp[r_{gs}(1 - (gs_t + \beta ip_t)/K_{gs})] \quad (1.5)$$

$$ip_{t+1} = ip_t \exp[r_{ip}(1 - (ip_t + \alpha gs_t)/K_{ip})] \quad (1.6)$$

At equilibrium these models reduce to the following linear zero-growth isoclines:

$$gs_{t+1} = gs_t = (K_{gs} - \beta ip) \quad (1.7)$$

$$ip_{t+1} = ip_t = (K_{ip} - \alpha gs) \quad (1.8)$$

Nonlinear zero-growth isoclines have been used in conjunction with the Lotka-Volterra models to represent nonlinear competitive relationships (Gilpin and Ayala 1973). Using (1.3) and (1.4) as zero-growth isoclines instead of (1.7) and (1.8) results in nonlinear models that have the same interpretation as (1.5) and (1.6).

$$gs_{t+1} = gs_t \exp[r_{gs}(1 - (gs_t(1 + \beta ip_t))/K_{gs})] \quad (1.9)$$

$$ip_{t+1} = ip_t \exp[r_{ip}(1 - (ip_t(1 + \alpha gs_t))/K_{ip})] \quad (1.10)$$

These models reduce to (1.7) and (1.8) at equilibrium. The following functions illustrate one of several ways that management and random error ($\epsilon \sim \log N(1, \sigma_\epsilon^2)$) can be included in (1.7) and (1.8):

$$gs_{t+1} = gs_t \exp[r_{gs}(1 - (gs_t(1 + \beta(1 - j)ip_t))/K_{gs})] \epsilon_{gs} \quad (1.11)$$

$$ip_{t+1} = (1 - j)ip_t \exp[r_{ip}(1 - ((1 - j)ip_t(1 + \alpha gs_t))/K_{ip})] \epsilon_{ip} \quad (1.12)$$

Models such as (1.11) and (1.12) could address the nonlinearity problem. For example, there is no well-defined protocol for using results from herbicide experiments to predict changes in grass biomass resulting from herbicide use when invasive plant biomasses within the management unit and at the herbicide experiment site are different. If experiments were used to estimate parameters of models (1.11) and (1.12), disparities between management unit and herbicide experiment invasive plant biomasses would be accounted for by estimating predictor variables (gs_t and ip_t) within management units and inserting these biomasses into the models.

Addressing the Sampling Problem

The deterministic relationship between plant species biomass in a sample and plant species biomass in an entire management unit is linear. The slope coefficient of this relationship has a known value that scales sample area to management unit area. The intercept of this relationship is at zero. This relationship and sample data will predict plant species biomass in management units. The magnitude of prediction error will depend upon the degree to which sample biomass reflects management unit biomass.

The number of samples required to predict management unit biomass with some specified level of accuracy will depend on the magnitude of between-sample variation in plant biomass (i.e. the number of samples required and the degree to which plant biomass varies within a management unit are positively related). The magnitude of within-management unit variation in plant biomass is a reflection of both the plant species that are present (some species are more patchily distributed than others) and the magnitude of within-management unit variation in growing conditions (e.g. variation in soil type). Spatial statistics, particularly interpolation techniques, can help predict management unit plant biomass from sample data. However, developing sampling and statistical techniques for estimating management unit plant biomass is not a goal of this paper.

Addressing the Competition, Growth Rate, Carrying Capacity, and Random Error Problems

An experiment that establishes a range of plant densities or manipulates plant density in a naturally occurring plant community can identify the appropriate forms of models that follow (1.1) and (1.2), and can also estimate site-specific α , β , r 's, K 's, and σ_ϵ 's. However, to represent the competition, growth rate, carrying capacity, and random error problems the variance of parameters should reflect all of the variation that exists in nature, and an experiment conducted at only one site over a short time frame (~3 – 5 years) will underestimate temporal and spatial variation in some parameters and may overestimate variation in other parameters. To best quantify parameter variation (i.e. to best represent prediction error caused by the competition, growth rate, carrying capacity,

and random error problem), data from as many years and locations as possible should be used.

Meta-Analysis. Meta-analysis will provide point-estimates of parameters of models that follow (1.1) and (1.2) from additional years and locations. For example, herbicide experiments are one source of information on the marginal probability distribution of β . These experiments require establishing herbicide-treated and not-treated plots in areas believed to have uniform vegetation characteristics. A zero-growth isocline, such as (1.3), can be fit to data from an herbicide experiment to yield a point-estimate of β if two assumptions are made and the experiment protocol adheres to two criteria. Assumption 1) Herbicides did not injure grasses. Visual symptoms of herbicide-caused grass injury have been characterized for all the major herbicide modes of action, and herbicide researchers usually report symptoms of herbicide grass injury in manuscripts (Gunsolus and Curran 1992). Assumption 2) Enough time elapsed for grass populations to fully respond to decreased invasive plant biomass before grass biomass was measured. Invasive plant and grass biomass are usually measured for multiple years after herbicides are applied, and it may be necessary to avoid using data from the first year after herbicide application. Criteria 1) Herbicides substantially reduced invasive plant biomass (>~30% invasive plant mortality). Criteria 2) Grass biomass was measured.

Experiments that meet these assumptions and criteria will provide one point-estimate of β for each year that plant biomass is measured, and some invasive plant species have been the subject of many herbicide experiments. For example, a survey of the literature revealed that herbicide experiments will provide 20 estimates of β from areas throughout

the northwestern United States, if this parameter is interpreted as a competition coefficient that describes the influence of leafy spurge on perennial grasses (Maxwell 1984, Vore 1984, Gylling and Arnold 1985, Lym and Messersmith 1985a, Hein 1988, Lym and Messersmith 1994, Markle and Lym 2001).

As another example, meta-analysis of seeding experiments can provide point-estimates of α . Seeding experiments require establishing grass-seeded and not-seeded plots in areas believed to have uniform vegetation characteristics: Each seeded grass species from each site that a grass species is studied can provide one point-estimate of α . To derive these estimates, a zero-growth isocline, such as (1.4), can be fit to data on each seeded species within each site the species is studied. A survey of the literature revealed that two seeding experiments would provide 19 point-estimates of α from two sites in North Dakota if this parameter is defined as a competition coefficient that describes the influence of perennial grasses on leafy spurge (Lym and Tober 1997).

The methods for estimating α and β from the invasive plant literature are provided as examples. Data on other parameters of models that follow (1.1) and (1.2) may also exist in the literature for some invasive plants and grasses. However, there is little or no data in the literature on some parameters, such as σ_e 's.

Bayesian Parameter Estimation Techniques. In most cases involving ecologically and economically important invasive plants two kinds of data will be available for developing models that follow (1.1) and (1.2). 1) Data from the elaborate experiment/experiments (e.g. selective plant removal experiment, addition series experiment) required for elucidating model forms. This data will provide site-specific information on each of the

model parameters. 2) Literature data, such as that generated in herbicide and seeding experiments. Literature data will provide information from more sites and years but will only provide information on a subset of the parameters. The flexibility that Bayesian parameter estimation techniques provide enables both sources of data to be used in estimating parameters of models that follow (1.1) and (1.2). Using both sources of data will best represent the uncertainty that exists in nature.

Literature data can be used to construct Bayesian prior probability distributions. Prior probability distributions describe understanding of model parameters before new data (e.g. competition experiment data) are considered. Formally, the prior probability distribution is a joint probability distribution that describes interrelationships among model parameters. In the absence of any knowledge about these interrelationships the prior probability distribution is comprised of independent marginal probability distributions. In estimating parameters of models that follow (1.1), for example, a separate marginal probability distribution might be used to describe knowledge of each parameter because of a lack of information about interrelationships among parameters. Estimates of β from herbicide experiments can be used to construct the marginal prior probability distribution of this parameter. Constructing this prior probability distribution would require grouping estimates of β into a histogram and matching the moments of a probability distribution to this histogram.

Uniform probability distributions indicate that all values in the parameter space have equal probability. Uniform prior probability distributions are used when there is no *a priori* information about model parameters (Hilborn and Mangel 1997). For example,

uniform probability distributions might describe (a lack of) understanding about r_{gs} , K_{gs} and ϵ_{gs} . The lower limit of support on the parameter space of r_{gs} , K_{gs} and σ_ϵ must be greater than zero (e.g. grass carrying capacity cannot be negative), and the upper limit can be positive infinity or can correspond to some logical judgment (Hilborn and Mangel 1997).

Competition experiment data can be used to elucidate forms of models that follow (1.1) and (1.2) and can also serve as the new data that is used to update prior probability distributions of model parameters. The new data (i.e. competition experiment data) can be compactly described with a likelihood function. Multiplying this likelihood function by the prior probability distribution and appropriately weighting (i.e. using Bayes formula) results in the Bayesian posterior probability distribution of model parameters. This joint probability distribution represents the complete understanding of model parameters that is supplied by all of the relevant data. If the competition experiment data (i.e. likelihood function) provides information about the model parameters, the posterior probability distribution will have a smaller variance than the prior probability distribution. This smaller variance represents increased certainty about model parameters provided by the competition experiment. If the competition experiment provides information about the parameters then updating the prior probability distribution with competition experiment data via Bayes formula will also result in more knowledge of interrelationships among model parameters because some parameter value combinations will be more probable than others.

Within-Management Unit Data. Bayesian techniques help quantify the competition, growth rate, carrying capacity, and random error problems by enabling data from many sites and years to be used in estimating parameters of models that follow (1.1) and (1.2). If within-management unit data are available, Bayesian techniques can also help alleviate these problems. If within-management unit data are available the goal of estimating model parameters is no longer to represent all of the variation that exists in nature. Instead, the goal is to estimate management unit-specific parameters. Estimating management unit-specific parameters will reduce the spatial variation that gives rise to the competition, growth rate, carrying capacity, and random error problems.

The joint posterior probability distribution of (1.1) and (1.2) parameters can serve as the prior probability distribution when within-management unit information is available. Updating this prior probability distribution with management unit-specific data will result in a management unit-specific posterior probability distribution of model parameters. These same techniques have been used to estimate soil erosion parameters. Prior probability distributions on soil erosion parameters were elicited from a soils database that was constructed from many sites throughout the United States, and likelihood functions constructed from on-site data were used to update parameter estimates and provide site-specific erosion predictions (Wilson and Haan 1991, Wilson et al. 1991).

Several forms of management unit-specific information can contribute to parameter estimation. For example, it is desirable to have management unit-specific understanding of carrying capacities, because K_{gs} and K_{ip} vary substantially from site to site (Figure 1.1). Removing invasive plants from small representative areas and measuring grass

biomass after grasses equilibrate to invasive plant removal can generate within-management unit data on K_{gs} . Using this data to update the prior probability distribution of parameters of a model that follows (1.1) requires updating the likelihood function. This function can be updated by simply adding within-management unit data on K_{gs} to the existing competition experiment data matrix. Competition experiment data will exist in every case because these data are required to elucidate the form of the model that follows (1.1). Management unit-specific r 's, α 's, σ_e 's, and β 's can be estimated by appending data from other types of simple plant removal experiments to existing competition experiment data matrices.

Bayesian parameter estimation techniques provide a logical method for using competition experiment data, data from other invasive plant experiments (e.g. herbicide and seeding experiments) and within-management unit data in estimating parameters of models that follow (1.1) and (1.2). Developing these models could help quantify and alleviate the competition, growth rate, carrying capacity, and random error problems.

Addressing the Species Problem

Experiments consisting of plant density gradients (i.e. addition series or selective plant removal experiments) are required to elucidate appropriate forms of model that follow (1.1) and (1.2). Once these elaborate competition experiments have been conducted on a set of invasive plant and grass species, the same model form can be used for newly considered species, if the newly considered species and the species used for selecting model forms have similarly shaped zero-growth isoclines. Inspection of linear Lotka-Volterra zero-growth isoclines (1.7 and 1.8) demonstrates that the shape of these isoclines

is determined by the nature of competitive interactions among species. The K parameters, which are the only feature of these isoclines that are not influenced by competition, establish only isocline position and have no bearing on isocline shape.

The same nonlinear functions (i.e. zero-growth isoclines) have been used to model biomass relationships between many competing plant species. Goldberg (1987) used (1.3) to model the effect per unit biomass of seven different species (some dicots and grasses) on the biomass per individual of an indicator (i.e. phytometer) species. Gaudet and Keddy (1988) illustrates that the influence per unit biomass of 44 species on the biomass of a phytometer species conformed to the same non-linear relationship. A small number of models that follow (1.1) and (1.2) will be sufficient for modeling invasive plants and associated grasses.

Generally Applicable Predictor Variables. Competition, growth rates, carrying capacities, random error, and management efficacy are the relevant processes in developing models that follow (1.1) and (1.2). It would be very unrealistic to expect knowledge of these processes (expressed as model parameters) to be at all similar across plant species if plant densities were used as predictor variables because the average size of individual plants varies dramatically by species. Knowledge of these processes for one set of plant species can be better extrapolated to other plant species because predictor variables of (1.1) and (1.2) have units of plant biomass. Several studies have demonstrated per unit biomass competitive effects that do not vary from species to species (e.g. Goldberg 1987, Mitchell et al. 1999, Peltzer and Koehy 2001, Keddy et al.

2002). It has long been recognized that plant ecology will advance more quickly if generally applicable variables, like biomass, are studied (Keddy 1989).

Estimating K's for New Sets of Species. Grass and invasive plant carrying capacities vary considerably between sites dominated by the same species of invasive plant (Figure 1.2). Within-management unit data on carrying capacity will be critical in estimating parameters of models that follow (1.1) and (1.2). Between-species variation in K's causes the same problem as between-site or between-year variation in this parameter. Therefore, addressing the carrying capacity problem and addressing between-species variation in carrying capacity requires the same considerations and within-management unit data.

Bayesian Analysis and the Functional Group Approach. The amount of species-specific data required for any given ecological inquiry depends on the nature of the questions being addressed (Day et al. 1988). In the case of managers attempting to develop invasive plant management plans that are based on herbicide, biological control, seeding, and grazing, the question is: "Which plan will provide optimal results?" This question, whether explicitly stated or not, is implicit in every invasive plant management decision. If the manager relies on invasive plant research results to answer this question, then the manager must rely on sparse amounts of species-specific information from a small number of sites and years. This reality is balanced against the fact that data from many sites and years are necessary for quantifying the competition, growth rate, carrying

capacity, random error, and efficacy problems. Therefore, managers typically need more than the available supply of species-specific data to answer the question.

In many cases the lack of species-specific data will make it desirable to use data on plant species that are functionally similar to a particular plant species in developing models that predict biomass of that plant species. An entire branch of ecology (i.e. comparative ecology) is devoted to screening and categorizing functionally similar plant species in functional groups. Comparative ecologists have long recognized the need for a framework within which studies that rely on species nomenclatures contribute to development of general principles that transcend species boundaries. The parameters of (1.1) and (1.2) describe characteristics that comparative ecologists use to categorize plants. Categorization has been based on intrinsic growth rates (r 's) (Grime and Hunt 1975, Keddy 1989) and tolerance to stress and disturbance (j 's and σ_ϵ 's) (Grime 1977, Hobbs 1997, Grime 2001). *A priori* grouping of plants by functional characteristics has explained variation in response of plants to climate (σ_ϵ 's) (Hobbs 1997). Some of the most problematic invasive plants, such as the tap-rooted knapweeds (*Centaurea* spp.); are in the same taxonomic group (James et al. 1991), and many functionally and taxonomically similar invasive plants are managed with the same tactics and respond similarly to these tactics (j 's) (Sheley and Petroff 1999). Methods for assigning perennial invasive plants and perennial grasses to functional groups based on the parameters of (1.1) and (1.2) have been developed, and assignment of plants to functional groups has proven to be an effective method for expanding the general applicability of ecological research.

