AN ABSTRACT OF THE DISSERTATION OF

D. Eric Hanson for the degree of Doctor of Philosophy in Forest Science presented on October 29, 1998. Title: Population Dynamics of Three Early Seral Herb Species in Pacific Northwest Forests.

Signature redacted for privacy.

Abstract approved: _____

Steven R. Radosevich

I investigated the population dynamics of fireweed (*Epilobium angustifolium*), foxglove (*Digitalis purpurea*), and woodland groundsel (*Senecio sylvaticus*) to understand their colonization, persistence, and extirpation in Pacific Northwest Douglas-fir forests. Factors affecting the species' frequency and abundance in forest communities were evaluated. Their population dynamics were modeled and field experiments examined nitrogen fertilization and competition effects on population parameters. Experimental variation made the population models stochastic and sequential transition matrices incorporated the effects of competition into them.

Plant community ordination suggested a negative relationship between foxglove and elevation. Indicator species analysis revealed that foxglove is favored by disturbance, *i.e.,* broadcast silvicultural treatments, and by high site productivity, while fireweed responds to low productivity and lack of disturbance. Regression analysis related the species' frequency and cover to factors such as stand age, elevation, and UTM meters east.

Simulated woodland groundsel population increased most rapidly. Increased competition tended to reduce its biomass accumulation and seed production per plant but did not affect seeds produced per unit area. Competition also reduced established immature plant survival. Incorporating these factors into the population model, the rate of population growth declined.

The projected foxglove population grew at a lower rate than did woodland groundsel but faster than fireweed. Foxglove was adversely affected by competition, which generally reduced its size, biomass, and seed production. Interspecific competition reduced established plant survival, rosette persistence, perenniation, and flowering. Nitrogen fertilization stimulated seed germination, rosette persistence, and flowering but decreased perenniation. Nitrogen fertilization rate did not influence population growth when modeled but application timing did. Nitrogen applied at transplanting resulted in extinction of the population. Transplanting one year after fertilization resulted in constant population growth.

Fireweed, with the most complex life cycle, had the lowest population growth rate. Its persistence was entirely due to vegetative reproduction--without it the population would rapidly become extinct. Competition and fertilization had little effect on this species and population projections based on the field experiments indicated constant growth.

These results suggest life history and competitive ability regulate succession of pioneer species in Douglas-fir forests and increases population persistence comes at the expense of their growth rate.

Population Dynamics of Three Early Seral Herb Species in Pacific Northwest Forests

by

D. Eric Hanson

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented October 29, 1998
Commencement June 2000

ACKNOWLEDGMENTS

First, I would like to thank my committee, Drs. Bruce Coblenz, Dave Hibbs, Peter McEvoy, Mary Lynn Roush, and Mark Wilson. Their guidance, support, and counsel were critical to success of my dissertation. Dave is due special recognition for agreeing to replace Mary Lynn on the committee when there was nothing left to do but read the dissertation and conduct the final exam. A special thanks to Dr. Steve Radosevich for serving as my Major Professor and for challenging me to think critically about my science and the societal context in which it rest.

Several other faculty members and students have also be helpful to me in completing this project. The statistical assistance of Tom Sabin, Lisa Ganio, and Manuela Huso were invaluable. Labor provided by Anne Marie Badeau, Keri Bush, Will Schneider, Jose Toledo, and Kathleen Wilson made the field experiments possible. Thanks also to Mike Rector, Research Coordinator of the McDonald-Dunn Research Forest, for assisting me in locating field sites.

Numerous friends have encouraged me through out my career at OSU. My comrades in the CRAFTS cooperative, Tim Harrington, Steve Knowe, Alex Pancheco, Bob Shula, and Will Schneider made the working environment more enjoyable for their presence. Graduate student friends, such as Kathleen Avina, Jeanne Panek, Bev Law, and Michelle Stubbs have eased the burden through a shared trial. Two special friends helped me through the toughest part of all--the writing. Dr. Barbara Bond provided motivation and encouragement, while Dr. Barbara Schrader was, as one recently successful in completing her dissertation, the voice of reassurance insisting that the task was truly possible.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

LIST OF APPENDICES

LIST OF APPENDIX FIGURES

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

CONTRIBUTIONS OF AUTHORS

Steve Radosevich assisted with the design of the project and interpretation of its results. He also provided laboratory and computer facilities as well as review of the manuscripts.

DEDICATION

I dedicate this work to the memory of my Grandfather, Dr. Herbert C. Hanson, who was also a plant ecologist.

All that is gold does not glitter,
　　Not all those who wander are lost;
The old that is strong does not wither,
　　Deep roots are not reached by the frost.
From the ashes fires shall be woken,
　　A light from the shadows shall spring;
Renewed shall be the blade that was broken,
　　The crownless again shall be king.

by Bilbo Baggins
from J.R.R. Tolkien's
Lord of the Ring

Population Dynamics of Three Early Seral Herb Species in Pacific Northwest Forests

CHAPTER 1

Dissertation Introduction

RESEARCH PROJECT GOALS AND OBJECTIVES

Woodland groundsel (*Senecio sylvaticus* L.), foxglove (*Digitalis purpurea* L.), and fireweed (*Epilobium angustifolium* L.)[1] are early seral herbs common to forests of western Oregon. The goal of this research was to use population dynamics models to project the change in abundance of these three species as they were influenced by nitrogen fertilization and competition. Four specific research questions were addressed:

1) How are populations of these species influenced by properties of their life cycles? Which life cycle components have the greatest effect?

2) How do nitrogen fertilization and competition, which have been suggested to have a strong influence, affect their population dynamics? Do these two factors interact in their effect on the species' population dynamics?

3) How does the introduction of experimentally-derived variability into the transition probabilities of population models for these species affect their projections? Does demographic stochasticity have a greater on the populations than do environmental factors, such as nitrogen and competition?

---

[1]Taxonomy follows Hitchcock and Cronquist (1973).

4) Do other environmental or silvicultural factors besides nitrogen fertilization and competition affect their abundance?

Two research approaches were used to address these questions and are described below.

Research Approaches

1. Environmental and Silvicultural Influences on Target Species - Objectives 1 & 4

Plant community data were collected from young forest plantations (less than 20 years old) in western Washington and Oregon and analyzed to determine the effects of environmental variables and silvicultural treatments on the three selected herb species (Chapter 2). The effects of selected environmental and silvicultural variables on both presence and abundance of woodland groundsel, foxglove, and fireweed were examined using ordination and other multivariate techniques (Objective 4). Logistic and linear regression were then used to assess the magnitude of the factors affecting the presence and abundance (*i.e.*, percent cover) of the species (Objective 1).

2. Population Modeling - Objectives 1, 2, & 3

The three species differ in life histories (*i.e.*, an annual, semalparous perennial, and iteroparous perennial, respectively). Therefore, a population model was developed for each species to evaluate how life cycles affect their population dynamics (Objective 1). Population data from the literature were used to parameterize the models. Asymptotic population growth rates (λ) were determined using computer simulation, as well as sensitivity, elasticity, and loop analyses where appropriate. These results are presented for woodland groundsel, foxglove, and fireweed in the initial sections of Chapters 3, 4, and 5,

respectively. Data from field experiments (see below) then were incorporated into the existing population models. Further simulations and analyses were conducted on the revised models, which were the bases for comparing the effects of nitrogen fertilization and competition on population changes in these species (Objective 2). These results are discussed at the end of Chapters 3, 4, and 5 for the respective species. The experimental data provided the means to introduce stochasticity into the population models for comparing its effects *vis a vis* fertilization and competition treatments (Objective 3) with the results presented at the end of those chapters as well.

Three field experiments assessed the effects of various nitrogen fertilizer levels and competition treatments on the survival, size, development, and reproduction of each species (Objective 2). In one experiment, transplanted seedlings developed for three years, permitting on-site sexual and vegetative reproduction rates to be determined. Growth and phenological state were monitored through each growing season in this experiment. After three years, all three species were harvested to determine the relative change in plant abundance over time. The other two experiments lasted only one growing season each and differed only in propagule source (transplants vs. seed). These experiments were used to assess treatment effects on survival, size, and reproduction of the species. The results of the experiments are presented for woodland groundsel in Chapter 3, for foxglove in Chapter 4, and for fireweed Chapter 5.

The three-year experiment also was used to determine persistence and colonization of the three species over time. The experimental approach was similar to that of van Andel and Nelissen (1981) where plots containing each species were contiguous with those

having the other species. Persistence of the species in a plot and/or its colonization of other plots was assessed over the duration of the experiment.

Understanding the population dynamics of these species allows consideration of the mechanisms of plant community development. Through linking the population dynamics to resource availability and competition, direct effects on populations can be scaled up to reflect on successional processes. In addition, it provides a means to evaluate a variety of successional theories and a comparison for other population models created for each life history type.

Research Relevance

Scientific

Conceptually, succession has progressed from the ontogeny of a "supra-organism" (Clements 1914) to the spatial and temporal distribution of populations in a shifting mosaic, which is regulated by factors such as disturbance, colonization, persistence, and interference. Disturbance and related patch dynamics are one important component of the successional process (Picket and White 1985). Patches, which are created by some disturbance, have a size and growth rate that can be simulated through modeling (Levin and Paine 1974, Shugart and Seagle 1985). Such models have been used to simulate the colonization of patches in intertidal areas (Paine and Levin 1981) and forests (Botkin *et al.* 1972). Populations occupying a patch are affected by colonization ability, life history process (i.e., reproduction, establishment, growth, and mortality), environmental heterogeniety, and inter-, as well as, intra-specific interactions. (Peet and Christensen 1980,

Thompson 1985). It is the process of disturbance creating vacant patches and this interaction of various populations occupying them that creates communities.

This research assesses changes in dominance among these species in newly disturbed forest communities. It suggests patterns of reproduction and persistence are unique to each life history type, an observation also made by Silvertown *et al.* (1993). These life history strategies can explain both theoretical and empirical successional patterns (Pickett *et al.* 1987, Piemeisel 1951). Earlier observational studies suggest that life history traits (*e.g.*, Halpern 1989), disturbance intensity (*e.g.*, Halpern 1988), and/or environmental and community characteristics (*e.g.*, Wiser *et al.* 1998) influence the ability of plant species to colonize and occupy forest communities. They do not, however, relate these factors to the mechanistic aspects of succession, specifically population dynamics, as this study does. Assessing both demographic and environmental mechanisms of succession is needed to better understand the process (Glenn-Lewin 1980, Pickett and McDonnell 1989).

Our research investigates a portion of the postulated mechanisms of successional change (Pickett *et al.* 1987): dispersal/propagule pools, resource availability, life history strategy, and competitive ability. The project addresses the linkage between population and community ecology through examining the interrelated effects of population dynamics, plant life history, soil fertility, and competition on early forest succession using the target species as a model system. Experiments to explore whether life history characteristics are mechanisms of niche differentiation among these species have been suggested to understand successional processes better (van Andel and Jager 1981). This project investigates such relationships in communities where two of the species, woodland

groundsel and foxglove, have been introduced and are naturalized. All three species are compared in Chapter 6 with respect to population models, experimental results, and community characteristics. Population dynamics modeling in relation to successional process of early seral, forest herb communities also is discussed there. Studies previously conducted on the population biology of these species generally have not included all three together, making comparisons among them difficult. Moreover, much of the earlier work was done in greenhouse studies that could produce different results from field research. Restrictions on root growth (as can occur in greenhouse studies) can cause both physiological (Tschaplinski and Blake 1985) and morphological (Harper and Ogden 1970) changes in plants.

Determining the effects of stochasticity on the species' populations is another important aspect of this project. Variation, and hence uncertainty, is incorporated into populations through stochastic processes (Burgman et al. 1993). Stochasticity occurs in several forms in populations: demographic, environmental, and catastrophic (Lande 1993). This project focused on both demographic stochasticity, i.e., the effects of variability on survival and reproductive probabilities of individuals in a population, and environmental variation, i.e., more or less favorable conditions for the population's persistence. The former type of stochasticity is most important for small populations (Lande 1993), such as plants colonizing a site after disturbance. Typically, demographic stochasticity is introduced in population models by sampling from a standard distribution (e.g., Lande 1993, Leberg 1998) or from observational data (e.g., Burgman and Lamont 1992, Saltz 1995). This project employed an approach similar to that used for Indian meal moth (Plodia interpunctella Hübner) population dynamics (Bjørnstad et al. 1998), where

experimental results introduced demographic stochasticity into the model through sample means and their associated variation. Experimental treatments, *i.e.*, nitrogen level and competition manipulation treatment, were used to determine the effects of environmental variation on transitions in the population and simulate their effects on its development.

Management

This project also has applications to forest management since all three species have the potential to dominate early forest sites and can affect forest regeneration (West and Chilcote 1968, Isaac 1940, and Bianco 1990). Understanding dispersal and persistence of potential weed species is important (Ghersa and Roush 1993) for weed management. Understanding why weed populations shift over time and how such changes affect management decisions also is important (Zimdahl 1993). Such understandings allow the formulation of management strategies that hinder, or at least do not enhance, weed population development.

LITERATURE REVIEW

Overview of Population Models

A model is a simplified representation of a system (Keen and Spain 1992). There are several types of models including conceptual, scale, mathematical, computer--or more properly computer simulation--and perhaps even social and philosophical models. Every model begins conceptually and diverges into other types depending on how the model is used. The conceptual model also defines and restricts the form of subsequent models.

This discussion will be limited to mathematical models and simulations since they are most relevant to understanding the mechanisms of population dynamics.

Simple Mathematical Equations

Population models, in their many forms, have the same general structure: the change in number of individuals (N) as a result of additions from births (B) and immigration (I) and losses from deaths (D) and emigration (E) (Silvertown 1987, Burgman *et al.* 1993). In its simplest form, the dynamics of a population is represented by the following difference equation:

$$N_{t+1} = N_t + B - D + I - E, \tag{1}$$

where N_t is the initial population and N_{t+1} is the resultant one. This equation indicates the population abundance after a period of time. More complex equations are required to understand rates of birth, death and migration. These include other difference, differential, and logistic equations. The net reproductive rate (R_0) is another example of a difference equation and is derived from:

$$R_0 = \frac{N_{t+1}}{N_t} \tag{2}$$

(Silvertown 1987). This equation indicates how rapidly the population size is changing through the slope of N_{t+1} plotted against N_t. The net reproductive rate equation can be modified by adding constants or other variables to reflect resource limitations or density dependance. The instantaneous population growth rate (r) can be calculated using the differential equation:

$$\frac{dN}{dt} = rN, \tag{3}$$

Which indicates what the rate of change in a population is anytime (t) (Keen and Spain 1992, Silvertown 1987). This equation describes populations where birth and death rates are the only limitations to growth. By adding a term for carrying capacity (K), the model responds to other restrictions on population increase such as resource limitation, and creates the logistic growth equation:

$$\frac{dN}{dt} = rN\frac{(K-N)}{K} \tag{4}$$

(Silvertown 1987). Either of these equations can be integrated to determine the population at time N_t:

$$N_t = N_0 e^{rt}, \qquad \text{and} \qquad N_t = \frac{K}{1 - N_0 e^{rt}}, \tag{5,6}$$

respectively (Silvertown 1987).

Population models can include the effects of species interactions. The Lotka-Voltera equation, for example, models the interactions of two competing species (Silvertown 1987, Keen and Spain 1992). In this case, a coefficient is added to the logistic growth equation to account for the effects of one species on the other. The population growth of the first species is described by the equation:

$$\frac{dN_1}{dt} = rN_1\frac{(K - N_1 - bN_2)}{K} \tag{7}$$

where N_1 is the population of the first species, N_2 is the population of the second species, and b is the coefficient for the effect of the second species on the first. The equation for

the second species is similar but with the position of the two species in the equation reversed and a new interaction coefficient, a, introduced. The values of r and K are likely to be different for the two species, as well.

Life Tables

The preceding equations describe the growth of a population as if it were a single entity, but populations are composed of individuals that persist for varying lengths of time. There are often probabilities associated with life expectancy and reproductive output of individuals in a population that are useful in determining its fate (Caswell 1989). Life tables can be useful in computing age-specific mortality and fecundity probabilities (Burgman *et al.* 1993). To develop a life table, the age, survivorship, and fecundity of individuals in the population are traced (Leverich and Levin 1979). The number of survivors and amount of reproduction for each age is recorded. These data are compiled into the life table to describe parameters of the population. Age-classified survival is used to calculate other parameters such as mortality at a specific age and daily mortality rate. Reproduction at a given age is use to calculate age-specific fecundity per individual and, when combined with survival, the population growth rate. These parameters can be used to determine when the population is vulnerable to mortality or prone to reproduce. Life tables can also be developed using phenological stages rather than age (Caswell 1989).

Equation Series and Matrices

The probability of survival from one age or stage to another is sometimes expressed as a series of equations. In a generalized model, for example, a plant population produces

some average number of seeds (Sagar and Mortimer 1976). A proportion of those seeds fall to the ground and enter the surface seed bank. The processes of seed production and dispersal can be described for the population by the following equations:

$$B = Aa, \qquad \text{and} \qquad C = G + Bb, \qquad \qquad (8,9)$$

where A is the number of plants·m^{-2}, a is the seed production·plant^{-1}, B is the seed production·m^{-2}, b is the rate of dispersal into the surface seed bank, G is the seed immigration into the population, and C is the surface seed bank·m^{-2}. Similar equations can be developed for all stages of the population.

A series of equations can be expressed more compactly as a matrix if it represents a linear system of equations (Caswell 1989). Using matrices, the computation of abundance is simplified and other properties of the population such as growth rate and influential stages in the life cycle can be easily determined. Two types of matrices are required for this population analysis: a population vector and a transition matrix[2]. The population vector is a column vector that contains the number of individuals in each age or stage class at a specific time. Each element in the vector represents a specific age or stage in the life history of the organism and are often called state variables. The transition matrix contains the probabilities (or rates) for movement of individuals from one class to another over time. There is one element (transition rate) in the transition matrix for every

---

[2]The transition matrix represents the coefficients for a system of linear equations, *i.e.*, $2x + y = 10$ and $3x - y = 0$, and the population vector (as well as the eigenvector) contains values for the variables x and y that satisfy the equation (Caswell 1989).

possible change in state variable. Expressed in matrix form the equations from Sagar and Mortimer (1976) above (page 8) would have the following population vector and transition matrix **n** and **T**, respectively[3]:

$$
\mathbf{n} = \begin{pmatrix} G \\ B \\ C \\ \vdots \\ A \end{pmatrix}, \quad \text{and} \quad \mathbf{T} = \begin{pmatrix} 1 & 0 & 0 & \dots & 0 \\ 0 & 0 & 0 & \dots & a \\ g & b & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \dots & 0 \end{pmatrix}. \quad (10,11)
$$

Because the linear equation series is incomplete, not all of the possible state variables and transition rates are included in the matrices above. If the matrix were complete, matrix multiplication could be used to create a new population vector, $\mathbf{n_1}$ that indicates the population change stage.

Matrices simplify the analysis of population characteristics as well as the computation of population size. The asymptotic population growth rate (λ) can be determined by calculating the dominant eigenvalue[4] of the transition matrix (Caswell 1989). Sensitivity and elasticity analyses are used to determine which stages in the life cycle have the greatest effect on the population dynamics. Sensitivity analysis can be conducted either numerically or analytically. For numerical sensitivity, small changes (*e.g.*, - 10%) are made in a value of the transition matrix and the resulting change in λ is

---

[3]Matrix notation follows the standard of bold capital letters for matrices and bold lower case letters for vectors. Variables and matrix elements are in italics with the latter having subscripted row and column numbers, respectively .

[4]An eigenvalue (λ) is a number that satisfies the following relationship for the square matrix A: $\mathbf{Ax} = \lambda\mathbf{x}$, where **x** is the eigenvector of A.

observed (Caswell 1989). Those variables that produce the greatest changes in λ have the greatest sensitivity and, therefore, the greatest effect on the population when they are varied. This method also works for other forms of mathematical models (Burgman and Lamont 1992). Sensitivity is also a characteristic of the matrix structure and can de determined analytically. The effect of a matrix element, a_{ij}, on the asymptotic population growth rate is a proportion of element i of the reproductive vector times element j of the stable age distribution (Caswell 1978). Elasticities are relativized sensitivities where the proportional change in λ relative to the change in the transition matrix element is assessed (de Kroon *et al.* 1986). This relativization is important since different elements of a matrix can vary over several orders of magnitude resulting in exaggerated sensitivities for those elements with large values. Integrated sensitivities and elasticities, which account for an element's direct and indirect effects on λ, can be calculated by including the correlation between the changed element and other matrix elements (van Tienderen 1995). The contributions of various components of the life cycle to population growth can be analyzed by loop analysis, in which the elasticities of different aspects of the life history (*e.g.*, early vs. delayed reproduction), are compared (van Groenendael *et al.* 1994).

Examples of Population Models

Each of the mathematical models discussed have been used to study plant populations. First, selected examples of how each type of model has been used will be presented. A discussion of the models' limitations follows next and the application of matrices to plant populations. Then, the application of population models to weed science is examined.

The simple difference and differential equations have been used widely in population modeling and for a variety of purposes (Kingsland 1985). Most people are at least acquainted with the concept of exponential growth from the work of Malthus (Odum 1959). In his "Essay on the Principle of Population Growth," Malthus (1992) documents the inherent tendency for populations to grow exponentially and to exceed their resources (Equation 1). Although true exponential population growth without limit cannot be observed in nature, the cycle of explosive increase and catastrophic decline does occur in both experimental and simple natural populations (May 1981). Experimental populations of *Paramecium*, yeast, bacteria, *Drosophila*, and *Tribolium* have been shown to exhibit exponential-type fluctuations. Shelford (1943) found natural lemming populations to have stable exponential cycles, where the population repeatedly rises dramatically and then declines catastrophically. These oscillations are best described by the logistic model (Equation 4) that was developed by Verhulst in the mid-Nineteenth Century and popularized by Pearl in the 1920's (Kingsland 1985). At that time, it was thought by some that this equation could accurately predict future populations and such predictions were attempted for the populations of several countries including the U.S. More recently, the logistic model has been used to describe reproductive strategies; the r- and K-strategies, to understand better how organisms respond to a resource limited environment (Southwood 1981). The Lotka-Voltera species interaction model (Equation 7) also works in simple experimental systems as was demonstrated by Gause and others (Kingsland 1985). The concept of competitive exclusion and niche as an n-dimensional hypervolume arose from Hutchinson's consideration of the two-species competition model (Kingsland 1985). In general, these types of equations have been most useful in theoretical ecology.

Life tables have been widely used in studies of animal populations especially for game and pest species. The life table was first developed by actuaries to predict human longevity (Silvertown 1987). They are less commonly used for plants. An example of a plant population life table is the one developed for *Phlox drummondii*, an annual (Leverich and Levin 1979). The population was censussed at intervals, and survival and reproduction were assessed. These data were then used to create a life table with age, survivorship, mortality during the interval, and daily mortality rate. The life table model demonstrated that mortality increased greatly near the end of the life cycle. A fecundity schedule also was created that contained seed production during the time interval, the population size, age-specific fecundity, survivorship, and population growth rate for the interval. The sum of the interval growth rates gives the overall growth rate, which increased in this example. It may be that plant life tables are less common because determining the plant's age can be difficult.

The linear equation series model has been used for plant populations and works well for species with numerous stage changes in a growing season (van Baalen and Prins 1983). The model is usually represented as a flow chart rather than an equation series for compactness and to highlight the interrelationships among the stages (*cf.* Sagar and Mortimer 1976, van Baalen and Prins 1983).

Matrices were first used on populations by Leslie (1945). A common age-classified transition matrix (**L**) now bears his name:

$$L = \begin{pmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & 0 \end{pmatrix}, \tag{12}$$

where the first row contains the fecundity for each age (F_i) and the subdiagonal contains the probability of surviving to the next age (P_i). Stage classified matrices were developed next with the top row having the fecundity for each stage and all other elements being the probability of moving to another stage (Lefkovitch 1965). This matrix type is sometimes called the Lefkovitch matrix. In stage-classified matrices, any element can have a value because it is conceivable that any stage could transition to any other, unlike the age-classified models where individuals must move to the next age class or die.

Transition matrices can be more complex than described above. Age and stage classification can be integrated by creating a Leslie matrix with Lefkovitch matrices as its elements (Goodman 1969). Another approach is to have a Lefkovitch matrix with each element the product of the survival probability and growth probability (Law 1983, Vandermeer 1975). Each transition matrix was unique for a given age and these matrices were combined to describe the population dynamics. Reproduction was then accounted for by the probability of entering the zero size class. These modifications can also be used with other interactions, such as stage and habitat. Physiological and environmental factors can modify the transition rates (Maxwell *et al.* 1988). For populations where the transition rates vary seasonally, the different matrices can be combined into one in order to test the overall effect of the various stages on the whole population (Maxwell 1990).

Limitation of Population Models

Each of the modeling techniques previously discussed also have their limitations. Many populations do not behave in the regular deterministic manner suggested by simple mathematical equations, which results from differential response of life stages within the population (Burgman *et al.* 1993). Life tables can be computationally cumbersome compared with matrices and are difficult to use for organisms more naturally stage-classified (Caswell 1989). The series of equations, while they do incorporate population structure unlike the single equation models, are often deterministic and may include superfluous elements that do not directly effect population dynamics. The elements of the transition matrix can be either scalars or functions[5]. The scalars have the same deterministic limitations as do the other equation types unless they are randomly selected from a distribution of values. Functions can be used to increase the generality of the model but also make it more difficult to determine growth rate, sensitivity, and elasticity. Classification method can affect the results of the matrix. Stage transition matrices were found to have fewer erroneous results than age-based ones for teasel (*Dipsacus sylvertris*) populations (Werner and Caswell 1977). Stage classified matrix models are forced to assume stable age distributions, which are unrealistic (Caswell 1989). The matrices developed from Sagar and Mortimer's equation series (1976) above (Equations 8 and 9) illustrate one of the most serious pitfalls of using them; it is easy to develop matrices that produce the wrong population values (*cf.* Caswell 1989). If, for example, the sample matrix model (Equations 10 and 11) were run with an annual timestep, seeds produced by

---

[5]Scalars are numbers with a specific value while functions imply some mathematical treatment of a variable (e.g., x^2).

the plant in one year would enter into the seed rain in the following year, which is not the case. The time step would need to be shortened to a few months or weeks to accommodate this problem but it creates another difficulty. Now, the plant produces seeds several times a year, which is also not correct. Therefore, this particular model is best simulated as a linear equation series and not a matrix. Such errors are common in plant population models (Silvertown *et al.* 1993).

The overall utility of population models depends on the purpose for which they are to be used. Theoretical models are valuable for testing hypotheses about how populations change but would have little utility in making management decisions. Caswell (1989) articulates two uses of matrix models that also apply to life tables and equation series: projection and prediction. Projection is a determination of what would happen to a population given a certain set of assumptions. The assumptions are often hypotheses to be tested. Prediction, on the other hand, is an attempt to assess what will happen to the population often in order to make a management decision. It, too, is dependant on assumptions that must be correct in order for the prediction to be correct. Given this caveat, population models should not be used to select specific management activities but rather as tools to understand the managed ecosystem better and develop informed management strategies.

Uses of Matrix Models in Plant Population Studies

Plant population matrix models have been used to study various aspects of population growth including the effects of density, spatial arrangement, and life history/physiognomy. One such model for a hypothetical perennial plant projects that

fitness of an individual will decrease with increasing density (Bishir and Namkoong 1992). This projection arises, in part, because reproduction is favored at lower densities while population maintenance occurs at higher ones. For species with variably-fit genotypes or sizes, the degree of fitness can vary depending on initial density as well. A density dependent matrix model for *Viola fimbritula* was developed that was divided into four sub-models: seed bank survival, dormant seed fecundity, dormant seed germination, and plant transition, which included seedling and adult survival, and non-dormant seed fecundity (Solbrig *et al.* 1988). The model produced stable oscillations when it was deterministic that became damped when the model was stochastic. This response suggested that variation in the population's transition rates had a homogenizing effect on the population growth rate. To address neighborhood effects of plant density and the plastic response to plant density, a three-component annual plant model was developed that included fecundity and survival of both seedlings and adults as well as seed dispersal (Pacala and Silander 1985). This model was field-tested on velvetleaf (*Abutilon theophrasti* Medic.) and pigweed (*Amaranthus retroflexus* L.) communities (Pacala and Silander 1990). It was found that the neighborhood model collapsed to a simple competition model for such annual plant communities. The relative influences of fecundity, survival, and growth were compared for 66 perennial herb and woody species (Silvertown *et al.* 1993). Species varied predictably by life history and habitat with regard to the importance of these three factors.

Population dynamics models also have been used to test the effects of higher order interactions. The effects of pre-dispersal seed predation on plant population dynamics were assessed in two studies using matrix models. Platte thistle (*Cirsium canescens* Nutt.)

seed production and seedling and mature plant density increased when seed predation was eliminated (Louda and Potvin 1995). In an investigation of herbivory effects on the perennial herb, *Lathyrus vernus* population development, λ was more sensitive to meristem damage than either grazing or seed predation (Ehrlén 1995). It was also observed that spatial rather than temporal variation in the population may determine population trajectories.

Population Models in Weed Science

Population models are commonly used in Weed Science. Such models serve several functions including creating a framework for available information, simplifying complex systems, and improving experimental designs, but they have largely been used for making predictions (*sensu* Caswell 1989). These models are most often used to calculate rates of increase in crop yield, compare management practices, develop economic thresholds, and describe detailed effects of weed control measures (Mortimer 1987). Most weed models are empirical and have one of several mathematical forms: exponential, complex exponential, density dependent, and matrix (Cousens *et al.* 1987). The modeling approach taken can also have two forms: crop-centered and weed-centered (van Groenendael 1988). Crop-centered models usually predict crop yield and its reduction by weeds. Weed-centered models are often used to predict thresholds--the density at which control can be justified by some criteria, usually economic. Both types of models typically assume monospecific, spatially homogeneous weed stands; which is an assumption that is seldom valid (van Groenendael 1988).

Numerous parameters can be included in a weed population model: seed production, survival, seed dormancy, propagule movement, germination, growth, survival, and effects on crop yield are all potential elements (Cousens *et al.* 1987). Weed population models tend to predict initially explosive behavior in the population, which then equilibrates due to negative feedbacks such as density dependance, that are incorporated into the model (Doyle 1991). This restricted growth rate model is often assumed to be a hyperbolic function of the form:

$$N_{t+1} = \frac{aN_t}{(1 + bN_t)} \tag{13}$$

where *a* and *b* are empirical coefficients and N_t and N_{t+1} are the initial and subsequent population levels, respectively. Weed population models in general tend to be temporal rather than spatial and focus on extant populations and not invasion (Cousens *et al.* 1987). Models that have incorporated invasion, in the form of seed dispersal, have employed a Gausian "plume" model for wind and a spatially-explicit matrix model for a seed bank (Doyle 1991). Spatial relationships among individuals could be addressed through stochastic or spatially-explicit models that would track both dispersal and safe site elements of the population. Neighborhood models could be used to determine the spatial area of effect (van Groenendael 1988). Interactions among the crop and weeds further complicate the modeling and require consideration of various other parameters including spatial relations, patchiness, and species assemblages.

In general, weed population models tend to be of two types: those that focus on the biology of weed management and those that are centered on its economics. Biological models can be further divided into two classes: (1) those that assess the efficacy of

treatment and (2) those that examine the impacts of biology on management (or vice versa).

The efficacy models simulate population growth and then determine what treatments, tools, and timings would be required to keep the population at an acceptable level. Simulations were done, for example, with herbicides applied to control grasses, such as couchgrass (*Agropyron repens* (L.)Beauv.) and wild oat (*Avena fatua* L.), in cereals (McMahon and Mortimer 1980, Manlove *et al.* 1982, Selman 1970). Models have been used to test the efficacy of non-chemical treatments, such as biological control of *Striga hermonthia* on millet in Africa (Smith *et al.* 1993). There is an implicit assumption that efficacy models should predict weed population decline. Typically these models indicate an annual treatment application and/or high treatment efficacy. For example, control levels of 91% and 97%, respectively, were required to prevent increase of velvetleaf and common sunflower (*Helianthus annus* L.) seed banks (Bauer and Mortensen 1992).

The other type of biological model examines weed population growth from the perspective of interaction between management practices and biological processes. The model may be linked to weed control tactics, but are not tacitly so as occurs with efficacy models (*e.g.*, Bauer and Mortensen 1992). An empirical model of Japanese brome (*Bromus japonicus* Thunb.) population development focused on density, seed production, and two seed banks to make population projections (Whisenant 1987). This model was then used to determine the effects of periodic fire on the population.

Biological management models need not be quantitative. A qualitative broom snakeweed (*Guiterrezai sarothrae* [Pursh] Britt. & Rusby) model, for example, predicted the change in relative density (*i.e.*, absent, low, medium, high) from one year to the next

based on age (Torell *et al.* 1992). Predictions were made using a Markov probability matrix (Caswell 1989). This model could be used to evaluate the need for broom snakeweed control treatments.

Still other types of management-oriented biological models for weeds use matrices that are spatially explicit. One such model for *Datura ferox* examined the weed's movement through the field by subdividing it into individual quadrats that either had the weed or did not (Ballaré *et al.* 1987). The model then described weed seed production for each quadrat, which was inversely proportional to seedling density, the proportion of seed falling into neighboring quadrats, and how much seed was lost as contamination in the crop. It was found that harvest methods had a strong influence on plant dispersal either as a seed "predator" or disperser. A model for yellow foxtail (*Setaria lutescens* (L.)Beauv.) and velvetleaf examined the differences between ridge- and furrow-weed populations in a ridge-till cultivation system (Jordan 1993). The model used germination, seed movement, survival and reproduction rates with four separate matrices each with four stages. Based on the results of the models, the cultivation system was effective in managing the weed populations.

Some biological population models become hierarchical, linking various levels of organization. For example, a model predicted Johnsongrass (*Sorghum halepense* (L.) Pers.) seedling emergence (a population stage--a higher organizational level) as a function of temperature (a physiological constraint--a lower organizational level) (Benech Arnold *et al.* 1990). A portion of seed was responsive to temperature, while some was not. This relationship could be used as a sub-model for a process-based population model that incorporated environmental factors, such as soil temperature. In another case, population

dynamics and genetic models were linked to study the development of herbicide resistance within a weed population (Maxwell *et al.* 1990). This model was used to project the growth of herbicide resistant weed populations based on management tactics.

While most weed management decisions are based on economics, the second class of weed population models includes economics explicitly in the model. Population models are used as the basis of weed economic thresholds, which are then used to dictate control measures (Jordan 1992). There are two types of thresholds used in economic models. The economic threshold (ET) is the weed density where crop loss equals treatment cost on an annual basis. The economic optimum threshold (EOT) takes a longer time horizon and establishes a threshold weed density that optimizes return across several years. The EOT is typically lower than the ET. The EOT was 7.5- and 3.6-times lower than the ET for velvetleaf and common sunflower, respectively, in soybeans (Bauer and Mortensen 1992). The ET for yellow nutsedge (*Cyperus esculentus* L.) in tobacco and for blackgrass (*Alopecurus myosuroides* Huds.) in winter wheat was greater than the EOT (Doyle *et al.* 1986, Lapham 1987). Economic population models often indicate the need for treatment at low weed densities. The ET for control of wild oats in winter wheat, for example, was between two and five seedling·m^{-2} (Cousens *et al.* 1986).

Caution must be used when evaluating the forecasts of a model. For example, a report on management options for yellow nutsedge using a matrix-based weed population model for assessing (Lapham 1987) contained no matrix, λ-value, or sensitivity analysis. Evaluating the model or the plant population levels on which the economic justification of control was based was, therefore, impossible.

CHAPTER 2

Three Early Seral Herbs' Response to Environmental and Silvicultural Variables in Western Washington and Oregon Forests

ABSTRACT

A study was conducted to evaluate the relationship of various environmental and silvicultural variables with the frequency and abundance of fireweed, foxglove, and woodland groundsel in the forests of western Washington and Oregon. Species' responses to the above variables were compared with that of the plant community as a whole. The questions investigated were 1) does residence time of the species in the forest community increase as their life history became more complex (*i.e.*, more reproductive pathways and/or life stages), 2) is stand age inversely related with change in abundance of the species, and 3) what additional environmental and/or silvicultural factors also affect the occurrence of these species and do those factors differ for each? Cover and height data by plant species were collected from young forest plantations. Regression analyses and several multivariate techniques including nonmetric multi-dimensional scaling (NMS) for ordination, multi-response permutation procedure (MRPP), and indicator species analysis (ISA) for species grouping were used to develop relationships between environmental and silvicultural characteristics and the occurrence of these selected species. A two-dimensional NMS ordination for the communities sampled was highly correlated with organic debris cover and forest stand age on one axis and bare ground cover and elevation on a second axis. UTM meters east[6], which approximates an increasing elevation and decreasing moisture gradient, was correlated with both axes. The three species investigated, however, were poorly correlated with the axes. MRPP failed to detect

---

[6]Universal Transverse Mercator is a cartographic coordinate system that indicates the distance (m) north from either the South Pole or the Equator (meters north) and the distance (m) east from a meridian established in one of 60 Mercator projection strips called zones [meters east (Clarke 1990)]. This study was located in zone 10.

meaningful groups for fireweed and woodland groundsel, but found a tendency for foxglove to group in the lower range of elevation and bare ground cover. ISA indicated positive relationships between fireweed and the following conditions: lack of competition release, low site productivity, and lack of stand thinning. Foxglove was found to be positively related to competition release, specifically broadcast chemical application, high site productivity, and stand thinning. Logistic regression determined that woodland groundsel frequency was related to UTM meters east and that fireweed frequency was affected by an interaction of stand age and elevation. Woodland groundsel cover was negatively correlated with stand age, foxglove cover was negatively related to organic debris cover, and fireweed was positively related to UTM meters east and associated herbaceous vegetation height. In general, there are weak relationships between target species and environmental and/or silvicultural variables. These results suggest that environmental characteristics have a limited role in determining frequency and abundance of these species relative to other species of western Douglas-fir forest communities.

INTRODUCTION

Understanding the process of revegetation after a disturbance (*i.e.*, succession) has been an objective of plant ecology for decades (McCook 1994). The sequential facilitation model of succession proposed by Clements (1916) initiated a long and complex debate over how succession occurs. Many subsequent theories of succession rely on characteristics of the individual species to describe the interrelations of plants in a community. Gleason (1926), one of the first proponents of the individual paradigm in succession, asserted that plant communities were assemblages derived from species and

environmental similarities. Others imparted more mechanistic explanations to this concept, such as (1) the ability to persist in a community (Egler 1954), (2) differential growth and survival (Drury and Nisbet 1973), or (3) variation in reproductive strategy (Nobel and Slatyer 1980). Another modification of the Clementsian view of succession is that species must pass through an "environmental sieve" (as proposed by Harper (1977) in relation to individuals of a population) to progress from one seral stage to the next. In Grime's successional model (1977), for example, plants' life history traits allow individual species to survive in various cells of a stress-disturbance matrix. Resource limitations (Tilman 1985), creation of safe sites (Johnstone 1986), and alteration of the environment by the extant vegetation (Connell and Slatyer 1977) are all proposed to erect or remove environmental barriers for different plant species in the community. Computer simulations suggest that succession is primarily driven by species characteristics, such as life history and competitive ability, but that the final composition of the plant community is modified by environmental characteristics (Huston and Smith 1987).

Secondary forest succession after timber harvest or other silvicultural activities have provided an opportunity to examine the interactions among species and environmental characteristics. Forest recovery after clearcutting in Oregon was related to disturbance intensity with greater disturbance resulting in occupation by ruderal and colonizing plants (Halpern 1988). In the Oregon Cascades, species were grouped according to their response to clearcutting and burning as well as the time required to become established (Halpern 1989). Species abundance in Ontario boreal forests was related to standing timber and/or burning (Johnson and Elliott 1996). In another Canadian boreal forest, species colonizing after harvest varied along an edaphic gradient with more ruderal and introduced species on

clay soils than on sandy ones (Harvey *et al.* 1995). Species abundance was found to relate to soil pH and moisture after clearcutting in an European, pine forest (Zobel 1993). Thinning in western Oregon Douglas-fir stands increased bracken fern (*Pteridium aquilinum* (L.) Kahn.) and salal (*Gaultheria shallon* (Pursh)) cover, which were related to tree density and stand age. Thinning did not affect the cover of Oregon-grape (*Berberis nervosa* Pursh.) or sword fern (*Polystichum munitum* (Kaulf.) Presl) (Bailey and Tappeiner 1998). Even without silvicultural activities, environmental characteristics can be related to abundance of a species. Invasion of an undisturbed New Zealand mountain beech (*Nothofagus solandri*) forest by an exotic herb, *Hieracium lepidulum*, was related to incident solar radiation, low elevation, soil fertility, and degree of topographic sheltering (*e.g.*, swales) (Wiser *et al.* 1998).

Selecting associated species with differing life histories and sampling their frequency and abundance across a range of environments provides a dataset to make comparative assessments of the effects of environmental variables upon their presence in a community. Three such species were compared in this study. The creeping perennial fireweed (*Epilobium angustifolium* L.), the facultatively iteroparous perennial foxglove (*Digitalis purpurea* L.), and the annual woodland groundsel (*Senecio sylvaticus* L.) commonly occupy woodland clearings in Europe (Tüxen 1950 as cited in Ellenberg 1986). They are associates in the willow-herb clearing community (Myerscough 1980) and are characterized as species of intermittent openings (Salisbury 1942). Woodland groundsel is abundant in areas of relatively warm climate, while foxglove is more common in the higher suboceanic mountains (Ellenberg 1986). Fireweed is found in woodlands, including broad-leaved and coniferous plantations, wastelands, heaths, various spoils, and open

habitats, such as rock outcrops and cliffs (Myerscough 1980). It is a principle and permanent component in the tall perennial herb communities of European alpine and arctic areas (Myerscough 1980). In most other communities, fireweed is transitory.

Fireweed, foxglove, and woodland groundsel are often found in the early seral stages of Oregon and Washington forests. Fireweed occurs in the tree-dominated *Tsuga heterophylla*, *Pinus ponderosa*, *Abies grandis*, and *A. lasiocarpa* vegetation zones and the subalpine *Rubus parviflorus-Epilobium angustifolium*, *Valeriana sitchensis-Veratrum viride*, and *Carex spectabilis* communities of the Pacific Northwest (Franklin and Dyrness 1988). It can be abundant in the *Tsuga* and *Rubus* vegetation types. It is also a minor component in riparian red alder stands (*Alnus rubra* Bong.) (Henderson 1970). Foxglove is an early seral dominant of red alder communities from ages 4 to 16 (Henderson 1970) and is common in other moist shady areas of the Pacific Coast Range (Rickett 1971). Woodland groundsel also is associated with the *Tsuga heterophylla* zone (Franklin and Dyrness 1988). In a phytosociological assessment 17 to 29 years after the Tillamook Burn, fireweed was found in five of the six plant associations (Bailey and Poulton 1968). Woodland groundsel was found in one association in this area, the *Acer macrophyllum/Symphoricarpos mollis* type that occurs on steep, xeric, rock outcrops and talus fields. Both fireweed and woodland groundsel were present in five plant associations of the mid-elevation Cascades five years after logging (Dyrness 1973). Of the literature reviewed, only Parendes (1998) mentions the occurrence of foxglove in the Cascade Range, specifically in the H. J. Andrews LTER site, although it is present in some areas (personal observation, Appendix 1).

Since its introduction to North America, woodland groundsel has become an important component of the early seral forest community in the Pacific Northwest. A pioneer species, it is associated with disturbance but is not limited by the type or magnitude. Woodland groundsel seed germination was unaffected by treatments that simulated logging disturbance including exposure to full sunlight, burning, and soil churning (Ingersoll and Wilson 1990). Its tendency to increase in abundance rapidly and dominate a site by the second or third year after disturbance; however, is widely documented (West and Chilcote 1968, Gholz et al. 1985, Dyrness 1973, Kraemer 1977, and Yerkes 1958). Its abundance is often associated with fire (West and Chilcote 1968, Dyrness 1973), but it can also occur on unburned, disturbed sites. For example, woodland groundsel was prodigious in an unburned clearcut during the first three years after timber harvest (Gholz et al. 1985). It often persists at reduced levels one or two years after peak abundance (Isaac 1940, Franklin and Dyrness 1988, Morris 1970), but it can remain in the plant community longer. It was present on 15 precent of plots sampled in clearcut areas of the Oregon Cascades six years after harvest, albeit with extremely low cover (Yerkes 1958). In another study, it was found 14 years after logging on unburned plots (Kraemer 1977).

Woodland groundsel has a similar disturbance response pattern in Europe. It was abundant (15% cover) 1 year after a fire in a 28-year-old European, pine plantation (Gisela 1980) but was not present in the second year. On the other hand, populations of woodland groundsel growing in open coastal forest of the Netherlands have persisted for up to 40 years (Ernst 1985).

Foxglove also can be abundant in early seral forests although its occurrence in Pacific Northwest forest types is poorly noted. It is commonly found in areas of intermittent disturbance such as clearcuts, windthrows, and burns (Oberdorfer 1973, Salisbury 1942), thus becoming established from a buried seedbank (Salisbury 1942, van Baalen and Prins 1983). After the eruption of Mount St. Helens, foxglove was found in debris flows, mud slides, and areas with blown-down or scorched trees (Adams and Dale 1987). It also can dominate a site and then become locally extinct although generally on a longer timescale than its associate, woodland groundsel (van Andel and Ernst 1985). Foxglove had 25 percent cover two years after clearcutting of a Welsh forest (Hill and Stevens 1981). Its cover declined to less than 10% by the third and subsequent years.