Accurate assignment of plants to functional categories has been based on “soft” plant characteristics, which include canopy height, lateral spread, leaf size, leaf weight, dry matter production, and other relatively undemanding plant measurements (Hodgson et al. 1999). Properties of the habitats (e.g. disturbed/not disturbed, productive/ not productive) where a plant species grows also provide insight into which category the plant species

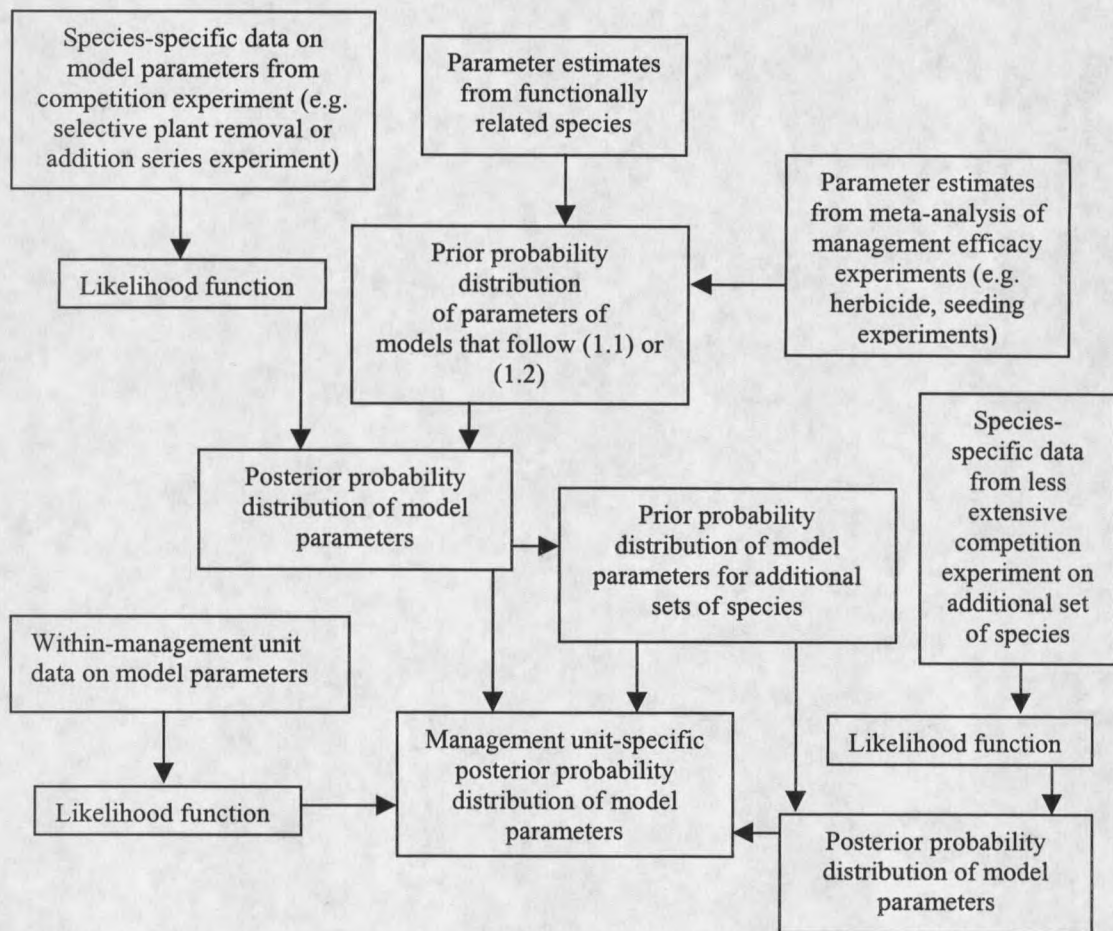


Figure 1.3. A protocol for developing models that follow (1.1) and (1.2). The “less extensive” competition experiment box represents the idea that less species-specific data will be required when broadly applicable model forms are elucidated and posterior probability distributions that serve as prior probability distributions for additional sets of species are developed.

belongs to with respect to growth rate (r), competitiveness (α or β), and response to stress and disturbance (j and σ_e) (Grime and Hunt 1975, Grime 2001). Which species data to use and reject in developing models that follow (1.1) and (1.2) for a particular species can be based on plant morphology and habitat associations.

One of the fundamental reasons for categorizing plants into functional groups is to facilitate development of plant ecology into a predictive science (Grime 1993). Models that follow (1.1) and (1.2) rely on ecological parameters to make quantitative predictions of plant biomass. Because there is insufficient species-specific data available for estimating these parameters, a data analysis framework that integrates species-specific data and comparative (i.e. functional group) data is required. Bayesian techniques supply this framework by providing a mathematical device (i.e. prior probability distribution) that quantifies the general understanding of processes and then uses this understanding, along with situation-specific information, to make situation-specific predictions (Edwards 1996, Hilborn and Mangel 1997). For example, comparative data on fish species have been used to elicit prior probability distributions on population dynamics-related parameters of other fish species, and these prior probability distributions have been used with species-specific data to make species-specific predictions (McAllister et al. 1994, Hilborn and Mangel 1997). Using general knowledge of processes, along with situation-specific data, to develop situation-specific predictions is a natural part of the scientific method (Edwards 1996, Hilborn and Mangel 1997).

Prior probability distributions on growth rate, competition, random error, and management parameters of a particular species can be derived from data on functionally

similar species when developing models that follow (1.1) and (1.2). However, because of inter-species and inter-site variation in model parameters, species- and/or management unit-specific data should play a more prevalent role in estimating parameters than the functional group data. By using species- and management unit-specific data to construct likelihood functions, prior probability distributions that are derived from functionally related species can be updated to reflect species- and management unit-specific information (Figure 1.3).

Conclusions

If prediction error is quantified it becomes more logical to base invasive plant management decisions on predictions derived from invasive plant research. This chapter provides a framework that quantifies error in perennial grass and dicotyledonous invasive plant biomass predictions. This framework then relies on within-management unit data to reduce and re-quantify prediction error. Decisions to use herbicide, biological control, seeding, and grazing strategies to manage invasive plants will become more informed, and therefore will more often be correct, when prediction error is diminished.

CHAPTER 2

INFLUENCE OF SOIL WATER AVAILABILITY ON COMPETITION
AMONG LEAFY SPURGE AND GRASSESSummary

Seeding mixtures of leafy spurge and two grasses were planted in experiments and grown for 127 d to determine if different water application regimes influenced competition among these three 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.

Introduction

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 necessitates 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 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 (Afyuni et 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 one invasive plant species can grow in association with different grasses within each of several habitats it infests. For example, spotted knapweed grows in association with western wheatgrass, Kentucky bluegrass, needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), crested wheatgrass (*Agropyron cristatum*), rough fescue (*Festuca scabrella*), bluebunch wheatgrass (*Pseudoroegneria spicatum*), 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 inquiry needed to understand competition between an invasive plant species and all grasses with which the invasive plant commonly coexists.

My objective was to determine the influence of plant-available water on competition among leafy spurge, Kentucky bluegrass and western wheatgrass in a greenhouse. Leafy spurge is a cool-season non-native perennial invasive plant that infests close to 1.2

million hectares in 29 states in the U.S.A. (Lajeunesse et al. 1999). Kentucky bluegrass is a cool-season non-native 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 factor/factors that limit plant growth are different at different levels of water availability, it was 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 factor/factors that limit plant growth (e.g. soil nutrient availability) at different levels of plant-available 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 kg 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. Seeds were covered with approximately 2 mm of soil, and the soil was misted with water every other

day for 20 d. The following ratio was then calculated: 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 m^{-2} for each species. Three addition series matrices consisting of all possible seed density combinations were established (4 Kentucky bluegrass densities x 4 western wheatgrass densities x 4 leafy spurge densities = 64 pots per density matrix x 3 density matrices = 192 pots per experiment) in the 7.6-L pots (Spitters 1983). These density matrices also contained between two and eight 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 h 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, the soil surface was misted with water every other day for 27 d. After the misting period (28 d after planting), all pots were watered to capacity. Pots in two density matrices were watered to capacity 61 d after planting, and one of these matrices was watered to capacity a third time 94 d after planting. Hereafter, pots watered once, twice, or three times will be said to have received the dry, intermediate, or wet treatments, respectively. After receiving final water applications, the plants in pots were harvested by clipping at the soil surface upon showing signs of severe water stress, or 127 d 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).

Plant-Available Water Sampling

To determine gravimetric water content, pots were weighed the day before each watering, and pots that were watered were re-weighed the day after watering. Pots were weighed after harvest, and soil was removed and thoroughly mixed. A uniform sample was taken from each pot. These samples were weighed, dried to a constant weight at 50 C and re-weighed to determine soil dry weight (soil dry weight = post-harvest soil weight x (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

Plants per pot of each species were counted at harvest. By-species aboveground biomass 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).

$$1/pw_{ls} = B + B_{ls,den} * den_{ls} + B_{kb,bio} * bio_{kb} + B_{ww,bio} * bio_{ww} \quad (2.1)$$

$$1/pw_{kb} = B + B_{kb,den} * den_{kb} + B_{ls,bio} * bio_{ls} + B_{ww,bio} * bio_{ww} \quad (2.2)$$

$$1/pw_{ww} = B + B_{ww,den} * den_{ww} + B_{ls,bio} * bio_{ls} + B_{kb,bio} * bio_{kb} \quad (2.3)$$

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 (B's) are intercept terms and B's 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 nine models (9 models = 3 water treatments x 3 species).

Regression coefficients of 2.1, 2.2 and 2.3 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:

$$\text{amp}_{sp} = B + B_{ls, bio} * \text{bio}_{ls} + B_{kb, bio} * \text{bio}_{kb} + B_{ww, bio} * \text{bio}_{ww} \quad (2.4)$$

was used to test the hypothesis that per-unit-abundance competitive effects do not vary by species. This model was fit to data from each separate water treatment to yield a total of three 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 (\underline{x} and \underline{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 $\underline{x} * \underline{y} = 1000000$ comparisons. The quantity $(1 - (\text{number of cases where } x_i > y_j) / 1000000) * 2$ is a two-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 "B", ";" will be replaced by "-", and the coefficients will not be subscripted. For example, $B_{ls,bio} = ls-bio$ and $B_{ls,den} = ls-den$. Because the dependent variable is inverse plant weight, the magnitude of competition coefficients and competition intensity are 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 2.1), 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 treatment 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

Table 2.1. Competition coefficient estimates, r^2 , standard deviations (SD) 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	SD	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	$=ww_{intermediate}$	$\neq kb_{wet}$	
	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			

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 2.2). 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 2.3). 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 this relationship was reversed in the wet treatment in Run 1. Kentucky bluegrass and leafy spurge had a similar effect on western wheatgrass plant weight in the wet treatment in Run 2.

Table 2.2. Competition coefficient estimates, r^2 , standard deviations (SD) 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	SD	Comparisons of Regression Coefficients		
1	Dry	0.44	kb-den	0.62	0.23	=kb _{intermediate}	≠kb _{wet}	
	Dry		ww-bio	11.58	3.87	=ls _{dry}	≠WW _{intermediate}	≠WW _{wet}
	Dry		ls-bio	24.50	6.64	≠ls _{intermediate}	≠ls _{wet}	
	Intermediate	0.83	kb-den	0.33	0.04	≠kb _{wet}		
	Intermediate		ww-bio	3.58	0.61	≠ls _{intermediate}	=WW _{wet}	
	Intermediate		ls-bio	7.93	1.59	≠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}	≠kb _{wet}	
	Dry		ww-bio	17.07	2.56	≠ls _{dry}	≠WW _{intermediate}	≠WW _{wet}
	Dry		ls-bio	46.99	9.17	≠ls _{intermediate}	≠ls _{wet}	
	Intermediate	0.71	kb-den	0.20	0.05	=kb _{wet}		
	Intermediate		ww-bio	4.71	0.53	≠ls _{intermediate}	≠WW _{wet}	
	Intermediate		ls-bio	11.45	2.59	≠ls _{wet}		
	Wet	0.41	kb-den	0.10	0.05			
	Wet		ww-bio	1.86	0.33	≠WW _{wet}		
	Wet		ls-bio	3.36	1.89			

Table 2.3. Competition coefficient estimates, r^2 , standard deviations (SD) 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	SD	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			

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 2.1, 2.2 and 2.3 (e.g. plant diseases and genetics and nutrient availability) caused greater random error when water was applied more frequently.

Table 2.4. 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.

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 2.4). In the dry treatment 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 two treatments in Run 2.

Discussion

There are two 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, Keddy 1989, Grime 2001). 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 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 (Table 2.1, 2.2, and 2.3), 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 three 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 (less than 25 cm in height) by the end of these greenhouse experiments, so 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 of these experiments is supplied by a theory that predicts 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 my 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 (Table 2.1, 2.2, and 2.3). However, there was no clear relationship between importance of competition (model r^2) and the number of water applications (Table 2.1, 2.2, and 2.3) (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 accepted.

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 2.1). The null hypothesis that per unit abundance competitive effects of the grasses are similar is accepted. Biesboer et al. (1994) reported that five 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 chapter, 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 results from this greenhouse study hold true in the field then it suggests that 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 the 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.

CHAPTER 3

DEVELOPMENT AND ACCURACY ASSESSMENT OF MODELS THAT PREDICT
GRASS AND LEAFY SPURGE RESPONSE TO
INVASIVE PLANT MANAGEMENTSummary

Managers use herbicide, biological control, seeding, and grazing strategies to manage invasive plants. Chapter 1 outlines challenges that managers face when they rely on invasive plant research results to select among these management strategies. Chapter 1 also describes how models that incorporate knowledge of invasive plant and grass carrying capacities, population growth rates and competitive interactions might facilitate the process of using research results to predict invasive plant management outcomes. This chapter develops these models for leafy spurge and perennial grasses using data from addition series experiments. To assess the level of realism attained by these models, predictions were compared to data from naturally occurring plant communities. Model predictions exhibited a considerable level of agreement with observed data from herbicide, seeding and selective plant removal experiments when on-site estimates of plant carrying capacity parameters were used to formulate model predictions.

Introduction

There are costs and benefits to using invasive plant management strategies. Biological control and herbicides can reduce invasive plant abundance (Kirby et al. 2000), and this reduction may result in increased desired species abundances (Lym and Messersmith

1985a), but biological control and herbicides often have non-target effects (Follett and Duan 2000), such as the consumption of native vegetation by introduced biological control agents (Louda 1998). Seeding of invaded areas can directly increase desired grass abundance and reduce invasive plant abundance but it is expensive (Lym and Tober 1997, Masters and Nissen 1998).

Monetary considerations, the magnitude of decreases in invasive plant production, increases in desired species production, and off-target effects are the major factors that determine whether or not use of any given invasive plant management strategy is warranted. These factors must be accurately predicted if managers are to consistently select optimal invasive plant management strategies. Plant competition and population dynamics models provide one means for predicting management-induced changes in invasive plant and desired species production, but little has been done to evaluate the feasibility of developing models that accurately predict these attributes.

Alternatively, many modeling projects have centered on interactions between annual weeds and annual crops, and these projects demonstrate that prediction accuracy depends on specific properties of predictor and response variables (Firbank et al. 1985, VanDevender et al. 1994, Rankins et al. 1998, Shaw et al. 1998, Vitta and Satorre 1999). For example, the competitive effects of annual weeds (predictor variable) on annual crop yield (response variable) has been estimated quite robustly in some cases (Freckleton and Watkinson 1998), but weed seed emergence and mortality have proven to be notoriously variable quantities that are difficult to predict (Kropff 1988, Freckleton and Watkinson 1998). Due to the highly variable nature of seed population dynamics, the accuracy of annual crop-annual weed population dynamics models does not reflect the prediction

accuracy to be expected from invasive plant population models. Many invasive plants are perennials that invade plant communities dominated by other perennials. Perennials rely more heavily on vegetative growth and propagation for population growth and maintenance. This type of growth and propagation has proven to be less tightly regulated by the random events and environmental conditions that determine whether or not seeds give rise to seedlings, juveniles and adult plants (Moloney 1988). Predictions of management-induced shifts in plant species abundances may therefore be more accurate in communities dominated by perennial plants.

Thus far, invasive plant model development and validation has emphasized the invasion process (Werner and Caswell 1977, Parker 2000, Higgins et al. 2001). Modeling efforts have also focused on within-patch population dynamics and predicting responses of invasive plants to management that affects particular plant growth stages, such as biological control (Lonsdale et al. 1995, Rees and Paynter 1997, Shea and Kelly 1998, McEvoy and Coombs 1999). Interactions among native and invasive plants have received considerable attention in recent years, but unlike the case of crops growing in association with weeds, little has been done to develop predictive models that are based on these interactions (Farnsworth and Meyerson 1999, Lavergne et al. 1999, Martin 1999, Almasi 2000, Case and Crawley 2000).

My overall goal was to develop models that describe interactions among perennial desired plants and perennial invasive plants and to explore the ability of these models to predict invasive plant management-induced shifts in plant community composition. Addition series field experiments were used to develop models that describe growth rates, competitive interactions, plant carrying capacities, and random error in communities

dominated by leafy spurge and grasses. To evaluate the ability of these models to predict changes in grass production resulting from decreased leafy spurge production, model output was compared to data from experiments where dicot-specific herbicides decreased leafy spurge production. To evaluate the ability of models to predict changes in leafy spurge production resulting from changes in grass production, model output was compared to data from experiments where monocot-specific herbicides or grass seeding altered grass production.

Materials and Methods

Addition Series Experiments

Plant System. Leafy spurge was selected for study because of its ecological and economic importance and because of the extensive data on this species. Leafy spurge is a cool-season rhizomatous perennial invasive plant that infests close to 1.2 million hectares in the United States (Lajeunesse et al. 1999). This plant is poisonous to some species of grazing animals (Kronberg 1993), can reduce forage production on pasture and rangeland (Lym and Messersmith 1985a) and may have other impacts. Kentucky bluegrass and western wheatgrass were selected for study because they commonly grow in association with leafy spurge (Nowierski and Harvey 1988). Kentucky bluegrass is a non-native cool-season rhizomatous 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).

Study Site. Two experiments were initiated 6.5 km west of Bozeman, MT at the Montana State University Arthur H. Post Research Farm (hereafter referred to as Post Farm) (45° 41' N, 111° 9' W). Elevation at this site is 1463 m, average annual precipitation is 457 mm and soils are Amsterdam silt loams (fine-silty, mixed, frigid Typic Haplustolls). Soil at the experiment sites was extensively tilled over several years because sites were previously used for agronomic research.

Experiments. Emergence ratios of grasses were estimated by uniformly sowing 30 seeds of each species in 1-L pots in a greenhouse. Seeds were covered with approximately 2 mm of soil. The soil was misted with water every other day for 20 d after which time the ratios of seedlings emerged : seeds planted was determined.

In May 1998, strips of Kentucky bluegrass sod (1-m wide) were laid around each 1 m x 1 m plot of an addition series experiment (hereafter this experiment is referred to as Experiment 1). In an addition series experiment target densities are combined factorially in every possible combination (Spitters 1983). To achieve target densities of 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), seeding rates were adjusted using the greenhouse-estimated seedling emergence ratios. Seeding levels were assigned to plots in a completely randomized design, and seeds were uniformly spread over plot surfaces in early June 1998. The seeds were covered with approximately 2 mm of soil, and plots were periodically irrigated until grasses became established.

The ability of leafy spurge to establish from seeds was unclear. Therefore, after allowing grasses to establish for one growing season, leafy spurge root pieces were

planted in the plots in May 1999. Plants did not establish from these propagules.

Consequently, leafy spurge seeds were collected from plants near Bozeman, MT in August 1999. Seedlings of leafy spurge were established in "conetainers" (3 cm diam. x 15 cm) (one seedling per container) in a greenhouse in August 1999.

Leafy spurge seedlings were approximately 10-cm tall and had extensive root systems by spring 2000. To kill grass and enhance leafy spurge establishment, glyphosate [*N*-(phosphonomethyl)glycine] was applied at 1.6 kg ae/ha to 36 evenly spaced cylindrical areas (diameter = 6.35 cm) in each plot in May, 2000. Six densities of leafy spurge (0, 4, 9, 16, 25, and 36 seedlings m⁻²) were hand planted in plots a few days after glyphosate application. Plants were evenly spaced and planted in the center of areas that received glyphosate. A pointed steel rod was used to make holes to accommodate seedlings, and soil was packed around the seedlings by hand. This experiment had 144 plots (4 Kentucky bluegrass densities x 6 western wheatgrass densities x 6 leafy spurge densities).

A second experiment (hereafter referred to as Experiment 2) was initiated adjacent to Experiment 1. Grasses were established in August of 2000 by uniformly spreading the same seeding rates as in Experiment 1. Leafy spurge seedlings were planted with uniform spacing at densities of 0, 4, 9, 16, 49, and 64 seedlings m⁻² in May 2000. All possible density combinations were not implemented in this experiment. Instead, half the combinations were omitted and the remaining combinations were replicated once. Density combinations were selected systematically to insure a wide range of grass and leafy spurge densities. The first, second and third numbers in the following three number sequences represent western wheatgrass, leafy spurge and Kentucky bluegrass target

densities, respectively:

000,002,011,013,022,031,033,040,051,053,100,101,103,110,112,121,123,130,132,
141,143,150,152,200,202,211,213,220,222,231,233,240,242,251,253,301,303,310,312,
321,322,323,330,332,341,343,350,352,400,402,411,413,420,422,431,433,440,442,451,
453,501,503,510,512,521,523,530,532,541,543,550,552. The seeding densities increase sequentially from 0 to 4 for Kentucky bluegrass and 0 to 6 for the other two species. For example, plot 051 received no western wheatgrass seeds, 49 leafy spurge seedlings and 156 Kentucky bluegrass seeds. Except for these differences, Experiments 1 and 2 were the same.

Plant Sampling. Height of each leafy spurge stem was measured in early September 2000, and again in late August 2001 and 2002 when repeated measurements of height over time indicated that growth had ceased. Total stem length per plot was used as an index of leafy spurge abundance, as opposed to plant biomass, because leafy spurge sheds considerable numbers of leaves during the growing season, which makes it difficult to measure leafy spurge biomass. Also, total stem length can be measured non-destructively at multiple time points, and non-destructive measures were required for developing time series models. Leafy spurge biomass was clipped at ground level, dried to a constant weight at 50 C and weighed in 10 plots in each experiment in late August 2001. These data were used to develop a relationship between stem length per unit area and biomass per unit area so that prediction accuracy of models developed from the Post Farm data could be evaluated using data from experiments in which leafy spurge biomass was measured.

Kentucky bluegrass and western wheatgrass biomass were estimated from two 15-cm x 15-cm frames that were placed in each plot in 2001. Frames were positioned in representative areas of plots in April 2001 and grass biomass was clipped at ground level, separated by species, dried to a constant weight at 50 C, and weighed in August 2001. Representative sampling, as opposed to random sampling, was conducted to control for patchy grass establishment in some plots. Because of patchy grass establishment, random sampling would have resulted in estimates of zero grass production in many plots that contained grass. In 2002, the 15-cm x 15-cm frames were re-clipped and resulting grass weights were compared to grass weights in entire plots to determine if representative sampling biased estimated grass biomass.

The inner 85-cm x 85-cm area of each plot (except the 20 plots harvested in 2001) was harvested in August 2002. The outer 15 cm was not harvested to avoid possible unrepresentative growing conditions near plot edges. Separating and drying were conducted as in 2001 except in plots that contained high biomasses of both grass species. Time constraints prevented separating western wheatgrass from Kentucky bluegrass in these plots, and therefore, grass biomass from a plot was thoroughly hand-mixed and three samples (dry weight = ~15 g per sample) were collected. The average ratio of dried western wheatgrass biomass to dried Kentucky bluegrass biomass in these samples was used to estimate grass biomass by species for entire plots.

Selective Plant Removal Experiments (SPRE)

Selective plant removal experiments (SPRE) were conducted throughout western Montana. These experiments were conducted to determine if competitive interactions in

Experiments 1 and 2 were similar to interactions in naturally occurring leafy spurge infestations.

Plant Species. Kentucky bluegrass grew in association with leafy spurge at almost all of the SPRE sites. Other grasses, including western wheatgrass, were present at a few sites.

Study Sites. Data for evaluating accuracy of the model that predicts leafy spurge production were collected from 12 experiments at five sites. Data for evaluating models that predict grass biomass were collected from 19 experiments at the same five sites. Because wide plant productivity gradients and different equilibrium abundances of leafy spurge and grasses occurred within sites, multiple experiments were conducted within some sites. Sites were located 1.2 km southeast, 1.5 km east, 86 km east, 154 km west and 249 km northwest of Bozeman, MT.

Experiments. Each of the 19 SPRE was comprised of three 1-m x 1-m plots and one 2-m x 2-m plot. Plots were carefully selected to ensure similar grass and leafy spurge production between plots within each experiment. Fencing was used to exclude ungulate grazing where necessary. Two 1-m² plots were not treated. To kill grass, the grass-specific herbicide sethoxydim (2-[1-(ethoxyimino)butyl]-5-[2-(ethylthio)propyl]-3-hydroxy-2-cyclohexen-1-one) and crop oil concentrate were applied in mid-May, 2001 to one 1-m² plot at rates of 0.086 kg ai ha⁻¹ and 382.10 ml ha⁻¹, respectively. To kill leafy spurge, the dicot-specific herbicide picloram (4-amino-3, 5, 6-trichloropicolinic acid) was applied during the same period to the 4-m² plot at a rate of 0.56 kg ai ha⁻¹. The larger

leafy spurge removal plot was selected to eliminate the edge effect that this tall plant might impose on plot borders. Small-scale spatial heterogeneity prevented selection of four 2-m x 2-m plots with uniform vegetation attributes. It was necessary to repeat herbicide applications once in some plots to remove targeted vegetation. Selective herbicides have been used to remove components of the vegetation and measure competition in other experiments (Peltzer and Kochy 2001).

Plant Data. Data were not collected from SPRE in which sethoxydim did not control grass and/or picloram caused twisting and yellowing of grass plants. Height of each leafy spurge stem was measured within an 85-cm x 85-cm frame that was centered in each plot when leafy spurge growth ceased in early August 2002. All grasses within these frames were harvested, dried and weighed as in Experiments 1 and 2. Plants other than grasses and leafy spurge, all of which were forbs, were also dried and weighed in the same manner.

Analysis, Results and Discussion

Biomass Relationships

To determine whether using representative 15-cm x 15-cm frames to estimate entire plot grass biomass in 2001 resulted in biased estimates, grass biomass in these same frames was re-measured in 2002. The 2002 15-cm x 15-cm frame biomass measurements were compared to the 2002 85-cm x 85-cm area frame biomass measurements after scaling both sets of measurements to the plot surface area (1 m^2) (figure 3.1).

The Post Farm models predict total leafy spurge stem length m^{-2} . The relationship between this metric and leafy spurge biomass was quantified so that seeding and herbicide experiments, which only measured leafy spurge biomass, could be used to evaluate predictive ability of Post Farm models (Figure 3.2). Leafy spurge density was also evaluated as a predictor of biomass, but this metric did not accurately predict

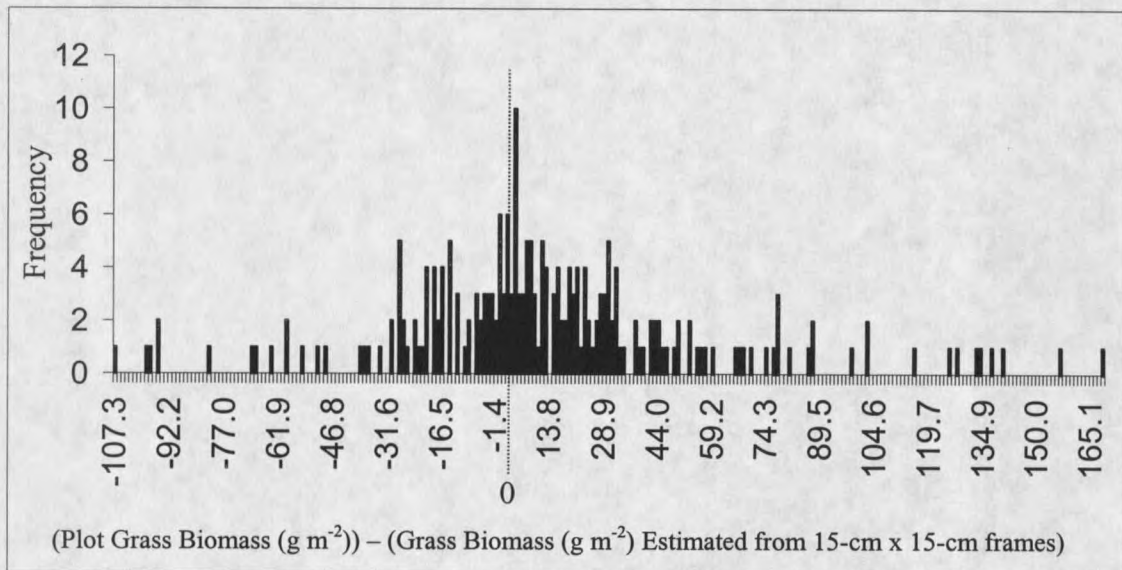


Figure 3.1. Histogram describing relationship between sampled grass biomass in 2002 and actual grass biomass in 2002 in Post Farm Experiment plots. Entire plots were not clipped in 2001 because clipping might have substantially affected 2002 plant measurements. Instead, clipping, drying and weighing of grass biomass in two 15-cm x 15-cm frames within each plot was used to derive estimates of grass biomass in entire plots. Grass was clipped, dried and weighed in 2002 in the same 15-cm x 15-cm frames, and grass biomass in entire plots (excluding outer 15 cm) was also clipped, dried and weighed in this year. The estimate of plot grass biomass derived from the 15-cm x 15-cm frames was subtracted from actual grass biomass in each plot after scaling both measurements to the same surface area ($1 m^2$), and the resulting values were arranged in a histogram. The lack of systematic variation (the histogram is nearly centered around the number 0) illustrates that selecting representative 15-cm x 15-cm frames did not bias 2001 estimates of plot grass biomass. The lack of systematic variation also indicates that clipping the 15-cm x 15-cm frames in 2001 did not substantially influence grass production in these same frames in 2002. Grasses were dormant when 2001 clipping occurred, which may help explain why clipping did not influence 2002 grass biomass production.

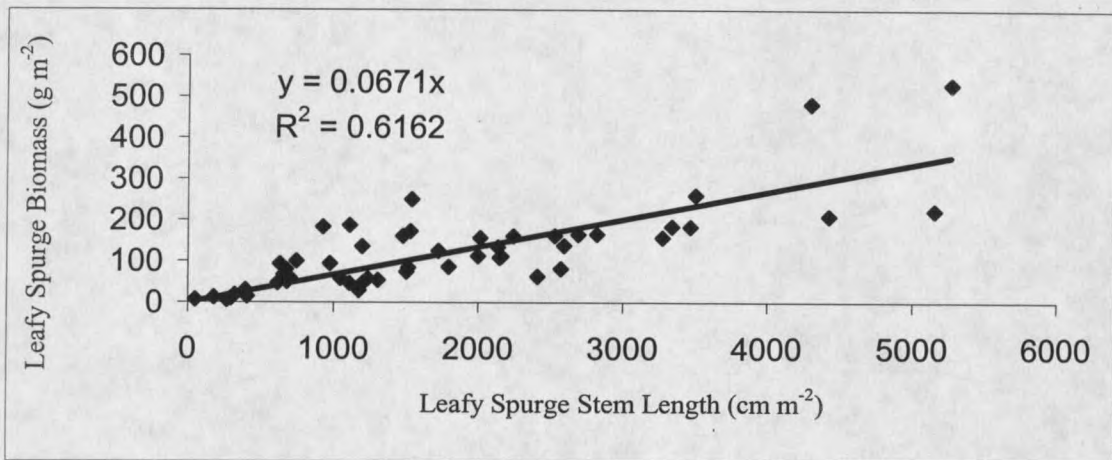


Figure 3.2. Linear regression relationship between leafy spurge stem length and leafy spurge biomass. Data come from end-of-growing-season measurements of 20 Post Farm Experiment plots from 2001 and 35 SPRE plots from 2002. The SPRE plots that were used did not receive herbicide.

biomass ($r^2 = 0.28$). Leafy spurge biomass was only quantified in 20 Post Farm Experiment plots because measuring biomass constitutes destructive sampling, and repeated measurements of leafy spurge over time were required to achieve the goals of this research.

Model Development

Models that Predict Leafy Spurge and Grass Production over Time. Some invasive plant management strategies temporarily alter species abundances (James et al. 1991). For example, herbicides often kill large proportions of invasive plant propagules, but invasive plant populations usually re-attain pre-herbicide application population sizes within a few years if herbicides are not reapplied (Bussan and Dyer 1999). Transient dynamics that occur between applications of invasive plant control measures are of interest to managers when they consider programs consisting of repeated control efforts. For example, livestock managers repeatedly use herbicides to control invasive plants in

rangelands with the goal of increasing grass forage production (Lym and Messersmith 1994). The length of the time period between herbicide application and recovery of an invasive plant population, and the change in forage production occurring during this time period, determine if herbicide use is cost-effective. Time series models containing parameters and predictor variables that might predict these time periods and changes in forage production were developed for perennial grasses and leafy spurge.

Except for 1gs and 1ls, which were eliminated in the early phases of model selection, time series models that have the following parameters and predictor variables were evaluated (Table 3.1).

$$ls_{t+1} = f(ls_t, gs_{t+1}, \alpha, r_{ls}, ls_{max}) \quad (3.1)$$

$$gs_{t+1} = f(gs_t, ls_t, \beta, r_{gs}, gs_{max}) \quad (3.2)$$

The response variable of (3.1) is end-of-the-growing-season leafy spurge stem length m^{-2} at year $t+1$. Predictor variables are leafy spurge stem length m^{-2} at year t (ls_t) and grass biomass m^{-2} at year $t+1$ (gs_{t+1}). The population growth rate parameter (r_{ls}) describes the rate of increase of leafy spurge when grass and leafy spurge abundances are very low, the competition coefficient (α) describes the influence of grass biomass on leafy spurge population growth, and ls_{max} is equilibrium leafy spurge abundance in the absence of grass (leafy spurge carrying capacity). Western wheatgrass and Kentucky bluegrass biomass were combined (gs) because model selection procedures indicated that competitive interactions between each of these grasses and leafy spurge were nearly identical, and prediction accuracy was not improved by modeling these grasses separately. When populations are modeled with time series models, interspecific competitor abundance at year t is typically used to predict abundances at year $t+1$. Using

Table 3.1. Time series models for predicting end-of-the-growing-season leafy spurge length of stem m^{-2} (ls_{t+1}) using leafy spurge length of stem m^{-2} from the previous growing season (ls_t) and grass biomass m^{-2} of the current growing season (gs_{t+1}) as predictor variables, and time series models for predicting gs_{t+1} using gs_t (grass biomass m^{-2} of the previous growing season) and ls_t as predictor variables. Source of models, Post Farm Experiments used for evaluating models, model jackknife mean square errors (JMSE), and r^2 are listed. Parameters describing intrinsic rates of population increase (r), plant carrying capacities (Max), and competitive interactions (competition coefficients) were estimated by minimizing the sum of squared errors. Parameter estimates, JMSE and r^2 were calculated after computing the natural logarithms of both sides of models.