Fireweed is another species common in the forested regions of the Pacific Northwest after disturbance and frequently colonizes after glaciation and volcanic eruption (Adams and Dale 1987). It was one of the first plant colonists after the eruption of Mount St. Helens and was found in debris flows, mud slides, and areas with blown-down or scorched trees (Adams and Dale 1987). The presence of woody debris may reduce fireweed cover on unburned sites (Kraemer 1977). In the Oregon Cascades, it had greater cover on burned clearcuts than on unburned ones (Yerkes 1958, Dyrness 1973).

Fireweed follows a similar pattern of rise and decline in abundance as the other two species but the change is more gradual. In general, its vegetative cover peaks in the third to fifth year after disturbance then declines slowly (Isaac 1940, Dyrness 1973, Yerkes 1958). Fireweed cover can be substantial: up to 30 percent cover was found the second year after a forest fire in Germany (Gisela 1980). Fireweed cover also increased to 10.5% in three years after timber harvest in Wales (Hill and Stevens 1981). The species will

persist in an established forest stand but is dependant on disturbance, *e.g.*, windthrow, to do so (Dyrness 1973). It was found in a 25-year-old stand in a chronosequential study (Kraemer 1977). Fireweed persisted in two Oregon clearcuts for over 20 years (Halpern 1989).

This study had two research objectives. The first objective was to compare how the environmental and silvicultural factors that affected the plant community as a whole influenced the presence and abundance of the three early seral forest herbs: fireweed, foxglove, and woodland groundsel (hereafter, target species, collectively) in western Oregon and Washington. This objective was met using multivariate analyses. Ordination was used to determine how the target species are related to continuous environmental variables and how their response compared with the entire plant community. Whether the target species occupy different areas of species-space was tested using a multivariate grouping technique. A third multivariate analysis assessed the effect of categorical variables on the presence and abundance of the target species.

The second objective was to address questions and test specific hypotheses about the effects of environmental and silvicultural variables on the presence and abundance of the target species. Each species has a different life history and response to environmental conditions. These differences make them well-suited to use in investigating how plant characteristics and environmental constraints affect their distribution in the plant community. The questions investigated were:

- Intuitively, it is expected that the length of time species are present in a plant community increases as the complexity of their life histories increases (*e.g.*, more life stages and/or reproductive methods). Can this be demonstrated for

these species in early seral Pacific Northwest forests? Do environmental factors, as described below, affect that relationship?

- Is there an inverse relationship between stand age (as a surrogate time since initial disturbance) and the presence and abundance of all three target species?

- How do other environmental (*e.g.*, slope, aspect, and elevation) and/or silvicultural factors (*e.g.*, site preparation, competition release, and thinning) affect species' presence and abundance. Are factors that are positively (or negatively) related with one species affect the other two species in the same way?

The following hypotheses were developed based on these questions. Woodland groundsel presence and abundance were hypothesized to decrease with increased time since initial disturbance and increase with the intensity of the disturbance (broadcast silvicultural treatments representing a more intense disturbance that spot or no treatments). It would have the shortest residence time in the community. Reduced competition (*i.e.*, silvicultural competition removal treatments) and increased available moisture (*i.e.*, decreasing UTM meters east) were anticipated to stimulate foxglove presence and abundance while they too would be inversely related to stand age. It was also expected to have an intermediate persistence in the community. Fireweed presence and abundance were projected to increase with increasing elevation (or UTM meters east) and protection from herbivory (*i.e.*, increased associated vegetation cover and height) and decline with stand age. It was expected to remain in the community longest. The hypotheses were tested using regression.

While these three species were selected because they are associated in some forest communities of the northern hemisphere, the differences among them do present difficulties in making generalizations. In addition to varying in their life histories, the target species also have differences in phylogeny, dispersal mechanism, seed bank characteristic, and susceptibility to herbivores. In order to support the conclusions drawn by this study, more closely related taxa (*e.g.*, congeners) differing only (or primarily) in life history need to be tested.

METHODS AND MATERIALS

Vegetation data was collected[7] between August, 1991 and May, 1995 from 196 plots established in young (20 years-old or less) Douglas-fir [PSME (*Pseudotsuga menziesii* (Mirbel) Franco)] plantations of western Washington and Oregon (Figure 2.1, Appendix 1). Each plot was sampled twice, with a two-year interval between samplings, following the procedures of Shula and Knowe (1991) (as cited in Shula 1998). A 0.045 ha PSME measurement plot (PMP) was established in each plantation and four 0.004 ha competition measurement plots (CMPs) were systematically located within it (Figure 2.2). Cover, to the nearest 5 percent, and average height (cm) of each species (or in some cases a larger taxa, *e.g.*, grasses) were visually estimated on each quadrant of the CMPs. Species with less than 5% cover were not included in the assessment. Species were divided into

---

[7]This vegetation data was collected as a part of the Regional Vegetation Management Model (RVMM) project. This project developed a young stand growth and yield simulation model for Douglas-fir in western Washington and Oregon (See Shula 1998 for details). Individuals primarily involved in the data collection were Eric Hanson, Steve Knowe, Alex Pancheco, Will Schneider, and Bob Shula.
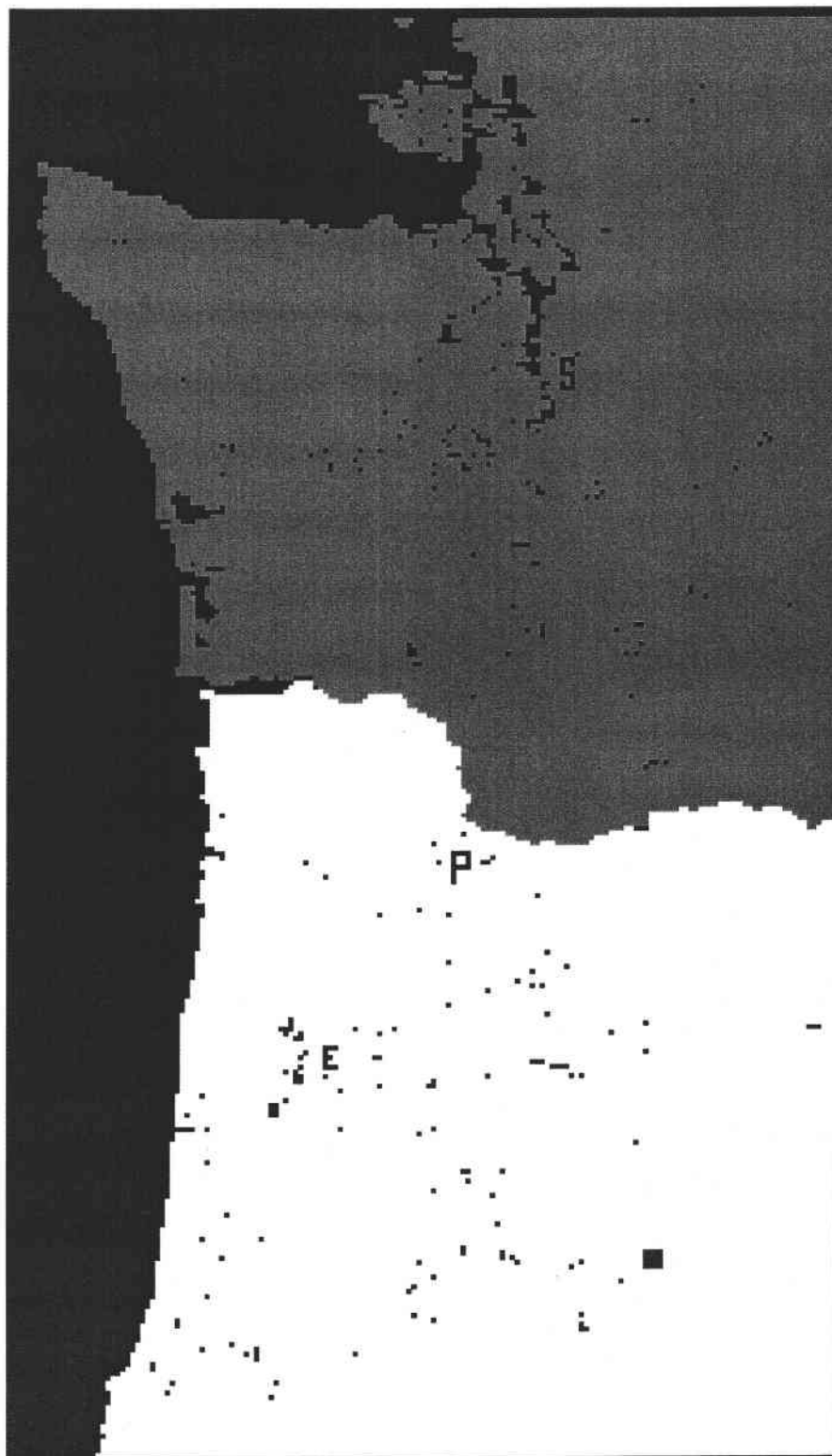
Figure 2.1. Location of 196 vegetation sampling plots. Plots are indicated (■) with the township, range, and section listed in Appendix 1. Eugene, OR, Portland, OR and Seattle, WA are indicated E, P, and S, respectively for reference.
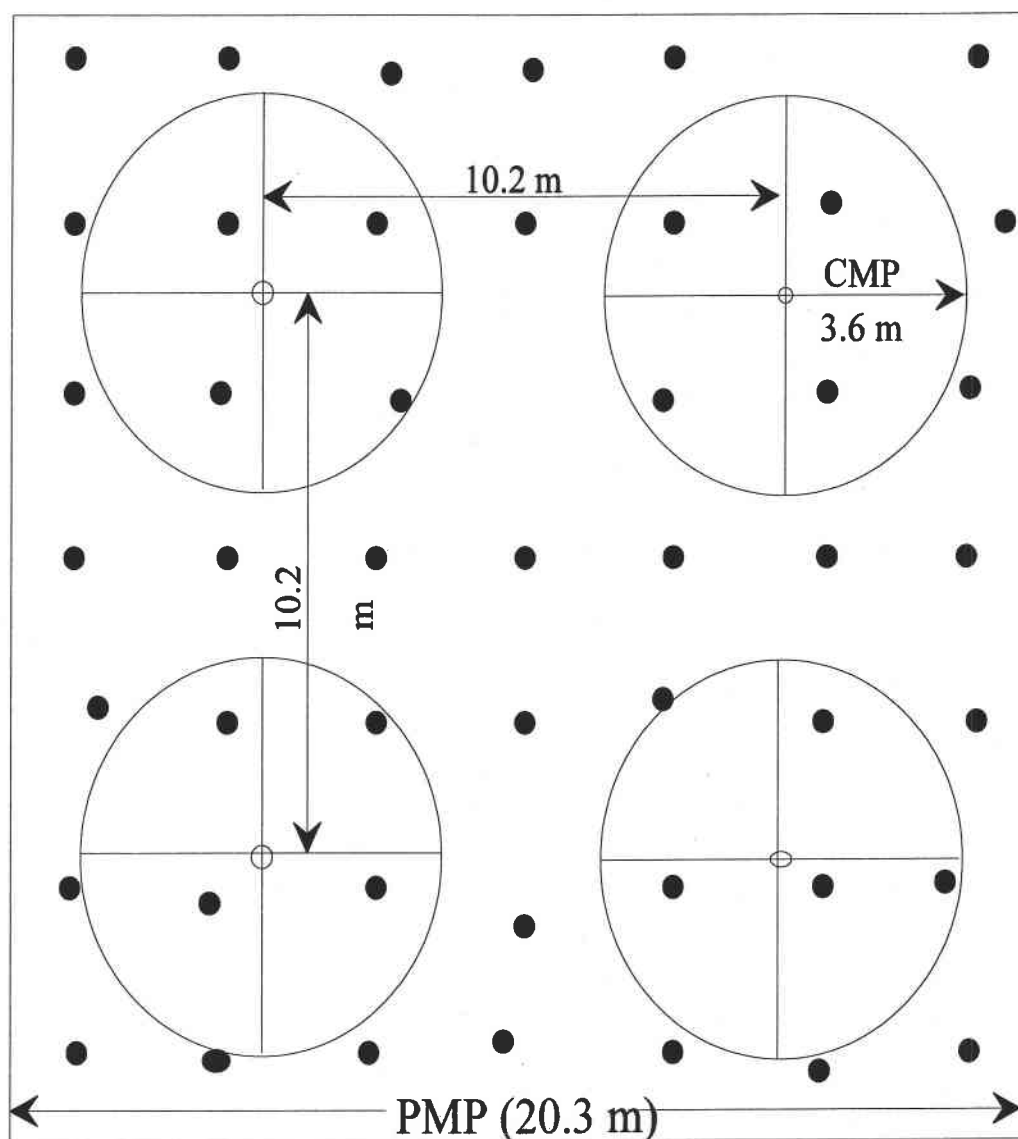
Figure 2.2. Arrangement of competition measurement plots (CMPs) for vegetation sampling within the PSME (Douglas-fir) measurement plot (PMP). CMPs were located systematically within the PMP Planted Douglas-fir trees are indicated (●). Adapted from Shula (1998).

two physiognomic layers for sampling: herbs, which included bare ground and organic debris, and shrubs. The herb layer was required to total to 100% cover; the shrub layer could not exceed 100% cover.

These data were used to assess how changes in target species frequency and abundance (*i.e.*, cover) related to continuous and categorical environmental variables including various silvicultural treatments (Tables 2.1 and 2.2). This study used several

Table 2.1. Continuous environmental and silvicultural variables used in the analysis of vegetation plots. The mean, standard deviation, and range of values are indicated.

Variable	Mean	Standard Deviation	Range
Aspect (°)	175	104	0 - 360
Bare Ground Cover (%)	4	9	0 - 85
Competition Release Applications	2	2	1-10[h]
Elevation (m)	440	295	0 - 1400
Last Competition Release Age (Years)	4	2.6	1-10
Slope (%)	15	10	0 - 40
Organic Debris Cover (%)	69	23	11 - 100
Stand Age (Years)	10.7	4.6	1- 20[i]
Thinning Age (Years)	10	4.5	9 - 14
UTM Meters East[j]	499,000	61,000	390,000 - 620,000
UTM Meters North	5,010,000	160,000	4,800,000 - 5,400,000

[h]No plots received release treatments 4, 5, or 7 times.

[i]There were no plots in the 18-year age class.

[j]Universal Transverse Mercator is a cartographic coordinate system that indicates the distance (m) north from either the South Pole or the Equator (UTM Meters North) and the distance (m) east from a meridian established in one of 60 Mercator projection strips called zones [UTM Meters East (Clarke 1990)]. This study was located in zone 10.

Table 2.2. Categorical environmental and silvicultural variables used in the analysis of vegetation plots.

Category	Level	N
Competition Release	Absent	228
	Broadcast Herbicide Spray	84
	Spot Herbicide Spray	18
	Total Vegetation Control	14
Site Preparation	Absent	102
	Broadcast Burn	26
	Broadcast Herbicide Spray	138
	Broadcast Herbicide Spray and Burn	52
	Mechanical	50
Site Productivity	High	140
	Medium	138
	Low	112
Slope Position	Ridge	6
	Upper Slope	136
	Middle Slope	172
	Lower Slope	30
Thinning	Absent	334
	Present	56

multivariate techniques to analyze the vegetation data: non-metric multidimensional scaling (NMS) for community ordination and to relate the continuous variables with the target species, multi-response permutation procedure (MRPP) to detect clustering among the target species within the ordination, and indicator species analysis (ISA) to determine the response of the target species to the categorical variables. Logistic and linear

regression were used to develop models relating target species frequency and cover to the environmental variables for hypothesis testing.

Multivariate Analyses

Species cover data from each quadrant on the CMPs of a vegetation plot were averaged to determine mean cover by species for the PMP. Occurrence frequency for each species was determined (Appendix 1, Table A1.2): those species found on only 1 PMP or in less than 10 quadrants in the entire study were considered rare and removed from the data by row using the general relativization[1] in PC-ORD (McCune and Mefford 1997) and then were arcsine-squareroot transformed. All multivariate analyses were conducted on these standardized data.

NMS ordination (see McCune and Mefford 1997 or Tong 1992 for a description of this technique) was conducted using PC-ORD (McCune and Mefford 1997). Sørensen distance[2] was used in all ordination procedures, which had 100 iterations and no *a priori* rotation[3]. The data was tested for outliers by graphing the frequency distribution of the Sørensen distance for the plots. Any plot distance greater than two standard deviations from the mean was considered for removal from the dataset (McCune and Mefford 1997). A six-axis NMS procedure was done first to determine the number of axes to use in the

---

[1]Cover for each species on a plot is divided the total vegetation cover on the plot.

[2]1-2W/(A+B), where A and B are the abundance of Species A and Species B, respectively, and W is their shared abundance.

[3]NMS in PC-ORD can maximize the relationship between the variables and the ordination axes during data reduction by varimax rotation (McCune and Medford 1997).

final ordination, which was based on the maximum reduction in stress[4] (Table 2.3). A two-axis NMS ordination was selected and was run several times until a solution was found that minimized stress within that number of axes (Table 2.3). Stress from this solution was graphed against iteration number to test the solution for stability, *i.e.*, the stress becoming constant within 100 iterations. A Monte Carlo test of significance[5] was conducted to

Table 2.3. Change in stress related to number of axes in NMS ordination. Initial and final stress are from the beginning and end of the NMS procedure, respectively. The change in final stress between an *n*-axis ordination and (*n*-1)-axis ordination is listed under Δ stress for the *n*-axis ordination. The ordination was conducted using the number of axes that produced the greatest Δ stress. The minimum final stress detected for the 2-axis ordination is indicated (*) and is associated with the ordination presented.

Number of Axes	Initial Stress	Final Stress	Δ Stress
6	27.1	9.7	14.3
5	29.8	24.0	-9.6
4	33.7	14.4	2.5
3	38.8	16.9	9.2
2	47.1	26.1	27.2
1	62.3	53.3	N/A
2	N/A	24.5*	N/A

[4]McCune and Mefford (1997) define stress as "a measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original *p*-dimensional space and the distance in the reduced *k*-dimensional ordination space." It indicates how much change occurs between the two matrices through the NMS ordination.

[5]In a Monte Carlo test of significance, data are randomly shuffled within each matrix column and the analysis repeated. This process is iterated and a distribution of results (*e.g.*, ordination scores) is created. The probability of a more extreme value than the one generated by the unshuffled matrix is then computed.

determine the probability of the ordination arising by chance. The coefficient of determination (R^2) was computed for the 2-dimensional NMS distances relative to the original N-dimensional distances as an indication of the information retained by the data reduction. The two-axis NMS ordination graph was rotated *a posteriori* to maximize the alignment between an environmental variable and Axis 1 to improve interpretability (Tueller *et al.* 1991). Correlations with the ordination axes for both the environmental variables and target species were computed. Correlation values greater than 0.098 were significant at the 5 percent level and those greater than 0.128 were significant at the 1 percent level (Gomez and Gomez 1984).

MRPP was also conducted using PC-ORD (McCune and Mefford 1997) on the standardized cover data to test for groups within the plots containing the target species. Sørensen distance and a weighting function:

$$C_i = \frac{n_i}{\sum n_i} \tag{14}$$

where n_i is the number of group members, were used in this analysis to compute the weighted mean within-group distance, δ. The probability of a smaller δ, which was determined with a Monte Carlo test of significance, and the within-group heterogeneity, $\mathscr{R}$[6], which indicated how the groups are dispersed compared with random chance, were

---

[6]The upper-case, script letter "r" ($\mathscr{R}$) is used to distinguish within group heterogeniety from Pearson's product-moment correlation (r) and the coefficient of variation (R^2).

computed. If $\mathscr{R}$ is greater than 0, the groups are more heterogeneous than would be expected by chance.

ISA was conducted in PC-ORD (McCune and Mefford 1997) using categorical variables (Table 2.2) test their relation to fireweed, foxglove, and woodland groundsel frequency and abundance. Each categorical variable consisted of at least two levels (*e.g.*, presence and absence). Relative frequency and cover percentages for each of the target species were computed for a level. The product of each species' relative frequency and cover gave the indicator value (IV) for that level. The maximum IV for each species for a given variable was compared with a population of random IVs developed using a Monte Carlo test of significance with 1000 permutations, which determined the probability of the observed maximum value arising by chance. If the probability were low, it suggested the species was associated with that variable level.

Regression Analysis

Regression was conducted only on the initial (*i.e.*, at the time of plot establishment) vegetation data because woodland groundsel was not present two years later on any of the plots.

Logistic regression was conducted on fireweed, foxglove, and woodland groundsel frequency (*i.e.*, plots with the species present/total plots) using Proc Genmod in SAS (SAS 1996). Potential independent variables were selected by plotting species frequency against categorical environmental variables. When a pattern suggesting an effect was detected, that variable was included in the logistic regression model. The following variables were used for fireweed and foxglove frequency models; stand age, elevation, and UTM meters

east. The woodland groundsel logistic model used only stand age and UTM meters east as independent variables. Because Proc Genmod does not have selection capability to add or remove variables from a model, all possible variable combinations were conducted. The most parsimonious model with the lowest deviance-to-degrees-of-freedom ratio was chosen.

Linear regression was used to assess the effect of environmental variables on cover of the target species, which was arcsine-squareroot transformed to meet the assumptions of normality and constant variance, where they occurred. Variables for these models were selected in a similar manner to those for the logistic regressions, through graphical inspection, except that categorical variables were considered and some variables were included to address the hypotheses (Page 33). Independent variables tested for fireweed cover included: UTM meters east, percent herb cover, stand age, percent slope, elevation, and a site preparation indicator. Organic matter cover, percent slope, competition release age, UTM meters east, and indicators for site productivity and middle slope position were used in foxglove cover models. Woodland groundsel cover models included stand age, number of competition release applications, aspect, elevation, and an indicator for competition release. Again, due to the lack of a selection system in Proc GLM (SAS 1990), numerous models were tested for each species but all models had at least one continuous variable. The most parsimonious model with the highest coefficient of determination was selected, but only if all the variables (or their interactions) were significant.

RESULTS AND DISCUSSION

Multivariate Analysis

No outliers were detected in the standardized data matrix used in the 2-dimensional nonmetric multi-dimensional scaling (NMS) ordination. The data reduction retained a satisfactory amount of information compared with the original matrix ($R^2 = 0.67$). The probability of the ordination arising by chance was slight based on the Monte Carlo test of significance ($P = 0.01$). MRPP detected no difference in average distance between the initial and final vegetation data ($P = 0.38$) indicating that samples collected at the two times occupied a similar space in the ordination.

The two-axis NMS ordination graph presented in Figure 2.3 was rotated to maximize the alignment between organic debris cover and Axis 1. This ordination had the greatest correlation between Axis 1 and both organic debris cover ($r = 0.81$) and stand age [$r = 0.44$ (Table 2.4)]. Axis 2 was most strongly correlated with bare ground cover ($r = 0.35$) and elevation [$r = 0.27$ (Table 2.4)]. UTM meters east was negatively correlated with Axis 1 ($r = -0.29$) and positively correlated with Axis 2 [$r = 0.24$ (Table 2.4)]. The other continuous variables had weaker correlations with both axes (Table 2.4).

In general, the target species were weakly correlated with the two ordination axes. Fireweed had the least correlation of the three species with Axis 1 and was poorly correlated with Axis 2 [$r = 0.03$ and 0.03, respectively (Table 2.5)]. Woodland groundsel correlation was greatest with Axis 1 and weakly correlated with Axis 2 [$r = -0.08$ and -0.03, respectively (Table 2.5)]. Foxglove had a weak negative correlation with Axis 1 and a relatively strong negative correlation with Axis 2 [$r = -0.07$ and 0.37, respectively (Table
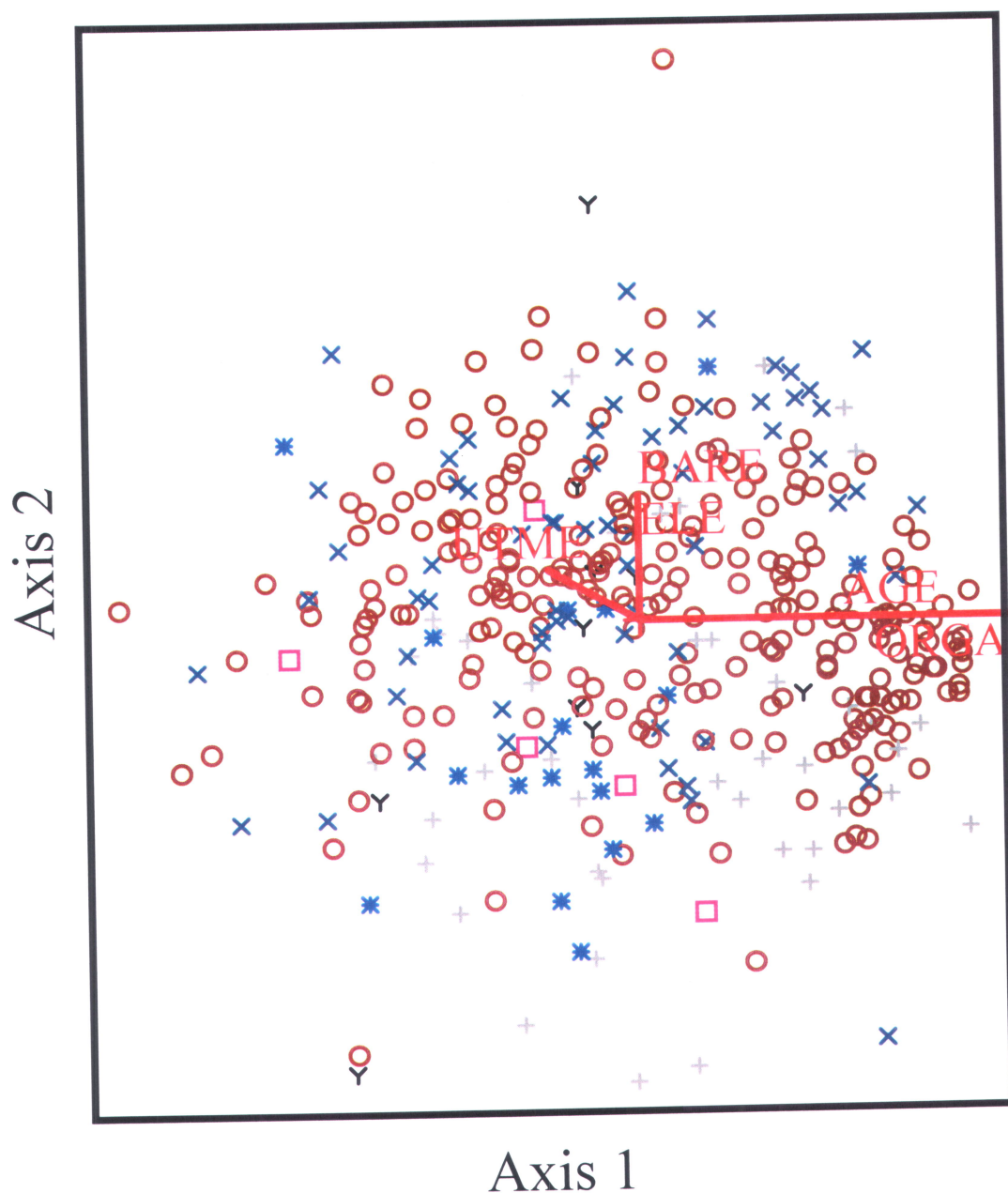
Figure 2.3. 2-dimensional NMS ordination of vegetation data. Graph was rotated to align Axis 1 with stand age. Length and direction of vectors indicate the degree of correlation with the axes. Organic debris cover, stand age, bare ground cover, elevation, and UTM meters east are indicated ORGA, AGE, BARE, ELE and UTME, respectively. Location of plots with none of the target species are indicated (○), those with woodland groundsel are indicated (Y), those with foxglove are indicated (+), those with fireweed are indicated (✗), those with woodland groundsel and foxglove are indicated (□) and those with fireweed and foxglove are indicated (✳).

Table 2.4. Pearson's product moment (linear) correlation of continuous variables to axes of 2-dimensional NMS ordination.

Variable	Axis 1	Axis 2
Aspect (°)	0.04	0.05
Bare Ground Cover (%)	-0.05	0.35
Competition Release Application	0.14	-0.05
Elevation (m)	-0.04	0.27
Last Competition Release Age (Years)	0.16	-0.20
Organic Debris Cover (%)	0.81	0.02
Slope (%)	0.25	0.04
Stand Age (Years)	0.44	0.01
Thinning Age (Years)	0.14	-0.12
UTM Meters east (m)	-0.29	0.24
UTM Meters north (m)	-0.13	0.01

Table 2.5. Pearson's product moment (linear) correlation with axes of 2-dimensional NMS ordinations and multi-response permutation procedure (MRPP) grouping of target species. P indicates the probability of any two different groups being different by chance. $\mathcal{R}$ indicates the within group heterogeneity, where $\mathcal{R} = 1$ is group identity and $\mathcal{R} = 0$ is the same heterogeneity as expected by chance.

	Correlation		MRPP	
Species	Axis 1	Axis2	P	$\mathcal{R}$
Fireweed	0.03	0.03	0.000	0.008
Foxglove	-0.07	-0.37	0.000	0.013
Woodland Groundsel	-0.08	-0.03	0.009	0.002

2.5)]. Only the correlation between foxglove and Axis 2 was significant at the 5 percent level (r= 0.098).

Plots with each of the target species were separated from those without them using the multi-response permutation procedure [MRPP (Table 2.5)]. Plots with fireweed, foxglove, and woodland groundsel were different from those without the respective species (P = 0.000, 0.000, and 0.009, respectively). The within group heterogeneity was not greater than expected by chance ($\mathscr{R}$= 0.008, 0.013, and 0.002, respectively), however, suggesting that the differences were minor and perhaps due to the large sample size (n=390).

Indicator species analysis (ISA) produced relationships between categorical environmental variables and both fireweed and foxglove, but not woodland groundsel. Competition release was indicative foxglove and fireweed but in an opposite manner (Table 2.6). Competition release presence was the indicator for foxglove (P = 0.003), while lack of competition release was a fireweed indicator (P = 0.0008). Of the three competition release types examined, broadcast herbicide application was the treatment related to foxglove [P = 0.008 (Table 2.6)]. Spot herbicide application was indicative of fireweed [P = 0.035 (Table 2.6)]. As might be expected, neither species was indicated by the absence of total vegetation control [P > 0.25 (Table 2.6)]. High site productivity suggested the presence of foxglove, and low site productivity indicated fireweed [P = 0.057 and 0.000, respectively (Table 2.6)]. There was a trend for ridges indicating foxglove (P = 0.075).

Table 2.6. Target species response to categorical environmental variables. Level represents the component of the variable having the greatest indicator value. The maximum product of the relative frequency and abundance for each species is the indicator value (IV). Specific competition release treatments were not tested where there was no difference between the presence and absence of such treatments detected and are indicated (N/A).

Variable	Fireweed			Foxglove			Woodland Groundsel		
	Level	IV	P-value	Level	IV	P-value	Level	IV	P-value
Competition Release	Absent	0.20	0.008	Present	0.15	0.003	Absent	0.03	0.373
Spot Herbicide	Present	0.20	0.035	Present	0.15	0.529	N/A	N/A	N/A
Broadcast Herbicide	Both	0.07	0.963	Present	0.23	0.008	N/A	N/A	N/A
Total Vegetation Control	Absent	0.15	0.259	Absent	0.18	0.356	N/A	N/A	N/A
Site Preparation	Absent	0.13	0.369	Present	0.12	0.102	Both	0.02	0.737
Site Productivity	Low	0.13	0.057	High	0.19	0.000	Low	0.03	0.372
Slope Position	Middle	0.11	0.408	Ridge	0.18	0.075	Upper	0.03	0.576
Thinning	Absent	0.21	0.018	Present	0.22	0.000	Absent	0.04	0.270

The NMS procedure developed an ordination that related several continuous environmental variables to its axes. Nevertheless, the target species were generally not correlated with either axis. The exception, foxglove's relation to Axis 2, is discussed below. All three species had the greatest frequency in the center of Axis 1, which is consistent with the gradual increase and decline of both fireweed and foxglove over time (van Andel 1975, van Baalen and Prins 1983, respectively) but is more difficult to explain for woodland groundsel. Woodland groundsel had the greatest frequency in the center of Axis 2, as well. It seems likely that there was too little data available for woodland groundsel abundance in this data set to relate it to the ordination. Fireweed tended to have

a roughly bimodal distribution relative to Axis 2 that would help explain the limited correlation.

MRPP detected only one group that could be explained independent of the power of large sample size--a clustering of foxglove on the negative side (*i.e.*, opposite of the environmental vectors in Figure 2.3) of Axis 2. This grouping is consistent with the correlation between foxglove and that axis in the ordination. Given that foxglove has a limited dispersal mechanism [*i.e.*, passive autochory[7] (van Baalen 1982)] compared with the other wind-dispersed species, it seems plausible that this relationship is due to elevation. Wind-dispersed seeds could move up or down slope with equal ease but foxglove seeds would be much more susceptible to gravity; moving up slope gradually as they are expelled uphill but rolling or washing downhill far more readily. Thus, up slope spread would be limited by how far the seeds were ejected and the establishment rate of mature individuals further uphill.

Some of the environmental variables that are target species indicators correspond well with their biology. High site productivity would favor foxglove, a poor competitor (van Baalen *et al.* 1984), if the species can become established before superior competitors. This observation is consistent with the results of the field experiment discussed in Chapter 4 (Page 131). Broadcast chemical release treatments would favor foxglove through reducing competition and increasing light availability for seed germination. Thinning would also be a likely foxglove indicator because canopy closure tends to cause its extinction (van Baalen and Prins 1983) and the increased light could stimulate seed

---

[7]A dispersal mechanism that relies on the parent plant for dispersal as opposed to external forces such as wind or animals and without specialized mechanisms.

germination (van Baalen 1982, Bliss and Smith 1985). Foxglove is more shade tolerant than the other target species (Johnson *et al.* 1993) allowing it to persist until thinning occurred. Lack of competition release for indication of fireweed suggests that, although the species colonizes an area after disturbance, its persistence on the site is not disturbance-dependent in the first 15 to 20 years of stand development. Since spot applications of herbicide for competition release are only made around the crop tree, this would represent a relatively minor disturbance to the forest community and be similar to no release treatment resulting in it being an indicator for fireweed.

Not all of the environmental indicator values are so easily explained. It seems that stand thinning would promote fireweed development given its response to disturbance in established stands (Dyrness 1973) resulting in thinning being an indicator for the species. The reverse is true, however, with lack of thinning tending to be indicative of fireweed. This may occur because the increased light stimulates other vegetation more than the fireweed (Lieffers and Stadt 1994) or because thinning is merely a surrogate for stand age since this treatment occurs in the latter stages of the stand ages sampled. Fireweed is also characterized as a species that uses abundant mineral resources when available although it does not require them (van Andel 1976), which suggests high site productivity is a fireweed indicator. Again, the reverse is true; fireweed is indicated by non-high site productivity. Other species may be better able to respond to the abundant resources in a highly productive site and hence out-compete fireweed, as is true of bluejoint (*Calamagrostis canadensis* (Michx.) Beauv.) (Landhausser & Lieffers 1994). It is equally unclear why ridges would tend to be indicative of foxglove. It is quite possible that indication is spurious since it is based on only 6 plots out of nearly 400.

Woodland groundsel did not respond to any of the categorical variables that might have been expected of it. It has been noted that, like fireweed, utilizes abundant nutrients when they are available but does not require them (van Andel and Vera 1977). Yet this species was not indicated by high site productivity, as one might expect. Since woodland groundsel absorbs nutrients rapidly (van Andel and Jager 1981), it may be less constrained by site productivity than other species. Broadcast site preparation treatments, such as burning, herbicides, or mechanical scarification, would also seem to be potential indicators for woodland groundsel given that it colonizes a site soon after disturbance (West and Chilcote 1968, Geyer 1995, Halpern *et al.* 1997). Again, this was not found in this study perhaps because of the limited presence of woodland groundsel in the data.

Regressions Analysis

Relationships between the environmental variables and both woodland groundsel and fireweed frequencies were examined but no relationship was found for foxglove frequency. Projected woodland groundsel frequency decreased with increasing UTM meters east [*i.e.,* moving eastward (P = 0.0023) (Figure 2.4)]. Fireweed frequency had a more complex relationship with the environmental variables: an interaction between stand age and elevation (P = 0.0009, 0.55, and 0.017 for the respective variables and their interaction). At low elevations, projected fireweed frequency declined rapidly with increasing stand age (Figure 2.5). As elevation increased, projected fireweed frequency at age 0 declined as did the rate of decline with increasing stand age until, at mid-elevations the frequency was relatively constant over time. Projected fireweed frequency increased with stand age at higher elevations reaching 100% around age 10. Linear relationships
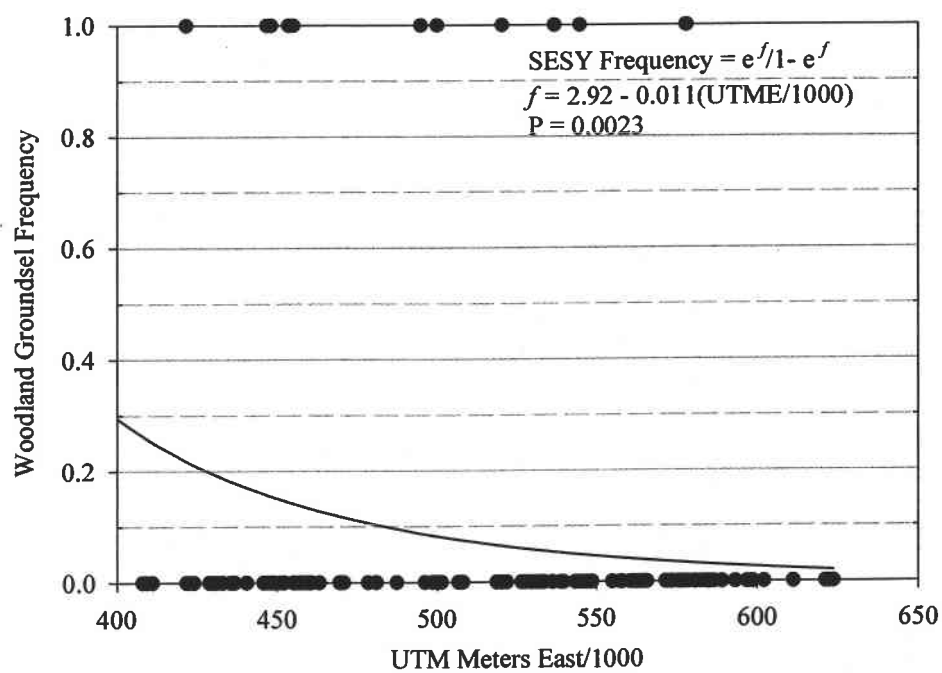
Figure 2.4. Relationship between woodland groundsel (SESY) frequency and UTM meters east (UTME). The regression is represented by (–) and the individual data are indicated (●).

EPAN Frequency = e^f/1- e^f
f = -0.021 - 0.27(Age) - 0.0008(El) + 0.003(Age*El)
P = 0.0009, 0.55, and 0.017, respectively
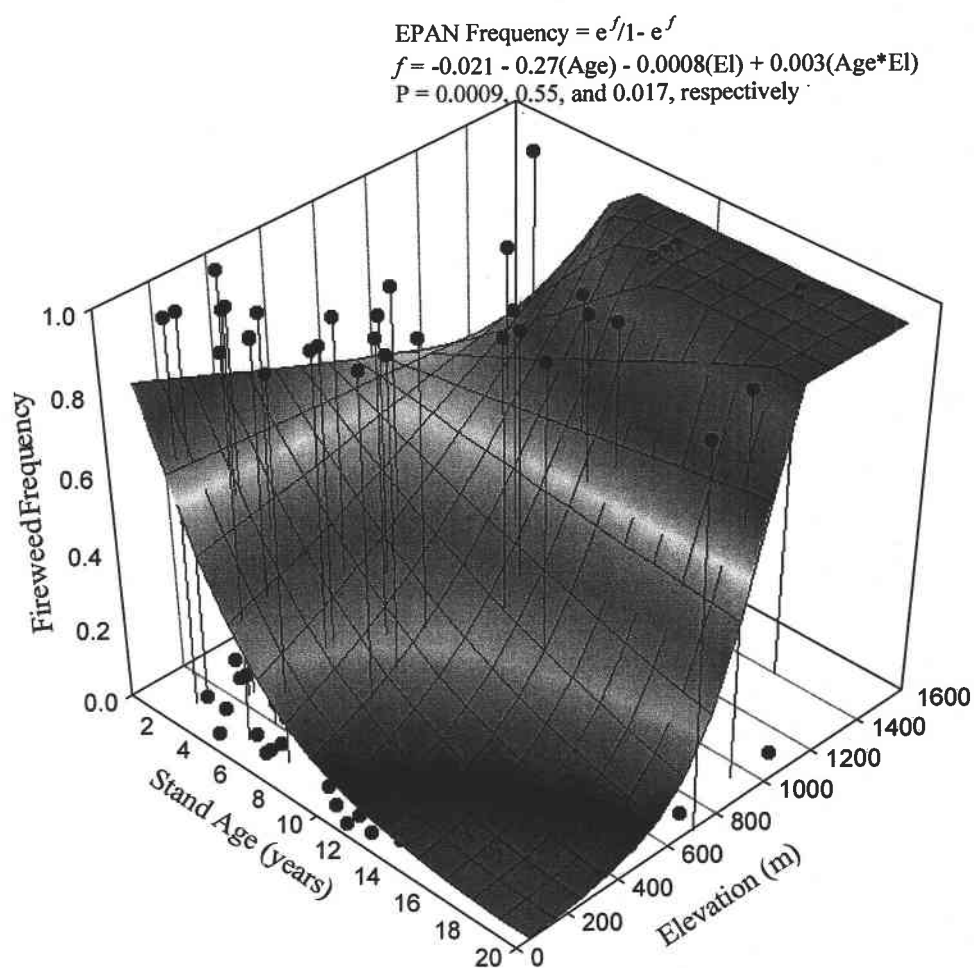
Figure 2.5. Relationship between fireweed (EPAN) frequency, stand age (years), and elevation [El (m)]. Regression is represented by the response surface (■) with the individual data indicated by (●).

were established between the environmental variables and cover of all three species. Woodland groundsel cover was projected to decline with increased stand age and increase with elevation [$P = 0.0052$ and 0.036, respectively (Figure 2.6)]. Increasing organic debris reduced foxglove cover [$P = 0.0042$ (Figure 2.7)]. Fireweed cover increased with increased herbaceous vegetation height (cm) and with increasing UTM meters east (Figure 2.8) but these variables did not interact ($P = 0.0029$, 0.024, and 0.37, respectively).

The independent variables derived for the logistic regressions of fireweed and woodland groundsel frequency differed in how closely they corresponded with the hypothesized responses (Page 33). The two hypothesized variables, stand age and broadcast herbicide site preparation (representing intense initial disturbance), did not predict woodland groundsel frequency as well as UTM Meters east. Since woodland groundsel migrated northward (and inland) from the southern Oregon Coast (Dennis 1980), it seems reasonable that its frequency should decrease moving eastward. It also seems likely that the relationship could be weak, since the species is not persistent in a community resulting in intermittent presence, (West and Chilcote 1968, Geyer 1995, Halpern *et al.* 1997), and is wind-dispersed allowing for greater dispersal distance (Parendes 1997). Fireweed frequency was predicted by an interaction between two of the hypothesized variables, elevation and stand age, although the regression elucidated a complexity in the relationship that was not anticipated. The interaction of stand age and elevation affecting fireweed frequency could result from competition. At low elevations, the fireweed could establish rapidly because of the favorable growing conditions, but be gradually excluded by more competitive vegetation (Landhauser and Lieffers 1997). As elevation increases, the growing conditions become more stressful, but fireweed is better
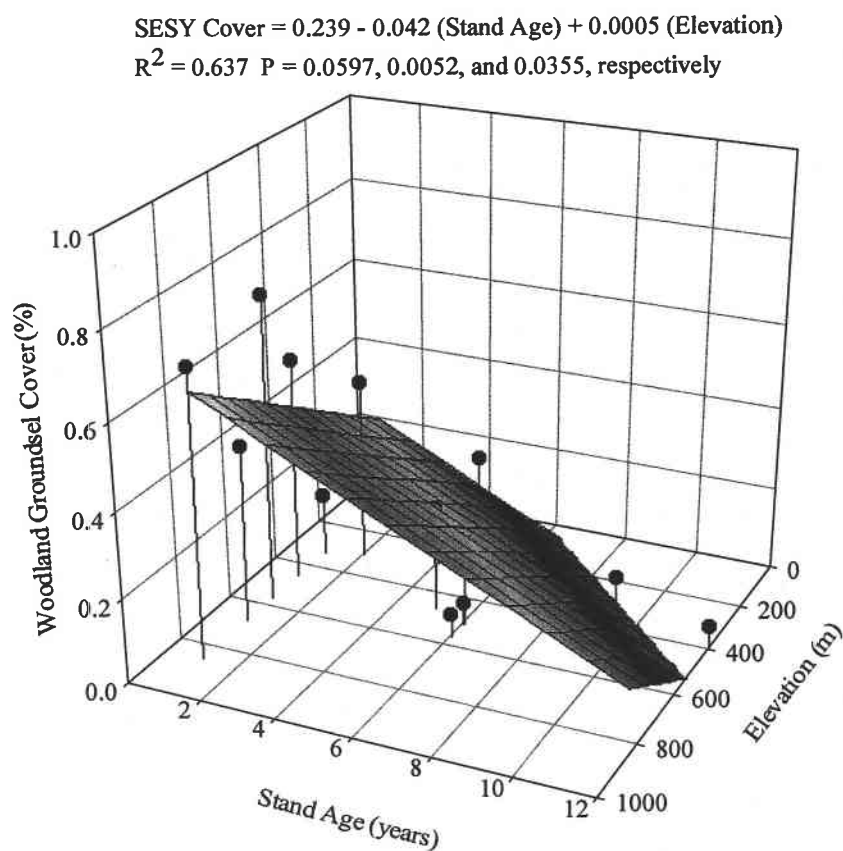
Figure 2.6. Woodland groundsel (SESY) cover (%) related to stand age (years) and elevation (m). Cover was arcsine-squareroot transformed. The response surface is represented by (■) while the individual data are indicated (●).
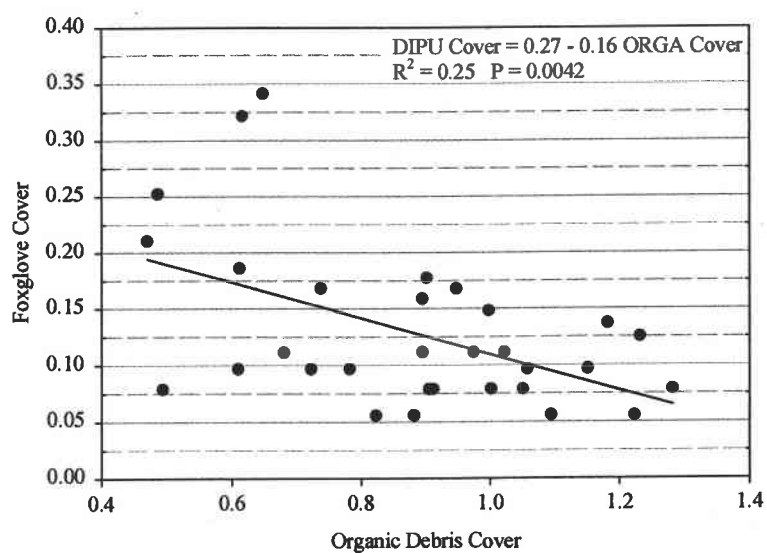
Figure 2.7. Relationship between foxglove (DIPU) and organic debris (ORGA) cover. Cover data were arcsine-squareroot transformed. The regression is indicated (−) and the individual data are indicated (●).