#	Model	Source	Experiment	JMSE	r^2	r	Max	Competition Coefficients
1ls	$ls_{t+1} = ls_t r_{ls} (1 + \alpha_1 ls_t + \alpha_2 gs_{t+1})^{-1}$	Cousens/ Mortimer (1995)	1 and 2	1.15	0.88	1.6		$\alpha_1=0.0003/\alpha_2=0.006$
2ls	$ls_{t+1} = ls_t + r_{ls} ls_t (1 - (ls_t + \alpha gs_{t+1})/ls_{max})$	Logistic	1 and 2	0.71	0.84	2.8	26317	28.7
3ls	$ls_{t+1} = ls_t \exp[r_{ls} (1 - (ls_t + \alpha gs_{t+1})/ls_{max})]$	Lotka-Volterra	1 and 2	0.61	0.87	1.6	20314	24.6
4ls	$ls_{t+1} = ls_t \exp[r_{ls} (1 - (\log(ls_t) + \alpha gs_{t+1})/\log(ls_{max}))]$	Lotka-Volterra	1 and 2	0.60	0.86	3.2	239426	0.008
5ls	$ls_{t+1} = ls_t \exp[r_{ls} (1 - (ls_t(1 + \alpha gs_{t+1}))/ls_{max})]$	Lotka-Volterra/ Watkinson (1981)	1 and 2	0.64	0.86	1.4	25506	0.008
1gs	$gs_{t+1} = gs_t r_{gs} (1 + \beta_1 gs_t + \beta_2 ls_t)^{-1}$	Cousens/ Mortimer (1995)	2	0.41	0.77	6.0		$\beta_1=0.0002/\beta_2=0.007$
2gs	$gs_{t+1} = gs_t + r_{gs} gs_t (1 - (gs_t + \beta ls_t)/gs_{max})$	Logistic	2	0.42	0.76	2.1	825	0.04
3gs	$gs_{t+1} = gs_t \exp[r_{gs} (1 - (gs_t + \beta ls_t)/gs_{max})]$	Lotka-Volterra	2	0.41	0.77	1.3	861	0.04
4gs	$gs_{t+1} = gs_t \exp[r_{gs} (1 - (\log(gs_t) + \beta ls_t)/\log(gs_{max}))]$	Lotka-Volterra	2	0.32	0.82	2.9	1835	0.0002
5gs	$gs_{t+1} = gs_t \exp[r_{gs} (1 - (gs_t(1 + \beta ls_t))/gs_{max})]$	Lotka-Volterra/ Watkinson (1981)	2	0.45	0.75	1.1	4462	0.005

grass at year $t+1$ to predict leafy spurge at year $t+1$ allowed for use of data from two time steps, as opposed to one time step, because grass biomass was only measured at the end of the 2001 and 2002 growing seasons, while leafy spurge was measured in 2000, 2001 and 2002. The parameter β of (3.2) describes the influence of leafy spurge on grass population growth, and $g_{s_{max}}$ is equilibrium grass biomass production in the absence of leafy spurge (grass carrying capacity).

Models that Predict Equilibrium and Carrying Capacity Leafy Spurge and Grass Production. Invasive plant management, such as seeding, and in some cases biological control, grazing and repeated herbicide use, can quasi-permanently change abundances of grasses and invasive plants. For example, seeding can quasi-permanently increase grass biomass production, and if a seeded grass competes with an invasive plant, establishing the grass will cause the equilibrium invasive plant abundance to decrease (Ferrell et al. 1998, Sheley et al. 2001). Alternatively, biological control, repeated herbicide use or grazing can quasi-permanently reduce invasive plant abundance, and if the invasive plant competes with grasses, this reduction will cause equilibrium grass biomass to increase. Models that predict equilibrium plant abundances will also predict non-equilibrium plant abundances in plant communities that are at carrying capacity. If a community is at carrying capacity but is not at equilibrium, then, for example, leafy spurge might replace grasses or grasses may displace leafy spurge over time, but grasses and leafy spurge will not simultaneously increase.

Models that were evaluated for predicting equilibrium leafy spurge and grass abundances have the following parameters and predictor variables.

$$ls = f(gs, \alpha, ls_{\max}) \quad (3.3)$$

$$gs = f(ls, \beta, gs_{\max}) \quad (3.4)$$

These models do not have population growth rate parameters (r 's) and year subscripts (t) because $ls_{t+1} = ls_t$ and $gs_{t+1} = gs_t$ at equilibrium. Because models that follow (3.1) and (3.2) reduce to models that follow (3.3) and (3.4) at equilibrium, interpretation of parameters and predictor variables are the same for all four models.

Model Forms. Scatter plots indicate a positive relationship between leafy spurge abundances of consecutive years and a negative relationship between grass and leafy spurge abundance within a year (Figure 3.3). This indicates that models that follow (3.1) and (3.3) will explain variation in leafy spurge abundance. Scatter plots indicate a positive relationship between leafy spurge abundance and variation in leafy spurge abundance. Therefore, when developing models that follow (3.1) and (3.3), it was assumed that prediction error is log-normally distributed. This assumption is often employed in modeling time series data (Hilborn and Mangel 1997). Scatter plots indicate that models that follow (3.2) and (3.4) will explain variation in grass biomass and also led to the assumption that prediction error is log-normally distributed (Figure 3.4).

Jackknife cross-validation was used to evaluate predictive abilities of three widely used time series models that follow (3.1) and (3.2) (Hjorth 1994). The models were used to predict Post Farm Experiment grass biomass m^{-2} (see 1gs, 2gs and 3gs Table 3.1) and leafy spurge stem length m^{-2} (see 1ls, 2ls and 3ls Table 3.1). The jackknife cross-validation protocol required deleting one plot's data (leafy spurge and grass abundances) from the Post Farm data set. The model being evaluated was then fit to remaining data

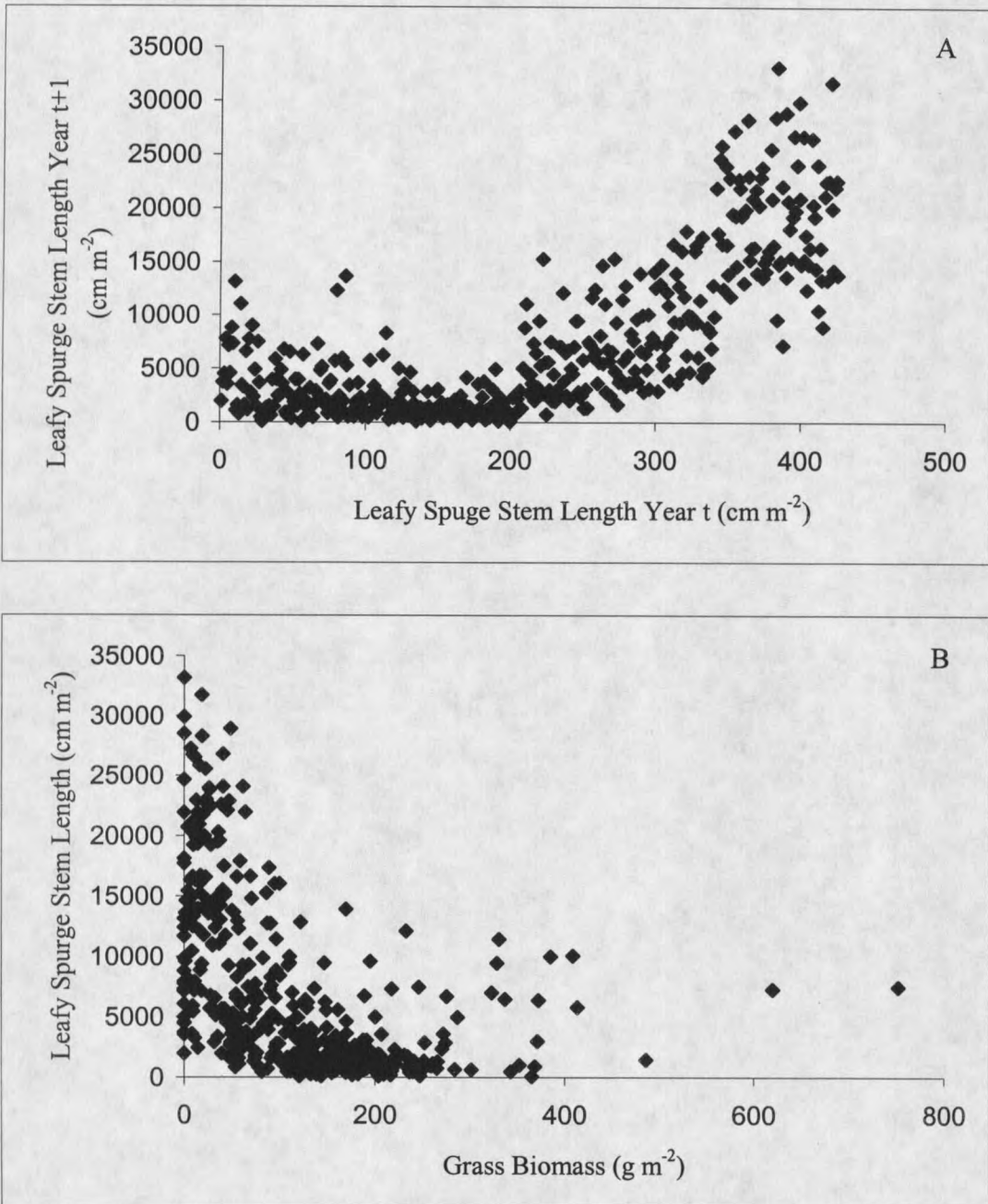


Figure 3.3. Leafy spurge stem length and grass biomass in two Post Farm Experiments. A) Leafy spurge in 2001 is plotted against leafy spurge in 2000, and leafy spurge in 2002 is plotted against leafy spurge in 2001. B) Leafy spurge in 2001 is plotted against grass in 2001 and leafy spurge in 2002 is plotted against grass in 2002.

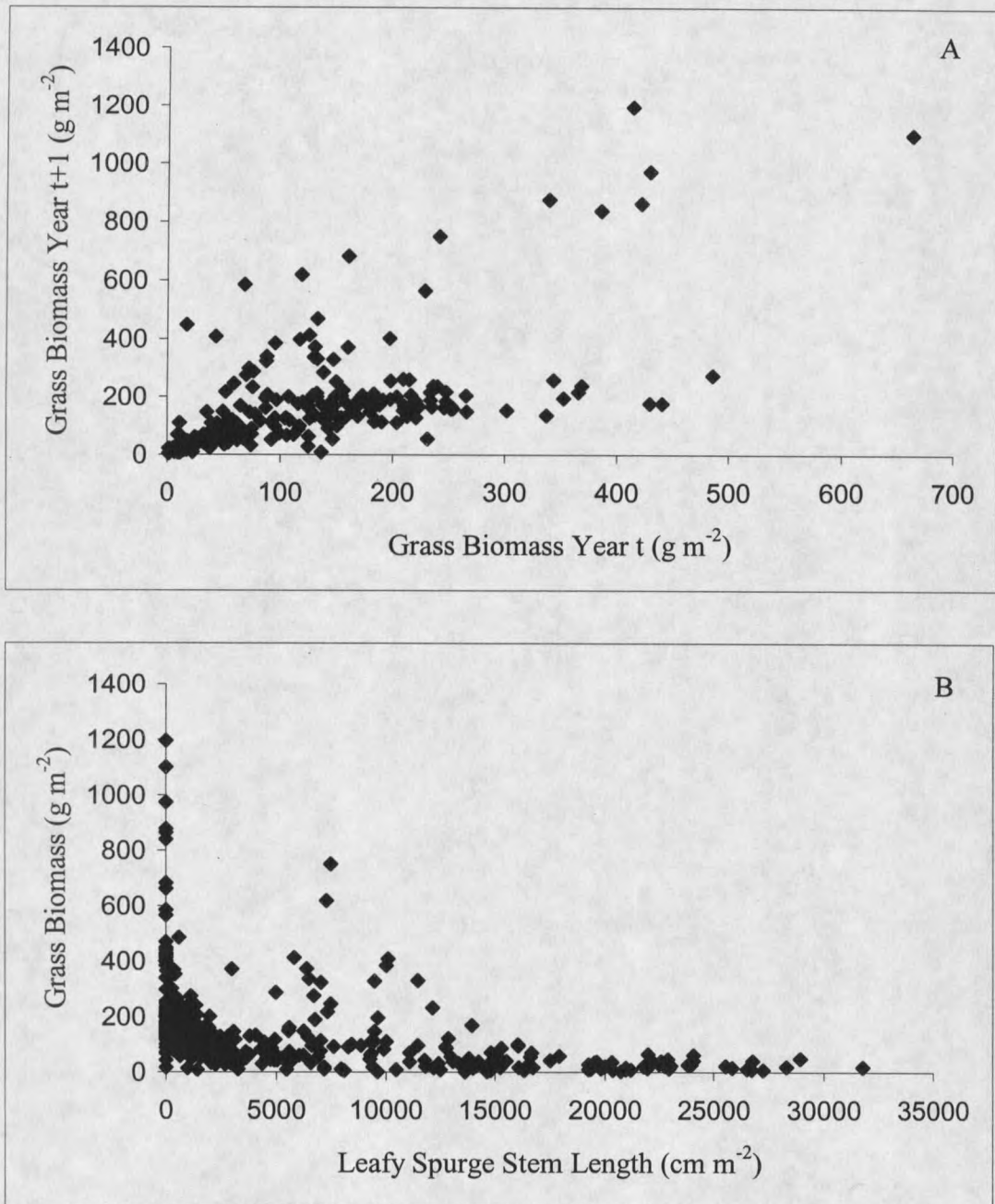


Figure 3.4. Grass biomass and leafy spurge stem length in two Post Farm Experiments. A) Grass biomass in 2002 is plotted against grass biomass in 2001. B) Grass biomass in 2001 is plotted against leafy spurge stem length in 2001 and grass biomass in 2002 is plotted against leafy spurge stem length in 2002.

by adjusting parameter values until the sum of squared residuals was minimized.

Because it is assumed that prediction error is log-normally distributed, model fitting was conducted by first computing the natural logarithm of both sides of the models. The model being evaluated, along with deleted values of the predictor variables, was then used to predict the deleted value of the response variable, and the following quantity was calculated: $(\log(\text{predicted response variable from deleted plot}) - \log(\text{observed response variable from deleted plot}))^2 = \text{squared residual}$. This procedure was repeated for every plot's data. Squared residuals were summed, and this sum was divided by the total number of plots. The jackknife mean square error that resulted from this procedure will hereafter be abbreviated as JMSE. Models with low JMSE predict Post Farm Experiment data better than models with high JMSE.

Jackknife cross-validation indicates that 3ls predicts leafy spurge more accurately than 1ls and 2ls (Table 3.1). All three models (1gs, 2gs and 3gs) predicted grass biomass in Experiment 2 with similar accuracy. Data from Experiment 1 were not used in developing a time series model that predicts grass biomass. The r_{gs} parameter could not be estimated in this experiment because grass biomass was near gs_{max} before measurement began, and gs_{max} in Experiment 1 was much lower than gs_{max} in Experiment 2. The lower gs_{max} of Experiment 1 may have resulted from a hardpan layer in the soil profile.

Models 3ls and 3gs were selected as a starting point for developing models that follow (3.1) and (3.2). These models had to be modified because the unmodified models do not accurately represent leafy spurge and grass dynamics. For example, least-square parameter estimates of 3ls and 3gs indicate the following: $gs_{max} > ls_{max}/\alpha$, $ls_{max} < gs_{max}/\beta$,

and it can be shown that these conditions will predict leafy spurge extinction within Post Farm Experiment plots. This prediction seems unrealistic because, in spite of extensive control efforts, leafy spurge currently coexists with Kentucky bluegrass and western wheatgrass in many areas within only a few kilometers of the Post Farm Experiment sites. Leafy spurge has also coexisted with Kentucky bluegrass and other grasses for several years in an area a few hundred meters from Post Farm Experiments 1 and 2.