EPAN Cover = -0.70 + 0.0009 (UTME/1000) + 0.09 (Herb)
$R^2 = 0.32$ $P = 0.0011, 0.0019, 0.0021$ and 0.024, respectively
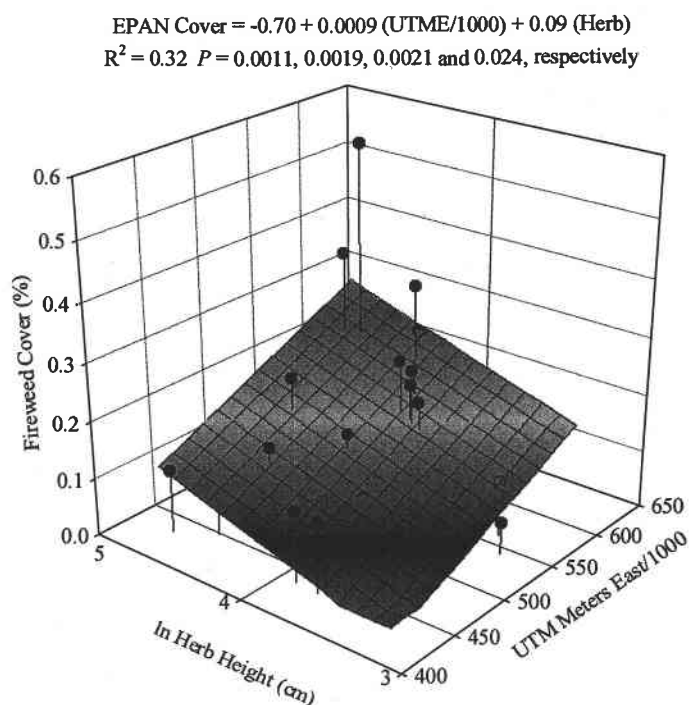
Figure 2.8. Relationship between fireweed (EPAN) cover (%), herbaceous vegetation (HERB) height (cm), and UTM Meters east (UTME). The cover was arcsine-squareroot transformed and the height was log-transformed. The regression is by the response surface (■) and the individual data are indicated (●).

able to survive under such marginal conditions than other species and becomes increasingly common in that plant community (Myerscough 1980, Chapin 1995). It may take time for fireweed to establish at the highest elevations but once there it can persist for an extended period of time resulting in 100% frequency in the communities (Myerscough 1980, Franklin and Dyrness 1988).

Predictive variables for cover of the target species were often different from those hypothesized. Woodland groundsel cover decreased as a function of stand age, which agrees with the results of other studies (West and Chilcote 1968, Geyer 1995, Halpern *et al.* 1997), but variables indicating disturbance intensity were not significant. The rise in woodland groundsel cover with increased elevation is similar to the results found by Morris (1970) where the species occurred in the Cascades but not in the Coast Range several years after disturbance. Organic debris cover was negatively correlated with foxglove cover instead of being related to stand age, competition reduction, or increased moisture. It is not obvious why such a relationship between organic debris and foxglove cover would exist. Foxglove seed requires light to germinate (van Baalen 1982), so increased organic debris could reduce germination, but that would not affect established plants. The amount of accumulated organic debris could be related to time since disturbance, which, in turn, could indicate a decline in available nutrients reducing foxglove's ability to persist in the plant community (Grime *et al.* 1990). Fireweed cover was positively related to herbaceous vegetation height, as was hypothesized, and UTM meters east, which was not. Moving eastward in the Pacific Northwest generally results in a decrease in precipitation (within the range of this study) and an increase in elevation (Franklin and Dyrness 1988). Elevation and/or reduced moisture may restrict competition for fireweed and allow the

species to become increasingly abundant in a manner similar to that discussed in its frequency. These two factors could be integrated by the UTM meters east variable. Height of the associated herbaceous vegetation could affect fireweed cover for an entirely different reason. Fireweed is a palatable forage for large mammals (Broderick 1990) and is often cropped just below the top of the surrounding herb canopy (personal observation). The field experiments suggested a relationship between vegetative cover and fireweed herbivory (Chapter 5, Page 183). Therefore, the taller the surrounding vegetation, the less herbivory the fireweed would be subjected to and the greater cover it could have.

The results of this study explain some factors affecting frequency, abundance, and vigor of fireweed, foxglove, and woodland groundsel. Many species in the NMS ordination were highly correlated with one or both of the ordination axes; however, the target species were not. Other ordinations have found fireweed occurrence to be related to burning and clear-cut logging (Johnson and Elloitt 1996). In this study, ISA suggested that fireweed was favored by lack of subsequent disturbance after the initial one required for establishment, and that foxglove was more abundant when disturbance was frequent. Regressions indicated that woodland groundsel abundance is affected by distance along an east-west gradient, stand age, and elevation. Fireweed abundance was related to these same variables and height of the surrounding herbaceous cover, while foxglove cover was weakly related to organic debris cover.

It has been argued that succession is the process of invasion, maintenance, and decline of plant populations (Johnstone 1986). Such population transitions, in turn, are often directly affected by changes in the plant's growing environment (Silvertown and Lovett-Doust 1993). Changes in age, organic debris cover, distance along a directional

gradient, elevation, and site productivity, as well as silvicultural treatments such as, site preparation, release, and thinning could all affect levels of competition and nutrient availability in a plant community (Smith 1986). These levels, in turn, can affect a species population dynamics that impacts its frequency and abundance.

This research indicates that these species respond less to environmental gradients assessed in this study than do other species in the same community. The success of the ordination procedure indicates that some of the species present in this study did reflect the effects of the environmental variables assessed. Other forest community work has found some species that responded to environmental gradients (Harvey *et al.* 1995, Johnson and Elliott 1996) or silvicultural treatments (Bailey and Tappeiner 1998, Avina 1997) while others did not. Abundance of one of the target species, fireweed, responded to the fire end of a fire-flood disturbance gradient (Timoney *et al.* 1997). This response may, however, have more to do with a gradient of suitable colonization sites (a life history characteristic) rather than changes in environmental properties.

The study also suggests that succession, for these species at least, is primarily a matter of life history expression, which concurs with the vital attributes hypothesis (Nobel and Slatyer 1980). The ability of each target species to persist in the plant community is reflected in its reproductive mode and characteristics of colonization after disturbance. Clearly, environmental constraints are imposed but they are expressed through the species' response within the restrictions of its life history. Foxglove seed's inability to germinate under a plant canopy, for example, is an environmental restriction imposed by both resource limitation (Tilman 1985) and inhibition resulting from the development of the associated vegetation (Connell and Slatyer 1977). Nevertheless, the mechanism of

foxglove's decline in the community is a direct result of its life history. The evolution of such a life history has been proposed to result from the forest's natural disturbance cycles (Ernst 1993). Whether life history has the same degree of influence on succession of species with a strong relation to environmental conditions, [*e.g.*, salal (Hanson, unpublished data)] as it does with these species, which have weak ones, is unclear and should be investigated. It may be that the greater intensity of selective forces on a species the more strongly it will be correlated to life history in terms of succession.

CONCLUSIONS

There were no definite relationships between life history and community persistence detected. Woodland groundsel presence was not related to stand age, while its abundance was inversely so. Neither its presence nor abundance was related to intensity disturbance. Reduced competition was associated with foxglove presence but not its abundance. Increased moisture availability and stand age were not related to either its presence or abundance. Fireweed presence inversely related to stand age at low elevation but directly related to it at high elevation. Its abundance was positively associated with increased associated vegetation height and UTM meters east, which represent protection from herbivory and increasing elevation/decreasing moisture.

LITERATURE CITED

Adams, A. B. and V. H. Dale. 1987. Vegetative succession following glacial and volcanic disturbances in the Cascade Mountain range of Washington, U.S.A. Pages 70-147 *in* D. E. Bilderback, ed. Mount St. Helens 1980: Botanical Consequences of the Explosive Eruptions. Berkeley, CA: University of California Press.

van Andel, J. 1975. A study on the population dynamics of the perennial plant species *Chamaenerion angustifolium* (L.) Scop. Oecologia 19:329-37.

van Andel, J. 1976. Growth and mineral nutrition of *Chamaenerion angustifolium* (L.) Scop. (=*Epilobium angustifolium* L.) on culture solutions. Oecol. Plant. 1:25-40.

van Andel, J. and W. H. O. Ernst. 1985. Ecophysiological adaptation, plastic responses, and genetic variation of annuals, biennials, and perennials in woodland clearings. Pages 27-49 *in* J. Haeck and J. W. Woldendorp, eds. Structure and Functioning of Plant Populations 2: Phenotypic and Genetic Variation in Plant Populations. Amsterdam: Noth-Holland Publishing.

van Andel, J. and J. C. Jager. 1981. Analysis of growth and nutrition of six plant species of woodland clearings. J. Ecol. 69:871-82.

van Andel, J. and F. Vera. 1977. Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. J. Ecol. 747-58.

Avina, K. A. 1997. Revegetation of Ferns and Herbs Following Different Methods of Timber Harvest in the Yurok Experimental Forest, A Coast Redwood Type. M.S. thesis, Arcada, CA: Humbolt State University. 58 pp.

van Baalen, J. 1982. Germination ecology and seed population dynamics of *Digitalis purpurea*. Oecologia 53:61-7.

van Baalen, J., A. Th. Kuiters, and C. S. C. van der Woude. 1984. Interference of *Scrophularia nodosa* and *Digitalis purpurea* in mixed seedling cultures, as affected by the specific emergence date. Acta Oecol. 5:279-90.

van Baalen, J. and E. G. M. Prins. 1983. Growth and reproduction of *Digitalis purpurea* in different stages of succession. Oecologia 58:84-91.

Bailey, A. W. and C. E. Poulton. 1968. Plant communities and the environmental interrelationships in a portion of the Tillamook Burn, northwestern Oregon. Ecology 49:1-13.

Bailey, J. D. and J. C. Tappeiner. 1998. Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon. Forest Ecol. Manage. 108:99-113.

Bliss, D. and H. Smith. 1985. Penetration of light into soil and its role in the control of seed germination. Plant Cell Environ. 8:475-83.

Broderick, D. H. 1990. The biology of Canadian weeds. 93. *Epilobium angustifolium* L. (Onagraceae). Can. J. Plant Sci. 70:247-59.

Chapin, D. M. 1995. Physiological and morphological attributes of two colonizing plant species on Mount St. Helens. Am. Mid. Nat. 133:76-87.

Clarke, K. C. 1990. Analytical and Computer Cartography. Englewood Cliffs, N.J.: Prentice Hall. 290 pp.

Clements, F. E. 1916. Plant Succession; An Analysis of the Development of Vegetation. Washington, D.C. Carnegie Inst. Wash. Publ. 242. Carnegie Institute of Washington. 512 pp.

Connell, J. and R. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111:1119-44.

Dennis, L. R. J. 1980. Gilkey's Weeds of the Pacific Northwest. Corvallis, OR: Oregon State University Press. 382 pp.

Drury, W. and I. Nisbet. 1973. Succession. J. Arn. Arbor. 54:331-68.

Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology 54:57-69.

Egler, F. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4:412-7.

Ellenberg, H. 1988. Vegetation Ecology of Central Europe [Vegetation Mitteleuropas mit den Alpen]. 4th ed. Cambridge, UK: Cambridge Universtiy Press. 731 pp.

Ernst, W. H. O. 1993. Population dynamics, evolution, and environment: Adaptation to environmental stress. Pages 19-44 *in* L. Fowden, T. Mansfield, and J. Stoddart, eds. Plant Adaptation to Environmental Stress. London: Chapman and Hall.

Ernst, W. H. O. 1985. The effects of forest management on the genetic variability of plant species in the herb layer. Pages 200-11 *in* H. R. Gregorius, ed. Population Genetics in Forestry. Berlin: Springer-Verlag.

Franklin, J. F. and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Corvallis, OR: Oregon State University Press. 452 pp.

Geyer, M. A. 1995. Autecological Studies of Two Annual Herbs, *Senecio sylvaticus* and *Epilobium paniculatum*: Effects of Biotic and Abiotic Factors. M.S. thesis, Corvallis, OR: Oregon State University. 83 pp.

Gholz, H. L., G. M. Hawk, A. Campbell, Jr. K. Cromack, and A. T. Brown. 1985. Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. Can. J. For. Res. 15:400-9.

Gisela, J. 1980. Die naturliche Wiederbesidlung von Waldbrandflähen in der Lüneburger Heide mit Mosses und Gefäßplanzen. Forstw. Cbl. 99:297-324.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torr. Bot. 53:7-26.

Gomez, K. A. and A. A. Gomez. 1984. Statistical Procedures for Agricultural Research. 2nd ed. New York: John Wiley & Sons. 680 pp.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111:1169-94.

Grime, J. P., J. G. Hodgson, and R. Hunt. 1990. The Abridged Comparative Plant Ecology. London: Unwin Hyman. 399 pp.

Halpern, C. B. 1989. Early successional patterns of forest species: Interactions of life history traits and disturbance. Ecology 70:704-20.

Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69:1703-15.

Halpern, C. B., J. A. Antos, M. A. Geyer, and A. M. Olson. 1997. Series replacement during early secondary succession: The abrupt decline of a winter annual. Ecology 78:621-31.

Harper, J. L. 1977. Population Biology of Plants. London: Academic Press. 892 pp.

Harvey, B. D., A. Leduc, and Y. Bergeron. 1985. Early Post Harvest Succession in relation to site type in the southern boreal forest of Quebec. Can. J. Forest Res. 25:1658-72.

Henderson, J. A. 1970. Biomass and Composition of the Understory Vegetation in some *Alnus rubra* Stands in Western Oregon. M.S. thesis, Corvallis, OR: Oregon State University. 64 pp.

Hill, M. O. and P. A. Stevens. 1981. The density of viable seeds in soils of forest plantations in upland Britain. J. Ecol. 69:693-709.

Huston, M. and T. Smith. 1987. Plant succession: Life history and competition. Am. Nat. 130:168-98.

Ingersoll, C. A. and M. V. Wilson. 1990. Buried propagules in an old-growth forest and their response to experimental disturbance. Can. J. Bot. 86:1156-162.

Isaac, L. A. 1940. Vegetative succession following logging in the Douglas fir region with special reference to fire. J. For. 38:716-21.

Johnson, G. N., A. J. Young, J. D. Scholes, and P. Horton. 1993. The dissipation of excess excitation energy in British plant species. Plant Cell Environ. 16:673-9.

Johnson, M. H. and J. A. Elliott. 1996. Impacts of logging and wildfire on an upland black spruce community in northwestern Ontario. Environ. Monitor. Assess. 39:283-97.

Johnstone, I. M. 1986. Plant invasion windows: A time-based classification of invasion potential. Biol. Rev. 61:369-94.

Kraemer, J. F. 1977. The Long Term Effect of Burning on Plant Succession. M.S. thesis, Corvallis, OR: Oregon State University. 123 pp.

Landhausser, S. M. and V. J. Lieffers. 1994. Competition between *Calamagrostis canadensis* and *Epilobium angustifolium* under different soil temperature and nutrient regimes. Can. J. For. Res. 24:2244-50.

Lieffers, V. J. and K. J. Stadt. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24:1193-8.

McCook, L. J. 1994. Understanding ecological community succession: Causal models and theories, a review. Vegetatio 110:115-47.

McCune, B. and M. J. Mefford. 1997. PC-ORD, Multivariate Analysis of Ecological Data. Version 3.0. Gleneden Beach, OR.: MjM Software Design.

Morris, W. G. 1970. Effects of slash burning in overmature stand of the Douglas-fir region. For. Sci. 16:258-70.

Myerscough, P. J. 1980. Biological flora of the British Isles. J. Ecol. 68:1047-74.

Noble, I. R. and R. O. Slatyer. 1980. The use of vital attributes to predict succession changes in plant communities subject to recurrent disturbances. Vegetatio 43:5-21.

Oberdorfer, E. 1973. Die Glierung der Epilobietea angustifolii Gesellschafften am Beispeil Süddeutcher Vegetationsaufnahmen. Acta Bot. Acad. Sci. Hung. 19:235-53.

Parendes, L. A. 1997. Spatial Patterns of Invasion by Exotic Plants in a Forested Landscape, Ph.D. Dissertation. Corvallis, OR: Oregon State University. 208 pp.

Rickett, H. W. 1971. Wild Flowers of the United States Volume 5: The Northwest States. New York: McGraw-Hill. 666 pp.

Salisbury, E. J. 1942. The Reproductive Capacity of Plants. London: Bell and Sons, Ltd. 244 pp.

SAS Institute Inc. 1996. SAS/STAT® Software: Changes and Enhancements through Release 6.11. Cary, NC: SAS Institute Inc. 233 - 315 pp.

SAS Institute Inc. 1990. SAS/STAT® User's Guide, Version 6. 4th ed. Volume 2. Cary, NC: SAS Institute, Inc. 846 pp.

Shula, R. G. 1998. Database development and application to characterize juvenile Douglas-fir (Pseduotsuga menziesii) and understory vegetation in the Oregon and Washington Coast Range Mountains. M. S. thesis, Corvallis, OR: Oregon State University. 101 pp.

Shula, R. G. and S. A. Knowe. 1991. Regional vegetation management model: Recommended dataset matrix, and sampling and data collection protocols. Corvallis, OR. Oregon State University. 11 pp.

Silvertown, J. W. and J. Lovett Doust. 1993. Introduction to Plant Population Biology. 3 ed. London: Blackwell Scientific. 210 pp.

Smith, D. M. 1986. The Practice of Silviculture. 7th ed. New York: Wiley and Sons. 578 pp.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125:827-52.

Timoney K. P., G. Peterson, and R. Wein. 1997. Vegetation development of boreal riparian plant communities after flooding, fire, and logging, Peace River, Canada. For. Ecol. Manage. 93:101-20.

Tong. S.T.Y. 1992. The use of non-metric multidimensional scaling as an ordination technique in resource survey and evaluation: a case study from southeast Spain. Appl. Geo. Sevenoaks 12:243-60.

Tueller, P. T., R. J. Tausch, and V. Bostick. 1991. Species and plant community distribution in a Mojave-Great Basin desert transition. Vegetatio 92:133-50.

Tüxen, R. 1950. Wanderwege der Flora in Stromtälern. Ebenda 2:52-3.

West, N. E. and W. W. Chilcote. 1968. *Senecio sylvaticus* in relation to Douglas-fir clear-cut succession in the Oregon Coast Range. Ecology 49:1101-7.

Wiser, S. K., R. B. Allen, P. W. Clinton, and K. H. Platt. 1998. Community structure and forest invasion by an exotic herb over 23 years. Ecology 79:2071-81.

Yerkes, V. P. 1958. Successional Trends of Lesser Vegetation Following Clearcutting in Old-growth Douglas-fir Stands. M.S. thesis, Corvallis, OR: Oregon State University. 98 pp.

Zobel, M. 1993. Changes in pine forest communities after clear-cutting: A comparison of two edaphic gradients. Ann. Bot. Fennici 30:131-7.

CHAPTER 3

Woodland Groundsel (*Senecio sylvaticus*) Populations as Affected By Competition and Nitrogen

ABSTRACT

A study was conducted to investigate the effects of nitrogen fertilization and competition on woodland groundsel population dynamics. Woodland groundsel is an introduced annual commonly found on newly harvested forest sites in western Oregon during the first several years after disturbance. Field experiments were conducted to quantify the effects of nitrogen fertilization and competition on survival, size, and population development of the species. The effects of fertilization on woodland groundsel size were timing-dependent: fertilizer applied at planting increased plant size, while application in the prior year had no effect. Woodland groundsel density and interspecific competition affected survival, size, and seed production. The experiments also assessed plant development from seed and transplants, as well as the species' ability to occupy and regenerate on a site. A population model was developed for woodland groundsel, and both deterministic simulations based on literature data and stochastic simulations that were parameterized from this study, were conducted to project the species' population growth. The model projections resembled observed behavior of woodland groundsel following disturbance suggesting that the populations undergo initial density-independent growth followed by density-dependent regulation.

Nomenclature: woodland groundsel, *Senecio sylvaticus* L. **SENSY**

Key Words: Succession, plant population modeling, annual plant population development

INTRODUCTION

Plant population models can be used to address a variety of scientific questions about annual plants. Jarry *et al.* (1995), for example, demonstrated that a persistent seed bank reduces the effect of year-to-year variation in adult fecundity on the stability of *Sebania vesicaria* populations. Using another model, Bazzaz *et al.* (1992) suggest that population dynamics of *Abutilon theophrasti* will be less stable under elevated CO_2 conditions. A theoretical model developed Latore *et al.* (1998) incorporated both rates of population change and a dispersal function to determine the critical patch size, *i.e.*, the minimum area required to maintain a population, of annual species. In simulations by Bonan (1991), plant size variation increased with stand density independently of how resources were distributed; a conclusion that contradicts existing competition theory. Further, a suite of population models for the annual grass *Sorghum intrans* (F. Muell. ex Benth) assessed the interrelated effects of density dependence, environmental variation, site quality, fire, and ants predation on the species' abundance (Watkinson *et al.* 1989). Our study uses such plant population models to investigate proposed mechanisms of population change, nitrogen fertilization and competition, in the exotic annual woodland groundsel (*Senecio sylvaticus* L. **SENSY**).

Since its introduction to North America, woodland groundsel has become an important component of early seral forest communities in the Pacific Northwest. A species common to temperate woodland clearings of Europe (Ernst 1985), it colonized the west coast of North America prior to the 1920's (West and Chilcote 1968, Robbin *et al.* 1951, Jepson 1925) and is now widely distributed in newly disturbed areas, such as clearcut forest stands, primarily west of the Cascade mountains (West and Chilcote 1968).

Woodland groundsel, which is associated with disturbance (West and Chilcote 1968, Gholz

et al. 1985), is considered by Dennis (1980) to be an unsightly weed due to its abundance

after disturbance, and may have adverse impacts on conifer seedling establishment in

plantation forestry (Carrier, personal communication[8]). It also may displace native annual

flora (Geyer 1995). Although not considered hazardous to livestock, woodland groundsel

contains the same alkaloids as tansy ragwort (*S. jacobeae* L.), which is toxic (Salisbury

1961).

Description and Life History

Woodland groundsel is an annual composite with rayless yellow flowers and a

single erect stem (Hitchcock and Cronquist 1973). It is distinguished from common

groundsel (*S. vulgaris* L.) by the absence of black-tipped bracts on the involucre.

Woodland groundsel seeds germinate readily and have no innate dormancy (Palmbald

1966, West and Chilcote 1968). Density of the parent generation does not affect

germination (Palmbald 1966). There is no persistent seed bank; populations are

maintained by wind-dispersed achenes (Ernst and Nelissen 1979). Seeds germinate in the

fall, then rosettes form that overwinter and continue vegetative growth in the spring. A

second cohort of seed often germinates in the spring. Fall germinants tolerate freezing

(Ernst 1985), but the spring ones do not (West and Chilcote 1968). Growth of the spring

race is more rapid than the fall one (Ernst 1985, West and Chilcote 1968) and by late

spring distinguishing between individuals of the two cohorts is difficult (West and Chilcote

[8]Byron Carrier, Research Forester, Weyerhaeuser Co., Springfield OR.

1968). Rosettes have 10 to 20 leaves·plant[-1] and can reach a diameter of 30 cm before bolting in mid-May. Shoots may grow to one meter by summer and flower from June through mid-July. The autogamous flowers (Ernst 1985) produce numerous stiffly-haired achenes with a pappus (Pojar and MacKinnon 1994) that develop about 15 days after anthesis. A dense population of woodland groundsel in the Oregon Coast Range produced 8,500 achenes·plant[-1] (West and Chilcote 1968). Similar results were reported in Britain (Salisbury 1942). Achenes are dispersed from mid-July through August. Although not studied for woodland groundsel, achene dispersal presumably follows a negative exponential curve with increasing distance from the parent plant similar to that observed for tansy ragwort (McEvoy and Cox 1987, Poole and Cairns 1940). Dispersal distance probably also increases in the prevailing wind's direction as it does for tansy ragwort (Poole and Cairns 1940). Woodland groundsel seed rain averaged 15 achenes·m^{-2} in seed traps set on a debris flow from the Mount St. Helens volcanic eruption (Adams and Dale 1987).

Effects of Fertility and Competition on Development

Woodland groundsel reproduction can be influenced by fertility and competition. Its seed production decreased from 3,800 achenes·plant[-1] at a planting density of 1 achene·pot[-1] (55 achenes·m^{-2}) to 62 achenes·plant[-1] at a planting density of 200 achenes·pot[-1] (11,000 achenes·m^{-2}) (Palmbald 1968a) indicating a strong response to intraspecific competition. In a similar experiment, achene weight, achenes·pot[-1], and achenes·plant[-1] all decreased with increasing density ranging from 1 to 10 plants·pot[-1] (39 to 390 plants·m^{-2}) (Geyer 1995). Thinning did not affect survival or reproduction (Palmbald 1968b).

Abundant nutrients, although beneficial when available, are not required for the species to grow and reproduce (van Andel and Vera 1977). With added nutrients, the number of flowers·plant^{-1} increased while the number of achenes per flower decreased, resulting in constant achene production·plant^{-1} in a greenhouse study (van Andel and Vera 1977). Fertilization and interspecific competition removal increased achene production in a field study (Geyer 1995). West and Chilcote (1968) studied woodland groundsel populations in the field and suggested they were regulated by soil fertility. However, a field comparison of fertilizer effects on woodland groundsel in clearcuts found that neither survival nor subsequent stand density were affected by fertilization (Geyer 1995). Woodland groundsel survival and reproduction are sensitive to competition (Geyer 1995, Halpern et al. 1997, Palmbald 1966). Nevertheless, competition removal did not affect woodland groundsel density in subsequent years relative to no removal (Halpern et al. 1997).

Study Objectives

This study addresses the question of woodland groundsel's rapid dominance and sudden decline on newly harvested forest sites. Specifically, this research examines the effects of nitrogen fertilization and competition manipulation on the survival, growth, and reproduction of woodland groundsel. Its objectives are to:

1) assess the impact of nitrogen fertilization and competition on woodland groundsel population dynamics, and

2) organize the available information about woodland groundsel population dynamics into a model, with stochasticity introduced using data from field

experiments, to test the effects of environmental variation and demographic stochasticity on the population.

Nitrogen fertilization was anticipated to increase reproductive output and increase both the growth rate and persistence of the population. Added levels of competition, on the other hand, were expected to reduce the population's persistence through a negative growth rate. Despite fluctuations in transition rates observed in other studies (van Andel and Vera 1977, Geyer 1995, Halpern et al. 1997, Palmbald 1966,1968a,b West and Chilcote 1968), environmental variation was projected to have a greater influence on population growth rates than demographic stochasticity.

The study is divided into three sections: (1) development of a deterministic population model using available literature, (2) field experimentation, and (3) stochastic population model development. Thus, the model was first developed, parameterized, and tested using data available in the literature, then modified using the results of our field experiments. In addition, field experiments assessed treatment effects on plant size and biomass. The models' ability to explain the rapid increase in woodland groundsel populations are discussed and compared with other work on this subject.

METHODS AND MATERIALS

Deterministic Population Model Development

A conceptual population model for woodland groundsel with an annual time step was developed following Sagar and Mortimer [1976 (Figure 3.1)] and was parameterized using data from the literature (Table 3.1). Woodland groundsel immigrated to new sites percent·year $^{-1}$, all of which entered the early seed bank. Seed viability and the early seed
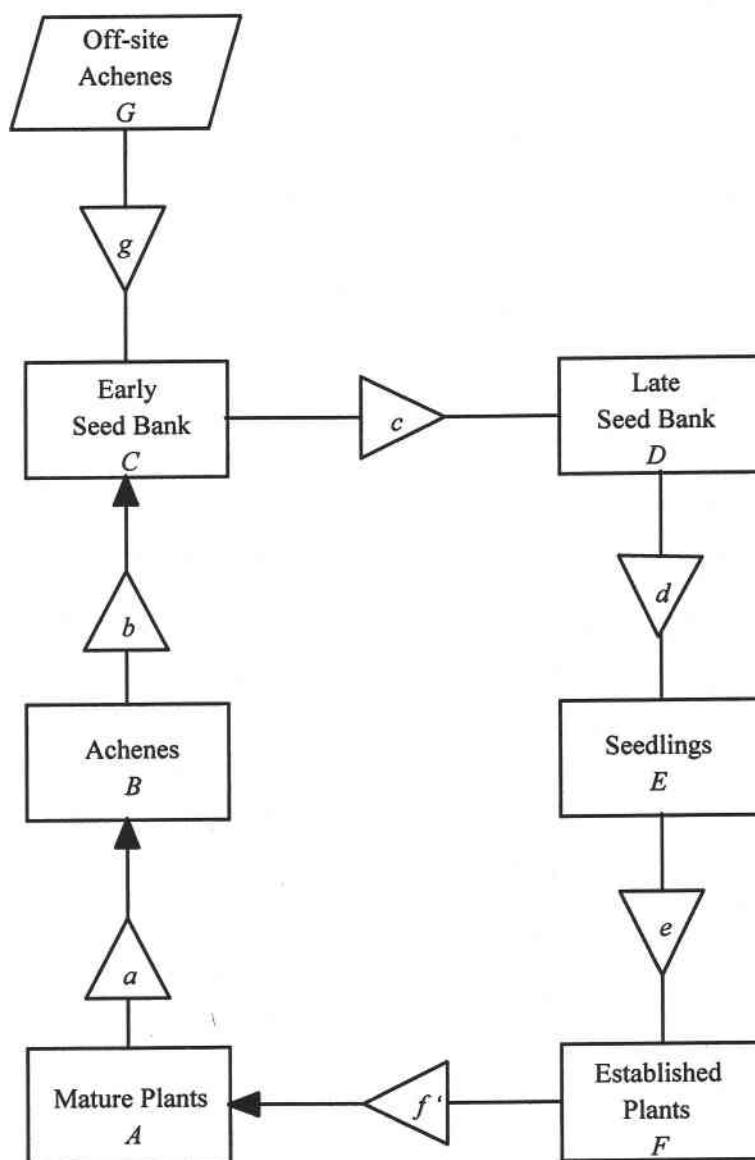
Figure 3.1. A conceptual population dynamics model for woodland groundsel. State variable equations are as follows; $C = G \cdot g + B \cdot b$, $D = C \cdot c$, $E = D \cdot d$, $F = E \cdot e$, $A = F f'$, $B = A \cdot a$. Rate definitions; g - immigration, c - post-dispersal mortality, d - late seed bank germination, e - seedling establishment, f' - flowering, a - achene production·plant^{-1}, b - seed viability.

Table 3.1. State variable and transition rate values for a deterministic woodland groundsel population model. Data were obtained from the literature. State variables are designated by uppercase letters in parentheses; variables for transition rates are in lowercase. Units for state variable are $\cdot m^{-2}$ while those for transition rates are $\cdot year^{-1}$ except for seed production, which is $\cdot plant^{-1} \cdot year^{-1}$. Values in italics are estimates not based on specific studies.

State/Transition	Value/Rate	Reference
Off-site Seeds (G)	190,400	West and Chilcote 1968
Early Seed Bank (C)	*15*	N/A
Late Seed Bank (D)	*1,042*	N/A
Seedlings (E)	1,000	Geyer 1995
Established Plants (F)	*23*	N/A
Mature Plants (A)	22	West and Chilcote 1968
	0.2	Halpern *et al.* 1997
	60	Halpern *et al.* 1997
	4.4	Halpern *et al.* 1997
Seeds (B)	190,400	West and Chilcote 1968
Immigration (g)	0.000079	Adams and Dale 1987
Post-dispersal Survival (c)	*0.95*	N/A
Late Seed Bank Germination (d)	0.96	West and Chilcote 1968
Seedling Establishment (e)	*0.02*	N/A
Flowering (f ΄)	*0.95*	N/A
Achene Production (a)	250	van Andel and Vera 1977
	625	van Andel and Vera 1977
	574	van Andel and Vera 1977
	10500	Salisbury 1942
	8564	West and Chilcote 1968
	267	Palmbald 1968
Seed Viability (b)	*0.9*	N/A

at a rate of 15 achenes $\cdot m^{-2} \cdot year^{-1}$ [Adams and Dale 1987 (Table 3.1)]. Given an achene production of 190,000 achenes $\cdot m^{-2}$, the estimated immigration rate was 0.000079 bank created by on-site populations were assumed to be high (McEvoy 1984, Poole and Cairns

1940) and estimated to be 90 percent·year^{-1} (Table 3.1). Given the small achene size, post-dispersal predation was assumed to be low (Eriksson *et al.* 1995), therefore the transition rate from the early seed bank to the late seed bank was estimated to be 95 percent·year^{-1}. Germination from the late seed bank was 96 percent·year^{-1} [Chilcote and West 1968 (Table 3.1)]. Because woodland groundsel seeds are not persistent (Ernst and Nelissen 1979), the model has no buried seed bank (Figure 3.1). An established woodland groundsel population was found to have 1,000 seedlings·m^{-2}, but low seedling survival (Geyer 1995), which results in an estimated survival rate of only 2 percent·year^{-1} (Table 3.1). Established plant survival and reproduction percentage were assumed to be high (95 percent·year^{-1}; Table 3.1) based on studies of annual reproductive biology (Palmbald 1968a, Grime 1977). Density of mature plants varied from 0.2 to 60 plants·m^{-2}·year^{-1}(West and Chilcote 1968, Halpern *et al.* 1997), with an average of 21.6 plants·m^{-2} (Table 3.1). Woodland groundsel produced between 8,500 and 10,500 achenes·plant^{-1}·year^{-1} in the field (West and Chilcote 1968, Salisbury 1942), while in a greenhouse study it produced only between 247 and 623 achenes·plant^{-1} (van Andel and Vera 1977), resulting in an average production of 4,155 achenes·plant^{-1}·year^{-1} (Table 3.1). An estimated 89,750 achenes·m^{-2} would be produced based on the average mature plant density and achene production. Achene production in an Oregon study by West and Chilcote (1968) was calculated to be more than 190,000 achenes·m^{-2} in a dense woodland groundsel stand (Table 3.1). Average values were used to calculate parameters if more than a single value was available in the literature. Some parameters were estimated by calculating transition rates from the appropriate state variable or general descriptive information (Sagar and Mortimer 1976).

Population vectors and transition matrices were derived from the state variable and transition rate values in Table 3.1. The rate parameters were incorporated into the following transition matrix (S1):

$$
S1 = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.9 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.96 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.02 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.95 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 4{,}155 & 0
\end{pmatrix}. \tag{15}
$$

These transition rates are for an annual time step, which was selected because the available data consisted of population changes among years. The first row and column represent immigration. The second one is for post-dispersal mortality and, the third, seed germination. Rows and columns four and five are seedling survival and plant flowering, respectively. Seed viability is in the sixth row and column, and seed production is in the seventh row and column. The population vector (n_t) represents the population colonizing a new after 1 year:

$$
n_t = \begin{pmatrix}
190{,}400 \\
14.25 \\
13.68 \\
0.27 \\
0.26 \\
1080 \\
972
\end{pmatrix} \tag{16}
$$

(where t=1) and the elements of the vector are in the same order as described for the transition matrix (See Appendix 3 for derivation of $\mathbf{n}_t$).

The conceptual and the initial deterministic model were created to accommodate the form of the available data: transition elements, and stage values having come from a variety of studies. The transition matrix, **S1**, was also used to simulate woodland groundsel population's behavior in RAMAS/Stage (Ferson 1991) because adult plant density and seed production were the stages of interest. However, this matrix is unsuitable for eigenanalysis that provides the asymptotic growth rate (λ) and sensitivity (Caswell 1978) and elasticity (de Kroon *et al.* 1986) indices. Therefore a reduced transition matrix,

$$S1' = \begin{pmatrix} 1 & 0 \\ 0.000075 & 64.8 \end{pmatrix}, \qquad (17)$$

S1', was created[9]:

and assessed λ for woodland groundsel. Sensitivity and elasticity indices were not computed for this model, because the reduced matrix is clearly dominated by element **S1'**$_{(2,2)}$.

Field Experiments

The field experiments were conducted in an afforested area of the MacDonald Research Forest north of Corvallis, OR (44° 40′ N and 123° 15′ W) at an elevation of 130

---

[9]The matrix reduction is achieved by multiplying transition rates *a, b, c, d, e,* and *f ′* from Table 1 and placing the product in element **S1'**$_{(2,2)}$.

m. Its slope is 10% with an aspect of 180°. The Jory silty clay loam soil, classified as a Xeric Haplohumults, supported a vegetation dominated by reed canarygrass, (*Phalaris arundinacea* L.), oats (*Avena sativa* L.), hairy cats-ear (*Hypochaeris radicata* L.) and Queen Anne's lace (*Daucus carrota* L.) with scattered Douglas-fir (*Pseduotsuga menseizii* [Mirbel] Franco) seedling and Himalayan blackberry (*Rubus discolor* Weike&Nees). The site receives approximately 1150 mm of precipitation annually, primarily from October to June.

Three experiments were conducted to determine the response of woodland groundsel to nitrogen fertilization and competition. Each experiment was conducted in a randomized complete block design with a factorial arrangement of three nitrogen fertilization levels and three competition treatments. The number of blocks varied among the experiments: four blocks in Experiments 1 and 2, two blocks in Experiment 3. The fertilizer levels used were ambient nitrogen with an average level of 12.5 kg·ha^{-1} (control), 62.5 kg·ha^{-1}, and 125 kg·ha^{-1} of added nitrogen. Fertilizer was applied by hand one year before planting in Experiment 1 and immediately prior to planting in Experiments 2 and 3. Intraspecific competition treatments were created from the number of planting sites used per plot, while landscape fabric was used to prevent interspecific competition from associated vegetation. Holes, 10-cm square, were cut in the fabric to allow woodland groundsel plants to grow. Competition treatments consisted of (1) one woodland groundsel planting site·m^{-2} with fabric present; (2) nine planting sites·m^{-2} with fabric present; and (3) nine planting sites·m^{-2} without fabric.

Experiment 1: Survival and Growth of Transplanted Woodland Groundsel

Woodland groundsel transplants were grown in the greenhouse by sowing 5 to 10 achenes into a peat pellet in the Fall of 1992. After germination, seedlings were thinned at the cotyledon stage to one plant per pellet. When individual seedlings developed two true leaves, they were placed outside to acclimate for two weeks. Experiment 1 was then established during the Winter of 1993 by transplanting seedlings into the plots at the density required for each competition treatment. At transplanting, plants were small rosettes; 3 to 5 cm in diameter with four to eight leaves.

The following data were collected for each woodland groundsel plant in the experiment during June 1993: Status (healthy, sick, flowering, browsed, dead, or missing), height (cm), and canopy diameter (cm, in two perpendicular directions). Plants then were harvested in August 1993 and root and shoot biomass (g) and achene production determined. At harvest, roots and shoots were separated, the roots were washed to remove soil, and then roots and shoots were dried at 60 C for 48 to 72 hours and weighed. Achenes were removed from the shoots of flowering plants prior to drying, then separated from the pappus and other flower parts by sieving, and weighed. An average achene weight (mg) was computed from a sample of 100 achenes, which was used to estimate the total number of achenes produced·plant^{-1} . The seed sample was germinated on moist blotter paper in a Petri dish at 25 C for 30 days to determine seed viability.

Experiment 2: Survival and Growth of Woodland Groundsel from Seed

Each planting location in Experiment 2 was sown with 10 woodland groundsel achenes in December 1994 and assessed in January and February 1995 to determine when

germination, seedling establishment, and mortality occurred. No germinants survived to March 1995.

Experiment 3: Regeneration of Planted Woodland Groundsel

Experiment 3 was established in Spring of 1992 using woodland groundsel transplants. The experiment was identical in layout to Experiment 1 except that only two replicates were used. Transplants were obtained and treated as in Experiment 1. There was also no end-of-season harvest as in Experiment 1 and the landscape fabric was removed at the end of the first growing season to allow natural seed dispersal and subsequent regeneration of the population. Data for plant status and size were collected in June 1992. An allometric equation (Appendix 2) relating woodland groundsel achene production to plant height from Experiment 1 was used to predict achene production from this experiment.

Data Analysis of Experiments

Binary data (*i.e.*, success or failure to meet a condition such as survival) collected in these experiments included mid-season survival, reproduction, seed viability, and germination. These data were analyzed by logistic regression using an indicator variable model (analysis of deviance) with Proc Genmod in the SAS statistical package (SAS Institute 1993). This statistical model uses the proportion of individuals having a positive response to the total number of individuals in a plot as the dependant variable. The independent variables included block, nitrogen fertilization level, and competition treatment, as well as their interactions. One fertilization level and one competition

treatment were selected to make comparisons (reference level). In these experiments, reference levels received no added nitrogen and had 9 woodland groundsel plants·m^{-2} without landscape fabric. The reference level for block was arbitrarily the last replicate in each experiment.

Analysis of variance was conducted on all continuous size and reproductive data including plant height, canopy diameter, root biomass, shoot biomass, achene number·plant^{-1}, achene number·m^{-2}, and individual achene weight. Tests were conducted independently on each response variable and used nitrogen level, competition treatment, and their interaction as independent variables. The analysis was conducted on plot means to avoid pseudoreplication (Hurlbert 1984). Data were tested for normality and constant variance and all variables were log transformed except individual achene weight, which required no transformation. Because of unbalanced data, means were separated using least-squares means pairwise comparison (SAS Institute 1990).

Stochastic Population Models

Stochastic population models for woodland groundsel were developed from the conceptual model previously described (Figure 3.1) and were parameterized using data collected during this study. Analysis of deviance was used to establish transition probabilities for the population models by eliminating block and non-significant treatment effects from the statistical model and obtaining parameter estimates. Probabilities were then computed using these parameters in the following equation:

$$\frac{e^{\alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2}}{1 + e^{\alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2}} \qquad (18)$$

where α is the parameter estimate for the intercept and the fertilization and competition reference levels, β_1 is the parameter estimate for the level of nitrogen addition, X_1; β_2 is the parameter estimate for the type of competition treatment, X_2, and β_3 is the parameter estimate for the interaction between nitrogen level, X_1, and competition treatment, X_2. As it was not possible to determine significantly different treatment levels, the probabilities for each level of a significant treatment were tested in the stochastic population models. The variance, V, was calculated for each parameter estimate using the following equation:

$$V = \frac{p \; q \; \phi}{n} \qquad (19)$$

where p is the estimated probability of response ($\hat{\mu}$), q is the estimated probability of no response (1- $\hat{\mu}$), ϕ is the scale parameter that is computed by Proc Genmod (SAS 1993) for the specific model being fit, and n is the number of observations. The parameter estimates were assumed to have an approximately normal distribution. Experimental variance was used to provide stochasticity in the population model.

The effects of nitrogen fertilization on the population were compared using the probability computed for each fertilizer level in model simulations when differences were detected. Where differences in parameter estimates for competition were found, the transition probabilities were arranged sequentially so that the level of competition increased from year to year (*i.e.*, Treatment 1 in Year 1, Treatment 2 in Year 2, and Treatment 3 in subsequent years). This arrangement simulated the increase in vegetation

expected over time after a disturbance. If no differences among treatments were detected, the transition probability from the experimental mean was used in the model. These models were analyzed and simulations conducted in the same manner as described for the deterministic model.

RESULTS AND DISCUSSION

Deterministic Population Model

The matrix **S1** was used to predict woodland groundsel population growth over three years (Figure 3.2). The model had a λ of 64.8. The projected plant density in the simulated second year was similar to that observed in western Oregon (West and Chilcote 1968), and followed a trajectory similar to one observed in the Oregon Cascades for the first two years (Halpern *et al.* 1997). Simulated achene production in the second year was higher than the observed level of 190,000 seeds·m^{-2} (West and Chilcote 1968) suggesting an inverse relationship between mature plant density and individual achene production, which has been observed in other studies (Palmbald 1966, Geyer 1995, Harper 1977).

This preliminary model has several limitations: (1) It contains numerous estimates, (2) data for some important model elements, especially transition rates, are limited, and (3) the deterministic nature of the model requires an assumption of constant population response, which does not allow for demographic variability. These limitations can be addressed using stochastic models.
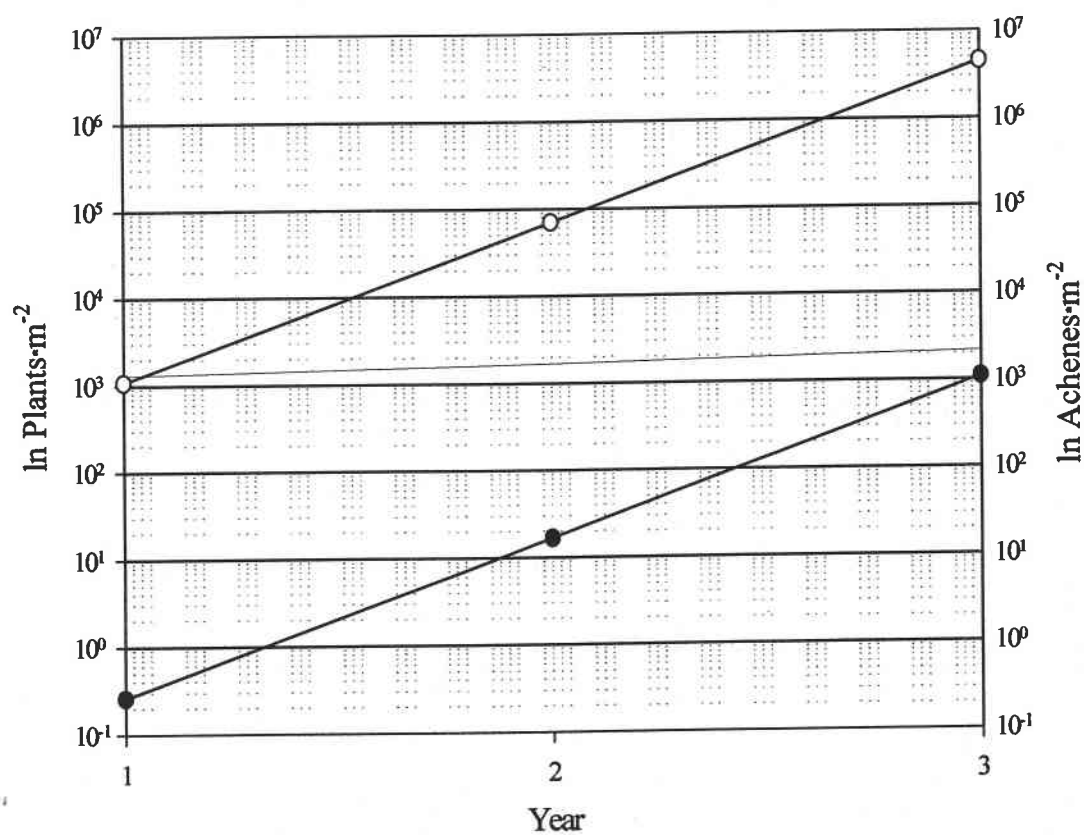
Figure 3.2. Woodland groundsel population development over projected three years using the deterministic model. Mature plant density [ln(plants·m⁻²)] is represented by (–O–). Achene density [ln(achenes·m⁻²)] is represented by (–●–).

Field Experiments

Experiment 1: Survival and Growth of Transplanted Woodland Groundsel

Nitrogen fertilization and competition manipulation did not affect plant size (Table 3.2). No differences in woodland groundsel height or canopy diameter detected among any of the nitrogen fertilization or competition treatments [P > 0.32 (Table 3.2)]. Similarly, there were no treatment responses in either root or shoot biomass to fertilization (P > 0.27), but competition treatments did affect biomass (Table 3.2). Both root and shoot biomass were reduced under Treatment 3 (9 plants·m^{-2} without landscape fabric) relative to plants grown in Treatment 1 [1 plant·m^{-2} with landscape fabric (P = 0.079 and 0.054, respectively)] but were not different from those for plants in Treatment 2 (9 plants·m^{-2} with landscape fabric). Other studies have detected similar biomass responses to competition (Geyer 1995, Halpern *et al.* 1997). No interactions were found between nitrogen levels and competition treatments for any of the size or allocation variables (P > 0.50) in this experiment.

Woodland groundsel reproduction was affected by competition treatment but not nitrogen level (Table 3.2). Achene production·plant^{-1} decreased with increasing competition; plants under Treatment 3 produced fewer achenes than those grown in Treatment 1 (P = 0.063). There was, however, no effect of competition on achene production·m^{-2} (P > 0.37). No effect of fertilization was detected on either achene production per plant or per m^2 (P > 0.22). Effects of competition on achene production have been found in other field studies (Geyer 1995, Halpern *et al.* 1997); fertilization also has shown an effect on achene production in both field and greenhouse studies (Geyer 1995, Halpern *et al.* 1997, van Andel and Vera 1977). Individual achene weight did not

Table 3.2. Woodland groundsel size as affected by nitrogen fertilization and competition manipulation. Competition treatments are as follows; (1) 1 plant·m⁻² with landscape fabric, (2) 9 plants·m⁻² with landscape fabric, and (3) 9 plants·m⁻² without landscape fabric. Analysis was conducted on log-transformed data except for individual seed weight, which did not require transformation. Mean separation was conducted using least-squares means. Back-transformed values are presented, with those in the same treatment and row followed by the same letter not being different. Untransformed plot means are presented where no differences were found.

Expt.	Variable	Nitrogen Added (kg·ha⁻¹)			Competition		
		0	62.5	125	1	2	3
1	Height (cm)	66.6 a	77.9 a	75.9 a	77.8 a	71.4 a	75.5 a
	Canopy Diameter (cm)	13.9 a	20.4 a	21.6 a	28.0 a	16.7 a	13.7 a
	Root Biomass (g)	2.5 a	3.0 a	3.8 a	5.41 a	1.1 ab	0.8 b
	Shoot Biomass (g)	13.4 a	16.5 a	24.5 a	21.0 a	4.7 ab	3.6 b
	Seeds·plant⁻¹	10,197 a	25,266 a	35,287 a	44,633 a	24,061 ab	8,339 b
	Seeds·m⁻²	30,580 a	72,333 a	49,787 a	50,661 a	63,552 a	12,190 a
	Achene Biomass (mg)	0.154 a	0.167 a	0.168 a	0.165 a	0.161 a	0.173 a
3	Height (cm)	7.1 a	13.8 a	31.8 b	4.8 a	15.7 b	22.8 b
	Canopy Diameter (cm)	5.4 a	4.0 a	11.6 a	3.8 a	9.7 a	4.5 a

vary with any nitrogen level or competition treatment (P > 0.10). There were no interactions between nitrogen level and competition treatment (P > 0.60).

Several possible reasons exist for woodland groundsel's limited treatment response in this experiment. Woodland groundsel is a poor competitor with other species (Halpern *et al.* 1997) since it competes by preempting resources through rapid growth and nutrient uptake (van Andel and Vera 1977). The one-year delay between fertilizer application the statistical power of the experiment. If, for example, the main plots are divided into 1-m^2 subplots and these data are used in an ANOVA of achene production·plant^{-1}, the p-value for the competition treatment effect is 0.0048 and all three treatments are different from one another. A study designed with experimental units of this size would increase the study's resolution power. Despite this limited ability to separate treatment differences for some variables, the data collected from this experiment were useful in creating a stochastic population model that provided a better understanding of potential variation in woodland groundsel reproduction.

Experiment 2: Survival and Growth of Woodland Groundsel from Seeds

Although woodland groundsel seed germination was high in the laboratory (Experiment 1), it was very low in this field experiment. Most of the seeds distributed either failed to germinate or died during early seedling development. There was, however, sufficient germination to assess its probability, which was 0.01 across the experiment. There were no differences in germination due to nitrogen fertilization levels but a competition treatment response was detected (P = 0.20 and 0.050, respectively) with increased germination occurring with Treatment 2 relative to Treatment 3. This response

is difficult to explain, however, since there was no associated vegetation present on the plots at the time of germination. Perhaps the soil temperature was increased by the black fabric used to prevent interspecific competition in Treatment 2, which may have resulted in increased woodland groundsel germination. There was no interaction between nitrogen levels and competition treatments (P = 0.36).

Most woodland groundsel seedlings in this experiment died in the cotyledon stage of growth. Few seedlings developed true leaves; thus there was insufficient survival to estimate the transition probability for changing from a seedling to an established plant. Other studies have also found very high seedling mortality rates of this species (West and Chilcote 1968, Geyer 1995). Given the wet soil conditions prevalent at the time of germination, the seedlings may have been subject to fungal diseases that have been observed in other studies (Geyer 1995, Palmbald 1966).

Experiment 3: Natural Regeneration of Planted Woodland Groundsel

This experiment was conducted similarly to Experiment 1, except that fertilization was done immediately prior to planting and there was no end-of-season harvest in the year of transplanting. The results of this experiment are in Table 3.2. Adding 125 kg·ha^{-1} nitrogen produced an increase in woodland groundsel height relative to the lower nitrogen levels (P = 0.026). Similarly, plant height was less in Treatment 1 than the other competition treatments (P = 0.045). These results are in contrast to those of Palmbald necessary in future studies to determine whether seed from other populations failed to reach this site or if conditions were not suitable for germination upon its arrival. It is not

clear what effect this lack of immigration may have had on the species failing to remain on-site.

Delaying planting until one year affected woodland groundsel as indicated by the interaction between fertilizer level and experiment timing detected in the plant height regression. There was a response in plant size to nitrogen when it was recently applied (Experiment 3) that was lacking when planting was delayed [Experiment 1 (Table 3.2)]. The lag between fertilization and planting in Experiment 1 may have eliminated any competitive effect on plant size, as occurred in Experiment 3. The delay may also have enhanced the effect of competition on mid-season survival observed in Experiment 1, by stimulating growth of the associated vegetation. These results raise interesting questions about how the timing of fertilization might influence the response of an annual species to both fertilization and competition in silvicultural systems.

Stochastic Population Models

The results of the field experiments (Tables 3.2 and 3.3) were used to develop parameter estimates, transition probabilities, and variances for the woodland groundsel population model (Figure 3.1). These experimental probabilities along with their variances were substituted for the appropriate literature-based probabilities in the model. If no experimental parameter estimate was determined, the previous probability value was retained. These estimated transition probabilities, along with their variances, were used in the model to create stochasticity that represented variation in the population response (Burgman *et al.* 1993).

Table 3.3. Woodland groundsel survival and reproduction as affected by nitrogen level and competition treatment. The proportion of plants responding are indicted with the number of plots indicated in parentheses. Experiments 1 and 2 had a maximum of 4 plots while Experiment 3 had 2. The specific stage is indicated; mid-season survival (MS), end-of-season survival (EOS), reproduction (Reprod), and germination (Germ).

Nitrogen	Competition	Expt 1			Expt 2	Expt 3
$(kg \cdot ha^{-1})$	Treatment	MS	EOS	Reprod	Germ	MS
0	1	0.08 (1)	0.08 (1)	0.08 (1)	0.000 (0)	0.17 (1)
	2	0.26 (4)	0.21 (4)	0.21 (4)	0.005 (2)	0.26 (2)
	3	0.01 (1)	0.01 (1)	0.00 (0)	0.000 (0)	0.04 (1)
62.5	1	0.25 (1)	0.08 (1)	0.08 (1)	0.009 (1)	0.00 (0)
	2	0.32 (4)	0.30 (4)	0.27 (4)	0.019 (3)	0.15 (2)
	3	0.05 (1)	0.04 (1)	0.04 (1)	0.009 (2)	0.09 (2)
125	1	0.58 (4)	0.58 (4)	0.33 (3)	0.008 (1)	0.51 (1)
	2	0.17 (4)	0.15 (3)	0.14 (3)	0.020 (3)	0.33 (2)
	3	0.09 (2)	0.09 (2)	0.09 (2)	0.004 (1)	0.20 (1)

Parameter estimates for transitions between stages in woodland groundsel development were variably affected by the nitrogen levels and competition treatments in Experiment 1. Mid-season survival, reproduction, and germination parameter estimates were all unaffected by added nitrogen (P > 0.10). The estimated parameters for mid-season survival increased with Treatments 1 and 2 relative to Treatment 3 (P = 0.0002). These results are consistent with those of Palmbald (1966), where woodland groundsel survival and reproduction decreased with increasing density when grown in a mixture of downy brome (*Bromus tectorum* L.). There was no effect of competition treatment on reproduction or seed viability parameter estimates (P > 0.33), and no interactions between nitrogen level and competition treatment were detected (P > 0.10).

The parameter estimates for mid-season survival responded differently to competition treatment in Experiment 3, where no effects were found (P > 0.18), and Experiment 1. There was no interaction between nitrogen level and competition treatments detected (P > 0.88). Transition probabilities were estimated based on the results of the field experiments. Mid-season survival probability for woodland groundsel in Experiment 1 differed among the three competition treatments (Figure 3.3). Plants in Treatment 1 had a 0.31 survival probability. The probability of survival was 0.25 for woodland groundsel grown with Treatment 2, while the survival probability was 0.048 for plants in Treatment 3. The probability of woodland groundsel reproducing was 0.81 and the probability of a seed being viable was 0.76 in Experiment 1, regardless of nitrogen level or competition treatment. Geyer (1995) also found that fertilization did not affect woodland groundsel survival, which is consistent with this experiment, but she did detect increased reproduction with added nitrogen that was not observed here. The estimated woodland
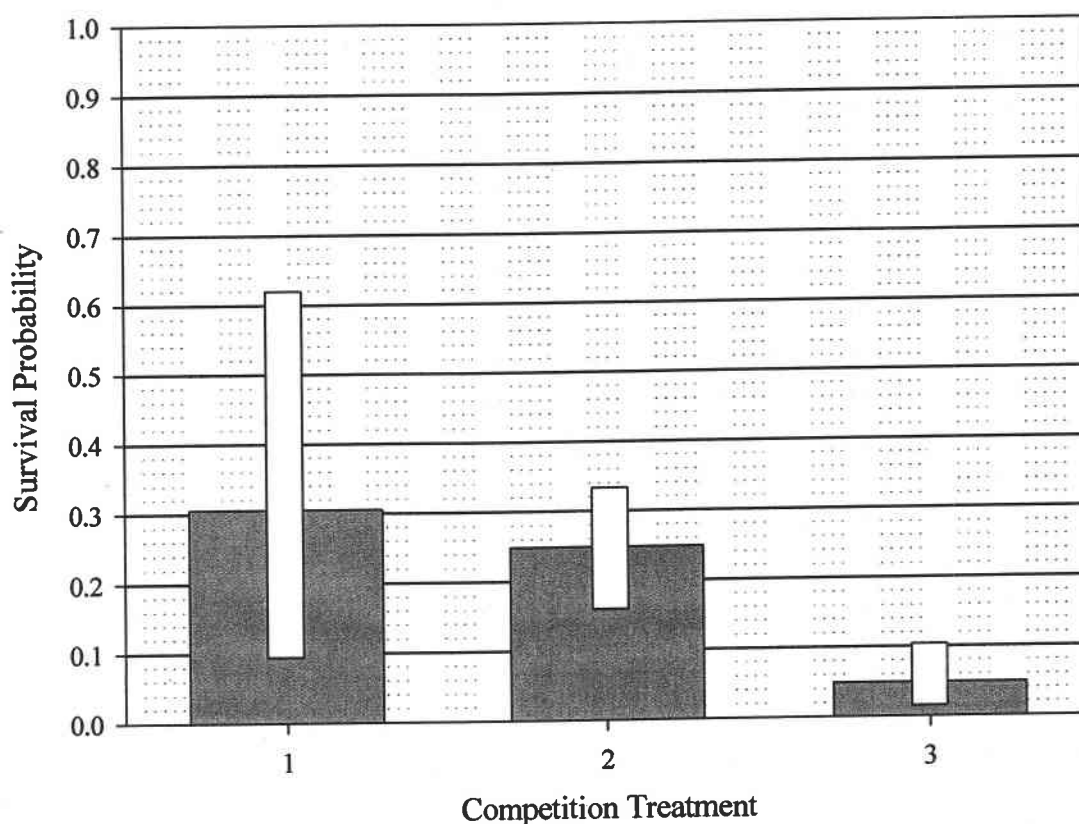
Figure 3.3. Estimated mid-season survival probability for woodland groundsel as affected by competition treatment in Experiment 1. Bars are the survival probability for each competition treatment and vertical lines represent the 95 percent confidence interval. Competition treatments are as follows; (1) 1 plant·m⁻² with landscape fabric, (2) 9 plants·m⁻² with landscape fabric, and (3) 9 plants·m⁻² without landscape fabric.

In order to model the effects of competition on population growth, a simulation was conducted using transition rates that were unaffected by competition and compared to projections from models groundsel survival at mid-growing season of the first year of Experiment 3 was 0.21, which is considered to be an approximation for plant establishment probability (e) that could not be estimated from Experiment 2.

where transition rates were influenced by competition. Because nitrogen fertilization had no effect on the population's transition rates, it was not included in the simulations.

An initial stochastic simulation for woodland groundsel was conducted using the following transition matrix, **S2**:

$$
\mathbf{S2} = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.76 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.01 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.21 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.81 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 29800 & 0
\end{pmatrix}, \tag{20}
$$

using transition rates that were not influenced by competition (Model 1). This matrix used the same structure as the one for the deterministic models (Page 79). The transition probabilities for flowering (f'), experimental mean achene production (a), and seed viability (b) from Experiment 1 were used in the simulation instead of the literature values. Similarly, germination probability (d) was derived from Experiment 2 and mid-season survival (e) from Experiment 3 was used (Table 3.4). The initial population vector, $\mathbf{n}_t$, remained unchanged.

Stochasticity was introduced into the model by providing RAMAS/Stage with a mean transition value, a variance for that transition, and a statistical distribution. In all cases a normal distribution was used. Each model simulation was iterated 100 times with the transition rates chosen at random based on the parameters described above. Calculations of λ for stochastic models were based on the mean value indicated in the reduced transition matrices, which are in Appendix 3.

Simulations using matrix S2 (Model 1 in Figure 3.4) caused the number of mature plants·m^{-2} to increase exponentially with a λ of 37.3. The first-year mean projected density was 0.03 plants·m^{-2}, rose to 0.75 plants·m^{-2} in the second, and reached 37 plants·m^{-2} by the third. This simulation was very different from the population increase projected from the literature values where the population reached over 1000 by the third year of simulation (Figure 3.2). It was also quite different from the 20 to 60 plants·m^{-2} that were observed in the field two years after disturbance (West and Chilcote 1968, Halpern *et al.* 1997). Due to the stochasticity introduced into the model the mature plant population could be substantially greater, as indicated by the upper confidence interval of one standard deviation generated from the stochastic simulation, or it could become locally extinct in any year.

Model 1 simulation (Figure 3.4) did not account for any of the differences in transition probabilities due to competition treatments. The mid-season survival probability in Experiment 1 (Table 3.4), where there were differences in mid-season survival among the competition treatments, was substituted for e (element $s2_{45}$) in matrix S2 to create a new matrix, S3 (Appendix 3). The three transition probabilities were arranged to reflect the change in associated vegetation over time. It was assumed that the plants grown

without competition (Treatment 1) would most resemble the environment during the first year, *i.e.*, with least associated vegetation and low density of woodland groundsel, and the plant establishment probability used was 0.31. By the second year, the woodland groundsel density was expected to have increased with limited other vegetation, which would most resemble Treatment 2 and 0.25 was used for the probability of *e*. The associated vegetation

Table 3.4. Transition probability for stochastic woodland groundsel population models. Values by treatment are listed where competition treatment affected them. Competition treatments are as follows; (1) 1 plant·m^{-2} with landscape fabric, (2) 9 plants·m^{-2} with landscape fabric, and (3) 9 plants·m^{-2} without landscape fabric. The mean value for the experiment is given where no treatment is indicated (N/A). The variables listed correspond to the transition probabilities from the woodland groundsel conceptual model (Figure 3. 1). The mean and variance of the probabilities are based on the analysis of significant treatment variables using logistic regression with an indicator variable model for the experiments indicated. The specific models in which the transition variables were used are indicated.

Experiment	Competition Treatment	Transition Variable	Mean	Variance	Model
2	N/A	*d*	0.009	0.0005	1, 2, 3
1	1	*e*	0.31	0.033	2, 3
1	2	*e*	0.25	0.027	2, 3
1	3	*e*	0.048	0.007	2, 3
3	N/A	*e*	0.21	0.023	1
1	N/A	*f ′*	0.81	0.006	1, 2, 3
1	N/A	*a*	29800	1.14e+09	1, 2
1	1	*a*	63700	3.43e+09	3
1	2	*a*	27000	9.87e+08	3
1	3	*a*	8750	5.63e+07	3
1	N/A	*b*	0.76	0.018	1, 2, 3
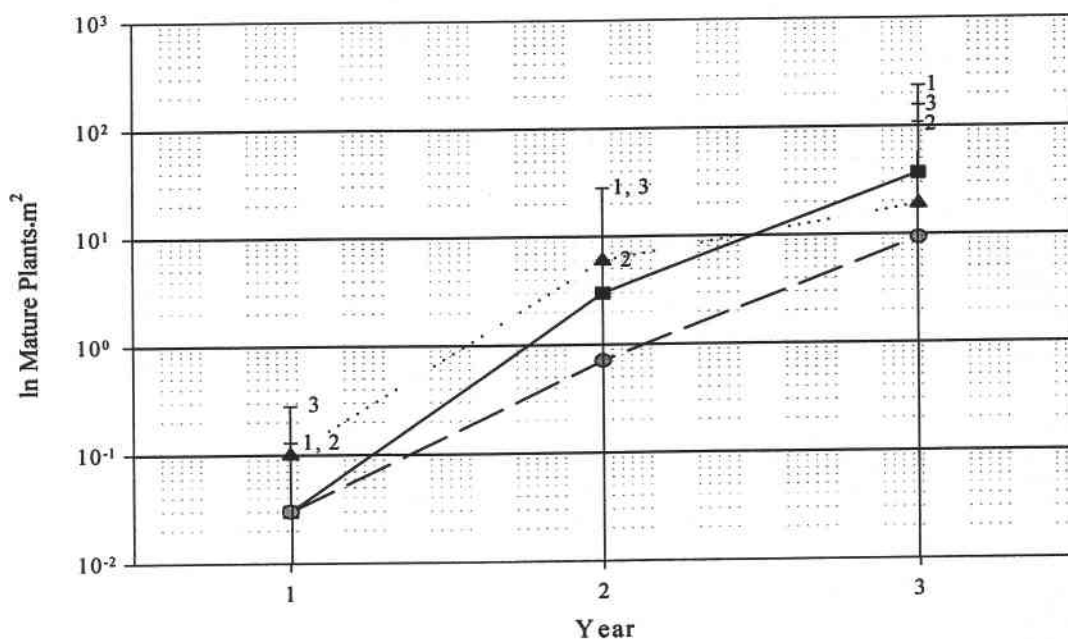
Figure 3.4. Woodland groundsel population projections over three years using stochastic models. Transition probabilities were from the field experiments. Projected mean mature plant density (ln Mature Plants·m^{-2}) is indicated for Models 1 (–■–), 2 (–●–), and 3 (- ▲ -) with the upper confidence limit of one standard deviation represented by a cross-bar on the vertical line with the model number. The confidence limits are the same for Models 1 and 2 in Year 1, and Models 2 and 3 in Year 2. Since the population cannot fall below zero the lower confidence limit is truncated at zero.

could develop substantially in subsequent years and be most similar to Treatment 3 where e was 0.048.

This projection from matrix **S3** (Model 2 in Figure 3.4) resulted in a decrease in the mature plant population growth rate (Figure 3.4). The mean projected density was the same as the previous simulation for the first year, but was only 0.71 plants·m^{-2} in the second and 9.3 plants·m^{-2} in the third year. The λ values for Model 2 were 52.8, 43.6, and 8.7 in years 1, 2, and 3, respectively.

A third modification in the parameters for this model was tested (Model 3 in Figure 3.4). The results of Experiment 1 (Appendix 2) and other studies (Palmbald 1968a, Geyer 1995) demonstrated that woodland groundsel achene production declines with increasing density, but the parameter estimates for this transition probability were not significantly different statistically due to excessive variation within the competition treatments. To simulate these differences, the mean achene production·plant^{-1} (a) for each competition treatment was used in the model in the same order as for plant establishment (Table 3.2). Matrix **S4** used the following values for a (element $s3_{76}$) in matrix **S3**: First-year 44,600 achenes·plant^{-1}, second-year 24,100 achenes·plant^{-1}, and third-year 8,300 achenes·plant^{-1}.

Model 3 created a mature plant population that increased exponentially and resulted in mean mature plant densities that were intermediate between the other two models (Figure 3.4). The λ values were 78.2, 35.2, and 2.4 for Years 1, 2, and 3, respectively. The projected population was greater in this simulation than the other two stochastic ones for the first two years, producing 0.10 mature plants·m^{-2} and 6.0 plants·m^{-2} in Years 1 and 2, respectively, but was lower than the other models in the third year, projecting only 19 plants·m^{-2}.

The stochastic models project exponentially growing woodland groundsel populations (Figure 3.4) as did the literature-based simulations. In these stochastic simulations, where the parameters changed over time, λ declined as time passed. Model 3 had the greatest change in λ and by the third year was projecting the most nearly constant population growth. Stochasticity introduced into the model allowed local extinction of the species to occur in some simulations. It also produced more variation in the population projections than modifying the transition parameters among the three models. The numbers of mature plants projected in the second growing season were at least an order of magnitude lower than what was observed in the field (West and Chilcote 1968, Halpern et al. 1997). Second-year plant density was better simulated by the deterministic literature-based model (Figure 3.2). The empirical germination rate was far lower for the stochastic simulations than the estimated one for the deterministic simulation and probably had a dramatic effect on projected population growth. It may also be that the variance in parameter estimates is lower in newly established populations than in later ones, allowing early populations to increase as the deterministic projection suggests. Over time the environment also may become more heterogeneous, increasing the variability in the population and reducing the population growth rate (Luken 1990).

There are several limitations in the parameter estimates of these models. In any future field study, the number of replicates would have to be increased to compensate for high mortality and to allow the statistical models sufficient power to detect treatment differences in transition probabilities of later growth stages. Several transitions were not assessed in this experiment either through assumption that they were unimportant (e.g., seed rain and post-dispersal mortality) or lack of experimental results (e.g., seedling

survival and establishment). Seed rain and post-dispersal mortality were assumed to be trivial given the size and apparent dispersal pattern of the woodland groundsel seed, but such assumptions should be tested in any future study since much of the population regulation in woodland groundsel is focused on seed production, dispersal, and germination processes. Evaluating losses from the late seed bank through seed predation and germinant disease would improve a critical step in the population model. Seedling survival probabilities were to have been estimated from the result of Experiment 2. Since these data were not available, transplant survival probability was used as an estimate for the transition from seedling to established plant, but it is likely a poor estimate. Although both seedlings and transplants must become established, the processes are different with potentially different success probabilities. The actual seedling establishment rate is probably much lower than the estimate based on the transplant probability, since seedling mortality is high.

The correlation structure of the parameter estimates is another factor to be considered. For example, both seedling establishment probability and seed production declined with increasing competition in Experiment 1 (Table 3.4). The amount of cross-correlation between these estimates would reflect the relative bias of a model containing both of them. Similarly, auto-correlation of a transition probability should be established for each variable across years.

The robustness of the models would also be improved by increased linkage with the environment. Monitoring ambient nitrogen levels through the course of the field experiments would allow explicit consideration of its influence on the population changes over time rather than creating a set of differing initial conditions. Similarly, assessment of temperature differences created by the use of landscape fabric to create varying

vegetation treatments would have eliminated potential confounding between the effects of the vegetation and fabric-induced temperature changes.

Metapopulation dynamics (Husband and Barrett 1996) may be more relevant to understanding the behavior of woodland groundsel populations in early seral forest communities than is its persistence on a given site. Large numbers of seeds can be produced in dense stands of woodland groundsel yet both observations and experiments indicate that the species will not remain in the community at a substantial density. What is the fate of all the seed? Moreover, how does woodland groundsel invade unoccupied areas? It has been demonstrated in this and other studies that woodland groundsel growth is plastic in its response to nitrogen availability and competition (van Andel and Vera 1977, Palmbald 1968a,b, Geyer 1995). Achene morphology is also highly plastic in response to mineral resources. Achene weight decreased as resource availability decreased while the pappus weight was unchanged (van Andel and Vera 1977). This reduced weight could create achenes with a greater potential dispersal distance by increasing the pappus-to-fruit ratio. It has also been observed that the stand density increases dramatically from the first to the second year (West and Chilcote 1968, Halpern *et al.* 1997). These changes in morphology and density could be factors in the rapid decline of woodland groundsel populations. With information about dispersion combined with demographic data a critical patch size could be determined (Latore *et al.* 1998) and used in the population model to determine how much immigration would be required to establish new populations.

Many population dynamics models used for annuals are difference equations (*e.g.*, Watkinson *et al.* 1989, Bonan 1991, Bazzaz *et al.* 1992, Latore *et al.* 1998). Only one study reviewed used a matrix model to simulate an annual population with a seed bank

(Jarry *et al.* 1995). The utility of matrix models increases as the interconnection among life cycle stages increases. The matrix approach also increases the ease with which transition rate can be systematically varied either to represent changes within a year (Maxwell 1990) or with the passage of years as was done in this study. Such flexibility allows the model to respond more closely to changes in environment that affect the population. Matrix models would work well for annuals with differing biotypes, such as the winter- and summer-annual varieties of woodland groundsel, occurring within a population. The three-stage model (seeds, seedlings, and adults) could have a time-step of less than one year, perhaps 3 months, and would easily track changes from one stage to another occurring at different rates at different times of the year. This would necessitate a suite of transition matrices similar to those described by Maxwell (1990). It would, however be simpler, and more congruous than a set of four difference equations creating a similar cycle.

CONCLUSIONS

Nitrogen fertilization did not increase population growth rate or persistence. Increased competition level did reduce individual transition parameters such as seedling establishment and seed production but did not cause a decline in population persistence or growth rate. Demographic stochasticity was more important than variation in either of these environmental factors in affecting woodland groundsel's population dynamics.

LITERATURE CITED

Adams, A. B. and V. H. Dale. 1987. Vegetative succession following glacial and volcanic disturbances in the Cascade Mountain range of Washington, U.S.A. Pages 70-147 *in* D. E. Bilderback, ed. Mount St. Helens 1980: Botanical Consequences of the Explosive Eruptions. Berkeley, CA: University of California Press.

van Andel, J. and F. Vera. 1977. Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. J. Ecol. 65:747-58.

Bazzaz, F. A., D. D. Ackerly, F. I. Woodward, and I. Rochefort. 1992. CO_2 enrichment and dependence of reproduction on density in an annual plant and a simulation of its population dynamics . Journal of Ecology 80:643-51.

Bonan, G. B. 1991. Density effects on the size structure of annual plant populations: An indication of neighbourhood competition. Annals of Botany 68:341-7.

Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. Risk Assessment in Conservation Biology. London: Chapman & Hall. 314 pp.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters . Theor. Popul. Biol. 14:215-30.

Dennis, L. R. J. 1980. Gilkey's Weeds of the Pacific Northwest. Corvallis, OR: Oregon State University Press. 382 pp.

Eriksson, O., J. Ehrlen, A. Telenius, and H. Froborg. 1995. Dynamics and abundance of field layer plants in a deciduous wood at Tullgarn, province of Sodermanland. *Sven. Bot. Tidskr.* 89:91-107.

Ernst, W. H. O. 1985. The effects of forest management on the genetic variability of plant species in the herb layer. Pages 200-11 *in* H. R. Gregorius, ed. Population Genetics in Forestry. Berlin: Springer-Verlag.

Ernst, W. H. O. and H. J. M. Nelissen. 1979. Growth and mineral nutrition of plant species from clearing on different horizons of an iron-humus podzol profile. Oecologia 41:175-82.

Ferson, S. 1991. RAMAS/Stage. Setauket NY: Applied Biomathematics.

Geyer, M. A. 1995. Autecological Studies of Two Annual Herbs, *Senecio sylvaticus* and *Epilobium paniculatum*: Effects of Biotic and Abiotic Factors. M.S. thesis, Corvallis, OR: Oregon State University. 83 pp.

Gholz, H. L., G. M. Hawk, A. Campbell, Jr. K. Cromack, and A. T. Brown. 1985. Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. Can. J. For. Res. 15:400-9.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111:1169-94.

Halpern, C. B., J. A. Antos, M. A. Geyer, and A. M. Olson. 1997. Series replacement during early secondary succession: The abrupt decline of a winter annual. Ecology 78:621-31.

Harper, J. L. 1977. Population Biology of Plants. London: Academic Press. 892 pp.

Hitchcock, C. L. and A. Crosnquist. 1973. Flora of the Pacific Northwest. Seattle, WA: University of Washington Press. 730 pp.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187-211.

Husband, B. C. and S. C. H. Barrett. 1996. A metapopulation perspective in plant population biology. J. Ecol. 84:461-9.

Jarry, M., M. Khaladi, M. Hossaert-McKey, and D. McKey. 1995. Modeling the population dynamics of annual plants with seed bank and density dependent effects. Acta Biotheor 43:53-65.

Jepson, W. L. 1925. A Manual of the Flowering Plants of California. Berkeley, CA: Associated Student Store, University of California. 1238 pp.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427-31.

Latore, J., P. Gould, and A. M. Mortimer. 1998. Spatial dynamics and critical patch size of annual plant populations. J. Theor. Bot. 190:277-85.

Luken, J. O. 1990. Directing Ecological Succession. London: Chapman and Hall. 251 pp.

Maxwell, B. D. 1990. The Population Dynamics and Growth of Salmonberry (*Rubus spectabilis*) and Thimbleberry (*Rubus parviflorus*). Ph.D. thesis, Corvallis, OR: Oregon State Univeristy. 286 pp.

McEvoy, P. B. 1984. Dormancy and dispersal in dimorphic achenes of tansy ragwort, Senecio jacobaea L. (Compositae). Oecologia 61:160-8.

McEvoy, P. B. and C. S. Cox. 1987. Wind dispersal distances in dimorphic achenes of ragwort, *Senecio jacobaea*. Ecology 68:2006-15.

Palmbald, I. G. 1968a. Competition in experimentally regulated populations of weeds with emphasis on the regulation of population size. Ecology 49:26-34.

Palmbald, I. G. 1968b. Comparative response of closely related species to reduced competition. I. *Senecio sylvaticus* and *S. viscosus*. Can. J. Bot. 46:225-8.

Palmbald, I. G. 1966. Experimental Studies on Interference in Weedy Plant Species. Ph.D. thesis, Seattle, WA: University of Washington. 227 pp.

Pojar, J. and A. MacKinnon. 1994. Plants of the Pacific Northwest Coast. Redmond, WA: Lone Pine Publishing. 527 pp.

Poole, A. L. and D. Cairns. 1940. Botanical aspects of ragwort (*Senecio jacobaea* L.). *Bull. N. Z. Sci. Ind. Res.* 82:1-61.

Robbin, W. W., M. K. Bullue, and W. S. Ball. 1951. Weeds of California. Sacramento, CA: Printing Division, State of California. 547 pp.

Sagar, G. R. and A. M. Mortimer. 1976. An approach to the study of the population dynamics of plants with special reference to weeds. Ann. Appl. Bot. 1:1-47.

Salisbury, E. J. 1961. Weeds and Aliens. London: Collins Publishing Co. 384 pp.

Salisbury, E. J. 1942. The Reproductive Capacity of Plants. London: Bell and Sons, Ltd. 244 pp.

SAS Institute, Inc. 1993. SAS Technical Report P-234, SAS/STAT® Software: The GENMOD Procedure, Release 6.09. Cary, NC: SAS Institute, Inc. 88 pp.

SAS Institute, Inc. 1990. SAS/STAT® User's Guide, Version 6. Fourth ed. Volume 2. Cary, NC: SAS Institute, Inc. 846 pp.

Watkinson, A. R., W. M. Lonsdale, and M. H. Andrew. 1989. Modelling the population dynamics of an annual plant *Sorguhm intrans* in the wet-dry tropics. Journal of Ecology 77:162-81.

West, N. E. and W. W. Chilcote. 1968. *Senecio sylvaticus* in relation to Douglas-fir clear-cut succession in the Oregon Coast Range. Ecology 49:1101-7.

CHAPTER 4

Foxglove (*Digitalis purpurea* L.) Populations as Affected by Competition and Nitrogen

ABSTRACT

Foxglove is an introduced semalparous perennial found throughout coastal forests of the Pacific Northwest. The species often dominates disturbed sites for several years. Models developed from literature data and field experiments were used to project changes in foxglove populations over time. Three experiments were conducted to test the effects of nitrogen fertilization and competition on survival, growth, and development of the species. The experiments included assessments of growth and development from seeds and transplants. The experiments demonstrated that foxglove was susceptible to competition and nitrogen fertilization enhanced that effect. Deterministic models based on literature data only projected exponentially increasing foxglove populations. However, two forms of a stochastic model projected (1) the population becoming locally extinct within a few years and (2) a steadily increasing population. The primary difference between the two stochastic simulations was the probability of mature plant persistence into subsequent generations. Further investigation of the factors affecting mature plant persistence and germination from buried seed banks is recommended to understand population regulation in this species better.

INTRODUCTION

Foxglove (*Digitalis purpurea* L. **DIKPU**) is a commonly studied species in biennial population dynamics research. It was one of the biennials evaluated by Sagar and Mortimer (1976) in their discussion of plant population modeling methods. This work was extended by van Baalen and Prins (1983) who modeled foxglove populations in various seral stages of European forests. Harper (1977) describes density dependent effects on growth and reproduction using work on foxglove by Oxley (unpublished data) that indicates reduced flowering with increased plant density. This study assesses how some life history characteristics, *e.g.*, facultative iteroparity, and variation in environmental conditions, *i.e.*, nitrogen fertilization and competition, affect foxglove's population dynamics as well as the effects of demographic stochasticity.

Foxglove is a plant native to European woodland clearings that was introduced to the West Coast of the United States as an ornamental and medicinal plant and later escaped cultivation (Dennis 1980). It is now well-established west of the Cascade Mountains (Hitchcock and Cronquist 1973) and is one of the most important exotic species in Pacific Northwest forests because of its rapid spread (Isaac 1940). Foxglove dominates disturbed areas for several years, "its rank growth crowding out the natural forage plants" (Dennis 1980), but is not persistent in a competitive environment (Hill 1989). Commonly found in areas of intermittent disturbance, *e.g.*, clearcuts, windthrown trees, and burns (Oberdorfer 1973, Salisbury 1942), it may become a management problem because of its persistent seed bank (Hill 1978). Cardiac glycosides, which have important medicinal value (Withering 1776, Pojar and MacKinnon 1994), also make foxglove toxic to humans

and livestock (Hill 1989, Dennis 1980, Pojar and MacKinnon 1994), but poisonings from foxglove are uncommon (Connor 1977, Isaac 1940, Robbins *et al.* 1951).

Description and Life History

Foxglove is a semalparous to iteroparous perennial (Silvertown 1984, van Baalen and Prins 1983) with an erect stem up to 2 m tall and a one-sided raceme of purple to white flowers (Pojar and MacKinnon 1994). The leaves are ovate to lanceolate and pubescent (Munz 1968, Hitchcock and Cronquist 1973, Pojar and MacKinnon 1994). Foxglove can germinate in either fall or spring but seedling survival is greatest for fall germinants (van Baalen 1982). Fall seedlings overwinter the first year, forming rosettes that overwinter a second year. Plants usually flower after a second year of vernalization (Yaniv 1985). A minimum size is necessary for vernalization (Chouard 1951 as cited in Klinkhamer *et al.* 1987), which is common in semalparous perennials (Klinkhamer *et al.* 1987). Foxglove flowers during June and July.

Seeds are dispersed by passive autochory[1] dehiscing from egg-shaped fruits as they ripen from late July through fall (van Baalen 1982) with a distribution distance pattern that is presumed to be similar to common mullen (*Verbascum thapsus* (*cf* Salisbury 1961), an associated species having a bell-shaped seed distribution pattern with a mean dispersal distance of about 4 m. A single foxglove plant can produce up to 500,000 seeds but average seed production is approximately 85,000 seeds·plant[-1] (Salisbury 1942). Reproduction can be reduced further by competition. In early- to mid-seral forest

---

[1] A dispersal mechanism that relies on the parent plant for dispersal as opposed to external forces such as wind or animals and without specialized mechanisms.

communities[2], foxglove plants produced about 12,000 seeds·m^{-2} (van Baalen and Prins 1983). In a late-seral forest community, with an extensive tree canopy, seed production dropped to between 1000 and 6000 seeds·m^{-2}.

Foxglove germination depends on several environmental factors: light, soil contact, soil moisture, and ambient temperature. Seed germination rates decline in response to both decreased light quality and quantity (van Baalen 1982, Bliss and Smith 1985). In the laboratory, van Baalen (1982) demonstrated that fewer seeds germinated under reduced light quantity and quality when in contact with soil than on moist blotter paper. The most seed germinated after adding 50 to 75 ml of water to 23 g (ca. 150 ml) of soil (van Baalen 1982). Germination decreased as the soil became either more xeric or hydric. Germination was unaffected by stratification but was sensitive to temperature (van Baalen *et al.* 1984), increasing from 40% at 10°C to 100% 35°C (van Baalen 1982, Bliss and Smith 1985). The innate fungus *Alternaria alternata* ([Fries] Keissler), found on seeds from ripe but unopened capsules, may be involved in breaking innate dormancy (Jacobsohn and Jacobsohn 1985).

The buried seed bank is vital in establishing foxglove after disturbance. For example, van Baalen and Prins (1983) found a seed bank in the Netherlands had 160 seeds·m^{-2}; 25% of those germinated after soil-mixing. Germinants emerged from disturbed soil cores obtained from foxglove stands (van Baalen 1982). Although the number of germinants declined over time, numerous seeds remained dormant in the soil after three disturbances. A buried seed bank in northern Wales contained more than 4000 foxglove

---

[2]Seral descriptions relate to succession of the herb/shrub community.

seeds·m^{-2} with germination ranging from 3 to 22% (Hill and Stevens 1981). Three years after clearcutting, this seed bank had a density of nearly 5000 seeds·m^{-2}. Seeds retrieved after two years of burial lost no viability (van Baalen 1982).

Foxglove is sensitive to interspecific competition, especially for light (van Baalen and Prins 1983, van Baalen *et al.* 1984). This can affect its reproductive output and, therefore, establishment of the next generation. When growing under a forest canopy, foxglove flowering and seed production decreased by an order of magnitude compared with an open-grown population. Seed germination decreased by six orders of magnitude in the same comparison (van Baalen and Prins 1983). Under competitive conditions, rosette dry weight and seed production decreased and secondary rosettes were not produced (van Baalen and Prins 1983).

Foxglove often dominates a site, then becomes locally extinct, although generally on a longer time scale than its associate, woodland groundsel (*Senecio sylvaticus* L.) (van Andel and Ernst 1985). After germination following disturbance (Salisbury 1942, van Baalen and Prins 1983), an additional generation is produced from seed. This population is maintained thereafter by producing secondary rosettes (van Baalen and Prins 1983) but that production declines over time. Following clearcutting in a Welsh forest, foxglove cover declined from 25% after two years to 8.8% in the fourth growing season (Hill and Stevens 1981).

Although not dominant, it also can be found in more advanced seral stages, such as in Oregon riparian red alder (*Alnus rubra* Bong.) communities, where it is maintained by minor disturbance (Henderson 1970). Foxglove has been found in stands of 4- to 16-year-old red alder and appeared again in 35- to 39- and 64-year-old stands of that species

(Henderson 1970). Even after catastrophic disturbances, such as the eruption of Mount St. Helens, foxglove has been found in debris flows, mud slides, and areas with blown-down or scorched trees (Adams and Dale 1987).

Study Objectives

This study explored the factors affecting foxglove's population dynamics. Its objectives were to:

1) assess the impact of nitrogen fertilization and competition on foxglove population dynamics,

2) orchestrate the available information about foxglove population dynamics into a model, which was parameterized with data from field experiments, and compare the results with other models for the species, and

3) determine how unique aspects of foxglove's life cycle affect population its, *e.g.*, whether lack of buried seed bank germination causes population decline and facultative iteroparity maintains it.

Nitrogen fertilization was predicted to increase reproductive output and increase both the growth rate and persistence of the foxglove population. Added levels of competition, on the other hand, were expected to reduce the population's persistence through a negative growth rate resulting in more rapid local extinction. As with woodland groundsel, environmental variation was projected to have a greater influence on population growth rates than demographic stochasticity. Populations were anticipated to deline without germination from the buried seed bank compared to simulations with it. Therefore, facultative iteroparity was expected to be vital to maintaining the populations.