Isocline analysis was used to further evaluate 3ls and 3gs and to suggest more realistic model forms. Zero-growth isoclines have the same parameters and predictor variables as (3.3) and (3.4). At equilibrium, each leafy spurge time series model that follows 3.1 reduces to an equilibrium model (i.e. zero-growth isocline) that follows (3.3), and each grass time series model that follows 3.2 reduces to an equilibrium model (i.e. zero-growth isocline) that follows (3.4). Zero-growth isoclines that follow (3.3) and (3.4) give values of ls and gs that yield zero population growth for leafy spurge and grasses, respectively. To derive the zero-growth isocline for 3ls, ls_{t+1} was set equal to ls_t and then 3ls was solved for ls_t . To derive the zero-growth isocline for 3gs, gs_{t+1} was set equal to gs_t , and 3gs was then solved for gs_t . Following are zero-growth isoclines for 3ls and 3gs:

$$ls = ls_{\max} - \alpha gs \quad (3.5)$$

$$gs = gs_{\max} - \beta ls \quad (3.6)$$

The apparent curvilinear relationship between leafy spurge and grass abundance suggests that linear zero-growth isoclines (3.5) and (3.6) are unrealistic (Figures 3.3B and 3.4B). The ability of leafy spurge to increase within a plot does not decrease linearly with increasing grass biomass, and the ability of grass biomass to increase within a plot does not decrease linearly with increasing leafy spurge abundance. Assuming that the zero-

growth isoclines are linear when they are in fact curvilinear could erroneously lead to the prediction that leafy spurge will go extinct in Post Farm Experiment plots.

Curvilinear zero-growth isoclines have been used in conjunction with Lotka-Volterra models (Gilpin and Ayala 1973). Two sets of curvilinear zero-growth isoclines were evaluated to determine if more realistic models could be developed for predicting leafy spurge and grass abundances. The following curvilinear zero-growth isoclines are similar to a model used to predict individual plant weight (Watkinson 1981, Goldberg 1987):

$$ls = ls_{\max}(1 + \alpha gs)^{-1} \quad (3.7)$$

$$gs = gs_{\max}(1 + \beta ls)^{-1} \quad (3.8)$$

It can be shown that (3.7) and (3.8) are the zero-growth isoclines for 5ls and 5gs, respectively (Table 3.1). It can also be shown that (3.9) and (3.10) are the zero-growth isoclines for 4gs and 4ls, respectively (Table 3.1). The following zero-growth isoclines are also similar to a model used to predict individual plant weight (Gaudet and Keddy 1988):

$$\log(ls) = \log(ls_{\max}) - \alpha gs \quad (3.9)$$

$$\log(gs) = \log(gs_{\max}) - \beta ls \quad (3.10)$$

Using curvilinear zero-growth isoclines, as opposed to the linear zero-growth isoclines of 3ls and 3gs, does not change interpretation of model parameters. Except for having nonlinear zero-growth isoclines, 4ls and 5ls are the same as (3ls) (i.e. the linear Lotka-Volterra model) and, 4gs and 5gs are the same as 3gs.

To select a model that predicts grass biomass, the predictive abilities of 4gs and 5gs were evaluated using Post Farm Experiment data, and the performance of these models was compared to that of the linear Lotka-Volterra model (3gs). Model 4gs has the lowest

JMSE of all the grass time series models, and this model was therefore selected for modeling grass biomass (Figure 3.5). The equilibrium model (i.e. zero-growth isocline) that corresponds with 4gs is (3.10).

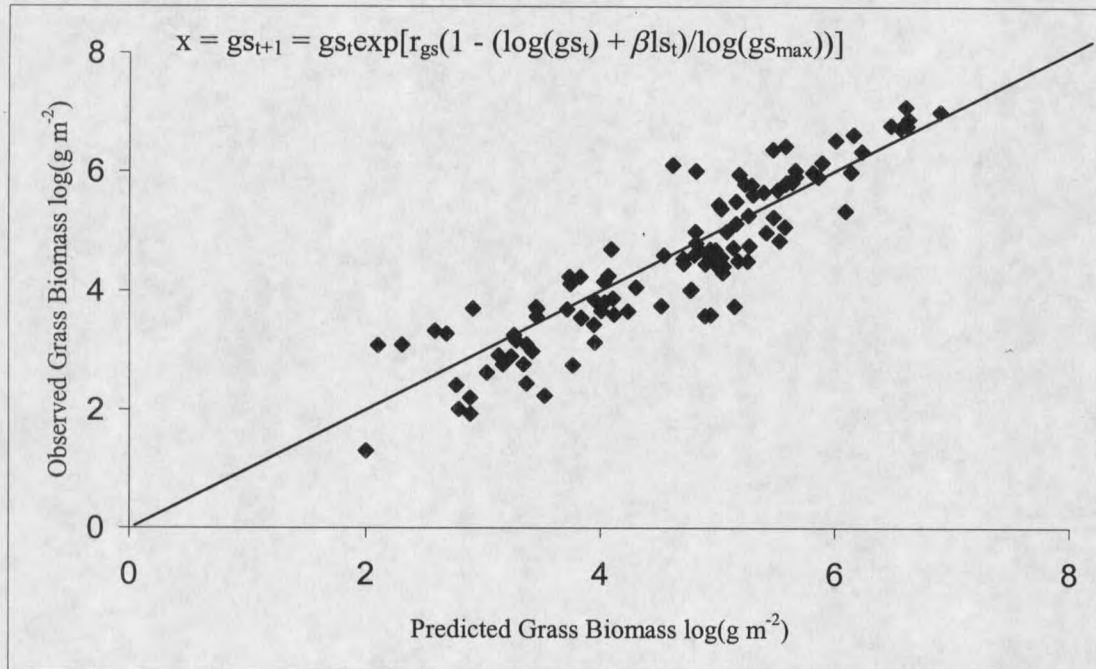


Figure 3.5. Predicted versus observed grass biomass data from Post Farm Experiment 2. Plot grass biomass was measured at the end of the 2001 (gs_t) and 2002 (gs_{t+1}) growing season, and leafy spurge stem length was measured at the end of the 2000 (ls_t) growing season. A Lotka-Volterra model that reduces to a nonlinear zero-growth isocline at equilibrium (i.e. when $gs_t = gs_{t+1}$) was used to derive predicted values. The parameter r_{gs} is the intrinsic population growth rate of grass biomass, gs_{max} is grass biomass at equilibrium in the absence of leafy spurge, and β is a competition coefficient that describes how leafy spurge influences the grass biomass growth rate.

To select a model that predicts leafy spurge abundance, the predictive abilities of 4ls and 5ls were evaluated using Post Farm Experiment data, and the performance of these models was compared to that of the model with the linear zero-growth isocline (3ls). Models 3ls, 4ls and 5ls have similar JMSE's. Model 3ls was rejected in favor of 4ls and 5ls because zero-growth isoclines of 4ls and 5ls are more consistent with the data.

The least-squares ls_{\max} estimate of model 4ls is too large to be realistic (Table 3.1), and isocline analysis revealed that using 4ls in combination with the grass model (4gs) predicts leafy spurge extinction. Therefore, Model 4ls was rejected, and 5ls was selected for modeling leafy spurge dynamics (Figure 3.6). The equilibrium model (i.e. zero-growth isocline) of 5ls is given by (3.7).

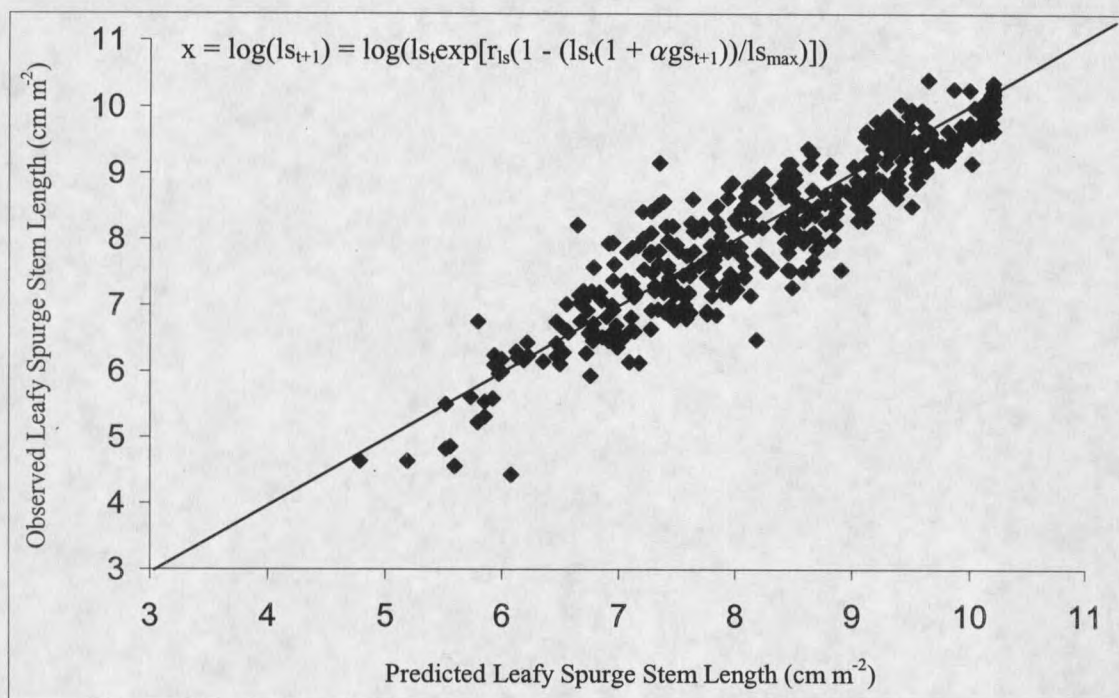


Figure 3.6. Predicted versus observed leafy spurge stem length data from Post Farm Experiment 1 and 2. Grass biomass (gs_t) was measured at the end of the growing season in 2001 and 2002, and leafy spurge stem length (ls_t , ls_{t+1}) was measured in 2000, 2001 and 2002. A Lotka-Volterra model that reduces to a nonlinear zero-growth isocline at equilibrium (i.e. when $ls_t = ls_{t+1}$) was used to derive predicted values. The parameter r_{ls} is the intrinsic population growth rate of leafy spurge, ls_{\max} is leafy spurge abundance at equilibrium in the absence of grass, β is a competition coefficient that describes how grass influences the population growth rate of leafy spurge, the subscript $t+1$ refers to plant abundances measured at the end of the current growing season, and the subscript t refers to the end of the previous growing season.

Assessments of Model Prediction Accuracy

Graphs of zero-growth isoclines for the grass (4gs) and leafy spurge (5ls) model suggest two competitive equilibriums (Figure 3.7). Effects of variation in the physical environment, predation and the other factors that constantly change plant abundances were somewhat taken into account in these equilibrium calculations because these factors influenced parameter estimates. Whether or not the estimated competitive equilibriums will eventually occur, and the length of time that equilibriums persist if they do occur, will depend upon the future intensity and frequency of the non-competition related factors that influence plant abundances (Huston 1979).

Competitive equilibriums will vary temporally and spatially with $l_{s_{max}}$, $g_{s_{max}}$, α , and β . Management actions can change equilibrium plant abundances within a site by changing these parameters. For example, grass seeding can cause a quasi-permanent increase in $g_{s_{max}}$, and this increase can cause equilibrium abundances of leafy spurge and grasses to decrease and increase, respectively (Ferrell et al. 1998). The parameters $l_{s_{max}}$ and $g_{s_{max}}$ vary spatially and must therefore be estimated site specifically when models that include these parameters are used to predict leafy spurge and grass production in management units (Figure 1.1). The magnitude of variation in r_{ls} , r_{gs} , α , and β is not known. To gain insight into the magnitude of this parameter variation, and to evaluate the ability of models 4gs and 5ls to predict leafy spurge and grass abundances, models were used to predict plant abundances that were observed in herbicide and seeding experiments and in SPRE.

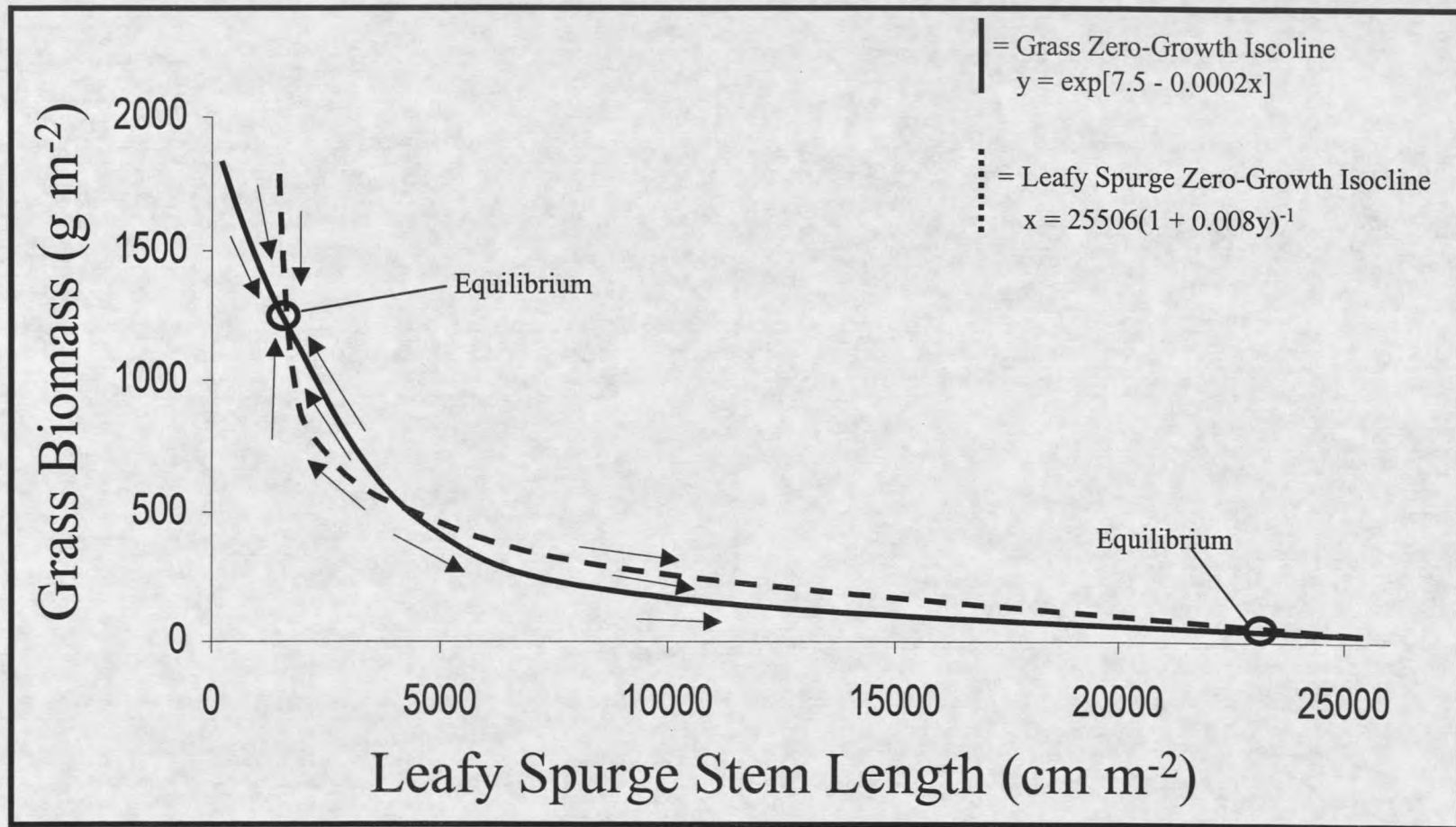


Figure 3.7. Zero-growth isoclines for leafy spurge and grass. Grass isocline parameters were estimated with 2001 and 2002 data from Post Farm Experiment 2. Leafy spurge isocline parameters were estimated with 2000, 2001 and 2002 data from Post Farm Experiments 1 and 2. Isoclines suggest that, depending on initial leafy spurge and grass abundances, one of two equilibrium states will be achieved.

Accuracy Evaluation of Grass Model using Herbicide Experiments. Data from published herbicide experiments were used to evaluate prediction accuracy of the grass model (4gs). Herbicide experiments consisted of herbicide-treated and not-treated plots in which leafy spurge, grass and other-plant abundance were estimated at the end of growing seasons. Although occasionally injuring grasses, herbicides used in these experiments target dicot plants such as leafy spurge. Data were not used if grass herbicide injury was reported or if herbicides did not reduce leafy spurge biomass. Leafy spurge biomass data were converted to stem length data using a linear regression relationship developed from Post Farm Experiments 1 and 2 data and SPRE data (Figure 3.2). Data from 20 site-year combinations were used ((Maxwell 1984) (one site for two years), (Vore 1984) (one site for four years and one site for one year), (Gylling and Arnold 1985) (one site, average of two years), (Lym and Messersmith 1985a) (one site for one year, two sites for two years), (Hein 1988) (one site for two years), (Lym and Messersmith 1994) (two sites for two years), (Markle and Lym 2001) (average of two sites for one year)).