This study was divided into three sections. A population model was developed from literature data as a framework for standardizing comparisons within this species and among others, then field experiments were used to determine the effects of competition and nitrogen fertilization on both plant and population development. Stochastic population models responsive to nitrogen level and competition were then constructed and simulations conducted to determine their effects on foxglove populations.

METHODS AND MATERIALS

Deterministic Population Models

This study used the same methods for modeling foxglove population development as for woodland groundsel (Chapter 3). The conceptual population model for foxglove had three stages; mature plants (A), immature plants (R), and buried seed bank ($D2$) (Figure 4.1). The persistent buried seed bank ($D2$) acted as a sink for seed production because there is no germination from it without disturbance (van Andel and Ernst 1985). Foxglove can sometimes be an iteroparous perennial (van Baalen and Prins 1983, Klinkhamer *et al.* 1987b), which the model (Figure 4.1) accommodated through mature plant persistence ($a*$ and a'). All state variable and transition rate values for this model were obtained from the literature and are shown in Table 4.1. Many of the state variables listed in Table 1 were not included in the conceptual model because they represent changes that occur within a year rather than between years. Transition rates for such variables were multiplied together to create compound transition rates (Figure 4.1).

Foxglove's perennial life history had more transition rates than did the annual woodland groundsel (Chapter 3). Among these transitions, second-year survival was
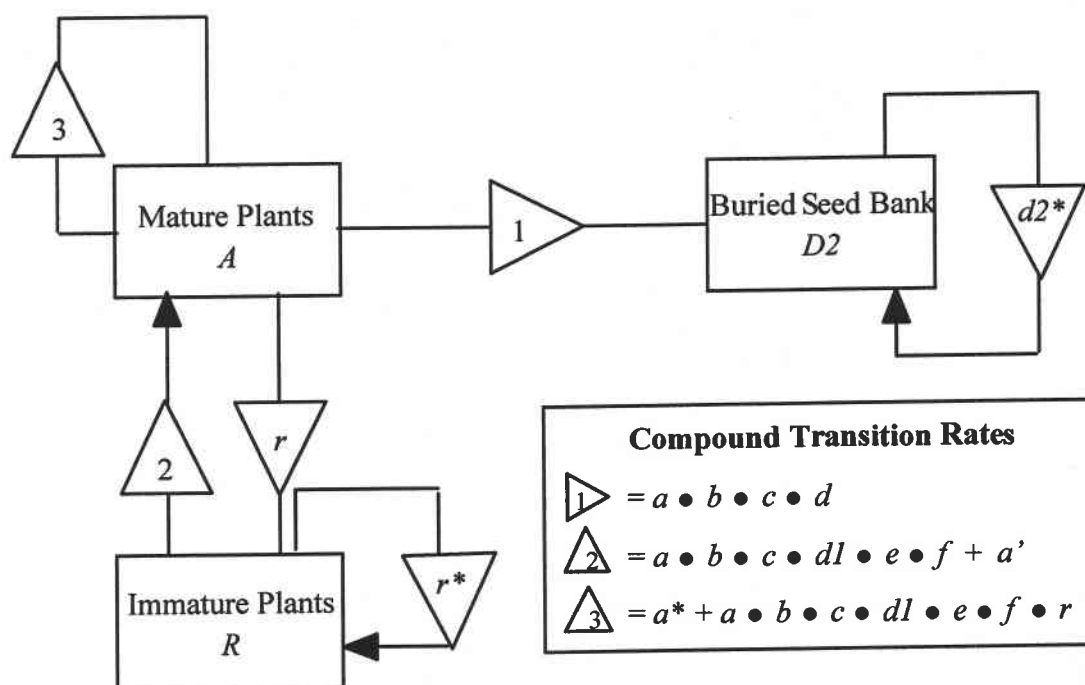
Figure 4.1. Conceptual population model for foxglove. State variables (boxes) and transition rates (triangles) were estimated from the literature (Table 4.1). Their abbreviations (or those for the equation components) also are in Table 4.1. Equations 1, 2, and 3 were used to aggregate transition rates for state variables not included in the model.

Table 4.1. State variable and transition rate values for foxglove obtained from the literature. All state variable are number·m⁻². Transition rates are ·year⁻¹ ; seed production (*a*) is number·plant⁻¹·year⁻¹ .

State	Value	Transition	Rate	Reference
Immigration (*G*)	0	NA	N/A	van Baalen 1982
Early seed bank (*C*)	28,800	Post-dispersal survival (*c*)	13%	Sagar & Mortimer 1976
	237,000		70%	van Baalen 1982
Late seed bank (*D1*)	167,000	SSB germination (*d1*)	65%	van Baalen 1982
	------		0.05%	van Baalen 1982
Buried seed bank (*D2*)	58,700	Seed incorporation (*d*)	35%	van Baalen 1982
	138,000		------	van Baalen 1982
	4,250	BSB persistence (*d2**)	100%	Hill & Stevens 1981
	4,900	BSB germination (*d2*)	3%	Hill & Stevens 1981
Seedlings (*E*)	115	Seedling establishment (*e*)	0.6%	Sagar & Mortimer 1976
	108,600		------	van Baalen 1982
	47		------	van Baalen 1982
	126		------	Hill & Stevens 1981
Established plants (*F*)	0.7	Mid-season survival (*f*)	100%	Sagar & Mortimer 1976
	------		75%	van Baalen 1982
Immature plants (*R*)	10.4	Flowering (*r*)	25%	van Baalen 1982
	------	Rosette persistence (*r**)	22%	Hill & Stevens 1981
Mature plants (*A*)	4.2	Iteroparity (*a**)	33%	Sagar & Mortimer 1976
	10.7	Seed production (*a*)	16,800	Sagar & Mortimer 1976
	7.8		41,700	van Baalen 1982
	2.9		32,600	van Baalen 1982
	------		85,500	Salisbury 1942
	------	Perenniation (*a*′)	N/A	N/A
Seeds (*B*)	180,000	Seed viability (b)	16%	Sagar & Mortimer 1976
	325,000		73%	van Baalen 1982
	95,000		------	van Baalen 1982

structured to accommodate foxglove's facultatively iteroparous perennial life cycle, and was divided into three categories: rosettes, flowering plants, and perennials. In this study, rosettes are defined as plants that are two-growing-seasons-old but still immature.

Persistence of the same rosettes from year to year can be difficult to distinguish from simple vegetative reproduction unless senescence of the preceding rosette is observed. The population was not separated by rosette age but both rosette types were considered as persistent for the model. Flowering plants reproduced sexually in their second growing season but showed no indication of further longevity (*i.e.*, producing more rosettes), thus typifying a biennial (Silvertown 1984). Perennial plants flowered, usually during their second year, and demonstrated a capacity to do so again. These plants could either flower or produce rosettes in the subsequent year, some of which may flower the following year. Rosette production by perennial plants was called 'perenniation' in this study to distinguish it from iteroparity (*i.e.*, sexual reproduction occurring more than once).

The transition rates for the foxglove population model from Table 4.1 were combined, using the equations in Figure 4.1, into matrix **D**:

$$\mathbf{D} = \begin{pmatrix} 1 & 0 & 31961 \\ 0 & 0.0546 & 0.13 \\ 0 & 0.9 & 1.967 \end{pmatrix} \tag{21}$$

The rows (from left to right) and columns (from top to bottom) in **D** are for buried seed bank, immature, and mature transitions, respectively. To simulate foxglove's limited germination window, no germination occurred in the transition matrix but was accounted for in the population vector $\mathbf{n}_t$:

$$\mathbf{n}_t = \begin{pmatrix} 0 \\ 1.3 \\ 0.09 \end{pmatrix} \tag{22}$$

(where t = 1), which represented population levels one year after disturbance. This hypothetical population was immigrating so no seed occurred in the buried seed bank (element one of n_t). Initial immature and mature plant densities were 1.3 and 0.09 plants·m^{-2}, respectively. Population projections from this model were analyzed as described for the reduced models in Chapter 3, except that only a submatrix (elements d_{22} to d_{33}) of the transition matrix **D** was analyzed because only these elements influenced the behavior of the extant population. Sensitivity (Caswell 1978) and elasticity analyses (de Kroon 1986) were also conducted on this submatrix using RAMAS/Stage (Ferson 1991).

Field Experiments

The field experiments to test the effects of nitrogen fertilizer and competition on foxglove development were similar to those described in Chapter 3. The same nitrogen levels of 0, 62.5, and 125 kg·ha^{-1} and competition treatments 1, 2, and 3 were used (see Chapter 3, page 81 for complete treatment descriptions). Experiment 1, established in Winter 1993, examined survival and growth of foxglove from transplants, including plant height, canopy diameter, and development status (see Chapter 3, page 82). These variables were evaluated in June 1993. Reproductive variables (such as seeds·plant^{-1}, seeds·m^{-2}, individual seed weight, seed viability, and plant biomass) and transition probabilities among life history stages were determined. Unlike woodland groundsel (Chapter 3), plant harvest in Experiment 1 was delayed until August 1994 to allow for seed production. Experiment 2 examined how foxglove population development from seed differed from that of transplants. Established in December 1994, it was evaluated in January and February 1995 for seed germination and seedling survival. Experiment 3 studied long-term

treatment effects on plant size and survival. Plants in Experiment 3 were transplanted in Spring 1992, assessed for survival, growth, and reproduction in June of 1992, 1993, and 1994 (Years 1, 2, and 3, respectively), then harvested in August 1994.

Statistical analysis was conducted as in Chapter 3. Continuous variables were tested by analysis of variance and means separated with Fischer's LSD. All plant size data in Experiment 1 required log transformation; seed number (per plant) was square-root transformed. In Experiment 3, data was log-transformed for the following variables: height and canopy diameter (Year 2), root biomass, shoot biomass, and seed number (both·plant^{-1} and ·m^{-2}). Logistic regression with an indicator variable model (analysis of deviance) was used for binomial data. Where analysis of deviance indicated significant main effects from nitrogen level and competition treatment, but with no interaction, the results are presented for each treatment combination. This is done because the model parameters for the treatments are not orthogonal with analysis of deviance, unlike in analysis of variance. In the case where both main effects are significant, each transition probability was dependent on an estimated parameter for the individual nitrogen level and competition treatment but not for the interactions of levels and treatments.

Stochastic Population Models

Transition rates for the foxglove model (Figure 4.1, Table 4.1) were modified, based on the results of the field experiments, to create stochastic models responsive to nitrogen level and competition. Populations were projected with several sets of matrices. Because some transition rates responded to nitrogen level, a separate matrix for each nitrogen level in Experiment 1 and Experiment 3 was created. In Experiment 1, the

probabilities from the competition treatments arranged as described for woodland groundsel (Chapter 3). Germination probability from Experiment 2 was used in all simulations. Data from Experiment 3 was used to test two sets of transition probabilities by varying rosette persistence and flowering probability between arranged competition and actual transition probabilities in the matrices for Year 2 and Years 3 (Appendix 3). The projections of the two sets of matrices from Experiment 3 were compared. Population projections were made and the models were analyzed in the same manner as for the deterministic model. It should be noted, however, that RAMAS/Stage computes eigenvalues and eigenvectors for stochastic models using only the mean transition value, which are used to derive λ, sensitivities, and elasticities, hence variability in these transition rates is not accounted for in the analysis.

RESULTS AND DISCUSSION

Deterministic Population Models

Eigen analysis was used to determine the properties of the foxglove population represented by matrix **D**. A dominant eigenvalue (λ) of 2.02 indicated that the simulated population will increase exponentially (Caswell 1989). Sensitivity analysis showed that the model submatrix would be most responsive to changes in the iteroparity rate (a^*; sensitivity index: 0.97) and elasticity analysis indicated the same (elasticity index: 0.94).

The increase in projected population density agreed with the analytical λ and was relatively near values observed in the field (Figure 4.2). The projected mature and immature plant populations increased exponentially reaching densities of 22 and 1.5 seeds·m^{-2} plants·m^{-2}, respectively, after four years. The buried seed bank density was
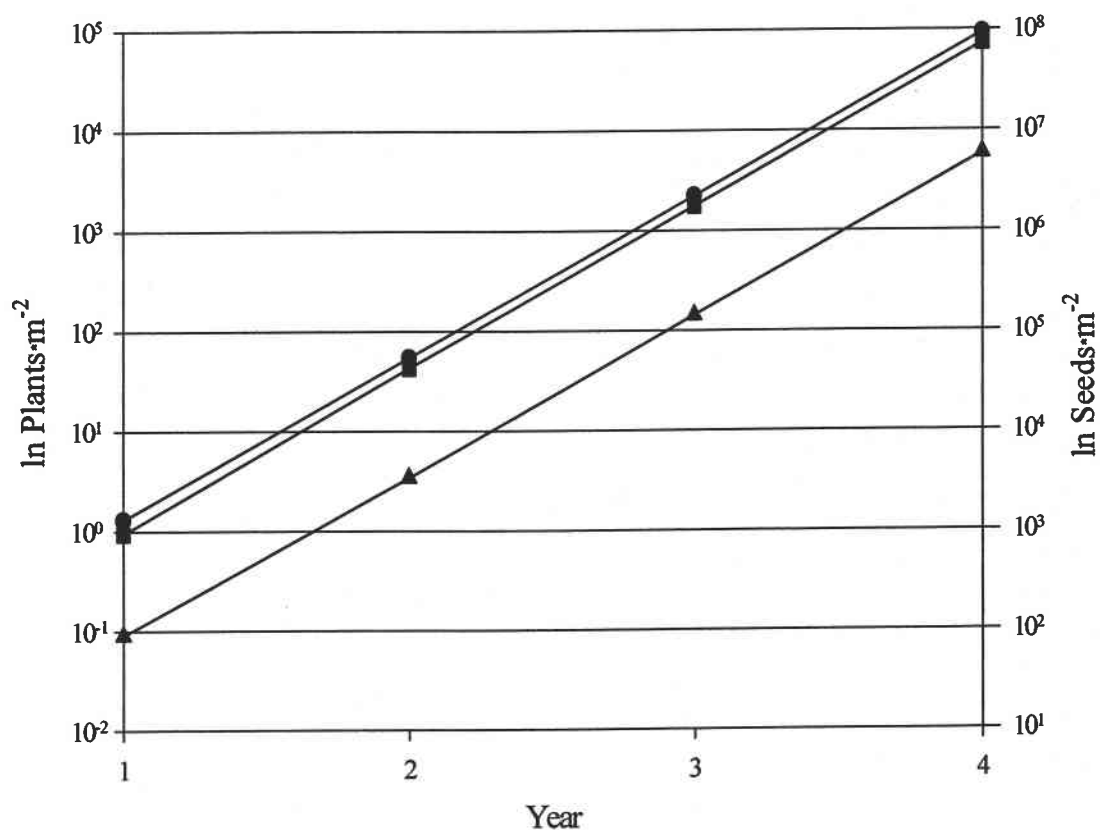
Figure 4.2. Foxglove population change over four years simulated by a deterministic population model. Mature and immature plant density [ln(plants·m⁻²] are represented by (—●— and –▲–, respectively). Buried seed bank density [ln(seeds·m⁻²)] is represented (–■–).

644,000 by the end of the simulation. Eliminating the possibility for germination from the buried seed bank, which does not occur without a disturbance (van Andel and Ernst 1985), restricted foxglove population growth in this model. Furthermore, this analysis demonstrated the importance of facultative iteroparity for persistence of foxglove in the plant community; without it, the population would become locally extinct after two or three years.

Field Experiments

Experiment 1: Survival and Growth of Transplanted Foxglove

Foxglove size and biomass were affected by nitrogen level and competition treatment in Experiment 1 (Table 4.2). Plant height and canopy diameter decreased in Treatments 2 and 3 [9 plants·m^{-2} with and without landscape fabric, respectively (see Chapter 3, page 81)] relative to Treatment 1 (1 plant·m^{-2} with landscape fabric; $P = 0.0001$). Treatment 3 reduced plant height and canopy diameter relative to Treatment 2 as well. Nitrogen fertilization did not affect foxglove height or canopy diameter ($P > 0.75$).

Plant biomass was similarly affected by competition treatment (Table 4.2). Both shoot and root biomass decreased for plants in Treatment 3 relative to those in Treatments 2 and 1 ($P = 0.0001$). Plants in Treatment 1 had greater root and shoot biomass than those in Treatment 2. Nitrogen level also affected shoot and root biomass, which was less following the application of 62 kg·ha^{-1} nitrogen relative to 125 kg·ha^{-1} nitrogen or no addition. There were no interactions between nitrogen level and competition treatment for any variable ($P > 0.08$) Individual seed wight was lower for plants in Treatment 2 relative

Table 4.2. Foxglove size, biomass, and seed production as affected by nitrogen fertilization and competition treatment in Experiments 1 and 3. Competition treatments were; (1) 1 plant·m^{-2} with landscape fabric, (2) 9 plants·m^{-2} with landscape fabric, and (3) 9 plants·m^{-2} without landscape fabric. Analysis of variance was conducted on log-transformed data except for seed production·plant^{-1} in Experiment 1, which was square root-transformed, and height and canopy diameter in Years 1 and 3, which did not require transformation. Mean separation was conducted with Fisher's protected LSD (P = 0.05). Back-transformed values are presented with those having the same letter not differing from one another. Untransformed plot means are presented where no differences were found.

Experiment	Variable		Nitrogen Fertilizer (kg·ha^{-1})			Competition Treatment #		
			0	62.5	125	1	2	3
1	Height (cm)		9.2 a	9.4 a	8.8 a	11.8 a	9.3 b	5.3 c
	Canopy diameter (cm)		11.9 a	11.4 a	10.7 a	16.1 a	11.5 b	5.4 c
	Root biomass (g)		2.3 a	1.1 b	2.0 a	6.3 a	2.4 b	0.4 c
	Shoot biomass (g)		15.1 a	7.6 b	14.8 a	52.2 a	16.3 b	2.6 c
	Seeds·plant^{-1}		77,300 a	68400 a	71,000 a	153,000 a	46,700 b	31,700 b
	Seeds·m^{-2}		230,000 a	217,000 a	138,000 a	185,000 a	245,000 a	61,600 b
	Seed biomass (mg·seed^{-1})		0.072 a	0.073 a	0.075 a	0.077 a	0.071 b	0.074 b
3	Height (cm)	Year 1	5.2 a	7.5 a	7.0 a	5.8 a	8.2 a	5.7 a
		Year 2	---------------------------------See Table 4.4---------------------------------					
		Year 3	83.7 a	63.1 a	57.8 a	118.8 a	64.6 b	48.4 b
	Canopy diameter (cm)	Year 1	6.5 a	10.5 a	10.1 a	8.4 a	11.5 a	7.1 a
		Year 2	18.4 a	18.1 a	14.2 a	22.2 a	13.3 b	12.2 b
		Year 3	19.8 a	15.6 a	16.9 a	27.0 a	16.8 b	13.4 b
	Root biomass (g)		3.6 a	3.0 a	5.2 a	6.6 a	2.8 b	1.5 b
	Shoot biomass (g)		30.2 a	14.5 a	20.5 a	42.2 a	11.8 b	4.9 b
	Seeds·plant^{-1}		21,900 a	11,200 a	19,200 a	49,000 a	15,400 b	10,000 b
	Seeds·m^{-2}		163,000 a	157,000 a	87,000 a	134,000 a	190,000 a	40,000 b
	Seed biomass (mg·seed^{-1})		0.064 a	0.048 a	0.054 a	0.071 a	0.054 a	0.051 a

to those in Treatment 1 but did not differ from seed weight of plants in Treatment 3 (P = 0.042). Plants grown in Treatment 3 produced fewer seeds·m^{-2} than those in either of the other competition treatments (P = 0.0015). Nitrogen fertilization had no effect on seed production and there also were no interactions between nitrogen level and competition treatment for seed production.

Experiment 2: Survival and Growth of Foxglove from Seeds

As occurred with woodland groundsel (Chapter 3), germination of foxglove seed in the field was poor. Nevertheless, both nitrogen level and competition treatment affected germination parameter estimates in Experiment 2 (P = 0.016 and 0.019, respectively) but without enough response to estimate the parameters for the interaction between the levels and treatments. Germination probability (*d1* in Figure 4.1) was greater with 125 kg·ha^{-1} nitrogen fertilizer than with no addition but was not different from the 62.5 kg·ha^{-1} level (Table 4.3). The probability of seeds germinating was greater in Treatment 1 than in Treatments 2 and 3, which did not differ from each other. None of the seedlings that emerged became established rosettes. Therefore, the probability of establishment could not be assessed and size, biomass, or reproduction data were not collected.

Two years later, in Summer 1996, foxglove rosettes were observed growing on some of the seeded plots. Some foxglove seed apparently requires more than one year to break dormancy in the field. This observation was similar to that of van Baalen (1982) in a laboratory experiment.

The treatment effects on germination are difficult to explain. The highest rate of added nitrogen may increase germination by stimulating growth of the *Alternaria* fungus,

Table 4.3. Transition probabilities (ŷ) and variances (s²) for stochastic foxglove population models. Transition probabilities abbreviations are defined in Table 4.1. Competition levels were: (1) 1 plant·m⁻² with landscape fabric, (2) 9 plants·m⁻² with landscape fabric, and (3) 9 plants·m⁻² without landscape fabric. N/A indicates a nitrogen level that had no effect and, when in the probability and variance of Treatments 2 and 3, indicates no competition treatment effects on probability. Transition probabilities from Year 2 of the Experiment 3 are designated by *(y2)* while those from Year 3 are denoted by *(y3)*. Probabilities were separated by comparing 95% confidence intervals and those with the same letter did not differ. Differences in competition treatment are represented by (a) and (b) while nitrogen level differences are indicated by (y) and (z). Decimal places for seed production (*a*) are indicated by (K) thousands, (M) millions, and (G) billions. The variance was only used in the stochastic simulations.

| | | | Competition Treatment # | | | | | |
| | | Fertilizer | 1 | | 2 | | 3 | |
Expt	Transition	(kg·ha⁻¹)	ŷ	s²	ŷ	s²	ŷ	s²
1	*f*	N/A	0.77 ab	0.04	0.69 a	0.05	0.50 b	0.06
3	*f*	0	0.94 ab y	0.05	0.99 a y	0.01	0.86 b y	0.10
	f	62.5	0.88 ab yz	0.09	0.98 a yz	0.02	0.73 b yz	0.17
	f	125	0.71 ab z	0.17	0.94 a z	0.05	0.48 b z	0.21
1	*r**	0	0.11 a y	0.04	0.14 a y	0.03	0.89 b y	0.03
	*r**	62.5	0.21 a z	0.06	0.26 a z	0.05	0.95 b z	0.01
	*r**	125	0.18 a z	0.04	0.23 a z	0.05	0.94 b z	0.02
3	*r** *(y2)*	0	0.27 y	0.03	N/A	N/A	N/A	N/A
	*r** *(y2)*	62.5	0.11 z	0.01	N/A	N/A	N/A	N/A
	*r** *(y2)*	125	0.04 z	0.01	N/A	N/A	N/A	N/A
3	*r** *(y3)*	N/A	0.18	0.01	N/A	N/A	N/A	N/A
1	*r*	0	0.48 a y	0.08	0.40 a y	0.06	0.06 b y	0.01
	r	62.5	0.54 a z	0.08	0.46 a z	0.06	0.07 b z	0.02
	r	125	0.57 a z	0.06	0.49 a z	0.06	0.08 b z	0.02

Table 4.3 Cont. Transition probabilities ($\hat{y}$) and variances (s^2) for stochastic foxglove population models.

		Nitrogen Fertilizer (kg·ha⁻¹)	Competition Treatment #					
			1		2		3	
Expt	Transition		$\hat{y}$	s^2	$\hat{y}$	s^2	$\hat{y}$	s^2
3	r (y2)	N/A	0.35 ab	0.10	0.61 a	0.10	0.30 b	0.09
3	r (y3)	N/A	0.65	0.03	N/A	N/A	N/A	N/A
1	a*	N/A	0.01	N/A	N/A	N/A	N/A	N/A
3	a*	N/A	0.17	0.01	N/A	N/A	N/A	N/A
1	a	N/A	185K a	20G	59K b	1G	35K b	36M
3	a	N/A	64K a	3G	32K a	550M	12K b	6M
1	a′	0	0.44 a y	0.08	0.48 a y	0.06	0.02 b y	0.004
	a′	62.5	0.24 a z	0.06	0.27 a z	0.05	0.01 b z	0.002
	a′	125	0.24 a z	0.04	0.27 a z	0.05	0.01 b z	0.002
3	a′	N/A	0.09	0.01	N/A	N/A	N/A	N/A
1	b	N/A	0.76	0.01	N/A	N/A	N/A	N/A
3	b	N/A	0.92 a	0.08	0.58 b	0.13	0.53 b	0.21
2	d1	0	0.01 a y	0.003	0.001 b y	0.001	0.001 b y	0.0004
	d1	62.5	0.03 a yz	0.02	0.007 b yz	0.003	0.01 b yz	0.002
	d1	125	0.05 a z	0.02	0.01 b z	0.005	0.01 b z	0.003

a member of the order Moniliaceae, that demonstrates increased growth with mineral fertilization (Guillemat and Montégut 1960). The response of germination to competition manipulation (via landscape fabric) is also perplexing because at the time of germination no associated vegetation was present on the plots. Germination may have increased because the black landscape fabric used to control the development of associated vegetation increased soil temperatures. Foxglove germination is stimulated by higher temperatures (van Baalen *et al.* 1984).

Experiment Three: Regeneration of Planted Foxglove

In Experiment 3, foxglove size and biomass responded more to competition manipulation than to nitrogen fertilization (Table 4.2). None of the variables assessed responded to nitrogen level in any year ($P > 0.11$) except for second year plant height, which interacted with competition treatment and is discussed below. Height and canopy diameter were not affected by competition manipulation in Year 1 of the experiment ($P > 0.15$) but were affected by it in subsequent years. Canopy diameter of plants growing under Treatment 1 was greater than those growing in Treatments 2 and 3 for both Years 2 and 3 ($P = 0.0058$, 0.015, 0.017, and 0.031, respectively). Plant height in Treatment 1 was greater than in Treatments 2 and 3 in Year 3 ($P = 0.0056$). Both root and shoot biomass also were greater for plants in Treatment 1 than those in Treatments 2 and 3 ($P = 0.022$ and 0.038, respectively). There were no differences in plant size or biomass between Treatments 2 and 3 in any year except as described below.

An interaction between nitrogen level and competition treatment was observed for second-year height (Table 4.4). Height was greatest for foxglove plants grown in

Table 4.4. Second-year foxglove height (cm) affected by an interaction between nitrogen fertilization level and competition treatment in Experiment 3. Competition levels were; (1) 1 plant·m^{-2} with landscape fabric, (2) 9 plants·m^{-2} with landscape fabric, and (3) 9 plants·m^{-2} without landscape fabric. Analysis of variance was conducted on log-transformed data. Mean separation was conducted using least square means (P = 0.05), with comparisons made among all treatment combinations. Back-transformed values are presented; those with the same letter did not differ from one another.

Nitrogen Fertilizer	Plant Height (cm) by Competition Treatment		
(kg·ha^{-1})	1	2	3
0	17.0 e	40.2 cd	49.9 bcd
62.5	138.9 a	88.8 ab	26.8 de
125	136.0 a	86.7 ab	70.2 bc

Treatments 1 and 2 and receiving nitrogen fertilizer (P = 0.001). Plants in Treatment 3 fertilized with 125 kg·ha^{-1} nitrogen did not differ in height from those that were unfertilized in that treatment, or from plants in Treatment 2 regardless of fertilization level. Plants fertilized with 62.5 kg·ha^{-1} nitrogen in Treatment 3 did not differ in height from unfertilized plants in any competition treatment. Unfertilized plants in Treatment 1 were shorter than all other treatment/level combinations except those receiving 62.5 kg·ha^{-1} nitrogen in Treatment 3. No other interactions were detected in the other size or biomass data (P > 0.075).

Nitrogen level and competition treatment effects on foxglove seed production in Experiment 3 were similar to those on plant size (Table 4.2). Nitrogen fertilizer did not affect seed production·plant^{-1}, individual seed biomass, or seed production·m^{-2} (P > 0.11). Likewise, there were no differences in individual seed weight among the competition treatments (P > 0.10). Seed production·plant^{-1} was greater for plants in Treatment 1 than

those in either Treatment 2 or 3 (P = 0.036). There were no differences in seeds·plant^{-1} between competition Treatments 2 and 3. In contrast, seed production·m^{-2} decreased with interspecific competition (Treatment 3) relative to plants grown alone and those with intraspecific competition (Treatments 1 and 2; P = 0.0007). No differences were found between these latter two treatments. There was no interaction between nitrogen level and competition treatment for seed production (P > 0.16).

Foxglove size did not respond to treatment in this experiment during Year 1, whereas it did in Experiment 1. This difference may have been caused by the timing of planting relative to fertilization. In Experiment 3, planting was done immediately after fertilization and the nitrogen may have been more accessible to the foxglove. Experiment 1 had a one-year delay between fertilization and planting. The extra nitrogen may have ameliorated any first-year competitive effects in Experiment 3 that were observed in Experiment 1. In Year 2, more analogous to Experiment 1 from a fertility standpoint, treatment responses were detected in Experiment 3. Competition for light may have stimulated height growth, which is a common response (Radosevich *et al.* 1997), without added nitrogen. Interspecific competition (Treatment 3) reduced height growth relative to the other two competition treatments with 62.5 kg·ha^{-1} of nitrogen. With 125 kg·ha^{-1} added nitrogen, this reduction in height growth occurred only between plants without competition (Treatment 1) and those with interspecific competition (Treatment 3). This result could have occurred through the same means as discussed for Experiment 1 where the intermediate nitrogen level stimulated competitors more than the foxglove, with the highest level of nitrogen compensating for that effect. The negative effects of both inter- and

intraspecific competition on plant size and biomass in Years 2 and 3, as well as on seed production, further confirm foxglove's poor competitive ability.

Stochastic Population Models

Foxglove mid-season survival parameter estimates in Experiment 1 were affected by competition treatments but not by nitrogen fertilizer levels (P = 0.0080 and > 0.52, respectively). There also were no interactions between nitrogen levels and competition treatments on the parameter estimates (P > 0.73). Mid-season survival probability (f) in Experiment 1 was greater under Treatment 2 (9 plants·m^{-2} with landscape fabric) than in Treatment 3 [(9 plants·m^{-2} without landscape fabric) Table 4.3]. The survival probability for plants grown in Treatment 1 (1 plant·m^{-2} with landscape fabric) did not differ from either of the other competition treatments.

In Experiment 3, parameter estimates for mid-season survival probability were affected by competition treatment and by nitrogen level (P = 0.0014 and 0.040, respectively). The effects of the interactions between nitrogen levels and competition treatments on the parameters could not be tested because of limited variation in survival. Treatment 3 caused a lower survival probability than did Treatment 2 (Table 4.3). The survival probability in Treatment 1 was not different from either of the other two competition treatments. Plants fertilized with 125 kg·ha^{-1} nitrogen had a lower survival probability than those where no fertilizer was applied, but did not differ from those with 62.5 kg·ha^{-1} nitrogen (Table 4.3).

Both nitrogen level and competition treatment affected the parameter estimates of rosette persistence ($r*$) in Experiment 1 (P = 0.058 and 0.0001, respectively), but the

interactions among the nitrogen levels and competition treatments did not affect the parameter estimates (P > 0.17). The probability of a rosette persisting was greater with Treatment 3 than for Treatments 1 and 2 (Table 4.3). Rosette persistence tended to have a greater probability with either amount of added nitrogen fertilizer than without it (Table 4.3).

In Experiment 3, the parameter estimates for the probability of remaining a rosette in Year 2 [$r*(y2)$] responded to nitrogen level but, unlike Experiment 1, were unaffected by competition treatments (P = 0.0021 and > 0.47, respectively). Interactions between nitrogen levels and competition treatments did not affect the parameter estimates (P > 0.20). The effect of nitrogen level on rosette persistence was more pronounced and opposite of that in Experiment 1. The probability of remaining a rosette was greater with 0 kg·ha^{-1} nitrogen than with either 62.5 or 125 kg·ha^{-1} nitrogen, which were not different from one another (Table 4.3).

The parameter estimates for flowering (r) were affected by both competition treatment and nitrogen level (P = 0.0001 and 0.055, respectively) in Experiment 1. There was a trend for an interaction between nitrogen level and competition treatment parameter estimates (P = 0.072), but these interaction parameters were not used since some of them could not be estimated because of limited response to treatment. Flowering probability (r) was greater for plants in Treatments 1 and 2 than with the interspecific competition Treatment 3, but there was no difference between the other treatments (Table 4.3). Plants in Treatment 3 had lower flowering probability without nitrogen fertilizer than with either 62.5 or 125 kg·ha^{-1} added nitrogen (Table 4.3).

The nitrogen level and competition treatment effects on second-year flowering probability [$r_{(y2)}$] parameter estimates in Experiment 3 also differed from Experiment 1. Competition treatment influenced these estimates, whereas nitrogen addition and the interactions between nitrogen levels and competition treatments did not (P = 0.0090, 0.16, and, 0.11 respectively). Flowering probability for plants grown in Treatment 1 did not differ from either of the other competition treatments (Table 4.3). The probability of flowering was greater, however, for plants in Treatment 2 than those in Treatment 3 (Table 4.3).

In Experiment 1, only 2 out of over 350 plants that flowered exhibited iteroparity (a^*), which was an insufficient response to analyze statistically but demonstrated the species' capacity for some repeat flowering. The iteroparity rate was estimated at 0.01 (Table 4.3). The perenniation (a') parameter estimates were affected both by nitrogen levels and competition treatments (P = 0.022 and 0.0001, respectively). There were no interaction parameter estimates between nitrogen levels and competition treatments (P > 0.35). Adding nitrogen at either 62.5 or 125 kg·ha^{-1} reduced the probability of perenniation (a') relative to no addition (Table 4.3). Perenniation probability was greater for plants in Treatments 1 and 2 than those in Treatment 3 (Table 4.3). There were no differences between the first two competition treatments.

By Year 3 of Experiment 3, there were no competition treatment or nitrogen level effects on the parameter estimates for any of the transition probabilities: rosette persistence [$r^*_{(y3)}$] (P > 0.43 and 0.50, respectively), rosette flowering [$r_{(y3)}$] (P > 0.37 and 0.21, respectively), perenniation (a'; P > 0.76 and 0.62, respectively), or iteroparity (a^*; P > 0.76 and 0.28, respectively; Table 4.3). Interactions between levels and treatments could

not be assessed for any third-year transition except iteroparity, for which there was no interaction detected (P > 0.27) because of the limited number of positive responses.

Nitrogen level or competition treatment did not affect the parameter estimates for the probability of a seed being viable (*b*) in Experiment 1 (Table 4.3). There were also no interaction parameter estimates between levels and treatments (P > 0.81, 0.88, and 0.37, respectively).

Foxglove seed viability (*b*) parameter estimates in Experiment 3 were affected by competition treatments but not nitrogen levels (P = 0.012 and > 0.20, respectively). The interactions between nitrogen levels and competition treatments did not affect the parameter estimates (P > 0.11). The probability of producing viable seed was greater for plants grown in Treatment 1 than for those grown in either Treatments 2 or 3 (Table 4.3).

The interactive effects of nitrogen fertilization, application timing, and interspecific competition on foxglove life history are demonstrated by the different response of the transition rates in Experiments 1 and 3. The reduction in mid-season survival under interspecific competition (Treatment 3) in both experiments confirms foxglove's lack of competitive ability (van Baalen *et al.* 1984). Increased rosette persistence and reduced flowering under interspecific competition (Treatment 3) in Experiment 1 resulted from reduced rosette growth, which is related to flowering probability (van Baalen and Prins 1983; Appendix 2, Figure A2.1). Flowering probability was also increased with increasing rosette diameter (Appendix 2, Figure A2.2), which was not included in the model. Reduced perenniation observed with interspecific competition (Treatment 3) or increased nitrogen levels indicates that competitive exclusion eliminates foxglove from the plant community. Increased fertility enhances that exclusion process (Table 4.3). Seed viability

in older foxglove plants is sensitive to both intra- and interspecific competition, as indicated by its response to Treatments 2 and 3 in Experiment 3 (Table 4.3). This could reduce foxglove's ability to become established after a disturbance.

The difference in transition rate response to added nitrogen between Experiments 1 and 3 (Table 4.3) suggests competing vegetation is stimulated more by the addition of nitrogen than is foxglove resulting in the species' negative response to increased nitrogen level. This interaction between competition and fertilization could explain the reduced perenniation after fertilization in Experiment 1 (Table 4.3). Interspecific competition (Treatment 3) reduced foxglove seed production, which was not compensated for by increased fertilization (Table 4.4). In Years 1 and 2 of Experiment 3, nitrogen fertilization increased the probability of rosette mortality (Table 4.3). Nitrogen-stimulated interspecific competition was the probable mechanism for this response. Treatment ineffectiveness on Year-3 transition probabilities in Experiment 3 suggests that sufficient time had elapsed since treatment so that they were no longer influential. Low rosette persistence in Year 3 was related to high flowering probability.

No new foxglove plants were established in Experiment 3 despite ample flowering. The observations from Experiment 2, where foxglove seed was sown, could explain why regeneration did not occur. Seeds produced in Experiment 3 were not dispersed until Fall 1993. Given their innate dormancy, it seems unlikely that these seeds could have germinated until Fall 1994. Because the landscape fabric was removed from competition treatments 1 and 2 at the end of Year 1 (Fall 1992), suppression of the associated vegetation would have been reduced. Foxglove has limited germination capacity under a plant canopy (van Baalen 1982, Bliss and Smith 1985) so few if any seeds probably

germinated. Foxglove seedling recruitment on the site seems improbable without prior vegetation-clearing or, perhaps, a soil-churning disturbance.

Transition probabilities and variances in Table 4.3 were incorporated into a stochastic population model for foxglove using the equations in Figure 4.1 to form the transition matrices (Appendix 3). These matrices were used to simulate the effects of competition treatment and nitrogen fertilization level on a hypothetical foxglove population. The probabilities from Experiment 1 were used in one set of simulations; those from Experiment 3 were used in two other sets. The population projections showed no difference between the two, Experiment 3 simulations so the results of the projections using arranged competition levels are presented.

The foxglove population was projected to increase using a stochastic model and transition parameters from Experiment 1 (Figure 4.3). Simulated mature plant density increased rapidly from Year 1 to Year 2 (Figure 4.3A). It then increased gradually to between 0.95 and 1.6 plants·m^{-2} by Year 6 of the simulation. Immature plant density was projected to declined sharply from Year 1 to Year 2, increasing again from Year 3 onward (Figure 4.3B), and ranging from 0.8 to 2.6 plants·m^{-2} by Year 6. Seed density in the simulated buried seed bank increased with the onset of sexual reproduction in Year 2, reaching between 39,000 and 52,000 seeds·m^{-2} by Year 6 (Figure 4.3C). Nitrogen fertilization did not affect the outcome of these projections.

The projected foxglove populations using the data from Experiment 3 differed from those based on Experiment 1 data (Figure 4.4). The mean mature plant density increased from Year 1 to Year 2 of the simulation but not to the same level as in simulations based on Experiment 1 data (Figures 4.4A and 4.3A, respectively). After Year 2, the projected
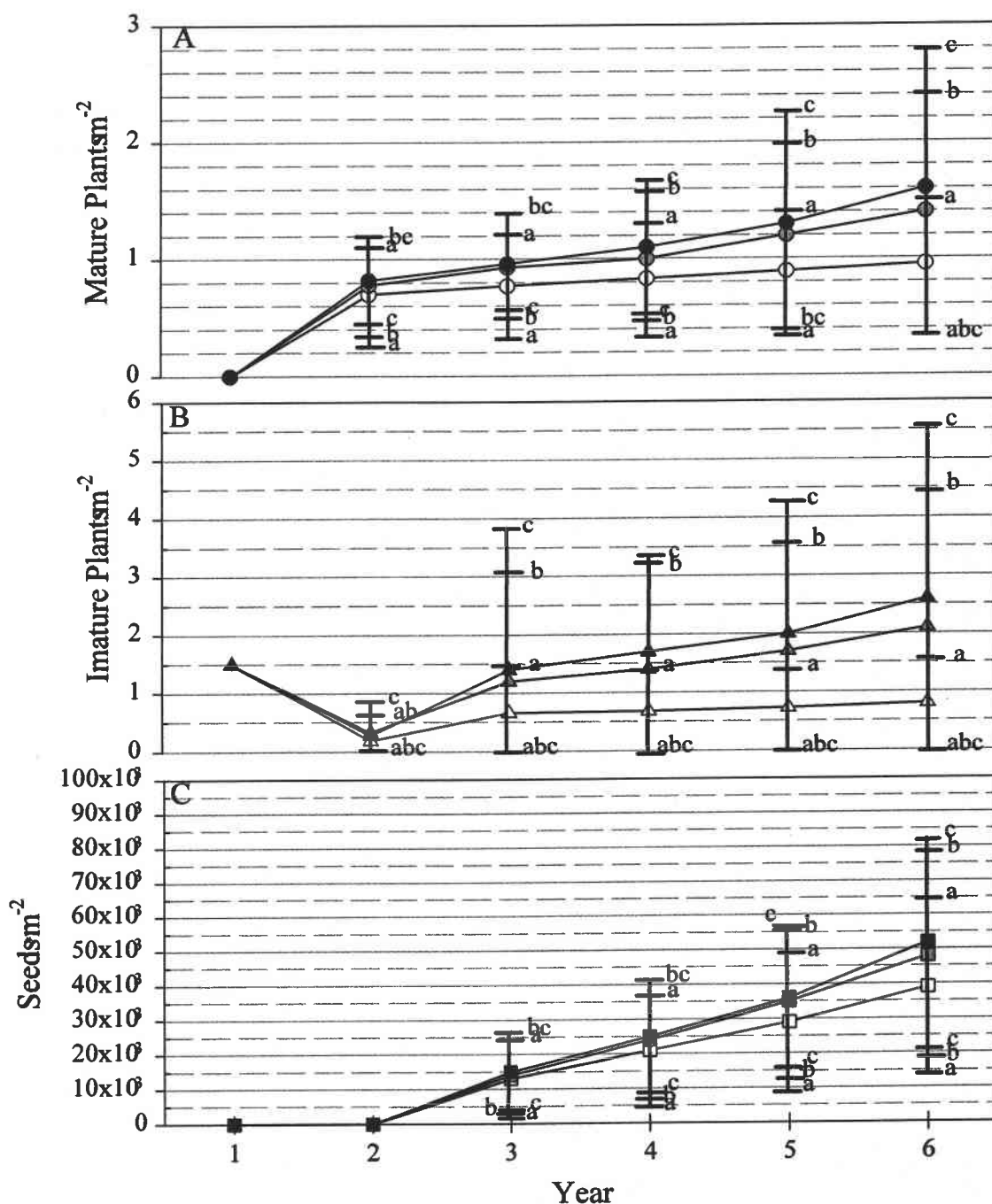
Figure 4.3. Projected mean foxglove population density (m⁻²) affected by nitrogen fertilization using transitions from Experiment 1. Responses are for (A) mature plants represented(—●—), (B) immature plants represented (–▲–), and (C) buried seed bank (seeds·m⁻²) represented (–■–). Nitrogen level is represented (□) for 0 kg·ha⁻¹, (▨) for 62.5 kg·ha⁻¹, and (■) for 125 kg·ha⁻¹. Vertical bars represent confidence intervals of ± one standard error. The standard error bars for their respective nitrogen levels are labeled; (a) 0 kg·ha⁻¹, (b) 62.5 kg·ha⁻¹, and (c) 125 kg·ha⁻¹. Since the population cannot fall below zero, all values are truncated at that level.

Figure 4.4. Projected mean foxglove population density (m⁻²) affected by nitrogen fertilization using transitions from Experiment 3. Responses are for (A) mature plants represented(—●—), (B) immature plants represented (–▲–), and (C) buried seed bank (seeds·m⁻²) represented (–■–). Nitrogen level is represented (□) for 0 kg·ha⁻¹, (▨) for 62.5 kg·ha⁻¹, and (■) for 125 kg·ha⁻¹. Vertical bars represent confidence intervals of ± one standard error. The standard error bars for their respective nitrogen levels are labeled; (a) 0 kg·ha⁻¹, (b) 62.5 kg·ha⁻¹, and (c) 125 kg·ha⁻¹. Since the population cannot fall below zero, all values are truncated at that level.

population declined until it was nearly extinct by Year 6. Unlike in simulations using Experiment 1 transitions, mean immature plant density declined from Year 1 in the simulations using Experiment 3 data (Figure 4.4B). No immature plants were projected by Year 6. Only the buried seed bank population increased, reaching about 4500 seeds·m^{-2} by Year 6 (Figure 4.4C). This simulated population was an order of magnitude less than that projected with transitions from Experiment 1. Again, nitrogen fertilization did not affect the population projections in Experiment 3 simulations.