There was very little or no vegetation other than grass and leafy spurge at many herbicide experiment sites. Other-plant biomass (other plants were almost exclusively forbs) was combined with leafy spurge. Because of similarity among growth forms, I feel the assumption that all non-grass plants have similar competitive influences on grasses is more tenable than assumptions embodied in combining other-plant abundances with grasses or leaving other plants out of the analysis.

To test 4gs, it was assumed that herbicide experiment plant communities were at carrying capacity and the zero-growth isocline of this model, which is given by (3.10),

was evaluated. To better ensure that grasses reached a zero-growth isocline after leafy spurge removal, only data from years subsequent to the year of herbicide application were used for the accuracy assessment.

Grass biomass in the absence of other plants (gs_{max}) was estimated independently for each site from a randomly selected herbicide treatment. Plots used to estimate gs_{max} were excluded from the accuracy analysis. The parameter gs_{max} was estimated by rearranging (3.10) where tr refers to herbicide treated plots:

$$\log(gs_{max}) = \log(gs_{tr}) + \beta ls_{tr} \quad (3.11)$$

The variable ls_{tr} refers to leafy spurge and all other non-grasses. The vast majority of non-grass plant biomass was leafy spurge biomass in all herbicide experiments. The parameter β is the least-squares Post Farm-estimated competition coefficient. Equation (3.11) was used to predict the grass biomass that would result from complete removal of all non-grass plants. In many instances non-grasses were completely controlled by herbicide treatment and $\log(gs_{max}) = \log(gs_{tr})$.

If herbicide experiment plots were measured for more than one year, gs_{max} was estimated from first-year data, and this gs_{max} estimate was used to predict grass biomass in that year and each subsequent year of the experiment. In cases where gs_{max} was estimated from a particular year's data and the prediction of grass biomass was formulated for that same year, the prediction was not formulated exclusively from observable quantities. Dashed lines are used to distinguish these cases from the more legitimate cases (solid lines), where gs_{max} was estimated in the first year and this gs_{max} estimate was used to formulate predictions of grass biomass for subsequent years (Figure 3.8). Assessment of the level of agreement between the Post Farm-estimated competition

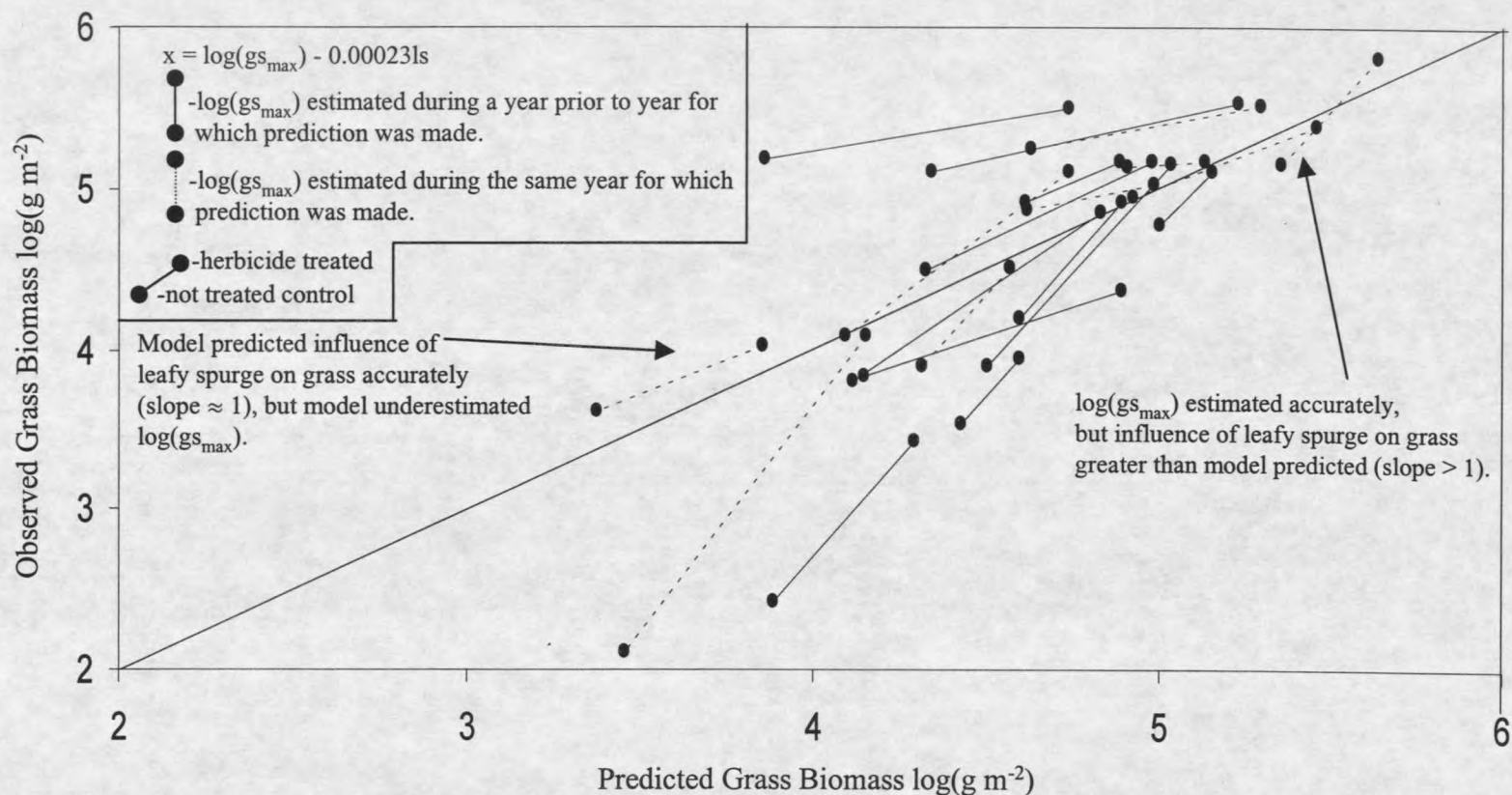


Figure 3.8. Predicted versus observed grass biomass data from herbicide experiments. Each set of two data points comes from a different herbicide experiment-year combination. Predicted values were formulated with a model developed from Post Farm experiments and the least-squares estimate of the Post Farm competition coefficient ($\beta = 0.00023$). Grass biomass production in the absence of leafy spurge (gs_{\max}) was estimated from randomly selected herbicide-treated plots. The predictor variable (ls) is leafy spurge stem length m^{-2} . This metric was estimated by applying a regression relationship to the leafy spurge biomass values that were reported in the herbicide experiment manuscripts (see Figure 3.2).

coefficient and the intensity of competition at herbicide experiment sites is equally legitimate in either case.

Because on-site estimates of gs_{\max} were used, this model accuracy assessment is equivalent to testing the level of agreement between the Post Farm estimate of β and the β value that is intrinsic to other sites. However, this assessment also tests the predictive ability of a system that relies on within-site estimates of gs_{\max} and ls , along with the Post Farm competition experiment-derived estimate of β , to predict grass biomass.

Grass biomass was averaged across all not-treated plots, and this average was calculated for herbicide-treated plots within an herbicide experiment-year combination. Model predictions were formulated for each plot, and predicted grass biomass values were then averaged across all not-treated plots within an herbicide experiment-year combination, and this average was calculated for predicted grass biomass in herbicide-treated plots. Average predicted and observed not-treated grass biomass were compared for this accuracy assessment, as were average predicted and observed herbicide-treated grass biomass (Figure 3.8).

Typically, accuracy assessments are conducted on raw data. Averages were used in this assessment because leafy spurge and grass abundances varied substantially among plots that did not receive herbicide, which suggests that there was considerable within-experiment variation in plant productivity. The rationale for averaging plant measurements is that if herbicide treatments are randomly assigned to plots then the following equality will hold:

$$\lim_{n \rightarrow +\infty} \left(\frac{1}{n} \sum_{i=1}^n gs_{\max, nt, i} - \frac{1}{n} \sum_{i=1}^n gs_{\max, tr, i} \right) = 0 \quad (3.12)$$

The subscript n is the number of plots and n_t and n_r subscripts denote not-treated and herbicide-treated plots, respectively. As plot number increases, the equality is more closely approximated. Within-site values of β are most accurately estimated by averaging plot biomass values so that the influence of small-scale variation in gs_{max} is minimized. In addition to better assessing within-site β , average-based model evaluations are particularly relevant to managers, because managers are interested in predicting average states of management units, not the state of a few small plots within management units.

The predictive ability of (3.10) appears to be similar across the range of grass biomasses observed (no obvious funneling or other patterns in the residuals) (Figure 3.8). Often upper right data points within pairs are closer to the predicted = observed line than are lower left data points, which suggests that the model predicts grass biomass in treated plots more accurately than in not-treated plots. This may have resulted because gs_{max} was estimated from plots where herbicides removed much of the leafy spurge biomass and inter-site differences in β will not influence prediction accuracy as dramatically if leafy spurge abundance is low.

Slopes between not-treated and treated data points are similar to the predicted = observed line for several site-year combinations, which suggests that competition intensity at the Post Farm is often similar to competition intensity in naturally occurring infestations (Figure 3.8). The similarity in competition intensity was observed in spite of differences between the grass species used to develop the models and grass species present at herbicide experiment sites. Slopes are more and less steep than that of the observed = predicted line for some site-year combinations, suggesting that competition

intensity at the Post Farm is between the extremes. There is a longstanding disagreement over whether competition becomes more intense (Grime 1973, Keddy 1989) or stays similar (Newman 1973, Wilson 1991) with increasing plant productivity. These data demonstrate that there are not strong relationships between competition intensity and plant productivity within the range of plant productivities that occurred at herbicide experiment sites.

Figure 3.8 must be appraised with some caution. If average plant productivity of not-treated plots was substantially less than average plant productivity of treated plots, slope > 1 would result. If average plant productivity of not-treated plots was substantially higher than in treated plots, herbicides injured grasses and/or grasses did not fully respond to invasive plant removal before data were collected, slope < 1 would result. The imperfect relationship between reported leafy spurge biomass and estimated stem length m^{-2} also influenced this accuracy assessment to some extent (Figure 3.2). It is logical to assert that most sources of error in the herbicide experiments will under-represent prediction accuracy of (3.10). However, slopes with values similar to 1.0 could also erroneously result from herbicide injury, trends in plant productivity, imperfect knowledge of the relationship between total stem length and leafy spurge biomass, and measurement of grass biomass that occurred before grasses equilibrated to leafy spurge removal.

Accuracy Evaluation of Grass Model using SPRE. Model (3.10) was also evaluated using SPRE data. Grass biomass in picloram-treated SPRE plots was predicted with (3.10). Picloram is a dicot-specific herbicide that occasionally injures grasses.

To conduct the accuracy assessment (3.10) was solved for $gs_p \approx gs_{max}$.

$$\log(gs_p) = \log(gs_n) + \beta(ls_n - ls_p) \quad (3.13)$$

Subscripts refer to not-treated plots (n) and picloram-treated plots (p). The term gs_p is analogous to gs_{max} because little or no leafy spurge remained after picloram was applied. The term ls_p accounts for leafy spurge and other non-grasses that were not killed. The ls terms denote all non-grass plants, and almost all non-grasses in SPRE were leafy spurge. Measurement of predictor and response variables occurred within the same year, and therefore, this assessment does not account for inter-year variation in plant productivity. Because small plots with uniform vegetation were carefully selected, this assessment was less hindered by small-scale intra-site variation in plant productivity than was the evaluation that relied on herbicide experiment data. Because stem length was measured in SPRE experiments, the imperfect relationship between this metric and leafy spurge biomass did not affect this accuracy assessment.

Model (3.13), which is analogous to (3.10), predicted low SPRE grass biomass values fairly accurately but over-predicted in the high-biomass region of the predicted space (Figure 3.9A). Over-predictions were greatest in SPRE that had high leafy spurge abundance and low grass biomass before picloram application. Over-predictions may have resulted because insufficient time elapsed between leafy spurge removal and grass measurement. If grasses were highly suppressed and did not have time to equilibrate to leafy spurge removal before biomass measurement (did not have time to reach a zero-growth isocline), the model would over-predict.

To test this possibility, prediction accuracy of 4gs was evaluated. Rates of biomass increase are taken into account with this model. Leafy spurge control efforts began in

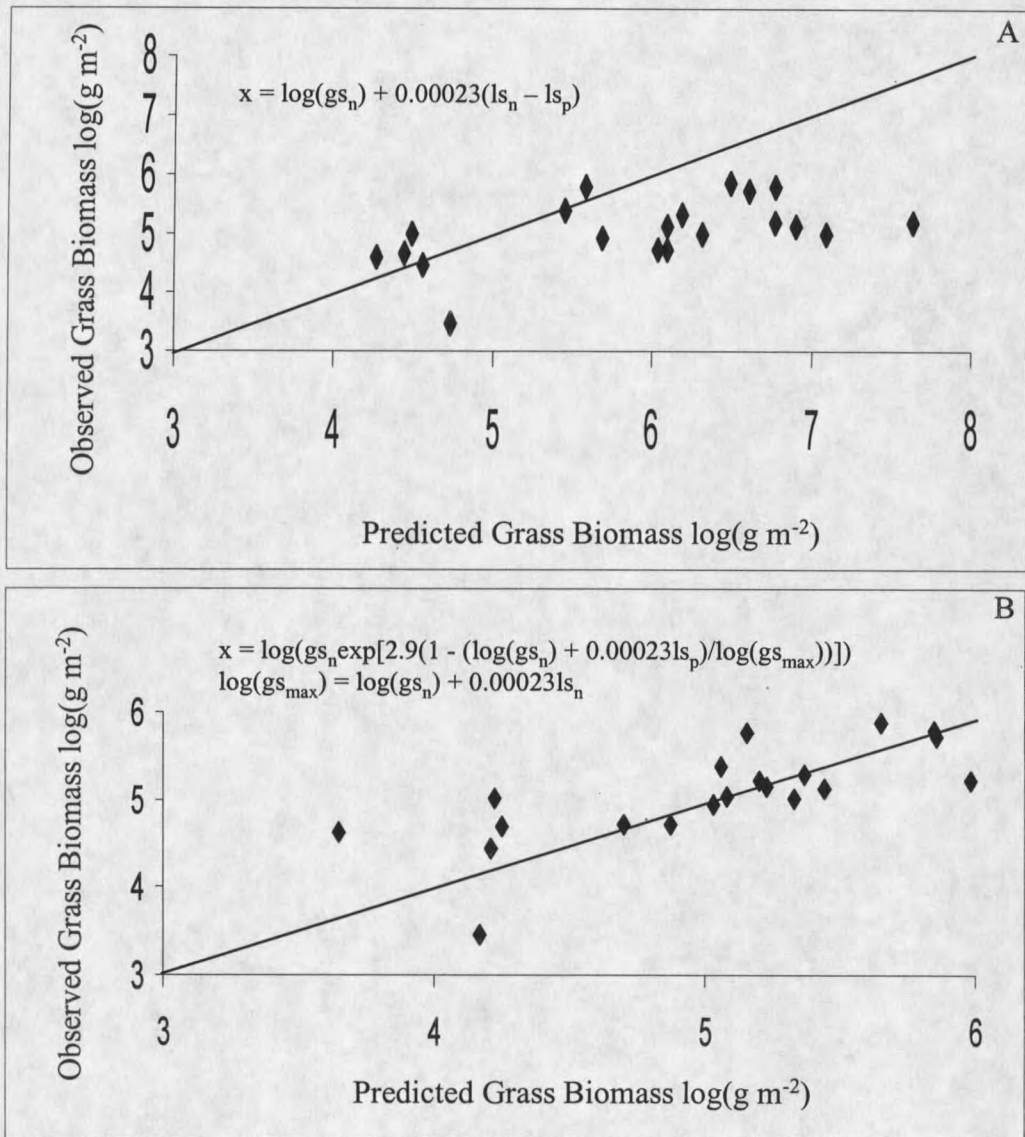


Figure 3.9. Predicted versus observed grass biomass data from SPRE. The n subscripts denote average plant abundances in the two untreated plots of each SPRE and p denotes the one picloram treated plot. Picloram is a dicot-specific herbicide, and little or no leafy spurge remained in picloram-treated plots (ls_p values were small). Observed values are grass biomasses in picloram-treated plots. Predicted values were derived from the zero-growth isocline of a time series model (A) and a time series model (B). The parameter $\beta = 0.00023$ is a competition coefficient that describes the influence of leafy spurge on grass population growth, and $r_{gs} = 2.9$ is the intrinsic grass population growth rate. These least-squares parameter estimates were derived using data from Post Farm Experiment 2. Each data point comes from a different SPRE, and experiments were conducted at different locations in western Montana.

spring of 2001, but leafy spurge did continue to compete with grasses during this year to some extent. Leafy spurge was almost completely controlled going into the spring of 2002, and grasses began an unhindered equilibration to leafy spurge removal. Therefore, grass biomass was projected one time step (one growing season) with a model that is analogous to (4gs).

$$\log(gs_p) = \log(gs_n \exp[r_{gs}(1 - (\log(gs_n) + \beta ls_p)/\log(gs_{max}))]) \quad (3.14)$$

The variables gs_p and gs_n were measured in the same year, but an analogy: $gs_p \approx gs_{t+1}$, $gs_n \approx gs_t$, $ls_p \approx ls_t$, is relied on for this accuracy assessment. The parameters r_{gs} and β are the Post Farm-estimated intrinsic rate of increase and interspecific competition coefficient, respectively (Table 3.1). The gs_{max} term was estimated as:

$$\log(gs_{max}) = \log(gs_n) + \beta ls_n \quad (3.15)$$

which is (3.10) solved for gs_{max} . The β value is the least-squares estimate of this parameter from Post Farm Experiment 2. The time series model (3.15) outperformed the zero-growth isocline of this same model (3.10) (Figure 3.9B), which indicates that more than one full growing season may be required for grass biomass to reach gs_{max} if grass is greatly suppressed prior to leafy spurge removal.

There are other phenomena that could explain over-predictions with the zero-growth isocline model. For example, leafy spurge produces large amounts of litter that can persist for several growing seasons. Perhaps grass biomass did not fully equilibrate to leafy spurge removal because leafy spurge litter competed with grass (Grime 2001). Figures 3.9A and 3.9B must be interpreted cautiously. In spite of efforts to carefully select uniform plots, there were inter-plot differences in plant productivity, and

undetected herbicide injury may have occurred. However, most likely these factors would lead to underestimated prediction accuracy.

Accuracy Evaluation of Leafy Spurge Model using Seeding Experiments. Data from two seeding experiments were used to evaluate prediction accuracy of (3.7), which is the zero-growth isocline of 5ls (Lym and Tober 1997) (Table 3.1). Seeding of several grass species followed application of the non-selective herbicide glyphosate, the dicot-specific herbicide 2,4-D and tillage at the Fargo and Jamestown, North Dakota research sites. Some plots received herbicide and tillage but were not seeded. Grass, leafy spurge and other-plant abundance were estimated at the end of the three sequential growing seasons following the year of grass seeding. Leafy spurge biomass was converted to stem length using the linear regression relationship developed from Post Farm data and SPRE (Figure 3.2).

Leafy spurge was predicted and observed for each grass species treatment in each experiment. Observed and predicted values were calculated for each of the three years of data. The ls_{max} parameter of (3.7) was estimated year- and site-specifically as:

$$ls_{max} = ls_{ns}(1 + \alpha gs_{ns}) \quad (3.16)$$

which is (3.7) solved for ls_{max} . The ns subscript refers to not-seeded plots. It was possible to use data from not-seeded plots to estimate ls_{max} because leafy spurge recovered from use of 2,4-D and glyphosate very quickly. These herbicides kill plants that exist at the time of application but have little or no residual effect. The α value was derived using least-squares estimation of Post Farm data (Table 3.1). All non-seeded plot data were used to estimate ls_{max} , and these data were subsequently excluded from the

accuracy evaluation. The predictive ability of the following model, which is analogous to (3.7), was evaluated:

$$\log(ls_{sd}) = \log(ls_{\max}(1 + \alpha g_{sd})^{-1}) \quad (3.17)$$

The ls terms represent the combined abundance of leafy spurge and all other forbs. The sd subscripts refer to seeded plots. Because ls_{\max} was estimated within each site-year combination, this accuracy evaluation does not take inter-annual variation in plant productivity into consideration.

Data from Fargo are scattered about the predicted = observed line (Figure 3.10) while the model consistently over-predicts leafy spurge abundance at Jamestown (Figure 3.11). Grasses may have been more competitive at Jamestown than at the Post Farm and Fargo, or leafy spurge may have equilibrated to herbicide use more slowly, which would indicate a smaller value of r_{ls} at Jamestown than at the Post Farm and Fargo. Each symbol within a graph represents a different grass species, and these data suggest that all grasses competed similarly with leafy spurge on a per unit biomass basis (Figures 3.10 and 3.11).

Cautions applied to the previously presented accuracy assessments are also relevant to this assessment. The imperfect relationship between leafy spurge biomass and stem length per unit area may be especially important because leafy spurge is the response variable in this assessment (Figure 3.2).

Accuracy Evaluation of Leafy Spurge Model using SPRE. Accuracy of (3.7) was evaluated using SPRE data. This model was used to predict leafy spurge abundance

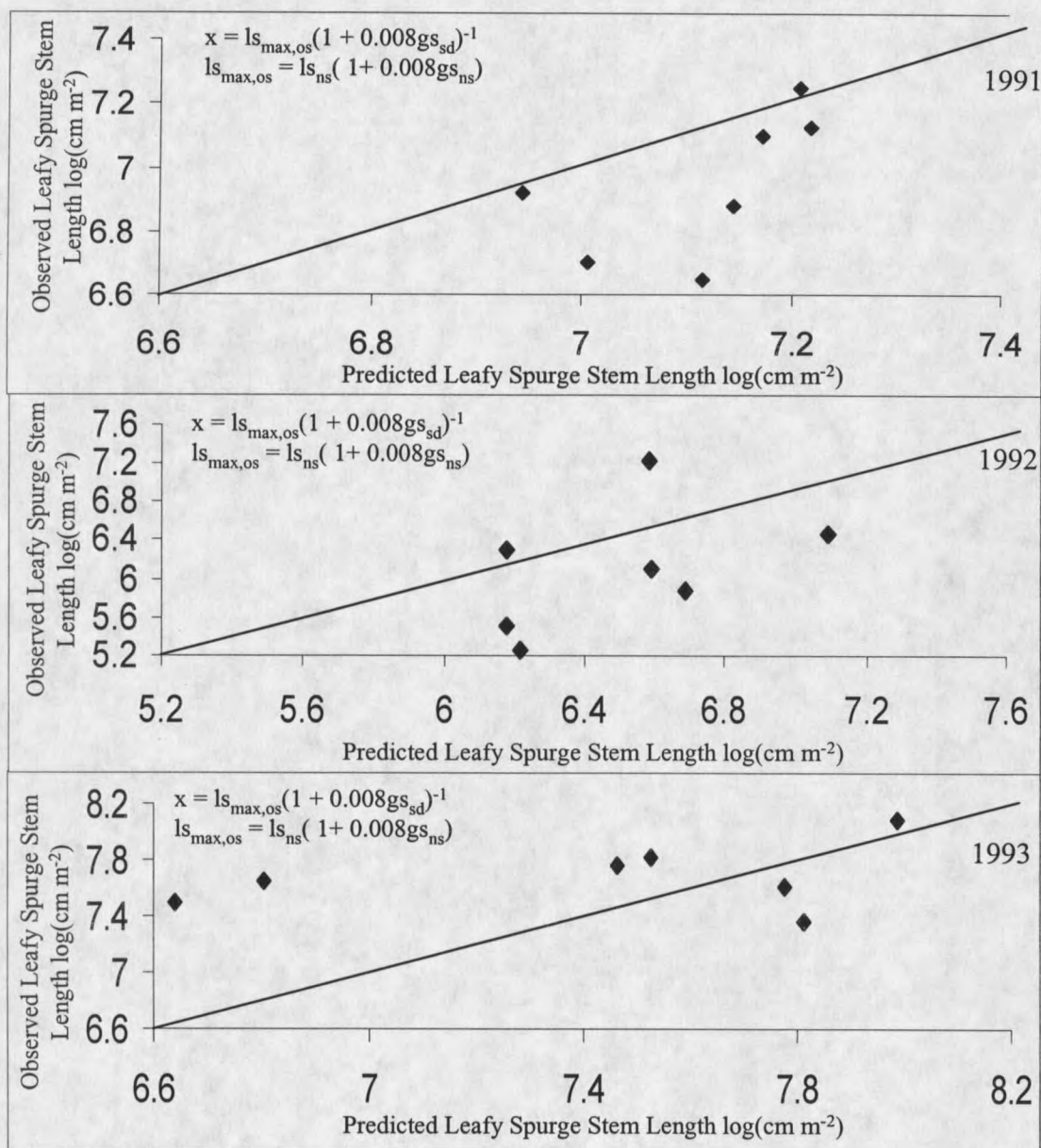


Figure 3.10. Predicted versus observed leafy spurge data from grass seeding experiment conducted near Fargo, North Dakota (Lym and Tober 1997). Predicted values were derived from the zero-growth isocline of a Post Farm model and the least-squares estimate of the competition coefficient ($\alpha = 0.008$) from the Post Farm. The parameter ls_{max} is leafy spurge stem length m⁻² in the absence of grass. This parameter was estimated from leafy spurge (ls_{ns}) and grass (gs_{ns}) abundance in unseeded plots. Stem length was estimated by applying a regression relationship to the leafy spurge biomass values that were reported in the seeding experiment manuscript (see Figure 3.2). The predictor variable (gs_{sd}) is grass biomass in seeded plots. Each data point within a graph corresponds to a different grass species.

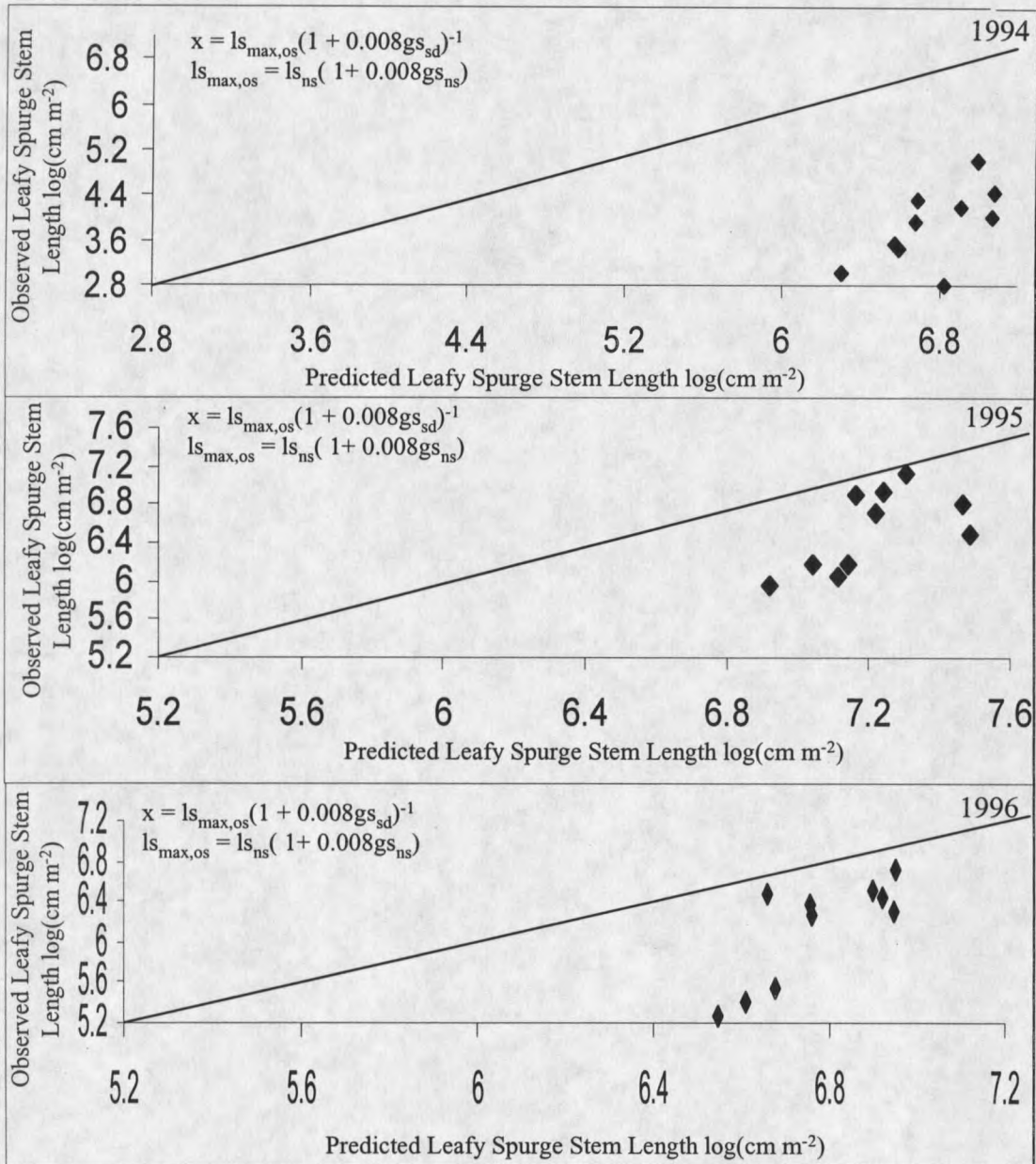


Figure 3.11. Predicted versus observed leafy spurge data from grass seeding experiment conducted near Jamestown, North Dakota (Lym and Tober 1997). Predicted values were derived from the zero-growth isocline of a Post Farm model and the least-squares estimate of the competition coefficient ($\alpha = 0.008$) from the Post Farm. The parameter $l_{s_{\max}}$ is leafy spurge stem length m^{-2} in the absence of grass. This parameter was estimated from leafy spurge ($l_{s_{ns}}$) and grass ($g_{s_{ns}}$) abundance in unseeded plots. Stem length was estimated by applying a regression relationship to leafy spurge biomass values that were reported in seeding experiment manuscript (see Figure 3.2). The predictor variable ($g_{s_{sd}}$) is grass biomass in seeded plots. Each data point within a graph corresponds to a different grass species.

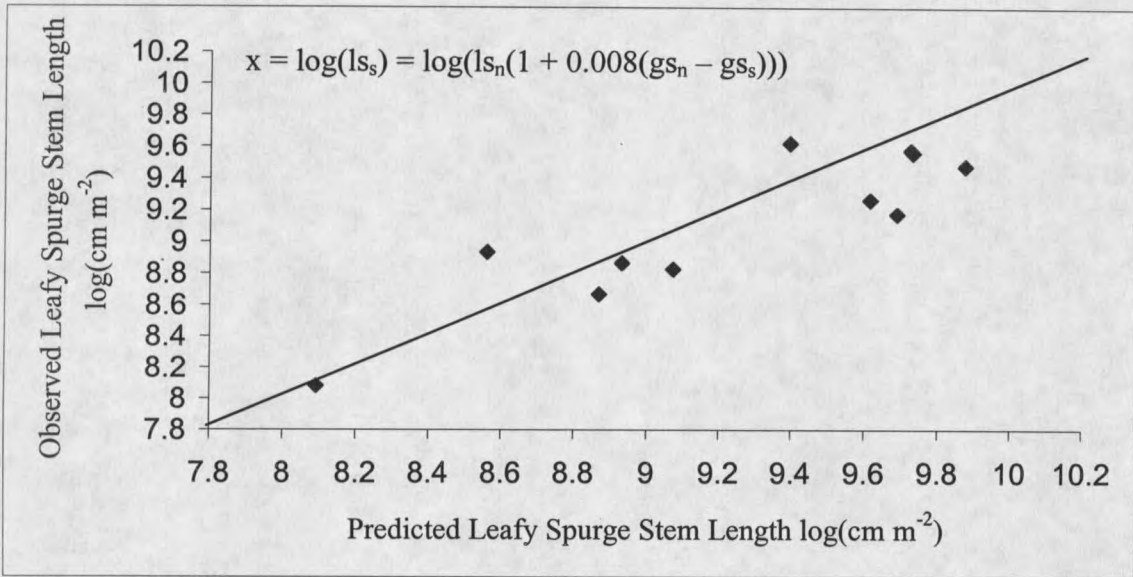


Figure 3.12. Predicted versus observed leafy spurge stem length data from SPRE. The n subscripts denote average grass (gs) and average leafy spurge (ls) production in the two not-treated plots of each SPRE, and s denotes abundances in one plot treated with sethoxydim, which is a grass-specific herbicide. Each observed value is leafy spurge abundance in a sethoxydim-treated plot. Little or no grass remained in sethoxydim-treated plots (gs_s values were small). Predicted values were derived from the zero-growth isocline of a time series model that was fit to data from Post Farm Experiments using least-squares. The $\alpha = 0.008$ parameter describes the influence of grass on leafy spurge production. Each data point comes from a different experiment, and experiments were conducted at different locations in western Montana.

in plots where sethoxydim removed grasses (Figure 3.12). Model (3.7) was solved for

ls_{\max} :

$$\log(ls_s) = \log(ls_n(1 + \alpha(gs_n - gs_s))) \quad (3.18)$$

with ls_s substituting for ls_{\max} . The s subscripts denote the one sethoxydim-treated plot in each experiment. The $ls_{\max} = ls_s$ substitution is appropriate because little or no grass remained in sethoxydim treated plots, and gs_s was included to account for grass that was not killed. The ls terms refer to leafy spurge and the small abundances of other forbs that were present in some SPRE. Because predictor and response variables were measured within the same growing season, this accuracy assessment does not take inter-annual

variation in plant productivity into consideration. Because leafy spurge stem length was measured in SPRE, this accuracy assessment is not hindered by the imperfect relationship between stem length and biomass. Other cautions applied to the other accuracy assessments also apply to this assessment.