For the transition submatrices derived from Experiment 1, λ ranged from 2.3 for Year 1 (with 125 kg·ha^{-1} nitrogen) to 1.1 in Year 3 (regardless of nitrogen level). These λ values indicate the foxglove population would grow exponentially but that its growth rate would slow with time (Caswell 1989). This observation was confirmed by the population projections in Figures 4.3A and 4.3B. The λ values also substantiate the limited impact of nitrogen fertilizer on the population over time. After three years different nitrogen levels produced no changes in the population growth rate. Matrices developed with data from plots fertilized with 125 kg·ha^{-1} nitrogen in Experiment 3 had extreme λ values ranging from 0.92 in Year 1 to 0.32 in Year 3. As in Experiment 1, λ for these matrices declined with time. This confirmed the exponential decline demonstrated by the population projections in Figures 4.4A and 4.4B (Caswell 1989). The data from both experiments demonstrate that higher nitrogen levels increase initial population growth rates. They are unable to maintain such levels, however, and can decline at an increased rate as, indicated by the λ from Year 3 with 125 kg·ha^{-1} nitrogen.

In general, the foxglove transition submatrix derived from Experiment 1 data was most responsive to iteroparity. Sensitivity indices ranged from 0.64 to 0.88 and elasticities

from 0.33 to 0.87. Two exceptions to this generalization occurred in matrices with data from plants without competition (Treatment 1) and either 62.5 or 125 kg·ha^{-1} nitrogen. These matrices were most sensitive to perenniation (sensitivity indices: 1.2 and 1.4, respectively). The matrix created from 62.5 kg·ha^{-1} nitrogen data responded equally to iteroparity, perenniation, and immature-plant flowering with elasticity indices of 0.33, 0.32, and 0.32, respectively. The other matrix responded only to perenniation, and immature-plant flowering (elasticity indices of 0.35 for both).

The transition matrices for Year 2 and Year 3-to-6 created from Experiment 3 data were most sensitive to perenniation regardless of nitrogen level (sensitivity indices from 1.2 to 0.71). The Year 1 matrices were most sensitive to rosette survival with 0 kg·ha^{-1} nitrogen, and to rosette flowering with 62.5 and 125 kg·ha^{-1} nitrogen (sensitivity indices: 0.57, 1.1, and 1.1, respectively). The Year 1 matrices were most responsive to perenniation and rosette flowering regardless of nitrogen level, elasticity indices of 0.30 to 0.44. Response was similar for Year 2 and Year 3-to-6 with 62.5 or 125 kg·ha^{-1} nitrogen (elasticity indices: 0.28 to 0.39). The Year 3-to-6 matrices at these nitrogen levels also were responsive to iteroparity (elasticity indices: 0.30 and 0.34, respectively). Elasticity analysis on the Year 2 and Year 3-to-6 matrices with 0 kg·ha^{-1} added nitrogen indicated they were most responsive to rosette survival (elasticity indices: 0.33 to 0.43, respectively).

The results of the sensitivity and elasticity analysis further demonstrate the role of iteroparity in foxglove population dynamics. The models that were most sensitive to iteroparity (deterministic and stochastic with Experiment 1 data) projected populations that increased. The model that was not sensitive to iteroparity (stochastic with Experiment 3

data) projected decreasing populations. The analyses also suggest that flowering and persistence of immature plants cannot sustain a foxglove population.

The results of the foxglove simulations are different from those reported by Silvertown et al. (1993). Our λ values were lower and, in some cases, indicate population decline, whereas Silvertown et al. (1993) suggested a rapidly growing population (λ = 11.8). They report that foxglove populations were most responsive to seedling recruitment and progression to a more developed stage. Our research did not assess seedling recruitment but found that, in many cases, foxglove was equally responsive to progression and retrogression (i.e., movement to an earlier stage). Furthermore, we found growing populations were often most responsive to stasis in the form of iteroparity.

Transition probabilities were lower in matrices created with Experiment 3 data than those using Experiment 1 transitions except for the perenniation rate (a'). The chief difference between the two models was that predicted iteroparity (a^*) was over five times greater in Experiment 1 than in Experiment 3 (1.0 and 0.17, respectively). Other transition values also differed between the two experiments. Seed production in Experiment 1 was twice that of Experiment 3, but seed entered only the buried seed bank in both simulations and did not influence the current population. Rosette persistence was one-third less in Experiment 1 because of an increased probability of flowering, but again sexual reproduction does not affect the extant population. Iteroparity was the difference between a foxglove population with a stable growth rate (Experiment 1 data; Figures 4.3A and B) and one that became extinct (Experiment 3 data; Figures 4.4A and B).

Poor competitive ability explains the difference in population projections of the two experiments. In Experiment 3, where planting occurred immediately after fertilization, the

additional nitrogen stimulated the competitors more than foxglove, resulting in its inferior performance with increased fertilization. Delayed planting, as in Experiment 1, reduced the effect of fertilization on the associated vegetation and improved foxglove's ability to compete.

Most of the transition rates either remained constant or declined with time, and were represented experimentally by increased competition. The exception was rosette persistence probability in Experiment 1, which increased dramatically. The population parameters would be expected to continue declining over time (van Baalen and Prins 1983). This decline should change the projections, with faster extinction where resources are initially abundant and stable populations where resources do not stimulate competition excessively.

Iteroparity is the primary factor that allows foxglove to be dominant in a plant community. If the species were highly semalparous--like the population described in simulations with Experiment 3 data--it would be only a minor component of the community, quickly becoming locally extinct. Seed germination would have greater impact on the population if foxglove were strictly semalparous. Experiment 3 transitions simulated how foxglove populations could develop when invading a new area. The projected plant population was not large nor persistent but it produced a substantial buried seed bank that could repopulate a site following a disturbance.

Simulations indicated that foxglove populations develop differently when they arise from a buried seed bank[3] after a disturbance. A germination probability of 0.65 from a buried seed bank was observed by van Baalen and Prins (1983). When this germination rate was used to create population vector n_d as input for the matrices developed from Experiment 3 transitions, the projected mature plant population rose to 3 plants·m^{-2} by Year 3, then declined. The increase occurred, in part, because the germination rate must be made invariant when seeds germinate from the buried seed bank. This tends to project larger populations than with the stochastic transitions. Nevertheless, the mature plant population also increases because of the numeric increase in germination rate. The germination rate from the buried seed bank is high enough to establish a foxglove population that can become dominant in the community. It could persist for some years, especially if a second cohort of germinants arises from the buried seed bank the following year.

Monocarpic perennial species typically become extinct after a generation or two in secondary seres (Klemow and Raynal 1985). This is true for foxglove, as well, although it is facultatively iteroparous (van Andel and Ernst 1985). Harper (1977) observes, "when they (biennials) are conspicuous enough to be chosen for study they are usually already in a condition of decline." Our work, starting with an immigrating foxglove population, found that projected populations could either increase gradually or decline to extinction locally depending on initial soil fertility. This study suggests that foxglove may remain in

---

[3]Strictly speaking, these are seeds moving from the buried to the surface seed bank. They are designated as buried seed bank seed to distinguish them from seeds produced by the current population.

the community longer under lower fertility conditions. Other biennials, such as *Picris hieraciodies* and *Echium vulgare*, can persist on infertile sites due to lack of competitive exclusion (Klemow and Raynal 1985).

Harper's comment also suggests that biennial populations should be studied in newly disturbed areas where the species was previously known to exist. Thus, both the increase and decline of the population can be monitored. This tactic was used by van Baalen and Prins (1983), but, by using a chronosequence rather than following a single population, failed to establish when and how the transition from increase to decline occurred. Our research suggests that this change from positive to negative growth rate may be an interaction of initial soil fertility and suppression of seed germination by soil contact. These effects should be studied in a continuously monitored population in the field.

Foxglove can present a management concern because of its ability to perenniate and its persistence in the soil seed bank (Hill 1989). Although not generally considered as competitive as associated species, it can form dense stands that persist for several years (van Andel and Ernst 1985) and interfere with other plants (Dennis 1980). Our research indicates that even a declining foxglove population can create a seed bank of several thousand seeds·m^{-2} in three years. Therefore, seed production should be closely managed in this species. Maintaining a competitive environment would reduce the probability of flowering--the first step in controlling seed production. Competition also reduces the probability of perenniation and seed viability. In less competitive settings, nitrogen fertilization could be used to reduce the probability of mid-season survival and perenniation. It would also increase the probability of foxglove flowering and seed germination. A combination of competition enhancement, perhaps through seeding, and

fertilization could provide effective management. Investigations of the environmental factors affecting perenniation also could lead to potential management tactics.

CONCLUSIONS

The effect of nitrogen fertilization on population growth rate varied depending on the application timing. The growth rate increased if fertilization occurred prior to population establishment but declined if they occurred simultaneously. Increased competition level did result in a decreased population growth rate. However, demographic stochasticity generally had a greater effect on population dynamics than either of these environmental variables. Lack of buried seed bank germination caused negative foxglove population growth rates but were compensated for by facultative iteroparity.

LITERATURE CITED

Adams, A. B. and V. H. Dale. 1987. Vegetative succession following glacial and volcanic disturbances in the Cascade Mountain range of Washington, U.S.A. Pages 70-147 *in* D. E. Bilderback, ed. Mount St. Helens 1980: Botanical Consequences of the Explosive Eruptions. Berkeley, CA: University of California Press.

van Andel, J. and W. H. O. Ernst. 1985. Ecophysiological adaptation, plastic responses, and genetic variation of annuals, biennials, and perennials in woodland clearings. Pages 27-49 *in* J. Haeck and J. W. Woldendorp, eds. Structure and Functioning of Plant Populations 2: Phenotypic and Genetic Variation in Plant Populations. Amsterdam: Noth-Holland Publishing.

van Baalen, J. 1982. Germination ecology and seed population dynamics of *Digitalis purpurea*. Oecologia 53:61-7.

van Baalen, J., A. Th. Kuiters, and C. S. C. van der Woude. 1984. Interference of *Scrophularia nodosa* and *Digitalis purpurea* in mixed seedling cultures, as affected by the specific emergence date. Acta Oecol. 5:279-90.

van Baalen, J. and E. G. M. Prins. 1983. Growth and reproduction of *Digitalis purpurea* in different stages of succession. Oecologia 58:84-91.

Bliss, D. and H. Smith. 1985. Penetration of light into soil and its role in the control of seed germination. Plant Cell Environ. 8:475-83.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters . Theor. Popul. Biol. 14:215-30.

Caswell, H. 1989. Matrix Population Models. Sunderland, MA: Sinauer Associates, Inc. 328 pp.

Chouard, P. 1951. Plantes bisannuelles vraies et fausses bisannuelles. 2) Relation entre la bisannualité et la vernalsation, le photoperiodisme, la dispersion geographique et la taxinomie. Bull. Soc. Bot. France 98:117-20.

Connor, H. E. 1977. The Poisonous Plants in New Zealand. Wellington, N.Z.: Government Printer. 246 pp.

Dennis, L. R. J. 1980. Gilkey's Weeds of the Pacific Northwest. Corvallis, OR: Oregon State University Press. 382 pp.

Ferson, S. 1991. RAMAS/Stage. Setauket NY: Applied Biomathematics.

Guillemat, J. and J. Montégut. 1960. The effects of mineral fertilizers on some soil fungi. Pages 98-111 *in* D. Parkinson and J. S. Waid, eds. The Ecology of Soil Fungi. Liverpool, U.K: Liverpool University Press.

Harper, J. L. 1977. Population Biology of Plants. London: Academic Press. 892 pp.

Henderson, J. A. 1970. Biomass and Composition of the Understory Vegetation in some *Alnus rubra* Stands in Western Oregon. M.S. thesis, Corvallis, OR: Oregon State University. 64 pp.

Hill, M. O. 1978. The development of a flora in even-aged plantations. Pages 175-92 *in* E. D. Ford, D. C. Malcolm, and J. Atterson, eds. The Ecology of Even-aged Forest Plantations. Cambridge, UK: Institute of Terrestrial Ecology.

Hill, M. O. and P. A. Stevens. 1981. The density of viable seeds in soils of forest plantations in upland Britain. J. Ecol. 69:693-709.

Hill, R. L. 1989. *Digitalis purpurea* L., foxglove (Scrophulariaceae). Pages 351-2 *in* P. J. Cameron, ed. A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874-1987. Oxon, U.K.: CAB International.

Hitchcock, C. L. and A. Crosnquist. 1973. Flora of the Pacific Northwest. Seattle, WA: University of Washington Press. 730 pp.

Isaac, L. A. 1940. Vegetative succession following logging in the Douglas fir region with special reference to fire. J. For. 38:716-21.

Jacobsohn, M. K. and G. M. Jacobsohn. 1985. Production of a fungistat and the role of fungi during germination of *Digitalis purpurea* L. cv. Gloxiniaflora seeds. Ann. Bot. 56:543-52.

Klemow, K. M. and D. J. Raynal. 1985. Demography of two facultative biennial plant species in an unproductive habitat. J. Ecol. 73:147-167.

Klinkhamer, P. G., T. J. de Jong, and E. Meelis. 1987. Life-history variation and the control of flowering in short-lived monocarps. Oikos 49:309-14.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427-31.

Munz, P. A. 1968. A California Flora. Berkeley, CA: University of California Press. 1681 pp.

Oberdorfer, E. 1973. Die Glierung der Epilobietea angustifolii Gesellschafften am Beispeil Süddeutcher Vegetationsaufnahmen. Acta Bot. Acad. Sci. Hung. 19:235-53.

Pojar, J. and A. MacKinnon. 1994. Plants of the Pacific Northwest Coast. Redmond, WA: Lone Pine Publishing. 527 pp.

Radosevich, S. R., J. S. Holt, and C. M. Ghersa. 1997. Weed Ecology: Implications for Management. 2 ed. New York: John Wiley & Sons. 589 pp.

Robbin, W. W., M. K. Bullue, and W. S. Ball. 1951. Weeds of California. Sacramento, CA: Printing Division, State of California. 547 pp.

Sagar, G. R. and A. M. Mortimer. 1976. An approach to the study of the population dynamics of plants with special reference to weeds. Ann. Appl. Bot. 1:1-47.

Salisbury, E. J. 1942. The Reproductive Capacity of Plants. London: Bell and Sons, Ltd. 244 pp.

Salisbury, E. J. 1961. Weeds and Aliens. London: Collins Publishing Co. 384 pp.

Silvertown, J. W. 1984. Death of the elusive biennial. Nature 310:271.

Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant demography--relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. J. Ecol. 81:465-76.

Withering, W. 1776. An Account of the Foxglove and some of Its Medicinal Uses. London: C.G.J. and J. Robinson. 207 pp.

Yaniv, Z. 1985. Digitalis. Pages 446-9 in A. H. Haley, ed. CRC Handbook of Flowering. Volume VII. Boca Raton, FL: CRC Press.

CHAPTER 5

Fireweed (*Epilobium angustifolium*) Populations
as Affected by Competition and Nitrogen

ABSTRACT

A study was conducted to investigate the population development of fireweed (*Epilobium angustifolium* L.) in newly disturbed forest areas of Oregon. Fireweed is a native iteroparous perennial that commonly becomes established in forests shortly after a disturbance and persists there for up to several decades. Experiments were conducted to test the effects of nitrogen fertilization and competition, which have been proposed as agents of population change, on survival, size, and development of this species. The experiments included assessing size and development from seeds and transplants, as well as its ability to regenerate on a site. First-year plant size was affected by nitrogen fertilization level and competition treatments. Interspecific competition reduced mid-season survival. Nitrogen fertilization increased survival and affected size of 2-year-old plants. Models based on the literature projected populations that had a lower growth rate than observed in the field. Vegetative reproduction was determined to be more important to the species' persistence on-site than sexual reproduction. Stochastic models projected the population growing at a slower rate than the deterministic model. They also indicated fertilization did not affect population development and that competition tended to result in linear population growth.

Nomenclature: Fireweed *Epilobium (Chamaenerion) angustifolium* L. **CHAAN**

Keywords: Succession, plant population model, iteroparous perennial population development

INTRODUCTION

Plant population dynamics models have been used to study a variety of factors affecting iteroparous perennial species. For example, mesquite (*Prosopis juliflora*), a competitive shrub, was found to reduce populations of two perennial grasses, black grama (*Bouteloua eriopoda*) and mesa dropseed (*Sporobolus flexuosus*), while grazing did not have any adverse effects on them (Wright and Van Dyne 1981). Protection from human trampling was projected to have a positive impact on survival of the endangered sentry milk-vetch (*Astragalus cremnophylax* var. *cremnophylax*) but these were subject to favorable climatic conditions (Maschinski *et al.* 1997). Bulb harvest was found to have a detrimental impact on wild leek (*Allium tricoccum*) populations because of the species reliance on asexual reproduction (Nault and Gagnon 1993). This study assessed the impacts of nitrogen fertilization and competition manipulation on fireweed (*Epilobium* (*Chamaenerion*) *angustifolium* L. **CHAAN**) population dynamics.

Fireweed is a native plant in the Pacific Northwest that commonly invades newly disturbed lands where it can become weedy. It inhibits regeneration of crop tree species in forest plantations (Bianco 1990) through competition for resources, creating unfavorable growing conditions (*e.g.*, cover for small herbivores), and by physical damage (Simard and Nicholson 1990). Dense fireweed stands can reduce light levels sufficiently to cause tree seedling mortality (Comeau 1988). It is a persistent weed in Alaskan grain fields (Conn and DeLapp 1983) and is becoming a problem in British perennial crops (Bailey and Hoogland 1983). This species is listed as a noxious weed in Manitoba (Broderick 1990) and has been associated with 11 pathogenic fungi including the agent for needle rust in *Abies balsamea* (Ginns 1986, Goodwin 1930).

As a native plant, fireweed also has beneficial aspects. It was used by the Native Americans of the Pacific Northwest for food and fiber and is an excellent source of nectar for honey bees (Pojar and MacKinnon 1994). It is eaten by numerous wild and domestic herbivores (Willms *et al.* 1980, Henderson *et al.* 1979). Its aesthetic value has also been noted as it is the territorial flower of the Yukon (Broderick 1990).

Description, Reproduction, and Population Development

Fireweed, which is in the Onagraceae family, is a creeping perennial found in temperate and polar regions of the Northern hemisphere (Rickett 1966, Bentham 1904, Czerepanov 1995, Dahlgren and Lassen 1972, Mosquin 1967). It grows up to 3 m tall with stems that are woody near the base and alternate, lanceolate leaves. The abundant flowers, clustered on the apical stem, are red to purple in color and produce a four-lobed capsular fruit that releases numerous small seeds enclosed in large white plumes.

Fireweed reproduces both generatively and vegetatively. The iteroparous plant is self-compatible (Myerscough 1980), but also is protandrous[4], forcing outcrossing (Myerscough and Whitehead 1966). Average seed production is 76,000 seeds·plant^{-1} (Salisbury 1942). A fireweed stand in Alaska produced an average of 77 fruits·shoot^{-1} containing a mean 420 seeds (Livingston 1977), resulting in an average seed production of 28,500 seeds·shoot^{-1}. High light intensity is required for successful fruiting (Salisbury 1942).

---

[4]Plants that produce pollen before the stigma is receptive are protandrous (Hanson 1962).

Fireweed seed has impressive dispersal capability due to its light weight, between 0.04 mg (Salisbury 1961) and 0.07 mg (Myerscough and Whitehead 1966), and a large plume, which expands during dry weather, when dispersal conditions are most favorable, and contracts with moisture (Salisbury 1961). With a still-air fall rate between 6.5 and 6.9 cm·s^{-1} (Salisbury 1961, Myerscough and Whitehead 1966), an estimated 20 to 50% of the seed dispersed rises to more than 100 m above the ground (Solbreck and Anderson 1987), which could result in seed being moved several hundred kilometers. Fireweed has a seed rain of 40 seeds·m^{-2} (Adams and Dale 1987, Henderson *et al.* 1979 as cited in Broderick 1990). Fireweed does not have a significant or persistent buried seed bank. This seed bank contained between 75 and 100 seeds·m^{-2} in a Welsh second-growth forest (Hill and Stevens 1981). Seed remains viable for up to 18 months but germination decreases with increasing seed burial depth and those below 2 mm do not germinate (Myerscough and Whitehead 1966).

Seeds are produced to colonize new areas (Salisbury 1942). Fireweed was seeded on debris from the Mount St. Helens eruption to assess its colonization ability (Wood and Morris 1990). Its greatest emergence rate was 4.7% on pumice (a coarse substrate with subsurface moisture). Only 15% of the plants seeded survived the duration of the study with those from large seed having the greatest survival. The establishment rate is low in fireweed with 5% seed produced becoming established seedlings (Hill and Stevens 1981).

Germination of fireweed seed is constrained by a variety of factors. The seed can germinate at anytime after dispersal, typically doing so in late summer or fall (Livingston 1977, Myerscough and Whitehead 1966, 1967). Dormancy is thought to be weak in fireweed (Myerscough and Whitehead 1967). Only a few seeds survive over the winter

(Myerscough and Whitehead 1967). The seeds require light for germination (Niethammer 1927). Emergence and germination rate decreased with decreased illumination, soil and atmospheric moisture, mineral nutrients (Myerscough and Whitehead 1966), and temperature (Livingston 1977, Jobidon 1968, Myerscough and Whitehead 1966). Fireweed seed dispersed early in the season had greater germination than those produced later (Livingston 1977), and larger seeds had a higher germination rate than smaller ones (Wood and Morris 1990).

Vegetative reproduction is important for fireweed's persistence in the plant community. It grows clonally from adventitious buds on the roots and rhizomes (Salisbury 1961), which remain dormant for 1 year (Vodlazsky 1979 as cited in van Andel and Jager 1981). In the greenhouse, 1 shoot per 10 cm rhizome developed independent of the collection date, planting date, or rhizome length (8-20 cm). Seedling shoot development is slow but roots grow rapidly, such that an 8-month-old seedling, with a rosette 6 cm in diameter, will have a complex root system and adventitious buds (Myerscough 1980).

Fireweed forms an extensive horizontal root system and a large taproot (Antos and Halpern 1996). In firm soil with associated vegetation, this species can spread 0.33 to 0.5 m·year^{-1} (Salisbury 1961). Under less rigorous growing conditions, it can spread up to 1 m·year^{-1}. The ability of older plants to cycle nutrients internally also aids in their persistence (van Andel and Nelissen 1979). It is suggested that the buds can re-establish fireweed after a disturbance such as logging (Livingston 1977).

Newly established stands of fireweed increase in shoot density for the first several years, then expand in area while shoot density declines (van Andel 1975). Shoots grow from late May (Broderick 1990) until the beginning of August (Livingston 1977) and

flower from June or July to September (Broderick 1980, Myerscough 1980). Seed is released beginning in late July (van Andel and Jager 1981, van Andel 1976). A stand with a mean age of 14 years had 112 shoots·m^{-2} (van Andel 1975). Shoot density also increases over the growing season (Livingston 1977, van Andel 1975). Shoot biomass increased for the first 7 years of fireweed stand development then remained relatively constant for the next 12 years (Myerscough 1980). Root growth decreases at about 15 years, which stresses the ability of the population to maintain itself (van Andel 1975). Fireweed populations can be very persistent, with ages of up to 35 years in Europe and 47 years in North America, having been recorded (van Andel and Nelissen 1979, Broderick 1980 as cited in Broderick 1990, respectively).

Population Response to Fertilization and Competition

Reproductive allocation in fireweed is not affected by soil nutrients but reproductive output is (van Andel and Vera 1977). In unamended soil, plants produced an average of 10 capsules and 792 seeds; in fertilized soil, they yielded 30 capsules and 1909 seeds·plant^{-1}. The seed to seed-plume weight ratio decreased from 0.25 to 0.16 with fertilization. Dry matter allocation to the roots increased during flowering, suggesting that vegetative reproduction dominates sexual reproduction.

Both interference and fertilization affect its establishment. In an old, dense fireweed stand, nitrogen fertilization reduced germination and seedling survival by stimulating the associated vegetation (van Andel and Rozema 1974). Associated vegetation also reduced survival without fertilization (van Andel and Nelissen 1979). There is little seedling recruitment in established fireweed stands (van Andel and Rozema

1974) unless they are cleared of vegetation and fertilized (Myerscough and Whitehead 1967).

Study Objectives

This study addresses the question of fireweed's persistence in early seral forest. Its objectives are to:

1) assess the impact of nitrogen fertilization and competition on fireweed population dynamics,

2) integrate the available information about fireweed population dynamics into a model, which is made stochastic using data from field experiments, and compare the effects of environmental variation and demographic stochasticity on the populations, and

3) determine how the sexual and vegetative portions of fireweed's life cycle affect its population, *e.g.*, which portion makes a greater contribution to the population growth rate.

Nitrogen fertilization was predicted to increase reproductive output and increase both the growth rate and persistence of the fireweed population. Added levels of competition, on the other hand, were expected have little effect on the population's persistence. Environmental variation was anticipated to have a more influence on population growth rates than demographic stochasticity. Populations were expected to respond more to factors affecting vegetative reproduction than sexual reproduction.

The population dynamics of fireweed are discussed in this study with regard to the influences of nitrogen fertilization and competition. First, the deterministic population model is developed and analyzed. Data from field experiments and stochastic population models are presented next.

METHODS AND MATERIALS

Deterministic Population Model

A fireweed conceptual population model with four states and an annual timestep was developed (Figure 5.1). Mature plants (A) produce new mature plants, immature plants (R), buds (B'), and seed that enter the buried seed bank ($D2$). Immature plants can either persist as immature plants or flower and become mature plants. Buds can produce both mature and immature plants or can remain dormant. Seed from the buried seed bank can also produce

mature and immature plants but, since the seed remains viable for only 18 months (Myerscough and Whitehead 1966), it is not persistent as are the other stages.

The model was parameterized using data from the literature (Table 5.1). Fireweed readily immigrates to new sites at a rate of 40 seeds$\cdot$m^{-2} $\cdot$year^{-1} [Henderson et $al.$ 1979, Adams and Dale 1987 (Table 5.1)]. Only a small percentage of the seeds produced, 0.1%$\cdot$year^{-1}, were estimated to return to the population in the seed rain given the seed's dispersal characteristics (Solbreck and Anderson 1987). Post-dispersal seed predation losses were presumed to be small, due to small seed size (Eriksson et $al.$ 1995), and the transition rate was estimated at 95%$\cdot$year^{-1}. Transition from the late seed bank to the buried one was estimated at 20%$\cdot$year^{-1} (Table 5.1). Only 0.7%$\cdot$year^{-1} of fireweed seed
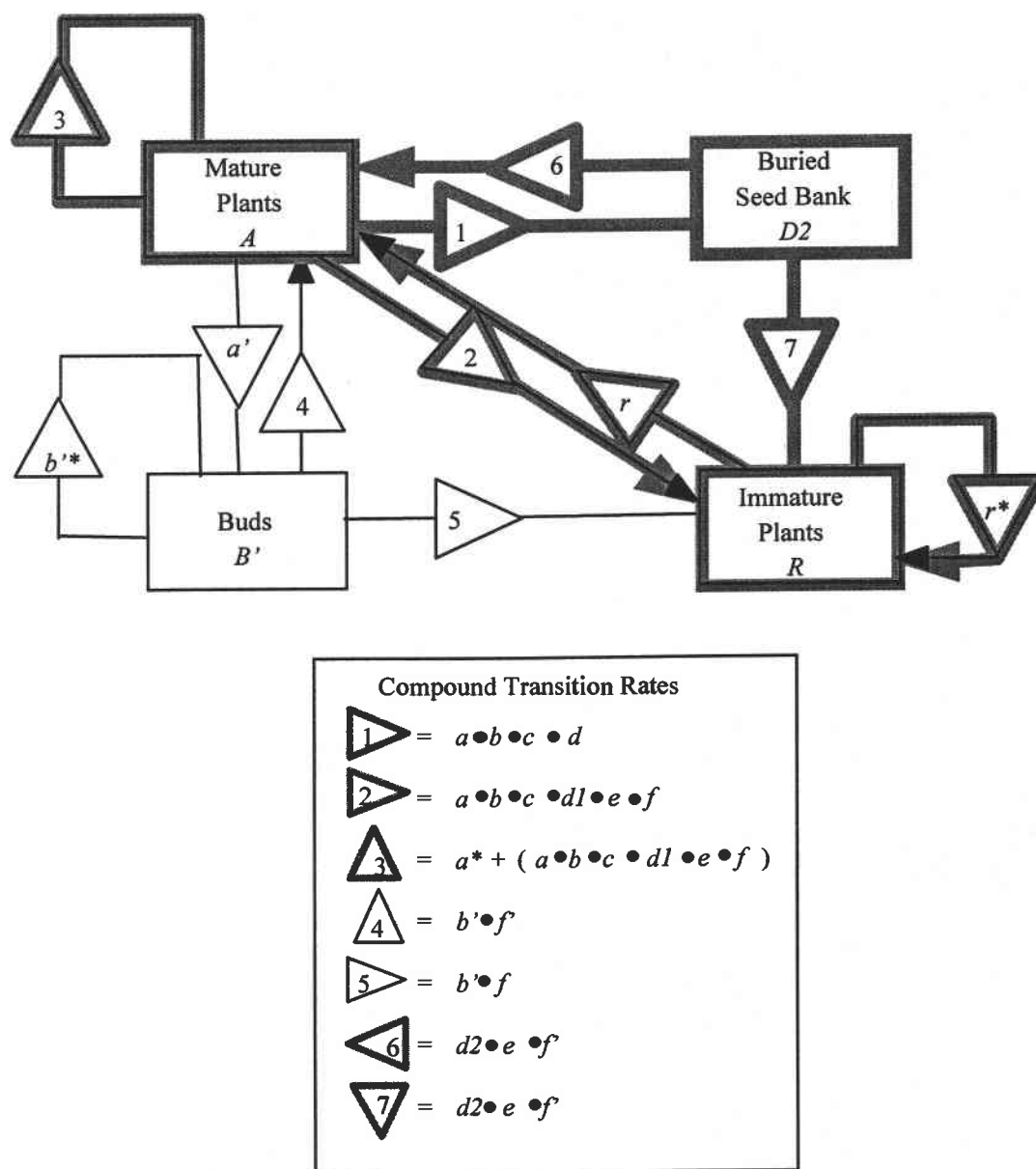
Figure 5.1. A conceptual population dynamics model for fireweed. The sexual portion of the model is indicated by (■) and the vegetative elements are designated by (▯). Transition rates and state values are from Table 5.1.

Table 5.1. State variable values and transition rates for a deterministic fireweed population model. Data were obtained from the literature. State variables are designated by upper-case letters in parentheses; variables for transition rates are in lowercase. All state variable units are $\cdot m^{-2}$; those for transition rates are $\cdot year^{-1}$ except, for seed and bud production (a and a', respectively), which are $\cdot plant^{-1} \cdot year^{-1}$. Values in italics are estimates not based on specific studies.

State/Transition	Value/Rate	Reference
Immigration (G)	40	Henderson *et al.* 1979
	40	Adams and Dale 1987
Early seed bank (C)	----	N/A
Late seed bank ($D1$)	----	N/A
Buried Seed Bank ($D2$)	79	Hill and Stevens 1981
Seedlings (E)	----	N/A
Established Plants (F)	----	N/A
Immature Plants (R)	----	N/A
Mature Plants (A)	30[5]	van Andel 1975
	53	van Andel 1975
	26	van Andel 1975
	61	van Andel 1975
	110	van Andel 1975
	112	van Andel 1975
Seeds (B)	----	N/A
Buds (B')	----	N/A
Post-dispersal Survival (c)	*0.95*	N/A
Seed Incorporation (d)	*0.20*	N/A
SSB Germination ($d1$)	0.007	Livingston 1977
SSB Germination ($d1$)	0.047	Wood and Morris 1990
BSB Germination ($d2$)	*0.35*	N/A

[5] Shoots $\cdot m^{-2}$ for mature plants with a maximum stand age of 1, 3, 6, 18, 22, and 27 years old, respectively.

Table 5.1 cont. State variable values and transition rates for a deterministic fireweed population model.

State/Transition	Value/Rate	Reference
Seedling Establishment (e)	0.05	Hill and Stevens 1981
Mid-season Survival (f)	0.20	N/A
First-Year Flowering (f')	0.50	N/A
Flowering (r)	0.75	N/A
Perenniation ($r*$)	0.75	N/A
Seed Production (a)	76,000	Salisbury 1942
	28,500[6]	Livingston 1977
	792	van Andel and Vera 1977
	1,909	van Andel and Vera 1977
Iteroparity ($a*$)	1.00	N/A
Bud Production (a')	3[7]	Salisbury 1961 Livingston 1977
	10	Salisbury 1961 Livingston 1977
Seed Viability (b)	0	N/A
Bud Survival ($b'*$)	0.75	N/A
Bud Germination (b')	0.25	N/A

[6]Seeds·shoot^{-1} .

[7]Buds·main root^{-1}·year^{-1}. Estimated from bud interval (Livingston 1977) times annual root growth (Salisbury 1961).

germinated from the late seed bank in the field [Livingston 1977 (Table 5.1)], and germination was assumed to be the same for the buried seed bank (BSB), given that light can stimulate seed germination under a shallow soil layer (Bliss and Smith 1985). Seedling establishment was 5%·$year^{-1}$ (Hill and Stevens 1981). Estimated established plant survival was reduced due to the palatability of fireweed (Ingram 1931). It was estimated that 50% of the established plants would flower in the first year and another 20% would survive as immature plants. Fireweed shoot density, sampled across stands from 1 to 27 years old, increased with time, ranging from 26 to 112 stems·m^{-2} [van Andel 1976 (Table 5.1)]. The average mature shoot density was 65.3 shoots·m^{-2}. All of the mature plants were presumed to survive--that is, to be replaced by a mature shoot in the same location--along with 75% of the immature ones. An estimated 75% of the immature plants became mature the following year. In the field, Salisbury (1942) found fireweed produces 76,000 seeds·$plant^{-1}$ while Livingston (1977) found that it yields 28,500 seeds·$shoot^{-1}$ (Table 5.1). It generated between 792 and 1,909 seeds·$plant^{-1}$ in a greenhouse study [van Andel and Vera 1977 (Table 5.1)]. Its bud production rate was estimated to be between 3 and 10·$year^{-1}$ on the main root (Table 5.1), based on a 10-cm interval between buds (Livingston 1977) and an average root growth of 0.3 to 1.0 m·$year^{-1}$ (Salisbury 1961). In the model, therefore, mature plants produced an average 26,800 seeds and 6.5 buds·$plant^{-1}$. Bud survival was estimated at 75%, and an estimated 25% germinated the following year to become established plants.

Transition rates for the model were calculated using data from the literature and estimates (Table 5.1) according to the equations in Figure 5. 1. Immigration produced 0.19 BSB seeds·$year^{-1}$, 0.00007 immature and 0.0002 mature plants·$year^{-1}$, and 0.0076

buds·year^{-1}. The BSB produced 0.0001 mature and 0.0002 immature plants·year^{-1} (Figure 5.1, compound transition rate Equations 6 and 7, respectively). Mature plants produced 6.5 buds, 1.004 mature plants, 0.002 immature plants, and 5.09 BSB seeds·year^{-1} (Figure 5.1, transition rate a' and Equations 3, 2, and 1, respectively). Twenty-five percent·year^{-1} of the immature plants did not flower the following year but the remaining 75%·year^{-1} flowered (Figure 5.1, transition rates $r*$ and r, respectively). The buds produced by mature plants can have three fates: 75%·year^{-1} of them remain buds, 12.5%·year^{-1} become mature plants, and 5%·year^{-1} develop into immature plants (Figure 5.1, transition rate $b'*$ and Equations 4 and 5, respectively). Buds produced by mature plants have a separate stage, while mature plant seeds do not, because the buds will not germinate until the following year. Any seeds that germinate from the BSB do so the next year, hence its separate stage. Germination of buds represents an increase in ramet number, while replacement of existing mature and immature plants is included, respectively, in Equation 3 and the variable $r*$ of Figure 5.1.

The transition values for the fireweed model were incorporated into the transition matrix, **E**:

$$\mathbf{E} = \begin{pmatrix} 0 & 0 & 5.092 & 0 \\ 0.0001 & 0.25 & 0.002 & 0.05 \\ 0.0002 & 0.75 & 1.004 & 0.125 \\ 0 & 0 & 6.5 & 0.75 \end{pmatrix} \qquad (23)$$

where the rows and columns represent the transition rates for the BSB, immature and mature plants and buds, respectively. The vector, $\mathbf{n}_t$:

$$\mathbf{n_t} = \begin{pmatrix} 7.6 \\ 0.0028 \\ 0.0072 \\ 0.304 \end{pmatrix} \tag{24}$$

(where t = 0) is the product of the immigration rate (40 seeds·m^{-2} ·year $^{-1}$) and the immigration production rates listed above. The elements of this vector are in the same order as for the transition matrix and indicate the population at the end of the first year. Immigration was used to establish the population but was not included in the transition matrix, which is consistent with the observation that seedlings do not readily establish in existing fireweed stands (van Andel and Rozema 1974, van Andel and Nelissen 1979). The effects of omitting immigration will be discussed later.

The deterministic model was used to make population projections and analyzed in the same manner as for foxglove [(*Digitalis purpurea*) Chapter 4]. In addition, loop analysis (van Groenendael *et al.* 1994) was used on the fireweed model to assess the effects of vegetative versus sexual reproduction. In this analysis, the life cycle was divided into its sexual and vegetative components (Figure 5.1). The sexual phase involves the buried seed bank, immature plant and mature plant stages and their transition rates. The stages included in the vegetative model were mature and immature plants and buds. Two transition matrices were used to simulate these reproductive strategies, $\mathbf{E_B}$ for vegetative and $\mathbf{E_S}$ for sexual reproduction:

$$
\mathbf{E_B} = \begin{pmatrix} 0.25 & 0 & 0.05 \\ 0.75 & 1 & 0.125 \\ 0 & 6.5 & 0.75 \end{pmatrix} \quad \text{and} \quad \mathbf{E_S} = \begin{pmatrix} 0 & 0 & 5.092 \\ 0.0001 & 0 & 0.0019 \\ 0.0002 & 0.75 & 0.0048 \end{pmatrix} \quad \text{(24,25)}
$$

The population vector, $\mathbf{n}_t$, was used with an initial pulse of immigration to establish the population, but was truncated to reflect only sexual (elements $n_{t\ (1-3)}$) or vegetative (elements $n_{t\ (2-4)}$) reproduction (Appendix 3). In addition, continuous immigration was simulated to determine its effects on fireweed populations using matrix $\mathbf{E_S}$.

Field Experiments

All field experiments were conducted with the same design and methodology as was used for woodland groundsel [*Senecio sylvaticus* L. (Chapter 3)]. Experiment 1, which was established in Winter 1993, used transplants to test the effects of nitrogen fertilization levels (0, 62.5, and 125 kg·ha⁻¹) and competition treatments [Treatment 1, 1 plant·m⁻¹ with landscape fabric; Treatment 2, 9 plants·m⁻¹ with landscape fabric; and Treatment 3, 9 plants·m⁻¹ with without landscape fabric; (See Chapter 3, page 81 for complete treatment descriptions)] on survival, size, and reproduction in fireweed. These variables were assessed in June 1994, and the experiment was harvested in August of that year for seed and biomass production. Experiment 2 assessed seed germination and seedling establishment. It was initiated in December 1994, and evaluated in January and February 1995. Begun in Spring 1992, Experiment 3 used transplants to determine the size, survival, and reproduction of fireweed over time, evaluating them in June 1992, 1993,

and 1994 (Years 1, 2, and 3, respectively); biomass and seed were harvested in August 1994. Size assessments for these experiments were conducted in the same manner as for woodland groundsel (Chapter 3). Biomass was also assessed in the same manner except that the number of adventitious buds on the roots was determined prior to drying.

The dispersal structure of the fireweed seed required a different seed separation technique than was employed for woodland groundsel and foxglove (Chapters 3 and 4, respectively). Prior to opening, the fruits were enclosed in a cloth bag. The plants were harvested and dried during which time the fruits opened. The contents of the bag were evacuated and trapped. This material, which included seed, plumes, and pieces of fruit, stem, and leaves, was ground in a blender to remove the seed from the plume. After the seeds were detached from the plumes, they were collected, along with the other parts previously mentioned. These parts were weighed and a subsample taken to determine the proportion of seeds present. The subsample was weighed, and the seeds it contained were counted and weighed. This information was used to estimate the number of seeds collected. Seed germination was conducted in the same manner as for woodland groundsel (Chapter 3).

The same statistical procedures described for woodland groundsel (Chapter 3) were used in this study. Binomial data were analyzed using logistic regression with an indicator variable model. Analysis of variance was conducted on continuous data, which was transformed when necessary. Crown diameter in Experiment 1 and all Year 1 size variables in Experiment 3 required log transformations to improve the consistency of variance and normality of the data.

Stochastic Population Models

Stochastic population models were developed following the methods described in Chapter 3. The data from Experiment 1 were used in one set of simulations, and data from Experiment 3 were used in another, as was done for foxglove (Chapter 4). Germination probability derived from Experiment 2 was used in all simulations. The data from Experiment 3 presented an opportunity to do two different simulations by varying the transition probabilities of immature plant persistence in the third and subsequent years as was done for foxglove (Chapter 4). The differing transition probabilities for the various levels of competition were arranged as described for woodland groundsel (Chapter 3); probabilities for interspecific competition (Treatment 3) were used for Year 3 and beyond. Estimated transition probabilities for immature plant persistence in Year 3 of Experiment 3 were substituted for the interspecific competition probabilities in the second set of simulations.

RESULTS AND DISCUSSION

Deterministic Population Model

All segments of the fireweed population increased but the projected populations were still low at six years (Figure 5.2) compared to field populations (van Andel 1975). The mature plant population was projected to be 0.61 plants·m^{-2} after six years, at which time values (van Andel 1975, Hill and Stevens 1981) and suggest that some probability estimates for the model are incorrect.

The asymptotic population growth rate (λ) for the deterministic fireweed model was 1.87. Vegetative reproduction was the prime driver for this population increase. The

model was most sensitive to the bud-to-mature transition and next most sensitive to the bud-to-immature transition and development of mature plants from the BSB (sensitivity indices of 3.14, 1.45, and 1.47, respectively). Because of differences in the matrix values, the elasticity may be a more reliable indicator. The model was most responsive to persistence of mature plants (elasticity index = 0.29); development of mature plants from buds as well as bud production by mature plants and persistence of buds were also primary drivers for the model (elasticity indices = 0.21, 0.25, and 0.17, respectively).

Comparison of Alternative Life History Pathways

Loop analysis confirmed the importance of vegetative reproduction in maintaining fireweed populations (Figure 5.2). Mature plant and bud density both increased over time in the vegetative part of the model and produced similar results to the whole model projections (Figure 5.2B and 5.2A). After six years, mature plant density was almost 0.6 plants·m^{-2} and bud density was 3.5 buds·m^{-2}. The vegetative segment of the model had a λ of 1.86, which was almost identical to the λ for the whole model.

The sexual pathway was affected by immigration. The mature plant population went extinct by Year 3 of the simulation. The buried seed bank density reached zero after 5 years when seed was the only means of reproduction and only a single initial pulse of immigration occurred (Figure 5.2C). When immigration was continuous, both the mature plant and buried seed bank densities remained constant (Figure 5.2C). The λ for the sexual part of the model was 0.080, indicating that if fireweed reproduced by seed alone, the population growth rate would go extinct as indicated by the numerical projections (Caswell 1989).
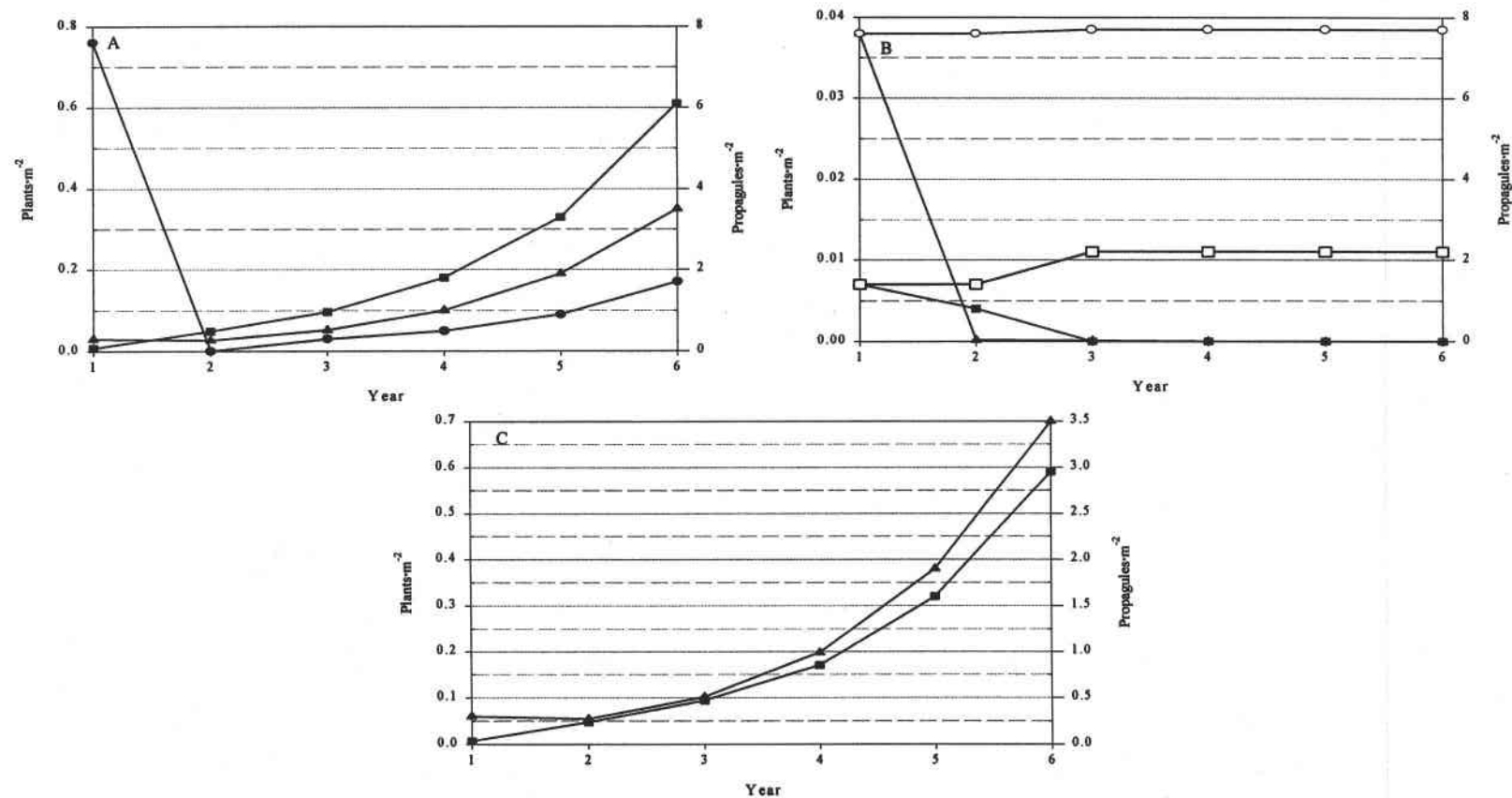
Figure 5.2. Simulated change in fireweed population over six years using deterministic models. Responses are for (A) full, (B) sexual, and (C) vegetative deterministic models (Table 5.1 and Figure 5.1). The effects of a single immigration event on mature plant density (plants·m^{-2}) are represented by (–■–) and those on buried seed bank density (propagules·m^{-2}) are represented by (–●–); effects of continuous immigration on mature plant and buried seed bank density are represented by (–□– and –Ο–, respectively). Bud density (propagules·m^{-2}) is represented by (–▲–).

168

Sensitivity and elasticity analyses were also conducted on the sexual and vegetative parts of the model. The sexual portion was most sensitive to the transitions from buried seed bank to immature and mature plants (sensitivity indices = 240 and 25, respectively). The greatest elasticity for the sexual component of model was derived from the flowering of immature plants, production of immature plants from the BSB, and seed entering the BSB (elasticity indices = 0.32, 0.29, and 0.23, respectively). The results for the vegetative part were similar to those for the whole model. The vegetative partial model was most sensitive to the bud-to-mature-plant transition and then to the transition from bud to immature plant (sensitivity indices = 3.14 and 1.46, respectively). Similarly, the elasticities indicate that the model was responsive to mature plant persistence, mature-to-bud and bud-to-mature transitions, and bud persistence (elasticity indices = 0.30, 0.25, 0.21, and 0.17, respectively).

The deterministic model required numerous probability estimates because literature values were not available. Although the values of the numerical projections are low compared with observed values, the projected increases in population over time and dominance of vegetative reproduction in maintaining that population do concur with the literature (van Andel 1975, Salisbury 1942, 1961). Thus, the model predicts sufficiently well to be useful in determining the effects of competition and nitrogen fertilization on fireweed populations.

Field Experiments

Experiment 1: Survival and Growth of Transplanted Fireweed

Fireweed size was variously affected by treatment in Experiment 1. There was an interaction between nitrogen level and competition treatment effects on plant height [(p=0.0042) Table 5.2]. Height was greatest with 125 kg·ha^{-1} nitrogen in Treatment 3 (9 plants·m^{-2} without

landscape fabric) and was least in that treatment without added fertilizer. Plants in Treatments 1

and 2 (1 and 9 plants·m⁻², both with landscape fabric) without added nitrogen were larger than

those that were fertilized under Treatment 2 but no different from those in Treatment 1. None of

the fireweed plants survived in Treatment 3 with 62.5 kg·ha⁻¹ added nitrogen.

Table 5.2. Fireweed height (cm) as affected by an interaction between nitrogen level and competition treatment. Competition treatments are as follow: (1) 1 plant·m⁻² with landscape fabric, (2) 9 plants·m⁻² with landscape fabric, and (3) 9 plants·m⁻² without landscape fabric. Analysis of variance was conducted without transformation. Mean separation was conducted using least square means (p=0.05). Comparisons were made among all nitrogen levels and competition treatment combinations; those values having the same letter are not different. Combinations where no plants survived are indicated by N/A.

Nitrogen (kg·ha⁻¹)	Competition Treatment		
	1	2	3
	----Height (cm)----		
0	11.8 b	11.1 b	2.0 d
62.5	9.5 bc	7.3 c	N/A
125	12.5 bc	7.1 c	20.0 a

Reduced competition increased fireweed's canopy diameter [(p=0.0006) Table 5.3].

Canopy diameter was greatest for plants in Treatment 1. Plants in Treatment 2 had greater canopy

diameters than those in Treatment 3. There were no effects of nitrogen level on canopy diameter,

nor was any interaction between nitrogen level and competition treatment (P > 0.67 and 0.39,

respectively).

As occurred with woodland groundsel (Chapter 3), fireweed survival in Experiment 1 was

too low to assess treatment effects on biomass (Table 5.4). Survival was so low that analysis on

a subplot level (as was done for woodland groundsel in Chapter 3) was not useful in detecting

Table 5.3. Fireweed height (cm) and canopy diameter (cm) as affected by nitrogen level and competition treatment in Experiments 1 and 3. Competition treatments are as follow: (1) 1 plant·m^{-2} with landscape fabric, (2) 9 plants·m^{-2} with landscape fabric, and (3) 9 plants·m^{-2} without landscape fabric. Analysis of variance was conducted on log-transformed data for Experiment 1 and for Year 1 of Experiment 3. Interaction between nitrogen levels and competition treatments could not be tested for Years 2 and 3 of Experiment 3 due to limited survival. Mean separation was conducted using Fisher's protected LSD (p=0.05). Back-transformed values are presented; those values having the same letter are not different. Biomass data were not analyzed due to insufficient survival; these and other data that could not be analyzed are indicated N/A. Where no differences were found, untransformed plot means are presented.

Expt	Variable		Nitrogen (kg·ha^{-1}) 0	62.5	125	Competition Treatment 1	2	3
1	Canopy Diameter (cm)		10.4 a	8.7 a	8.0 a	11.5 a	7.9 b	3.0 c
	Root Biomass (g)		4.53	N/A	1.50	1.18	3.17	N/A
	Shoot Biomass (g)		2.26	N/A	2.32	0.57	2.88	N/A
3	Height (cm)	Year 1	5.8 b	7.1 ab	8.6 a	5.2 a	8.7 b	9.4 b
		Year 2	27.5 a	39.8 a	16.9 a	10.0 a	29.2 a	N/A
		Year 3	35.0 a	59.2 a	30.4 a	15.0 a	45.9 a	N/A
	Canopy Diameter (cm)	Year 1	7.2 a	10.7 a	10.9 a	5.8 b	8.3 ab	12.5 a
		Year 2	22.8 a	25.4 a	16.4 a	20.0 a	20.1 a	N/A
		Year 3	18.0 a	23.3 a	29.4 a	35.0 a	23.5 a	N/A
	Root Biomass (g)		N/A	6.2	5.8	10.6	4.4	N/A
	Shoot Biomass (g)		N/A	9.6	7.0	N/A	7.9	N/A

Table 5.4. Fireweed survival and reproduction as affected by nitrogen level and competition treatment. The proportion of plants responding are indicated, with the number of plots indicated in parentheses. Experiments 1 and 2 had a maximum of 4 plots, and Experiment 3 had 2 plots. MS - mid-season survival, EOS - end-of-season survival, Reprod - reproduction, and Germ - germination.

Nitrogen (kg·ha⁻¹)	Competition Treatment	Expt 1			Expt 2	Expt 3			
		MS	EOS	Reprod	Germ	MS-Y1	MS-Y2	MS-Y3	Reprod
0	1	0.54 (4)	0.00 (0)	0.00 (0)	0.00 (0)	0.29 (2)	0.00 (0)	0.00 (0)	0.00 (0)
	2	0.11 (3)	0.03 (1)	0.02 (1)	0.09 (2)	0.25 (2)	0.03 (1)	0.02 (1)	0.03 (1)
	3	0.01 (1)	0.00 (0)	0.00 (0)	0.01 (1)	0.06 (1)	0.00 (0)	0.00 (0)	0.00 (0)
62.5	1	0.15 (1)	0.00 (0)	0.00 (0)	0.14 (2)	0.29 (2)	0.00 (0)	0.00 (0)	0.00 (0)
	2	0.11 (4)	0.00 (0)	0.00 (0)	0.14 (4)	0.57 (2)	0.06 (2)	0.06 (2)	0.02 (1)
	3	0.00 (0)	0.00 (0)	0.00 (0)	0.06 (2)	0.06 (0)	0.00 (0)	0.00 (0)	0.00 (0)
125	1	0.14 (1)	0.07 (1)	0.07 (1)	0.15 (2)	0.15 (2)	0.13 (1)	0.13 (1)	0.00 (0)
	2	0.11 (3)	0.03 (2)	0.02 (2)	0.13 (3)	0.57 (2)	0.19 (2)	0.11 (2)	0.03 (2)
	3	0.01 (1)	0.00 (0)	0.00 (0)	0.07 (2)	0.05 (1)	0.00 (0)	0.00 (0)	0.00 (0)

effects. In a future experiment, fireweed would have to be planted at far greater densities, protected from herbivory, and/or propagated from buds to ensure sufficient survival for analysis.

The response of fireweed height to fertilization and competition demonstrates the variable effects of these two parameters when planting is done a year after fertilization. When no nitrogen was added, interspecific competition (Treatment 3) dramatically reduced plant height because the resources were too limited for the plant to grow. When 125 kg·ha^{-1} of nitrogen was added, fireweed height increased with interspecific competition (Treatment 3) since more resources were available for growth and the plant could respond to reduce light competition (Radosevich *et al.* 1997). Added nitrogen did not increase canopy diameter, which indicates preferential allocation to height growth for light capture rather than diameter growth for space. Some other resource or condition may have had a greater effect on canopy diameter than nitrogen, for example the adjacent plant canopies and their influence on light quality (Ballaré *et al.* 1990) resulting in competition avoidance by fireweed.

Experiment 2: Survival and Growth of Fireweed from Seed

As with woodland groundsel and foxglove (Chapters 3 and 4), germination of fireweed in Experiment 2 was limited (discussed on Page 182) but was sufficient to estimate germination probability (Table 5.4). Seedling establishment was also limited, and its probability could not be estimated. No seedlings survived beyond March 1995. Therefore, size, biomass, and reproduction data were not collected.

The low seed germination rate in this experiment prevented successful establishment. Insufficient seeds were sown for a population to develop, given a 5% seedling establishment rate (Hill and Stevens 1981).

Experiment 3: Regeneration of Fireweed

In Experiment 3, fireweed responded to nitrogen level in Year 1 but not in Years 2 or 3 (Table 5.3). Nitrogen level affected plant height in Year 1 but not canopy diameter (P = 0.017 and 0.255). Year 1 height was greater with 125 kg·ha^{-1} added nitrogen than with no addition; with 62.5 kg·ha^{-1} added nitrogen, height was not different from either of the other treatments.   There was a trend for an interaction between nitrogen level and competition treatment with respect to fireweed height in Year 1, as was observed in Experiment 1 (P = 0.068). Interactions between nitrogen levels and competition treatment could not be tested in Years 2 and 3 because of limited survival (Table 5.4).

Similarly, in that experiment, fireweed responded to competition treatment in Year 1 but not in Years 2 or 3 (Table 5.3). Competition treatments influenced both height and canopy diameter in Year 1 (P = 0.005 and 0.062, respectively). Height was less for plants in Treatment 1 than for those in Treatments 2 and 3, which were not different from one another (Table 5.3). Canopy diameter was less in Treatment 1 than in Treatment 3, but neither was different from that in Treatment 2 (Table 5.3).

Survival was insufficient for analyzing the nitrogen level and competition treatment effects on root and shoot biomass (Table 5.4).

Increased nitrogen level increased fireweed height in Experiment 3, where transplanting occurred immediately after fertilization, as would be expected, whereas it

reduced plant height in Experiment 1 except in the presence of interspecific competition (Treatment 3). Competition (Treatments 2 and 3) in Experiment 3 increased plant height independent of nitrogen level. The competition treatments in Experiment 3 had the opposite effect on canopy diameter from Experiment 1 and increased with interspecific competition (Treatment 3) relative to no competition (Treatment 1). Since the fertilizer in Experiment 3 was applied immediately prior to transplanting, it is likely that more nutrients were available for fireweed to respond to the increased competition with increased height and canopy diameter. The associated vegetation (Treatment 3) also provided cover for the fireweed that tended to reduce large mammal herbivory, allowing greater height and diameter growth. Although the vegetation also provided cover in Experiment 1, nitrogen was less available due to the delayed transplanting so that height could not respond to fertilization below the maximum level.

Stochastic Population Models

Fireweed did not flower in sufficient quantity in Experiment 1 to estimate its probability statistically, so only the transition probabilities for mid-season and end-of-season survival were predicted. Mid-season survival, which was used to estimate seedling establishment (e), was affected by competition treatment but not nitrogen level (p=0.0001 and 0.3943, respectively). The probability of survival was greatest for plants grown in Treatment 1 (Table 5.5). Plants growing in Treatment 3 had the lowest probability of surviving to mid-season (Table 5.5). The survival probability for plants under Treatment 2 was not different from either of the other two (Table 5.5). There were no competition treatment or nitrogen level effects on end-of-season survival, which was used to estimate

Table 5.5. Transition probabilities ($\hat{y}$) and variances (s^2) for fireweed as affected by nitrogen level and competition treatment. Variables are defined in Table 5.1. These transitions were developed into stochastic population models using the equations in Figure 5.5.1. Competition treatments are as follow: (1) 1 plant·m^{-2} with landscape fabric, (2) 9 plants·m^{-2} with landscape fabric, and (3) 9 plants·m^{-2} without landscape fabric. Transition probabilities from Year 2 of Experiment 3 are indicated by *y2*; those from Year 3 denoted by *y3*. No effect of nitrogen on transition probabilities is indicated by N/A in the column Nitrogen. Variables where competition had no effect is indicated by N/A in Treatments 2 and 3. Probabilities were separated by comparing 95% confidence intervals and those with the same letter did not differ. Differences in competition treatment are represented by (a) and (b) while nitrogen level differences are indicated by (y) and (z).

| | | | Competition Treatment | | | | | |
| | | | 1 | | 2 | | 3 | |
Experiment	Variable	Nitrogen (kg·ha^{-1})	$\hat{y}$	s^2	$\hat{y}$	s^2	$\hat{y}$	s^2
1	*e*	N/A	0.28 a	0.15	0.11 ab	0.11	0.01 b	0.03
	f	N/A	0.17	0.1	N/A	N/A	N/A	N/A
	f'	N/A	0.02	N/A	N/A	N/A	N/A	N/A
	a	N/A	9975	N/A	N/A	N/A	N/A	N/A
2	*d1*	N/A	0.01 ab	0.04	0.02 a	0.05	0.01 b	0.03
3	*e*	N/A	0.36 a	0.26	0.47 a	0.26	0.04 b	0.10
	r* (y2)	0	0.06 a y	0.11	0.12 a y	0.15	0 b y	0
	r* (y2)	62.5	0.05 a y	0.11	0.11 a y	0.15	0 b y	0
	r* (y2)	125	0.19 a z	0.19	0.34 a z	0.22	0 b z	0
	r* (y3)	N/A	0.53	0.22	N/A	N/A	N/A	N/A

Table 5.5 cont. Transition probabilities ($\hat{y}$) and variances (s^2) for fireweed as affected nitrogen level and competition treatment.

| | | | Competition Treatment | | | | | |
| | | | 1 | | 2 | | 3 | |
Experiment	Variable	Nitrogen (kg·ha⁻¹)	$\hat{y}$	s^2	$\hat{y}$	s^2	$\hat{y}$	s^2
3	r (y3)	N/A	0.16	0.14	N/A	N/A	N/A	N/A
	a	N/A	27000	1.0e+08	N/A	N/A	N/A	N/A
	a'	N/A	2	2	N/A	N/A	N/A	N/A
	b'	N/A	0.5	0	N/A	N/A	N/A	N/A

the transition (*f*), detected due to limited treatment response (Table 5.5). The end-of-season survival across Experiment 1 was 0.167.

Seed was harvested from the one fireweed plant that flowered in Experiment 1. The flowering probability (*f* ′) in Experiment 1 was estimated to be 0.02 (Table 5.5). The plant produced 9775 seeds (*a* in Table 5.5) with an average individual seed weight of 0.25 mg. Many of the seeds produced were unfilled and none germinated when tested in the laboratory.

Germination probability (*d1*) in Experiment 2 was influenced by competition (Table 5.5). It was greater in Treatment 2 than in Treatment 3, but Treatment 1 did not differ from either. Nitrogen fertilization did not affect germination (P = 0.096). No interaction between nitrogen levels and competition treatments was detected (P = 0.70).

0.0002) but nitrogen level did not (P = 0.31). Mid-season survival was greater for plants growing in Treatments 1 and 2 than for those in Treatment 3 (Table 5.5). There was no interaction between nitrogen level and competition treatment for mid-season survival (p=0.25). In Year 2, perenniation (*r*(y2)*) was affected by both nitrogen level and competition treatment [p=0.0017 and 0.0128, respectively (Table 5.5)]. Due to limited survival, analyzing the interaction between treatments was not possible (Table 5.4). Year 2 perenniation was greater in Treatments 1 and 2 than in Treatment 3 (Table 5.5). It was also greater with 125 kg·ha⁻¹ added nitrogen than with 62.5 kg·ha⁻¹ or no addition (Table 5.5).

Enough fireweed plants flowered in Year 3 to allow the assessment of flowering probability (*r(y3)*), which was 0.158 (Table 5.5), but treatment effects could not be assessed due to limited survival (Table 5.4). The probability of perenniation in Year 3 was

predicted. There were no effects of competition treatment or nitrogen level on perenniation probability ($r*(y3)$), which was 0.526 across the experiment (Table 5.5). In both cases the interaction between treatments could not be analyzed due to limited survival (Table 5.4).

Despite greater flowering than in Experiment 1, only four plants in Experiment 3 produced seed, which was harvested, but was insufficient for an analysis of treatment response. The mean number of seeds produced (a) was over 27,000·plant^{-1} (Table 5.5). The average individual seed weight without the plume was 0.19 mg. Many of the seeds harvested were unfilled, and none germinated when tested in the laboratory. Harvested plants produced an average of two buds (a' in Table 5.5). The bud germination rate (b') was 0.5 (Table 5.5).

Large mammal herbivory was an important influence on fireweed that did not affect woodland groundsel or foxglove (Chapters 3 and 4). Herbivory, in turn, was affected by an interaction between nitrogen level and competition treatment (p=0.032). Plants fertilized with 125 kg·ha^{-1} nitrogen had a greater probability of being browsed than those fertilized with 62.5 kg·ha^{-1} nitrogen or receiving no fertilization when grown in Treatment 2 (Figure 5.3). Plants grown in Treatment 1 without nitrogen fertilizer were least likely to be browsed. There were no effects of nitrogen fertilization level on herbivory for plants in Treatment 3.

The effects of competition on fireweed survival in Experiments 1 and 3 are consistent with those observed in other studies where associated vegetation reduces seedling survival (van Andel and Rozema 1974, van Andel and Nelissen 1979). The year-end survival probability from Experiment 1 was similar to that at Mount St. Helens (Wood and Morris 1990). The lack of flowering response to fertilization was similar to the results
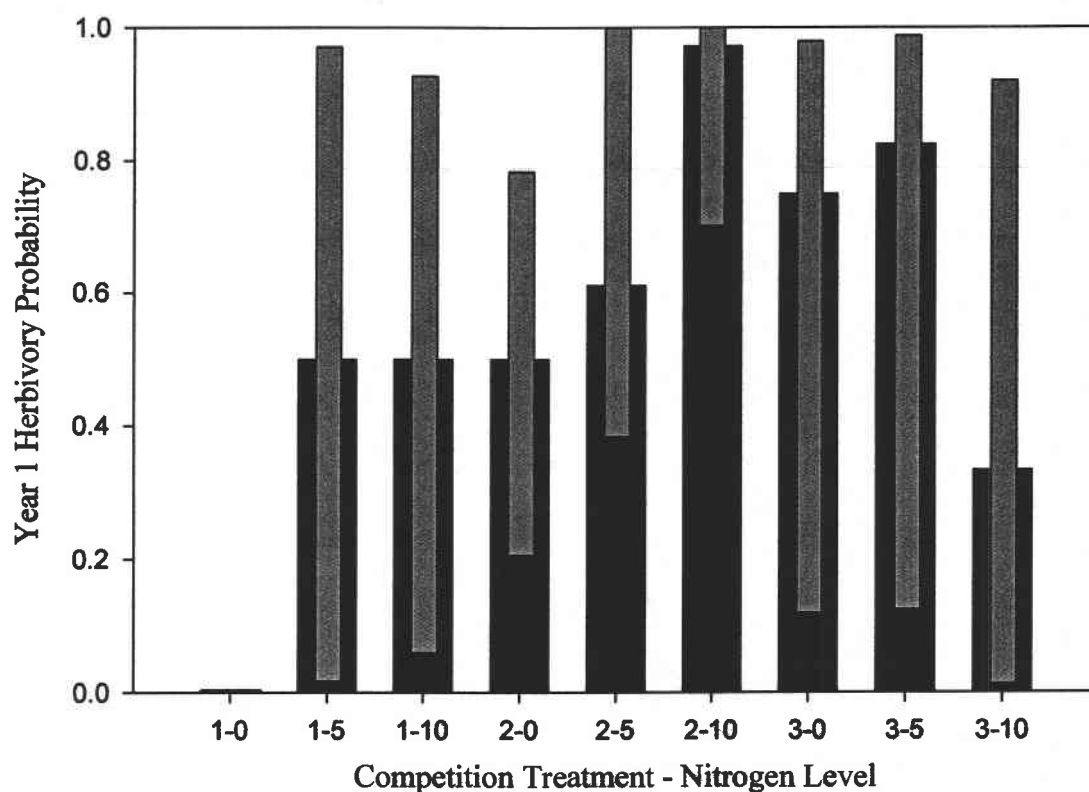
Figure 5.3. Estimated probability for fireweed Year 1 herbivory as affected by competition treatment and nitrogen level in Experiment 3. Competition treatments are as follows; (1) 1 plant·m^{-2} with landscape fabric, (2) 9 plants·m^{-2} with landscape fabric, and (3) 9 plants·m^{-2} without landscape fabric. Nitrogen levels are; (0) no added nitrogen (12.5 kg·ha^{-1} ambient), (5) 62.5 kg·ha^{-1} added nitrogen, and (10) 125 kg·ha^{-1} added nitrogen. Larger bars (▌) indicate the mean probability for each combination and the smaller bars (▯) represent the upper and lower 95 percent confidence limits. There was no interaction between nitrogen level and competition treatment for perenniation but there was for herbivory.

of a greenhouse study (van Andel and Vera 1977). The differences in germination observed among the competition treatments in Experiment 2 were likely due to temperature as postulated for the other two species studied (Chapters 3 and 4) rather than differences in competition. Fireweed seed germination responds to warm temperatures (Livingston 1977, Jobidon 1968, Myerscough and Whitehead 1966). The landscape fabric used in Treatments 1 and 2 could have raised the ambient temperature sufficiently to affect germination. Fertilization effects on germination and seedling establishment like those observed by van Andel and Vera (1977) were not found in Experiment 2, since associated vegetation was not present at germination.

The transition probabilities used in the stochastic population model for fireweed were developed from the field experiments (Table 5.5). Incorporating these values into the conceptual model (Figure 5.1) results in two different transition matrices. For Experiment 1, the following matrix was created:

$$E_1 = \begin{pmatrix} 0 & 0 & 1.857 & 0 \\ 0.017 & 0.25 & 0.005 & 0.041 \\ 0.002 & 0.75 & 1.001 & 0.005 \\ 0 & 0 & 1 & 0.75 \end{pmatrix} \qquad (26)$$

Despite the effects of nitrogen level on the estimated transition parameters in Experiment 3, the transition matrices developed from these data were essentially unaffected by it. The matrix produced for the no nitrogen level was:

$$
E_3 = \begin{pmatrix} 0 & 0 & 5.155 & 0 \\ 0.023 & 0.059 & 0.019 & 0.167 \\ 0 & 0.158 & 1 & 0 \\ 0 & 0 & 2 & 0.75 \end{pmatrix} \qquad (27)
$$

There were only trivial changes in the transition matrix with 62.5 kg·ha^{-1} added nitrogen (differences that would be lost in rounding). With 125 kg·ha^{-1} added nitrogen, the element for survival of immature plants, $e_{3(2,2)}$, changed to 0.194.

The projected fireweed population was unaffected by treatment, nor did it differ between Experiments 1 and 3 (Figure 5.4). In Experiment 1, the projected mature plant population rose to 0.3 plants·m^{-2} in Year 6 (Figure 5.4A). The immature population was over 0.2 plants·m^{-2} in Year 1 then dropped below 0.1 plants·m^{-2} for subsequent years in the simulation (Figure 5.4A). The buried seed bank and buds rose to over 0.5 and 0.6 propagules·m^{-2}, respectively, at Year 6 (Figure 5.4B). Six simulations were conducted to account for the differences in competition treatment and nitrogen fertilization level effects in Experiment 3. The maximum and minimum projected mean populations for these simulations are presented for each stage (Figure 5.4C and 5.4D). Data from plots without fertilization and with "arranged competition" produced the minimum populations and data from plots with 125 kg·ha^{-1} nitrogen and the actual, year-to-year transitions produced the maximum populations, but these population values were not statistically different. The simulated mature plant population reached 0.15 and 0.2 plants·m^{-2}, for the maximum and minimum, respectively (Figure 5.4C). The projected maximum and minimum values for the immature population were 0.25 and 0.15 plants·m^{-2}, respectively (Figure 5.4C). The
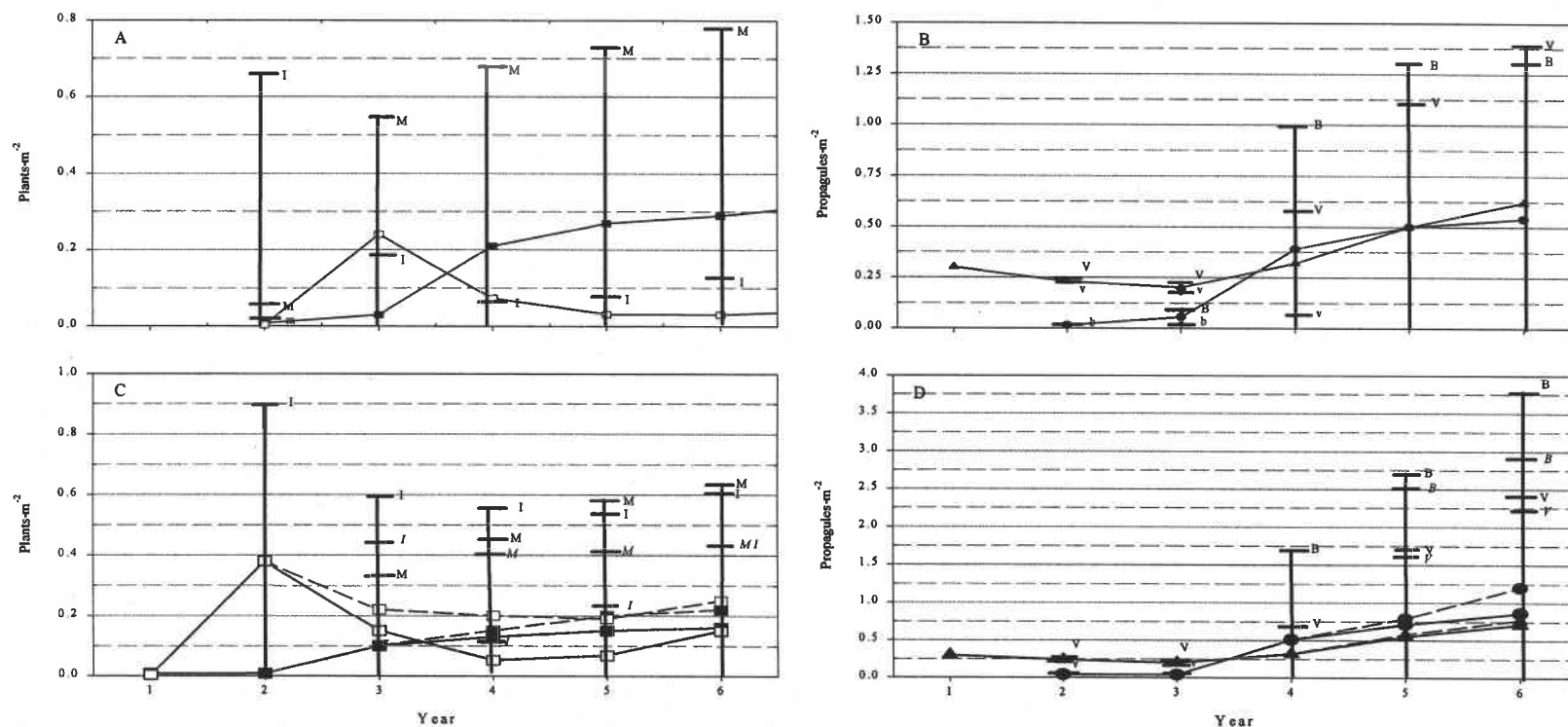
Figure 5.4. Projected mean population density of fireweed in stochastic simulations. Responses are for (A) plants and (B) propagules in Experiment 1 and (C) plants and (D) propagules in Experiment 3. Mature and immature plants (plants·m^{-2}) are represented by (—■— and —⊠—, respectively) while buried seed bank (seeds·m^{-2}) and bud densities (buds·m^{-2}) are represented by (—●— and —▲—, respectively). When two means for the same state are presented maximum projections are indicated by (- - -) while minimum projections are represented by (——). Vertical bars represent confidence intervals of ± one standard error. The horizontal lines on each bar indicate where the standard errors are for the matching state and are labeled as follows; (M) mature, (I) immature, (B) buried seed bank, and (V) buds with the lower confidence interval in italics. Again, where two means are presented, the standard error for the maximum projection is represented by uppercase letter while that for the minimum projection has a lowercase one. Since the population cannot fall below zero, the lower confidence intervals are truncated at that level.

maximum projected bud population was 0.85 buds·m^{-2} and the minimum was 0.7 buds·m^{-2} (Figure 5.4D). The buried seed bank was somewhat larger, with a minimum population of 0.85 seeds·m^{-2} and a maximum of 1.2 seeds·m^{-2} (Figure 5.4D).

The asymptotic population growth rate, λ, did not vary substantially among the various forms of the stochastic population model. For Experiment 1's model, λ was 1.14 in Year 1 and declined to 1.12 for subsequent years. For Experiment 3, it was 1.14 in Year 1 with no added nitrogen or with 62.5 kg·ha^{-1} added and 1.16 with 125 kg·ha^{-1} added nitrogen. The λ value increased in subsequent years of Experiment 3, reaching 1.19 in Year 6 for both the minimum- and maximum-producing models. In all cases, the value of λ indicates exponential growth but at a low rate (Caswell 1989).

Sensitivity analysis was conducted on the transition matrices for Experiment 1 ($\mathbf{E}_1$) and Experiment 3 ($\mathbf{E}_3$), including the variants for the different elements arising from nitrogen levels. Matrix $\mathbf{E}_1$ was most sensitive to the transitions from buds to mature and immature plants, with values of 1.811 and 1.532, respectively, in Year 1. Despite changes in immature plant survival due to fertilization, matrix $\mathbf{E}_3$ was most sensitive to the development of buds and BSB seed to mature plants in all cases. The sensitivities in Year 1 were 3.1 and 3.5 for seed and buds, respectively, both without fertilization and with 62.5 kg·ha^{-1} nitrogen; with 125 kg·ha^{-1} of added nitrogen they were 3.0 for seeds and 3.3 for buds. The sensitivity indices varied slightly among years but the same stages were always most responsive.

Elasticities, the relativized sensitivities, indicated that all the models for fireweed were most influenced by the survival of mature plants. Elasticities ranged from 0.49 for $\mathbf{E}_3$ with 125 kg·ha^{-1} added nitrogen in Year 3, to 0.62 for $\mathbf{E}_1$. The next most important

element was survival of buds, with elasticities ranging from 0.13 for E_1, to 0.16 for E_3 with 125 kg·ha^{-1} added nitrogen in Year 3.

The projections of the deterministic and stochastic models are not substantially different. Both project exponentially growing populations, although the average growth rate is higher with the deterministic simulations. Both also project populations far lower than those observed in the field. The models projected a mean shoot density of between 0.3 and 0.6 shoot·m^{-2} after six years. This is much lower than observed densities of 26 shoots·m^{-2} at the same age in the field (van Andel 1975). Given that elasticity analysis for both model types indicated that the transitions involving mature plants and buds were most influential, these parameter estimates are the ones requiring close inspection. The transition rates for bud survival and germination into mature and immature shoots were educated guesses. It seems plausible that the estimates for bud production and, perhaps, bud germination are too low. An experiment conducted specifically to address those transition rates would improve the projections of these models.

This study determined that vegetative reproduction is the critical mode for fireweed regeneration on a site. These results are similar to those for northern populations of wild leek (Nault and Gagnon 1993). Sexual reproduction was found to have a minimal impact of the population dynamics of both species where they were established. Large mammal herbivory is also suspected of playing a role fireweed's persistence but the mode of action was not determined. The development *Lathyrus vernus* populations were more sensitive to meristem damage than to grazing (Ehrlén 1995) and the apical meristem of fireweed would be most susceptible feeding by large mammals. Whether the effects of herbivory are due to loss of shoot tissue or damage to the meristem is worthy of investigation. Unlike

other work that used multiple transition matrices (Maschinski *et al.* 1997, Nault and Gagnon 1993), this study arranged them in a sequence to reflect changes in the environment over time. If, for example, the good and bad years for sentry milk-vetch (Maschinski *et al.* 1997), reflected a cyclic climatic pattern, the transition matrices could be arranged in yearly sequence. This arrangement could produce a more cyclic population trend differing greatly from the results of evaluating the years individually where populations become extinct in less than 100 years or increase continuously.

Several considerations for fireweed management are raised by this research. Seed germination and seedling establishment are both sensitive to environmental conditions, some of which can be manipulated. Both processes are adversely affected by competition; therefore maintaining groundcover could provide an effective means of management. After a population has become established, management of the seed population is no longer important locally. At that point, factors that affect vegetative reproduction are more effective for management. This research has not specifically identified factors that influence bud production, but interspecific competition does reduce shoot survival and could be used as a management tactic. Nitrogen fertilization could also be used to increase herbivory, which in turn would reduce plant vigor.

CONCLUSIONS

Competition level and nitrogen fertilization both affected individual transition rates but did not impact the overall population growth rate. As with foxglove (Chapter 4), demographic stochasticity generally had a greater effect on population dynamics than either

of these environmental variables.   Vegetative reproduction was far more important to

population growth rate on a site than was sexual reproduction.

LITERATURE CITED

Adams, A. B. and V. H. Dale. 1987. Vegetative succession following glacial and volcanic disturbances in the Cascade Mountain range of Washington, U.S.A. Pages 70-147 *in* D. E. Bilderback, ed. Mount St. Helens 1980: Botanical Consequences of the Explosive Eruptions. Berkeley, CA: University of California Press.

van Andel, J. 1976. Growth and mineral nutrition of *Chamaenerion angustifolium* (L.) Scop. (=*Epilobium angustifolium* L.) on culture solutions. Oecol. Plant. 1:25-40.

van Andel, J. 1975. A study on the population dynamics of the perennial plant species *Chamaenerion angustifolium* (L.) Scop. Oecologia 19:329-37.

van Andel, J. and J. C. Jager. 1981. Analysis of growth and nutrition of six plant species of woodland clearings. J. Ecol. 69:871-82.

van Andel, J. and H. J. M. Nelissen. 1979. Nutritional status of soil and plant species in several clearings in coniferous woods compared to that in two related habitats. Vegetatio 39:115-21.

van Andel, J. and J. Rozema. 1974. An experiment on reproduction from seed within existing populations of *Chamaenerion angustifolium* (L.) Scop. Plant Soil 41:415-9.

van Andel, J. and F. Vera. 1977. Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. J. Ecol. 65:747-58.

Antos, J. A. and C. B. Halpern. 1997. Root system differences among species: Implications for early successional changes in forests of western Oregon. Am. Midl. Nat. 138:97-108.

Bailey, J. A. and D. Hoogland. 1984. The response of *Epilobium* species to a range of soil and foliar acting herbicides. Aspects Appl. Biol. 8:43-52.

Ballaré, C. L., A. L. Scopel, and R. A. Sanchez. 1990. Far-red radiation reflected from adjacent leaves: An early signal of competition in plant canopies. Science 247:329-32.

Bentham, G. 1904. Handbook of British Flora. London: L. Reeve and Co. 584 pp.

Bianco, J. 1990. Managing fireweed on problem coastal sites. FRDA Memo No. 163. British Columbia Ministry of Forests. 8 pp.

Bliss, D. and H. Smith. 1985. Penetration of light into soil and its role in the control of seed germination. Plant Cell Environ. 8:475-83.

Broderick, D. H. 1990. The biology of Canadian weeds. 93. *Epilobium angustifolium* L. (Onagraceae). Can. J. Plant Sci. 70:247-59.

Broderick, D. H. 1980. The Establishment and Maintenance of Fireweed in Disturbed and Undisturbed Sites at Schefferville. M.S. thesis, Montreal, Quebec, Canada: McGill University. 162 pp.

Caswell, H. 1989. Matrix Population Models. Sunderland, MA: Sinauer Associates, Inc. 328 pp.

Comeau, P. 1988. Light attenuation by thimbleberry-fireweed communities in the ICH zone and its potential effects on conifer growth. Pages 5-7 *in* E. Hamilton and S. Watts, eds.Vegetation Competition and Response: Proceedings of the Third Annual Vegetation Management Workshop.Vancouver, B.C., Canada : BC Ministry of Forests.

Conn, J. J. and J. A. DeLapp. 1983. Changes in weed-species assemblages with increasing field age. Agroborealis 15:39-41.

Czerepanov, S. K. 1995. Vascular Plants of Russia and Adjacent States (the Former USSR). Cambridge, U.K.: Cambridge University Press. 516 pp.

Dahlgren, R. and P. Lassen. 1972. Studies in the flora of northern Morocco. I. Some poor fen communities and notes on a number of northern and Atlantic plant species. Bot. Not. 125:439-64.

Ehrlén, J. 1995. Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population dynamics. J. Ecol. 83:297-308.

Eriksson, O., J. Ehrlen, A. Telenius, and H. Froborg. 1995. Dynamics and abundance of field layer plants in a deciduous wood at Tullgarn, province of Sodermanland. *Sven. Bot. Tidskr.* 89:91-107.

Ginns, J. H. 1986. Compendium of Plant Disease and Decay Fungi in Canada, 1960 to 1980 Volume Agriculture Canada Publ. V. 1812. Ottawa, Ontario, Canada: Ottawa Research Branch, Series A. 416 pp.

Goodwin, W. 1930. Fungal Diseases of Plants in Agriculture, Horticulture, and Forestry. London: Balliere, Tindel, and Co. 526 pp.

van Groenendael, J. M., H. de Kroon, S. Kalisz, and S. Tuljapurkar. 1994. Loop analysis: Evaluating life history pathways in population projection matrices. Ecology 75:2410-5.

Hanson, H. C. 1962. Dictionary of Ecology. New York: Philosophical Library. 278 pp.

Henderson, G., P. G. Holland, and G. L. Werren. 1979. The natural history of a subarctic adventive: *Epilobium angustifolium* (Onagraceae) at Schefferville, Quebec. Nat. Can. 106:425-37.

Hill, M. O. and P. A. Stevens. 1981. The density of viable seeds in soils of forest plantations in upland Britain. J. Ecol. 69:693-709.

Ingram, D. C. 1931. Vegetative changes in grazing use on Douglas-fir cutover land. J. Agric. Res. 43:387-417.

Jobidon, R. 1968. Allelopathic potential of coniferous species to old-field weeds in eastern Canada. For. Sci. 32:112-8.

Livingston, P. L. 1977. The Reproductive Biology and Revegetation Potential of Fireweed in Alaska. Division III thesis, 60 pp.

Maschinski, J., R. Frye, and S. Rutman. 1977. Demography and population viability of an endangered plant species before and after protection from trampling. Conserv. Biol. 11:990-9.

Mosquin, T. 1967. Evidence for autopolyploidy in *Epilobium angustifolium* (Onagraceae). Evolution 21:713-9.

Myerscough, P. J. 1980. Biological flora of the British Isles. J. Ecol. 68:1047-74.

Myerscough, P. J. and F. H. Whitehead. 1967. Comparative biology of *Tussilago farfara* L., *Chamaenerion angustifolium* (L.) Scop., *Epilobium montanum* L. and *Epilobium adenocaulon* Hausskn. 1. Growth and ecology. New Phytol. 66:785-823.

Myerscough, P. J. and F. H. Whitehead. 1966. Comparative biology of *Tussilago farfara* L., *Chamaenerion angustifolium* (L.) Scop., *Epilobium montanum* L. And *Epilobium adenocaulon* Hausskn. 1. General biology and germination. New Phytol. 65:193-210.

Nault, A. and D. Gagnon. 1993. Ramet demography of *Allium tricoccum*, a spring ephemeral, perennial forest herb. J. Ecol. 81:101-19.

Niethammer, A. 1927. Keimungsphysiologische Studien unter Herborhebung des Lichtkeimungsproblems. Biochem. Z. 185:205-15.

Pojar, J. and A. MacKinnon. 1994. Plants of the Pacific Northwest Coast. Redmond, WA: Lone Pine Publishing. 527 pp.

Radosevich, S. R., J. S. Holt, and C. M. Ghersa. 1997. Weed Ecology: Implications for Management. 2 ed. New York: John Wiley & Sons. 589 pp.

Rickett, H. W. 1973. Wild Flowers of the United States Volume 6; The Central Mountains and Plains. New York: McGraw-Hill. 784 pp.

Salisbury, E. J. 1942. The Reproductive Capacity of Plants. London: Bell and Sons, Ltd. 244 pp.

Salisbury, E. J. 1961. Weeds and Aliens. London: Collins Publishing Co. 384 pp.

Simard, S. and Nicholson A. 1990. Balancing the positive and negative effects of non-crop plants on conifers: Pinegrass, fireweed, Sitka alder and paper birch--friend or foe. Pages 45-48 in E. Hamilton, ed. Vegetation Management: An Integrated Approach; Proceedings of the Fourth Annual Vegetation Management WorkshopVictoria, B.C. Canada: B.C. Ministry of Forests.

Solbreck, C. and D. Andersson. 1987. Vertical distribution of fireweed, *Epilobium angustifolium*, seeds in the air. Can. J. Bot. 65:2177-8.

Vodlazsky, L. E. 1979. Concerning variation of adventive buds and shoots from root-offspring of the herbaceous perennial *Chamaenerion angustifolium* (L.) Scop. (Onagraceae). Bot. J. Acad. Sci., SSSR 64:734-9.

Willms, W., A. McLean, R. Tucker, and R. Ritcey. 1980. Deer and cattle diets on summer range in British Columbia. *J. Range Manage.* 33:55-9.

Wood, D. M. and W. F. Morris. 1990. Ecological constraints to seedling establishment on the Pumice Plains, Mount St. Helens, Washington. Am. J. Bot. 77:1411-8.

Wright, R. G. and G. Van Dyne. 1981. Population age structure and its relationship to the maintenance of a semidesert grassland undergoing invasion by mesquite. Southwest. Nat. 26:13-22.

CHAPTER 6: SUMMARY

This research examined many of the factors that are associated with the longevity of fireweed, foxglove, and woodland groundsel in early seral stages of Douglas-fir communities of western Washington and Oregon. Environmental factors affected all three species. Increased complexity of the species' life history (*i.e.*, increased linkages among the states in the population model) resulted in greater influence of environmental conditions, either through increased number of environmental factors having an effect or through interactions among them. The population dynamics models developed described limiting factors that were intrinsic in each species' life cycle. Field-level fertilization/competition experiments provided the data for these models. This information provides a basis for more species-specific management and allows testing of the hypothesis that populations of other species with similar life history characteristics will respond in the same manner as did the target species.

The three species had different responses to environmental conditions. Woodland groundsel frequency was negatively related to UTM meters east. This variable indicates a decline in frequency moving eastward that may reflect its dispersal pattern since invading the region. Woodland groundsel cover was negatively related to stand age. Foxglove was negatively correlated with elevation and positively related to disturbance, as indicated by broadcast silvicultural treatments such as burning or spraying, and to site productivity. Its cover was negatively related to organic debris cover. In contrast to foxglove, fireweed was negatively correlated with disturbance and site productivity. Its frequency was related to an interaction between stand age, which had a negative effect, and elevation, which had a

positive one. Fireweed cover was positively related to moving eastward and herbaceous vegetation height.

Based on these results, other factors besides stand age were found to affect the species residence time in the forest community depending on its geographic location and disturbance characteristics. Foxglove, while being negatively related to stand age empirically, was not explicitly found to be so in this study. Fireweed would be expected to be more abundant in a more easterly community than either woodland groundsel or foxglove. A decline in woodland groundsel cover and fireweed frequency (at low elevation) is anticipated with increasing stand age, while in stands at higher elevations fireweed would be expected to show a positive effect of age. This decline would occur more rapidly for woodland groundsel than fireweed. Woodland groundsel and foxglove have more similar environmental requirements than fireweed. Foxglove and fireweed are inversely related in their environmental requirements. Foxglove's response to organic debris cover, silvicultural treatments, and site productivity suggest that it is stimulated by disturbance while fireweed is reduced by it. This relationship suggests that in communities where one species is increasing, the other would decline.