The Post Farm model predicted leafy spurge abundances in SPRE with considerable accuracy. Observations are scattered about the predicted = observed line in a manner that suggests that the model does not systematically over- or under-predict.

Conclusions

Models that contain growth rate, competition and carrying capacity parameters explain some variation in leafy spurge and grass production within Post Farm addition series experiments (Table 3.1). Ability of these models to predict plant community response to two types of invasive plant management-caused perturbations was tested. Quasi-permanent changes in species abundances, such as those that result from species introductions (e.g. grass seeding of invasive plant-infested communities), represent the PRESS perturbations of (Bender et al. 1984). Invasive plant management-caused perturbations that alter invasive plant abundances temporarily and then allow communities to relax toward equilibrium (e.g. herbicides) are of the PULSE variety (Bender et al. 1984). The Post Farm models explained variation in the response of leafy spurge and grass production to both kinds of perturbations in several naturally occurring communities.

Models with combined western wheatgrass and Kentucky bluegrass biomass predicted data from addition series experiments as accurately as models that have separate terms

for each grass species. There also did not seem to be any consistent by-species differences in the competitive abilities of the several other grasses that were present in herbicide and seeding experiments (Lym and Tober 1997) (Figures 3.11 and 3.12).

Several studies support the theory that per unit biomass competitive effects of many plant species are similar (Goldberg 1987, Mitchell et al. 1999, Peltzer and Kochy 2001). These findings suggest that the grasses that grow in association with leafy spurge might be considered collectively in a modeling and prediction context.

To apply this chapter's models to management situations, managers would need to provide an estimate of the effect of management strategies on targeted vegetation (e.g. the proportional increase in grass production caused by grass seeding or the proportional decrease in leafy spurge reduction caused by herbicides). Therefore, the models will become more useful with an improved ability to predict the direct effects of management.

Models described in this chapter should be viewed as a portion of a more comprehensive project focused on modeling interactions among leafy spurge and grasses. This chapter describes a successful attempt to select models with realistic properties. However, prediction error was substantial in every accuracy assessment, and this error must be quantified to fully represent the predictive ability provided by the models. The deterministic models of this chapter are transformed into stochastic models in Chapter 4. The stochastic models quantify prediction uncertainty by predicting the probabilities that given leafy spurge and grass abundances will occur in response to management actions.

CHAPTER 4

STOCHASTIC MODELS FOR FORECASTING RESPONSE OF INVASIVE PLANT-INFESTED COMMUNITIES TO MANAGEMENT

Summary

In this chapter, Bayesian techniques are used to transform deterministic models from Chapter 3 into stochastic models. The stochastic models are used to estimate probabilities that leafy spurge and grass abundances will exceed specified values or occupy specified intervals in response to management actions. Bayesian prior probability distributions are often used to describe understanding of model parameters before newly available data are considered. Prior probability distributions of competition coefficients were developed from meta-analysis of herbicide, seeding and selective plant removal experiments. These prior probability distributions and non-informative prior probability distributions describing plant population growth rate, carrying capacity and random error parameters were updated with data from competition experiments using likelihood functions. This updating resulted in Bayesian joint posterior probability distributions that describe complete understanding of parameters in light of all available data. By using posterior probability distributions of this chapter as prior probability distributions when within-management unit data become available, within-management unit refinement of parameter estimates can be accomplished and management unit-specific forecasts of grass and leafy spurge abundances can be formulated. Posterior probability distributions of this chapter can also be used as prior probability distributions when predictive models are developed for other invasive plant and grass species.

Introduction

Managers use herbicides, biological control, seeding, and grazing to minimize invasive plant abundance and impact. Monetary costs and species compositions resulting from management are the primary considerations that drive selection of management strategies. Species compositions are unknown quantities that must be predicted. Managers will become better equipped to select optimal invasive plant management strategies as predictions of management-induced shifts in species compositions improve.

In the future managers may consider ecological impact of invasive plants when selecting management strategies, but current understanding of impact is such that many ecological factors cannot be considered. However, species compositions play a large role in determining ecological condition, and researchers are beginning to explore the relationships between species compositions and ecological impact (D'Antonio and Vitousek 1992, Blossey 1999, Blossey et al. 2001). By predicting species compositions, insight is gained into the future state of the entire suite of ecological, aesthetic and monetary factors that establish whether or not use of any given invasive plant management strategy is warranted.

Predictive population and competition models have been developed for invasive plants (Kroon et al. 1987, Solbrig et al. 1988, Lonsdale et al. 1995), and in some cases model-based predictions of plant abundances have been fairly accurate (Gillman et al. 1993). Some researchers have suggested that population models might be used to predict plant abundances resulting from proposed invasive plant management actions (Shea and Kelly 1998, Parker 2000). However, several random processes cause uncertainty in model-

based predictions of plant abundances. These random processes, all of which are outlined in detail in Chapter 1, include efficacy of invasive plant management strategies, competition intensity, intrinsic plant growth rates, plant carrying capacities, plant abundances per unit area within management units, species compositions, random error, and magnitude of random error. Stochastic models have been used to quantify some of these random processes (Solbrig et al. 1988, Pandey and Medd 1991, Jordan 1992). This chapter relies on Bayesian techniques to develop stochastic models that quantify and reduce many of the sources of prediction uncertainty described in Chapter 1. To the best of my knowledge, these models constitute the first attempt to forecast invasive and desired plant abundances resulting from management actions. Bayesian techniques provide enough flexibility to allow data from various invasive plant research projects (e.g. herbicide and seeding experiments) to contribute to parameter estimation, and estimate probabilities that grass and invasive plant abundances will occupy specified intervals or exceed or fall below specified values.

Model Development

In Chapter 3, deterministic leafy spurge and grass models were developed/selected using data from competition experiments. Model predictive ability was evaluated using data from herbicide, seeding and selective plant removal experiments. In this chapter, all data described in Chapter 3 are used to develop stochastic versions of the deterministic models. The stochastic models forecast leafy spurge and grass abundances (i.e. these models predict the probability that particular leafy spurge and grass abundances will occur in response to management).

Model that Forecasts Grass Biomass over Time

Management applications of models that forecast grass biomass over time are outlined in Chapters 1 and 3. In Chapter 3, the following model, which is based on the Lotka-Volterra model, was selected for predicting grass biomass:

$$gs_{t+1} = (gs_t \exp[r_{gs}(1 - (\log(gs_t) + \beta ls_t)/\log(gs_{max}))])\epsilon_{gs} \quad (4.1)$$

The combined biomass ($g\ m^{-2}$) of all perennial grasses that grow in association with leafy spurge is represented by gs . The t and $t+1$ subscripts refer to the end of the current and next growing season, respectively. The r_{gs} parameter is the intrinsic rate of grass biomass increase, ls is leafy spurge stem length ($cm\ m^{-2}$), β is a competition coefficient that describes impact of leafy spurge on grass biomass production, and gs_{max} is equilibrium end-of-the-growing-season grass biomass ($g\ m^{-2}$) in the absence of leafy spurge. The error term accounts for all factors that influence gs_{t+1} (e.g. insect herbivory, hailstorms), except for the factors that are explicitly governed by other model terms. It is assumed that error is lognormally distributed ($\epsilon_{gs} \sim \log N(1, \sigma_{\epsilon_{gs}}^2)$). This assumption is often invoked with the use of logistic population growth models (Hilborn and Mangel 1997).

Herbicide and selective plant removal experiment (hereafter SPRE) data and 2001 and 2002 data from Post Farm Experiment 2 were used to estimate model (4.1) parameters. Data from Experiment 1 were not used because: 1) r_{gs} cannot be estimated because scatter plots indicate that Experiment 1 plant abundances were near equilibrium before measurement began, and 2) Experiment 1 $\log(gs_{max})$ was much lower than Experiment 2 $\log(gs_{max})$. The average weight of grass biomass in leafy spurge-free plots was 175 g in Experiment 1 and 627 g in Experiment 2. The lower $\log(gs_{max})$ of Experiment 1 may have resulted from a soil hardpan layer.

Good introductions to Bayesian statistics are available (Ellison 1996, Hilborn and Mangel 1997). Bayesian techniques were used to estimate the Bayesian joint posterior probability distribution of model (4.1) parameters ($P(r_{gs}, \beta, \log(gs_{max}), \sigma_{\epsilon,gs} | \text{data})$). This probability distribution represents the understanding of model parameters that results from all available data. This distribution is proportional to the product of the likelihood function ($L(\text{data} | r_{gs}, \beta, \log(gs_{max}), \sigma_{\epsilon,gs})$) and the joint prior probability distribution of model parameters ($P(r_{gs}, \beta, \log(gs_{max}), \sigma_{\epsilon,gs})$).

$$P(r_{gs}, \beta, \log(gs_{max}), \sigma_{\epsilon,gs} | \text{data}) \propto$$

$$L(\text{data} | r_{gs}, \beta, \log(gs_{max}), \sigma_{\epsilon,gs})P(r_{gs}, \beta, \log(gs_{max}), \sigma_{\epsilon,gs}) \quad (4.2)$$

Likelihood Function for Parameters of Model that Forecasts Grass Biomass over Time. A likelihood function that follows the normal distribution in the natural log space was used because of the assumption that (4.1) error is lognormally distributed. The following likelihood function represents data from Post Farm Experiment 2:

$$L(\text{data} | r_{gs}, \beta, \log(gs_{max}), \sigma_{\epsilon,gs}) =$$

$$\prod_{i=1}^n \frac{1}{\sigma_{\epsilon,gs} \sqrt{2\pi}} \exp\left(-\frac{(\log(gs_{t+1,i}) - \log(f(r_{gs}, \beta, ls_{t,i}, gs_{t,i}, \log(gs_{max}))))^2}{2\sigma_{\epsilon,gs}^2}\right) \quad (4.3)$$

The deviation is the squared difference between the natural log of the observed ($gs_{t+1,i}$) and predicted ($f(r_{gs}, \beta, ls_{t,i}, gs_{t,i}, \log(gs_{max}))$) grass biomass. The n subscript denotes the number of plots (i.e. rows in the data matrix) used in the analysis ($n = 108$).

Prior Probability Distribution of Parameters of Model that Forecasts Grass Biomass over Time. The Bayesian joint prior probability distribution describes understanding of model parameters before data that make up the likelihood function (i.e. Post Farm data)

are considered. A prior probability distribution with no interdependence among model parameters was selected for this analysis because of a lack of knowledge about interrelationships among parameters. Specifying a prior probability distribution with no relationships among parameters can be thought of as specifying a separate prior probability distribution for each parameter. If the likelihood function contains information about interrelationships among parameters, then multiplying the prior probability distributions by the likelihood function will result in a posterior probability distribution that reflects these interrelationships.

Uniform prior probability distributions were used for r_{gs} , $\log(gs_{max})$ and $\sigma_{\epsilon,gs}$ ($r_{gs} \sim U(0,4.47)$, $\log(gs_{max}) \sim U(0,7.60)$, $\sigma_{\epsilon,gs} \sim U(0,0.83)$). Uniform prior probability distributions are often referred to as non-informative or flat prior probability distributions. When uniform prior probability distributions are used, only the data that make up the likelihood function (in this case the Post Farm data) determine the shape of the posterior probability distribution over established limits of the parameter space. Uniform prior probability distributions were used because, other than Post Farm data, there was no information on these parameters. The lower limit of the r_{gs} , $\log(gs_{max})$ and $\sigma_{\epsilon,gs}$ parameter space was set at 0 because these parameters must be positive. The upper limits of r_{gs} and $\sigma_{\epsilon,gs}$ were set to correspond with $L(\text{data} | r_{gs}) \approx 0$ and $L(\text{data} | \sigma_{\epsilon,gs}) \approx 0$, respectively. If the likelihood of data given parameter values is very small (≈ 0) then the values of $P(r_{gs})$ and $P(\sigma_{\epsilon})$ are irrelevant in computing the posterior probability distribution of parameters. Unless otherwise specified, this same rationale was used in setting upper limits on uniform prior probability distributions throughout this chapter.

The probability distribution of $\log(g_{s_{\max}})$ had an unrealistically long right-hand tail when the upper limit on the parameter space was set to correspond with $L(\text{data} | \log(g_{s_{\max}})) \approx 0$. Consequently, the upper limit was set at $\log(2000 \text{ g m}^{-2}) = 7.60 \text{ g m}^{-2}$. This boundary is justified because plots from other Post Farm Experiments did not produce even half this much grass biomass (Carpinelli 2000, Sheley et al. 2002). Furthermore, the greatest grass biomass of any plot in Post Farm Experiment 1 and 2 was only 1196 g m^{-2} .

Herbicide experiment and SPRE data were used to develop a prior probability distribution for β . In herbicide experiments, leafy spurge, grass and other-plant abundances were estimated at the end of growing seasons in herbicide-treated and not-treated plots. Although occasionally injuring grasses, herbicides in these experiments target leafy spurge and other dicot plants. To allow grasses to equilibrate to dicot removal, only data from years subsequent to the first year of herbicide application were used. There was very little or no vegetation other than grass and leafy spurge at most herbicide experiment sites. Other-plant abundance was combined with leafy spurge. I feel the assumption that all non-grass plants have similar competitive influences on grasses is more tenable than assumptions embodied in combining other-plant abundance (other plants were primarily forbs) with grasses or leaving other plants out of the analysis. Leafy spurge biomass was measured in herbicide experiments, and these data were converted to stem length m^{-2} using a linear regression relationship developed from Post Farm and SPRE data (Figure 3.2). Data were not used if grass herbicide injury was reported or if herbicides did not reduce leafy spurge biomass. Data from 20 site-year combinations were used ((Maxwell 1984) (one site for two years), (Vore 1984) (one site

for four years and one site for one year), (Gylling and Arnold 1985) (one site, average of two years), (Lym and Messersmith 1985a) (one site for one year, two sites for two years), (Hein 1988) (one site for two years), (Lym and Messersmith 1994) (two sites for two years), (Markle and Lym 2001) (average of two sites for one year)). Each site-year combination had a large gradient in leafy spurge abundance because some herbicides killed a large proportion of leafy spurge in each site-year combination and each experiment had some plots that did not receive herbicide.

The following model was fit to data from each site-year combination to generate 20 point estimates of β :

$$\log(gs) = \log(gs_{\max}) - \beta ls \quad (4.4)$$

This model is the zero-growth isocline of model (4.1). The ls predictor variable refers collectively to leafy spurge and all other non-grass plants within herbicide experiments. It was assumed that herbicide experiment plant communities were at carrying capacity in order to generate estimates of β with (4.1). At carrying capacity there are not simultaneous net gains in the abundances of both leafy spurge and grasses, but grasses may be displacing leafy spurge or leafy spurge may be displacing grasses over time. Therefore, the ratio of leafy spurge to grass abundance at carrying capacity may not be the same as this ratio at equilibrium. To better justify the carrying capacity assumption, data from the first year that herbicides were applied were not used so that grasses were given more time to respond to leafy spurge removal.

One point estimate of β was derived from each of 19 SPRE using the following equation, which is analogous to (4.4):

$$\beta = (\log(gs_p) - \log(gs_n)) / (ls_n - ls_p). \quad (4.5)$$

The ls predictor variable refers collectively to leafy spurge and the few other non-grasses that were present at some SPRE sites. The p subscript refers to grass (gs_p) or non-grass (ls_p) abundance in the plot within a SPRE that received picloram to remove non-grasses, and the n subscript refers to average plant abundances (gs_n and ls_n) in the two plots that were not treated with herbicide. Little or no leafy spurge and other non-grass abundance remained in picloram-treated plots ($ls_p \approx 0$). To generate estimates of β with (4.5), was assumed that SPRE plant communities were at carrying capacity. Herbicides were applied in mid-May 2001 and grasses were not measured until early August 2002. Allowing nearly two growing seasons for SPRE plant communities to equilibrate to leafy spurge removal helped justify this assumption.

To estimate the prior probability distribution of β ($\beta \sim \log N(-9.0, 0.83)$), herbicide experiment and SPRE estimates of this parameter were grouped in a histogram, and a lognormal probability distribution was fit to this histogram (Figure 4.1).

Posterior Probability Distribution of Parameters of Model that Forecasts Grass Biomass over Time. The Bayesian joint posterior probability distribution of model (4.1) ($P(r_{gs}, \beta, \log(gs_{max}), \sigma_{\epsilon,gs} | \text{data})$) parameters was simulated by using a form of Markov chain Monte Carlo integration (Gilks et al. 1998). Hereafter, θ will denote a vector that contains one parameter value for each model parameter. Initial values were set for each parameter of 4.1, and $L(\text{data} | \theta_t)P(\theta_t)$ was evaluated for the parameter vector (θ_t). New parameter values were then proposed, and $L(\text{data} | \theta_{t+1})P(\theta_{t+1})$ was evaluated for the proposed vector (θ_{t+1}). The proposed vector was determined by adding