Among the three species, two different types of population models were developed in this study. The model for woodland groundsel, an annual, involved transitions among stages within a year. This transition structure resulted in more stages for the model than for the other two species. The foxglove and fireweed models had fewer stages and the transitions among them occurred between years. Both latter models had numerous potential intra-annual transitions that were not explicitly expressed because of the model structure selected.

The models indicated which transition(s) controlled the plant population's development. For woodland groundsel, the simulated population was regulated by seed production. Iteroparity was the limiting transition rate for modeled foxglove populations-- an interesting condition for a biennial species that by definition should be monocarpic. Two cohorts of germinants from the seed bank increased the persistence of the foxglove population dramatically over a single one in these simulations. Mature plant persistence constrained simulated fireweed population growth most, which was followed closely by bud persistence and the transitions between mature plants and buds. Further analysis of the model indicated that maintenance of the extant fireweed population was entirely due to vegetative reproduction. The models suggest that as the life cycle of the species became more complex, their reliance on vegetative reproduction increased. The results of these simulations represent possible hypotheses to be tested in field experiments.

Growth of all three species responded less to nitrogen fertilization than to competition, although timing of the fertilizer application was important in affecting both variables. Woodland groundsel height increased when the highest fertilizer rate was applied at transplanting. Plant height also increased under competition with nitrogen fertilization at transplanting. Both shoot and root biomass along with individual seed production decreased with competition when fertilizer was applied the previous year. The intermediate fertilizer level applied the previous year resulted in decreased foxglove root and shoot biomass that was not observed when fertilization occurred at transplanting. Increased competition generally reduced foxglove size, biomass, and seed production and the effects were more pronounced when transplanting was delayed relative to fertilization. Second-year foxglove height was affected by an interaction between fertilizer rate and

competition when fertilizer was applied at transplanting. Fireweed height exhibited a similar interaction between nitrogen and competition but it occurred when transplanting was delayed one year relative to fertilization. Fertilizing immediately prior to transplanting resulted in an increase in fireweed height, which was the only other fertilizer effect detected for the species. Competition resulted in increased fireweed canopy diameter and height with fertilization at transplanting, but canopy diameter decreased when fertilizer was applied the previous year.

Population transition rates responded to competition and fertilization treatments. Interspecific competition affected woodland groundsel establishment and seed production when transplanting was delayed relative to fertilization. Increased competition affected many of foxglove's transition rates independent of fertilization timing. Fertilization primarily affected foxglove reproduction, specifically rosette persistence and flowering. Persistence of two-year-old, immature fireweed plants increased with fertilization and intraspecific competition, while interspecific competition reduced establishment and eliminated immature persistence.

Despite all the differences detected among individuals responding to fertilization and competition treatments, the population models indicated that these factors had relatively little influence on population development. Mature woodland groundsel populations generally increased less rapidly using empirically-derived parameter estimates than the literature-based ones but there were no effects of the experimental treatments on the values of the empirical parameters. Similarly, projected fireweed plant and propagule density were unaffected by fertilization or competition despite the fact that there were treatment differences in the transition rate estimates. The simulated foxglove populations

did respond to fertilizer timing, however. Establishment a year after fertilizing resulted in an increasing projected population, while population decline was projected for foxglove establishing immediately after fertilization. Competition treatments and fertilization levels within an application timing, however, did not affect the projected populations of foxglove.

These results suggest that, although individuals may have detectable responses to the competition and fertilization treatments, the populations are less sensitive to these effects. For these species, the limited population probability response results from the plasticity of individuals within the population. Plasticity creates greater variation in the population damping the effects of individual performance.

These results also suggest that the species may respond to factors on a larger scale than the population. For example, both fireweed and woodland groundsel had minimal responses to population-level treatments such as nitrogen fertilization and competition manipulation. Since both species are wind-dispersed, the role of metapopulation dynamics, *i.e.*, movement of population over a landscape in time and space, may have a greater affect on their presence and persistence in a plant community. This possibility maybe especially true for woodland groundsel, which lacks the capability of vegetative reproduction. In contrast to the spatial dynamics of woodland groundsel, foxglove's own form of metapopulation dynamics is strictly temporal. Foxglove's buried seedbank serves the same function as the wind-dispersed seeds in the other two species. It allows foxglove to colonize communities that are temporally disjunct rather than spatially so.

Although there are a variety of plant population dynamics models, two of the most common types are difference equations and matrices. Difference equations are more commonly used for species with relatively simple life histories, such as annuals, while

matrices are chosen for those species with more numerous life stages and complex interactions among them. Sagar and Mortimer's (1976) different approaches to modeling semalparous and iteroparous plant species illustrate this point. Semalparous species' models were designed in a manner best suited for a difference equation, while ones for iteroparous species would fit a matrix model. Many of the models created are species specific incorporating unique life history aspects. Many of the stages for these different models are the same, however, mature, immature, and buried seed bank in the foxglove and fireweed models, for example. It seems plausible that a general plant population model could be created that would allow simulation of population dynamics for all species of plant independent of life history. A matrix model could be used to accommodate more complex life cycles by increasing the number of stages for species with numerous stages. Both the types and rates of transitions among the stages would vary from species to species but the uniform structure would ease comparisons of population response among species to various perturbations.

This research has implications for vegetation management because the populations of undesirable species can be indirectly affected by silvicultural tactics. Fireweed, for example, is favored by lack of disturbance, while foxglove is stimulated by it. Thus, silvicultural treatments to control one species could favor the other if both are present on the site. Woodland groundsel, on the other hand, may be relatively unaffected by silvicultural treatments other than stand removal. It may be a naturalized component of very early seral forest communities and will decline rapidly after an initial colonization following tree harvest. The effects of metapopulations on vegetation management are poorly understood, but must be considered strategically. This strategic approach would

involve managing not only existing population, but also potential sites for colonization

considering both spatial and temporal elements of those uncolonized areas.

BIBLIOGRAPHY

Adams, A. B. and V. H. Dale. 1987. Vegetative succession following glacial and volcanic disturbances in the Cascade Mountain range of Washington, U.S.A. Pages 70-147 *in* D. E. Bilderback, ed. Mount St. Helens 1980: Botanical Consequences of the Explosive Eruptions. Berkeley, CA: University of California Press.

van Andel, J. 1976. Growth and mineral nutrition of *Chamaenerion angustifolium* (L.) Scop. (=*Epilobium angustifolium* L.) on culture solutions. Oecol. Plant. 1:25-40.

van Andel, J. 1975. A study on the population dynamics of the perennial plant species *Chamaenerion angustifolium* (L.) Scop. Oecologia 19:329-37.

van Andel, J. and W. H. O. Ernst. 1985. Ecophysiological adaptation, plastic responses, and genetic variation of annuals, biennials, and perennials in woodland clearings. Pages 27-49 *in* J. Haeck and J. W. Woldendorp, eds. Structure and Functioning of Plant Populations 2: Phenotypic and Genetic Variation in Plant Populations. Amsterdam: Noth-Holland Publishing.

van Andel, J. and J. C. Jager. 1981. Analysis of growth and nutrition of six plant species of woodland clearings. J. Ecol. 69:871-82.

van Andel, J. and H. J. M. Nelissen. 1981. An experimental approach to the study of species interference in a patchy vegetation. Vegetatio 45:155-63.

van Andel, J. and H. J. M. Nelissen. 1979. Nutritional status of soil and plant species in several clearings in coniferous woods compared to that in two related habitats. Vegetatio 39:115-21.

van Andel, J. and J. Rozema. 1974. An experiment on reproduction from seed within existing populations of *Chamaenerion angustifolium* (L.) Scop. Plant Soil 41:415-9.

van Andel, J. and F. Vera. 1977. Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. J. Ecol. 747-58.

Antos, J. A. and C. B. Halpern. 1997. Root system differences among species: Implications for early successional changes in forests of western Oregon. Am. Midl. Nat. 138:97-108.

Avina, K. A. 1997. Revegetation of Ferns and Herbs Following Different Methods of Timber Harvest in the Yurok Experimental Forest, A Coast Redwood Type. M.S. thesis, Arcada, CA: Humbolt State University. 58 pp.

van Baalen, J. 1982. Germination ecology and seed population dynamics of *Digitalis purpurea*. Oecologia 53:61-7.

van Baalen, J., A. Th. Kuiters, and C. S. C. van der Woude. 1984. Interference of *Scrophularia nodosa* and *Digitalis purpurea* in mixed seedling cultures, as affected by the specific emergence date. Acta Oecol. 5:279-90.

van Baalen, J. and E. G. M. Prins. 1983. Growth and reproduction of *Digitalis purpurea* in different stages of succession. Oecologia 58:84-91.

Bailey, A. W. and C. E. Poulton. 1968. Plant communities and the environmental interrelationships in a portion of the Tillamook Burn, northwestern Oregon. Ecology 49:1-13.

Bailey, J. A. and D. Hoogland. 1984. The response of *Epilobium* species to a range of soil and foliar acting herbicides. Aspects Appl. Biol. 8:43-52.

Bailey, J. D. and J. C. Tappeiner. 1998. Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon. Forest Ecol. Manage. 108:99-113.

Ballaré, C. L., A. L. Scopel, C. M. Ghersa, and R. A. Sanchez. 1987. The population ecology of *Datura ferox* in soybean crops: A simulation approach incorporating seed dispersal. Agric. Ecosyst. Envir. 19:177-88.

Ballaré, C. L., A. L. Scopel, and R. A. Sanchez. 1990. Far-red radiation reflected from adjacent leaves: An early signal of competition in plant canopies. Science 247:329-32.

Bauer, T. A. and D. A. Mortensen. 1992. A comparison of economic and economic optimum thresholds for two annual weeds in soybeans. Weed Tech. 6:228-35.

Bazzaz, F. A., D. D. Ackerly, F. I. Woodward, and I. Rochefort. 1992. CO_2 enrichment and dependence of reproduction on density in an annual plant and a simulation of its population dynamics . J. Ecol. 80:643-51.

Benech Arnold, R. L., C. M. Ghersa, R. A. Sanchez, and P. Insauti. 1990. A mathematical model to predict *Sorghum halepense* (L.)Pers. seedling emergence in relation to soil temperature. Weed Res. 30:91-9.

Bentham, G. 1904. Handbook of British Flora. London: L. Reeve and Co. 584 pp.

Bianco, J. 1990. Managing fireweed on problem coastal sites. FRDA Memo No. 163. British Columbia Ministry of Forests. 8 pp.

Bishir, J. and Namkoong G. 1992. Density-dependent dynamics in size-structured plant populations. J. Theor. Biol. 154:163-88.

Bjørnstad, O. N., M. Begon, N. C. Stenseth, W. Falck, S. M. Sait, and D. J. Thompson. 1998. Population dynamics of the Indian meal moth: demographic stochasticity and delayed regulatory mechamisms. J. Animal Ecol. 67:110-26.

Bliss, D. and H. Smith. 1985. Penetration of light into soil and its role in the control of seed germination. Plant Cell Environ. 8:475-83.

Bonan, G. B. 1991. Density effects on the size structure of annual plant populations: An indication of neighbourhood competition. Ann. Bot. 68:341-7.

Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60:849-73.

Broderick, D. H. 1990. The biology of Canadian weeds. 93. *Epilobium angustifolium* L. (Onagraceae). Can. J. Plant Sci. 70:247-59.

Broderick, D. H. 1980. The Establishment and Maintenance of Fireweed in Disturbed and Undisturbed Sites at Schefferville. M.S. thesis, Montreal, Quebec, Canada: McGill University. 162 pp.

Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. Risk Assessment in Conservation Biology. London: Chapman & Hall. 314 pp.

Burgman, M. A. and B. B. Lamont. 1992. A stochastic model for the viability of *Banksia cuneata* populations: Environmental, demographic, and genetic effects. J. Appl. Ecol. 29:719-27.

Caswell, H. 1989. Matrix Population Models. Sunderland, MA: Sinauer Associates, Inc. 328 pp.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters . Theor. Popul. Biol. 14:215-30.

Chapin, D. M. 1995. Physiological and morphological attributes of two colonizing plant species on Mount St. Helens. Am. Mid. Nat. 133:76-87.

Chouard, P. 1951. Plantes bisannuelles vraies et fausses bisannuelles. 2) Relation entre la bisannualité et la vernalsation, le photoperiodisme, la dispersion geographique et la taxinomie. Bull. Soc. Bot. France 98:117-20.

Clarke, K. C. 1990. Analytical and Computer Cartography. Englewood Cliffs, N.J.: Prentice Hall. 290 pp.

Clements, F. E. 1916. Plant Succession; An Analysis of the Development of Vegetation. Washington, D.C. Carnegie Inst. Wash. Publ. 242. Carnegie Institute of Washington. 512 pp.

Comeau, P. 1988. Light attenuation by thimbleberry-fireweed communities in the ICH zone and its potential effects on conifer growth. Pages 5-7 *in* E. Hamilton and S. Watts, eds. Vegetation Competition and Response: Proceedings of the Third Annual Vegetation Management Workshop. Vancouver, B.C., Canada : BC Ministry of Forests.

Conn, J. J. and J. A. DeLapp. 1983. Changes in weed-species assemblages with increasing field age. Agroborealis 15:39-41.

Connell, J. and R. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111:1119-44.

Connor, H. E. 1977. The Poisonous Plants in New Zealand. Wellington, N.Z.: Government Printer. 246 pp.

Cousens, R., C. J. Doyle, B. J. Wilson, and G. W. Cussans. 1986. Modelling the economics of controlling *Avena fatua* in winter wheat. Pest. Sci. 17:1-12.

Cousens, R., S. R. Moss, G. W. Cussans, and B. J. Wilson. 1987. Modeling weed populations in cereals. Pages 93-108 *in* C. L. Foy, ed. Reviews of Weed Science. Volume 3. Champaign, IL: Weed Science Society of America.

Czerepanov, S. K. 1995. Vascular Plants of Russia and Adjacent States (the Former USSR). Cambridge, U.K.: Cambridge University Press. 516 pp.

Dahlgren, R. and P. Lassen. 1972. Studies in the flora of northern Morocco. I. Some poor fen communities and notes on a number of northern and Atlantic plant species. Bot. Not. 125:439-64.

Dennis, L. R. J. 1980. Gilkey's Weeds of the Pacific Northwest. Corvallis, OR: Oregon State University Press. 382 pp.

Doyle, C. J. 1991. Mathematical models in weed management. CP 10:432-44.

Doyle, C. J., R. Cousens, and S. R. Moss. 1986. A model of the economics of controlling *Alopecurus myosuroides* Huds. in winter wheat. CP 5:143-50.

Drury, W. and I. Nisbet. 1973. Succession. J. Arn. Arbor. 54:331-68.

Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology 54:57-69.

Egler, F. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio :412-7.

Ehrlén, J. 1995. Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population dynamics. J. Ecol. 83:297-308.

Ellenberg, H. 1988. Vegetation Ecology of Central Europe [Vegetation Mitteleuropas mit den Alpen]. 4th ed. Cambridge, UK: Cambridge Universtiy Press. 731 pp.

Eriksson, O., J. Ehrlen, A. Telenius, and H. Froborg. 1995. Dynamics and abundance of field layer plants in a deciduous wood at Tullgarn, province of Sodermanland. Sven. Bot. Tidskr. 89:91-107.

Ernst, W. H. O. 1993. Population dynamics, evolution, and environment: Adaptation to environmental stress. Pages 19-44 *in* L. Fowden, T. Mansfield, and J. Stoddart, eds. Plant Adaptation to Environmental Stress. London: Chapman and Hall.

Ernst, W. H. O. 1985. The effects of forest management on the genetic variability of plant species in the herb layer. Pages 200-11 *in* H. R. Gregorius, ed. Population Genetics in Forestry. Berlin: Springer-Verlag.

Ernst, W. H. O. and H. J. M. Nelissen. 1979. Growth and mineral nutrition of plant species from clearing on different horizons of an iron-humus podzol profile. Oecologia 41:175-82.

Ferson, S. 1991. RAMAS/Stage. Setauket NY: Applied Biomathematics.

Franklin, J. F. and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Corvallis, OR: Oregon State University Press. 452 pp.

Garrison, G. A., J. M. Skovlin, C. E. Poulton, and A. H. Winward. 1976. Northwest Plant Names and Symbols for Ecosystem Inventory and Analysis. 4th ed. Portland, OR: USDA PNW Forest and Range Experiment Station. 263 pp.

Geyer, M. A. 1995. Autecological Studies of Two Annual Herbs, *Senecio sylvaticus* and *Epilobium paniculatum*: Effects of Biotic and Abiotic Factors. M.S. thesis, Corvallis, OR: Oregon State University. 83 pp.

Ghersa, C. M. and M. L. Roush. 1993. Searching for solutions to weed problems: Do we study competition or dispersal. Biosci. 43:104-9.

Gholz, H. L., G. M. Hawk, A. Campbell, Jr. K. Cromack, and A. T. Brown. 1985. Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. Can. J. For. Res. 15:400-9.

Ginns, J. H. 1986. Compendium of Plant Disease and Decay Fungi in Canada, 1960 to 1980 Volume Agriculture Canada Publ. V. 1812. Ottawa, Ontario, Canada: Ottawa Research Branch, Series A. 416 pp.

Gisela, J. 1980. Die naturliche Wiederbesidlung von Waldbrandflähen in der Lüneburger Heide mit Mosses und Gefäßplanzen. Forstw. Cbl. 99:297-324.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torr. Bot. 53:7-26.

Glenn-Lewin, D. C. 1980. The individualistic nature of plant community development. Vegetatio 43:141-46.

Gomez, K. A. and A. A. Gomez. 1984. Statistical Procedures for Agricultural Research. 2nd ed. New York: John Wiley & Sons. 680 pp.

Goodman, L. A. 1969. The analysis of population growth when the birth and death rates depend on several factors. Biometrics 25:659-81.

Goodwin, W. 1930. Fungal Diseases of Plants in Agriculture, Horticulture, and Forestry. London: Balliere, Tindel, and Co. 526 pp.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111:1169-94.

Grime, J. P., J. G. Hodgson, and R. Hunt. 1990. The Abridged Comparative Plant Ecology. London: Unwin Hyman Ltd. 399 pp.

van Groenendael, J. M. 1988. Patchy distribution of weeds and some implications for modelling population dynamics: A short literature review. Weed Res. 28:437-41.

van Groenendael, J. M., H. de Kroon, S. Kalisz, and S. Tuljapurkar. 1994. Loop analysis: Evaluating life history pathways in population projection matrices. Ecology 75:2410-5.

Guillemat, J. and J. Montégut. 1960. The effects of mineral fertilizers on some soil fungi. Pages 98-111 in D. Parkinson and J. S. Waid, eds. The Ecology of Soil Fungi. Liverpool, U.K: Liverpool University Press.

Halpern, C. B. 1989. Early successional patterns of forest species: Interactions of life history traits and disturbance. Ecology 70:704-20.

Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69:1703-15.

Halpern, C. B., J. A. Antos, M. A. Geyer, and A. M. Olson. 1997. Series replacement during early secondary succession: The abrupt decline of a winter annual. Ecology 78:621-31.

Hanson, H. C. 1962. Dictionary of Ecology. New York: Philosophical Library. 278 pp.

Harper, J. L. 1977. Population Biology of Plants. London: Academic Press. 892 pp.

Harper, J. L. and J. Ogden. 1970. The reproductive strategy of higher plants. 1. The concept of strategy with special reference to *Senecio vulgaris* L. J. Ecol. 58:681-98.

Harvey, B. D., Leduc A., and Y. Bergeron. 1995. Early Post Harvest Succession in relation to site type in the southern boreal forest of Quebec. Can. J. For. Res. 25:1658-72.

Henderson, G., P. G. Holland, and G. L. Werren. 1979. The natural history of a subarctic adventive: *Epilobium angustifolium* (Onagraceae) at Schefferville, Quebec. Nat. Can. 106:425-37.

Henderson, J. A. 1970. Biomass and Composition of the Understory Vegetation in some *Alnus rubra* Stands in Western Oregon. M.S. thesis, Corvallis, OR: Oregon State University. 64 pp.

Hill, M. O. 1978. The development of a flora in even-aged plantations. Pages 175-92 *in* E. D. Ford, D. C. Malcolm, and J. Atterson, eds. The Ecology of Even-aged Forest Plantations. Cambridge, UK: Institute of Terrestrial Ecology.

Hill, M. O. and P. A. Stevens. 1981. The density of viable seeds in soils of forest plantations in upland Britain. J. Ecol. 69:693-709.

Hill, R. L. 1989. *Digitalis purpurea* L., foxglove (Scrophulariaceae). Pages 351-2 *in* P. J. Cameron, ed. A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874-1987. Oxon, U.K.: CAB International.

Hitchcock, C. L. and A. Crosnquist. 1973. Flora of the Pacific Northwest. Seattle, WA: University of Washington Press. 730 pp.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187-211.

Husband, B. C. and S. C. H. Barrett. 1996. A metapopulation perspective in plant population biology. J. Ecol. 84:461-9.

Huston, M. and T. Smith. 1987. Plant succession: Life history and competition. Am. Nat. 130:168-98.

Ingersoll, C. A. and M. V. Wilson. 1990. Buried propagules in an old-growth forest and their response to experimental disturbance. Can. J. Bot. 86:1156-162.

Ingram, D. C. 1931. Vegetative changes in grazing use on Douglas-fir cutover land. J. Agric. Res. 43:387-417.

Isaac, L. A. 1940. Vegetative succession following logging in the Douglas fir region with special reference to fire. J. For. 38:716-21.

Jacobsohn, M. K. and G. M. Jacobsohn. 1985. Production of a fungistat and the role of fungi during germination of *Digitalis purpurea* L. cv. Gloxiniaflora seeds. Ann. Bot. 56:543-52.

Jarry, M., M. Khaladi, M. Hossaert-McKey, and D. McKey. 1995. Modeling the population dynamics of annual plants with seed bank and desity dependent effects. Acta Biotheor 43:53-65.

Jepson, W. L. 1925. A Manual of the Flowering Plants of California. Berkeley, CA: Associated Student Store, University of California. 1238 pp.

Jobidon, R. 1968. Allelopathic potential of coniferous species to old-field weeds in eastern Canada. For. Sci. 32:112-8.

Johnson, G. N., A. J. Young, J. D. Scholes, and P. Horton. 1993. The dissipation of excess excitation energy in British plant species. Plant Cell Environ. 16:673-9.

Johnson, M. H. and J. A. Elliott. 1996. Impacts of logging and wildfire on an upland black spruce community in northwestern Ontario. Environ. Monitor. Assess. 39:283-97.

Johnstone, I. M. 1986. Plant invasion windows: A time-based classification of invasion potential. Biol. Rev. 61:369-94.

Jordan, N. 1993. Simulation analysis of weed population dynamics in ridgetilled fields. Weed Sci. 41:468-74.

Jordan, N. 1992. Weed demography and population dynamics: Implications for threshold management. Weed Tech. 6:184-90.

Keen, R. E. and J. D. Spain . 1992. Computer Simulation in Biology: A BASIC Introduction. New York: Wiley-Liss. 498 pp.

Klemow, K. M. and D. J. Raynal. 1985. Demography of two facultative biennial plant species in an unproductive habitat. J. Ecol. 73:147-167.

Kingsland, S. E. 1985. Modeling Nature: Episodes in the History of Population Ecology. Chicago, IL: University of Chicago Press. 267 pp.

Klinkhamer, P. G., T. J. de Jong, and E. Meelis. 1987. Life-history variation and the control of flowering in short-lived monocarps. Oikos 49:309-14.

Kraemer, J. F. 1977. The Long Term Effect of Burning on Plant Succession. M.S. thesis, Corvallis, OR: Oregon State University . 123 pp.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427-31.

Lande, R. 1993. Risks of population extinction from demographic and environmental stoachsticity and randon catastrophies. Am. Nat. 142:911-27.

Landhausser, S. M. and V. J. Lieffers. 1994. Competition between *Calamagrostis canadensis* and *Epilobium angustifolium* under different soil temperature and nutrient regimes. Can. J. For. Res. 24:2244-50.

Lapham, J. 1987. Population dynamics and competitive effects of *Cyperus esculentus* (yellow nutsedge)--prediction of cost-effective control strategies. Pages 1043-1050 *in* Proceeding of the 1987 British Crop Protection Conference--Weeds.

Latore, J., P. Gould, and A. M. Mortimer. 1998. Spatial dynamics and critical patch size of annual plant populations. J. Theor. Bot 190:277-85.

Law, R. 1983. A model for the dynamics of a plant population containing individuals classified by age and size. Ecology 64:224-30.

Leberg, P. Influence of complex sex determination on demographic stochasticity and population viability. Conserv. Biol. 12:456-9.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1-18.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometricka 33:183-212.

Leverich, W. J. and D. A. Levin. 1979. Age-specific survivorship and reproduction in *Phlox drummondii*. Am. Nat. 113:881-903.

Levin, S. A. and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proc. Nat. Acad. Sci. USA 71:2744-2747.

Lieffers, V. J. and K. J. Stadt. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24:1193-8.

Livingston, P. L. 1977. The Reproductive Biology and Revegetation Potential Of Fireweed in Alaska. Division III thesis, 60 pp.

Louda, S. M. and M. A. Potvin. 1995. Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. Ecology 76:229-45.

Luken, J. O. 1990. Directing Ecological Succession. London: Chapman and Hall. 251 pp.

Malthus, T. R. 1992. An Essay on Population. Cambridge: Cambridge University Press. 392 pp.

Manlove, R. J., A. M. Mortimer, and P. D. Patwain. 1982. Modeling wild oat populations and their control. Pages 749-756 *in* Proceeding of the 1982 British Crop Protection Conference--Weeds.

Maschinski, J., R. Frye, and S. Rutman. 1977. Demography and population viability of an endangered plant species before and after protection from trampling. Conserv. Biol. 11:990-9.

Maxwell, B. D. 1990. The Population Dynamics and Growth of Salmonberry (*Rubus spectabilis*) and Thimbleberry (*Rubus parviflorus*). Ph.D. thesis, Corvallis, OR: Oregon State Univeristy. 286 pp.

Maxwell, B. D., M. L. Roush, and S. R. Radosevich. 1990. Predicting the evolution and dynamics of herbicide resistance in weed populations. Weed Tech. 4:2-13.

Maxwell, B. D., M. V. Wilson, and S. R. Radosevich. 1988. Population modeling approach for evaluating leafy spurge (*Euphorbia esula*) development and control. Weed Tech. 2:132-8.

May, R. M. 1981. Models for single populations. Pages 5-29 *in* R.M. May. Theoretical Ecology: Principles and Applications. Oxford, U.K.: Blackwell Scientific Publications.

McCook, L. J. 1994. Understanding ecological community succession: Causal models and theories, a review. Vegetatio 110:115-47.

McCune, B. and M. J. Mefford. 1997. PC-ORD, Multivariate Analysis of Ecological Data. Version 3.0. Gleneden Beach, OR.: MjM Software Design.

McEvoy, P. B. 1984. Dormancy and dispersal in dimorphic achenes of tansy ragwort, *Senecio jacobaea* L. (Compositae). Oecologia 61:160-8.

McEvoy, P. B. and C. S. Cox. 1987. Wind dispersal distances in dimorphic achenes of ragwort, *Senecio jacobaea*. Ecology 68:2006-15.

McMahon, D. J. and A. M. Mortimer. 1980. The prediction of couch infestations--a modeling approach. Pages 601-606 *in* Proceeding of the 1980 British Crop Protection Conference--Weeds.

Morris, W. G. 1970. Effects of slash burning in overmature stand of the Douglas-fir region. For. Sci. 16:258-70.

Mortimer, A. M. 1987. The population ecology of weeds--implications for integrated weed management, forecasting and conservation. Pages 377-386 *in* Proceedings of the 1987 British Crop Protection Conference--Weeds.

Mosquin, T. 1967. Evidence for autopolyploidy in *Epilobium angustifolium* (Onagraceae). Evolution 21:713-9.

Munz, P. A. 1968. A California Flora. Berkeley, CA: University of California Press. 1681 pp.

Myerscough, P. J. 1980. Biological flora of the British Isles. J. Ecol. 68:1047-74.

Myerscough, P. J. and F. H. Whitehead. 1967. Comparative biology of *Tussilago farfara* L., *Chamaenerion angustifolium* (L.) Scop., *Epilobium montanum* L. and *Epilobium adenocaulon* Hausskn. 1. Growth and ecology. New Phytol. 66:785-823.

Myerscough, P. J. and F. H. Whitehead. 1966. Comparative biology of *Tussilago farfara* L., *Chamaenerion angustifolium* (L.) Scop., *Epilobium montanum* L. And *Epilobium adenocaulon* Hausskn. 1. General biology and germination. New Phytol. 65:193-210.

Nault, A. and D. Gagnon. 1993. Ramet demography of *Allium tricoccum*, a spring ephemeral, perennial forest herb. J. Ecol. 81:101-19.

Niethammer, A. 1927. Keimungsphysiologische Studien unter Herborhebung des Lichtkeimungsproblems. Biochem. Z. 185:205-15.

Noble, I. R. and R. O. Slatyer. 1980. The use of vital attributes to predict succession changes in plant communities subject to recurrent disturbances. Vegetatio 43:5-21.

Oberdorfer, E. 1973. Die Glierung der Epilobietea angustifolii Gesellschafften am Beispeil Süddeutcher Vegetationsaufnahmen. Acta Bot. Acad. Sci. Hung. 19:235-53.

Odum, E. P. 1959. Fundamentals of Ecology. Philadelphia, PA: W. B. Saunders Co. 546 pp.

Pacala, S. W. and J. A. Silander, Jr. 1990. Field tests of neighborhood population dynamic models of two annual weed species. Ecol. Mon. 60:113-34.

Pacala, S. W. and J. A. Silander, Jr. 1985. Neighborhood models of plant population dynamics. I. Single-species models of annuals. Am. Nat. 125:385-411.

Paine, R. T. and Levin, S. A. 1981. Intertidal landscapes: Disturbance and the dynamics of pattern. Ecol. Monogr. 51:145-178.

Palmbald, I. G. 1968a. Competition in experimentally regulated populations of weeds with emphasis on the regulation of population size. Ecology 49:26-34.

Palmbald, I. G. 1968b. Comparative response of closely related species to reduced competition. I. *Senecio sylvaticus* and *S. viscosus*. Can. J. Bot. 46:225-8.

Palmbald, I. G. 1966. Experimental Studies on Interference in Weedy Plant Species . Ph.D. thesis, Seattle, WA: University of Washington. 227 pp.

Parendes, L. A. 1997. Spatial Patterns of Invasion by Exotic Plants in a Forested Landscape. Ph. D. dissertation, Corvallis, OR: Oregon State University. 208 pp.

Peet, R. K. and N. L. Christensen. 1980. Succession: A population process. Vegetatio 43:131-40.

Pickett, S.T.A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms, and pathways of succession. Bot. Rev. 53:335-371.

Pickett, S.T.A. and M. J. McDonnell. 1989. Changing perspectives in community dynamics: A theory of successional forces. TREE 4:241-245.

Pickett S.T.A. and P. S. White. 1985. Natural disturbance and patch dynamics: An introduction. Pages 3-13 in S.T.A. Pickett and P. S. White, eds. The Ecology of Natural Disturbance and Patch Dynamics. Orlando, Academic Press, Inc.

Piemeisel, R. L. 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. Ecology 32:53-72.

Pojar, J. and A. MacKinnon. 1994. Plants of the Pacific Northwest Coast. Redmond, WA: Lone Pine Publishing. 527 pp.

Poole, A. L. and D. Cairns. 1940. Botanical aspects of ragwort (Senecio jacobaea L.). Bull. N. Z. Sci. Ind. Res. 82:1-61.

Radosevich, S. R., J. S. Holt, and C. M. Ghersa. 1997. Weed Ecology: Implications for Management. 2 ed. New York: John Wiley & Sons. 589 pp.

Rickett, H. W. 1971. Wild Flowers of the United States Volume 5: The Northwest States. New York: McGraw-Hill. 666 pp.

Rickett, H. W. 1973. Wild Flowers of the United States Volume 6; The Central Mountains and Plains. New York: McGraw-Hill. 784 pp.

Robbin, W. W., M. K. Bullue, and W. S. Ball. 1951. Weeds of California. Sacramento, CA: Printing Division, State of California. 547 pp.

Sagar, G. R. and A. M. Mortimer. 1976. An approach to the study of the population dynamics of plants with special reference to weeds. Ann. Appl. Bot. 1:1-47.

Salisbury, E. J. 1961. Weeds and Aliens. London: Collins Publishing Co. 384 pp.

Salisbury, E. J. 1942. The Reproductive Capacity of Plants. London: Bell and Sons, Ltd. 244 pp.

SAS Institute Inc. 1996. SAS/STAT® Software: Changes and Enhancements through Release 6.11. Cary, NC: SAS Institute Inc. 233 - 315 pp.

SAS Institute Inc. 1993. SAS Technical Report P-234, SAS/STAT® Software: The GENMOD Procedure, Release 6.09. Cary, NC: SAS Institute, Inc. 88 pp.

SAS Institute Inc. 1990. SAS/STAT® User's Guide, Version 6. 4th ed. Volume 2. Cary, NC: SAS Institute, Inc. 846 pp.

Saltz, D. 1995. Minimizing extinction probability due to demographic staochasticity in a reintroduced herd of Persian fallow deer *Dama dama mesopotamica*. Biol. Conserv. 75:27-33.

Selman, M. 1970. The population dynamics of *Avena fatua* (wild oats) in continuous barley; desirable frequency of spraying with tri-allate. Pages 1176-1188 *in* Proceeding of the 10th British Weed Control Conference.

Shelford, V. E. 1943. The relation of snowy owl migration to the abundance of the collared lemming. Auk 62:592-4.

Shugart, H. H. and S. W. Seagle. 1985. Modeling forest landscapes and the role of disturbance in ecosystems and communities. Pages 353-68 *in* S.T.A. Pickett and P. S. White, eds. The Ecology of Natural Disturbance and Patch Dynamics. Orlando, Academic Press, Inc.

Shula, R. G. 1998. Database development and application to characterize juvenile Douglas-fir (Pseduotsuga menziesii) and understory vegetation in the Oregon and Washington Coast Range Mountains. M. S. thesis, Corvallis, OR: Oregon State University. 101 pp.

Shula, R. G. and S. A. Knowe. 1991. Regional vegetation management model: Recommended dataset matrix, and sampling and data collection protocols. Corvallis, OR. Oregon State University. 11 pp.

Silvertown, J. W. 1984. Death of the elusive biennial. Nature 310:271.

Silvertown, J. W. 1987. Introduction to Plant Population Ecology. Essex, England: Longman Scientific & Technical. 229 pp.

Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant demography--relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. J. Ecol. 81:465-76.

Silvertown, J. W. and J. Lovett Doust. 1993. Introduction to Plant Population Biology. 3 ed. London: Blackwell Scientific. 210 pp.

Simard, S. and A. Nicholson. 1990. Balancing the positive and negative effects of non-crop plants on conifers: Pinegrass, fireweed, Sitka alder and paper birch--friend or foe. Pages 45-48 *in* E. Hamilton, ed.Vegetation Management: An Integrated Approach; Proceedings of the Fourth Annual Vegetation Management WorkshopVictoria, B.C. Canada: B.C. Ministry of Forests.

Smith, D. M. 1986. The Practice of Silviculture. 7th ed. New York: Wiley and Sons. 578 pp.

Smith, M. C., J. Holt, and M. Webb. 1993. Population model of the parasitic weed *Striga hermonthia* (Scrophulariaceae) to investigate the potential of *Smicronyx umbrinus* (Coleoptera:Curculionidae) for biological control in Mali. CP 12:470-6.

Solbreck, C. and D. Andersson. 1987. Vertical distribution of fireweed, *Epilobium angustifolium*, seeds in the air. Can. J. Bot. 65:2177-8.

Solbrig, O. T., R. Sarandon, and W. Bossert. 1988. A density-dependent growth model of a perennial herb, *Viola frimbriatula*. Am. Nat. 131:385-400.

Southwood, T. R. E. 1981. Bionomic strategies and populations parameters. Pages 30-52 *in* R.M. May, ed. Theoretical Ecology: Principles and Applications. Oxford, U.K.: Blackwell Scientific Publications.

van Tienderen, P. H. 1995. Life cycle trade-offs in matrix population models. Ecology 76:2482-9.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125:827-52.

Timoney, K. P., Peterson G., and Wein R. 1997. Vegetation development of boreal riparian plant communities after flooding, fire, and logging, Peace River, Canada. Forest Ecol. Manage. 93:101-20.

Thompson, J. N. 1985. Within-patch dynamics of life histories, populations, and interactions: Selection over time in small spaces. Pages 253-64 *in* S.T.A. Pickett and P. S. White, eds. The Ecology of Natural Disturbance and Patch Dynamics. Orlando, Academic Press, Inc.

Tong. S.T.Y. 1992. The use of non-metric multidimensional scaling as an ordination technique in resource survey and evaluation: a case study from southeast Spain. Appl. Geo. Sevenoaks 12:243-60.

Torell, L. A., K. C. McDaniel, and K. Williams. 1992. Estimating the life of short-lived cyclic weeds with Markov processes. Weed Tech. 6:62-7.

Tschaplinski, T. J. and T. J. Blake. 1985. Effects of root restriction on growth correlations, water relations, and senescence of alder seedlings. Physiol. Plant. 64:167-76.

Tueller, P. T., R. J. Tausch, and V. Bostick. 1991. Species and plant community distribution in a Mojave-Great Basin desert transition. Vegetatio 92:133-50.

Tüxen, R. 1950. Wanderwege der Flora in Stromtälern. Ebenda 2:52-3.

Vandermeer, J. H. 1975. On the construction of the population projection matrix for a population grouped into unequal stages. Biometrics 31:239-42.

Vodlazsky, L. E. 1979. Concerning variation of adventive buds and shoots from root-offspring of the herbaceous perennial *Chamaenerion angustifolium* (L.) Scop. (Onagraceae). Bot. J. Acad. Sci., SSSR 64:734-9.

Watkinson, A. R., W. M. Lonsdale, and M. H. Andrew. 1989. Modelling the population dynamics of an annual plant *Sorguhm intrans* in the wet-dry tropics. J. Ecol. 77:162-81.

Werner, P. A. and H. Caswell. 1977. Population growth rates and age versus stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). Ecology 58:1103-11.

West, N. E. and W. W. Chilcote. 1968. *Senecio sylvaticus* in relation to Douglas-fir clear-cut succession in the Oregon Coast Range. Ecology 49:1101-7.

Whisenant, S. G. 1989. Modeling Japanese brome population dynamics. Pages 176-185 *in* Proc. West. Soc. Weed Sci..

Wiser, S. K., R. B. Allen, P. W. Clinton, and K. H. Platt. 1998. Community structure and forest invasion by an exotic herb over 23 years. Ecology 79:2071-81.

Willms, W., A. McLean, R. Tucker, and R. Ritcey. 1980. Deer and cattle diets on summer range in British Columbia. *J. Range Manage.* 33:55-9.

Withering, W. 1776. An Account of the Foxglove and some of Its Medicinal Uses. London: C.G.J. and J. Robinson. 207 pp.

Wood, D. M. and W. F. Morris. 1990. Ecological constraints to seedling establishment on the Pumice Plains, Mount St. Helens, Washington. Am. J. Bot. 77:1411-8.

Wright, R. G. and G. van Dyne. 1981. Population age structure and its relationship to the maintenance of a semidesert grassland undergoing invasion by mesquite. Southwest. Nat. 26:13-22.

Yaniv, Z. 1985. Digitalis. Pages 446-9 *in* A. H. Haley, ed. CRC Handbook of Flowering. Volume VII. Boca Raton, FL: CRC Press.

Yerkes, V. P. 1958. Successional Trends of Lesser Vegetation Following Clearcutting in Old-growth Douglas-fir Stands. M.S. thesis, Corvallis, OR: Oregon State University. 98 pp.

Zimdahl, R. L. 1993. Fundamentals of Weed Science. San Diego, CA: Academic Press. 450 pp.

Zobel, M. 1993. Changes in pine forest communities after clear-cutting: A comparison of two edaphic gradients. Ann. Bot. Fennici 30:131-7.

APPENDICES

Appendix 1: Community vegetation data.

Table A1.1. Vegetation Sampling Plot (PMP) location. Region indicates the general location while locale is a nearby town or other geographic reference.

Plot	Region	Locale	Township	Range	Section
1	Coast Range	Forks, WA	30 N	13 W	21
2	Coast Range	Forks, WA	30 N	13 W	22
3	Coast Range	Forks, WA	30 N	13 W	21
4	Coast Range	Forks, WA	30 N	13 W	21
5	Coast Range	Coos Bay, OR	26 S	12 W	15
6	Coast Range	Coos Bay, OR	26 S	12 W	15
7	Coast Range	Coos Bay, OR	26 S	12 W	15
8	Coast Range	Tillamook, OR	1 S	7 W	13
9	Coast Range	Tillamook, OR	1 S	7 W	13
10	Coast Range	Tillamook, OR	1 S	7 W	13
11	Coast Range	Mapleton, OR	18 S	10 W	14
12	Coast Range	Mapleton, OR	18 S	10 W	14
13	Coast Range	Reedsport, OR	20 S	10 W	15
14	Coast Range	Reedsport, OR	20 S	10 W	15
15	Coast Range	Yachets, OR	19 S	11 W	14
16	Coast Range	Yachets, OR	19 S	11 W	14
17	Coast Range	Yachets, OR	19 S	11 W	14
18	Coast Range	Yachets, OR	19 S	11 W	14
19	Coast Range	Yachets, OR	19 S	11 W	14
20	Coast Range	Yachets, OR	19 S	11 W	14
21	Coast Range	Yachets, OR	19 S	11 W	14
22	Coast Range	Yachets, OR	12 S	11 W	23
23	Coast Range	Yachets, OR	19 S	11 W	14
24	Coast Range	Yachets, OR	19 S	11 W	14

Table A1.1 cont. Vegetation Sampling Plot (PMP) location.

Plot	Region	Locale	Township	Range	Section
25	Coast Range	Yachets, OR	15 S	11 W	25
26	Coast Range	Yachets, OR	15 S	11 W	25
27	Coast Range	Yachets, OR	15 S	11 W	25
28	Coast Range	Yachets, OR	15 S	11 W	25
29	Coast Range	Yachets, OR	15 S	11 W	25
30	Coast Range	Yachets, OR	15 S	11 W	25
31	Coast Range	Yachets, OR	15 S	11 W	25
32	Coast Range	Yachets, OR	15 S	11 W	25
33	Coast Range	Yachets, OR	15 S	11 W	25
34	Coast Range	Yachets, OR	15 S	11 W	25
35	Coast Range	Summit, OR	11 S	7 W	18
36	Coast Range	Blodgett. OR	11 S	7 W	33
37	Coast Range	Blodgett. OR	11 S	7 W	27
38	Coast Range	Blodgett. OR	11 S	7 W	35
39	Coast Range	Blodgett. OR	11 S	7 W	34
40	Coast Range	Lakeside, OR	23 S	12 W	23
41	Coast Range	Lakeside, OR	23 S	12 W	23
42	Coast Range	Lakeside, OR	23 S	12 W	14
43	Coast Range	Blodgett. OR	10 S	7 W	35
44	Coast Range	Blodgett. OR	11 S	7 W	10
45	Coast Range	Alsea, OR	13 S	8 W	22
46	Coast Range	Alsea, OR	13 S	8 W	16
47	Coast Range	Alsea, OR	13 S	8 W	16
48	Coast Range	Alsea, OR	13 S	8 W	10

Table A1.1 cont. Vegetation Sampling Plot (PMP) location.

Plot	Region	Locale	Township	Range	Section
49	Coast Range	Alsea, OR	13 S	8 W	4
50	Coast Range	Alsea, OR	13 S	8 W	14
51	Coast Range	Longview, WA	10 N	2 W	30
52	Coast Range	Longview, WA	10 N	3 W	25
53	Coast Range	Longview, WA	10 N	3 W	12
54	Coast Range	Longview, WA	10 N	3 W	12
55	Coast Range	Longview, WA	10 N	3 W	13
56	Coast Range	Longview, WA	10 N	2 W	30
57	Coast Range	Pedee, OR	9 S	8 W	13
58	Coast Range	Pedee, OR	9 S	7 W	26
59	Coast Range	Pedee, OR	9 S	7 W	27
60	Coast Range	Longview, WA	10 N	3 W	2
61	Coast Range	Longview, WA	10 N	3 W	2
62	Coast Range	Longview, WA	11 N	3 W	36
63	Coast Range	Longview, WA	10 N	3 W	11
64	Coast Range	Pedee, OR	8 S	7 W	32
65	Coast Range	Pedee, OR	9 S	7 W	5
66	Coast Range	Pedee, OR	9 S	7 W	34
67	Coast Range	Pedee, OR	9 S	7 W	19
68	Coast Range	Pedee, OR	9 S	7 W	19
69	Coast Range	Hoquiam, WA	19 N	10 W	26
70	Coast Range	Hoquiam, WA	20 N	9 W	8
71	Coast Range	Hoquiam, WA	20 N	9 W	18
72	Coast Range	Hoquiam, WA	20 N	9 W	17
73	Coast Range	Hoquiam, WA	20 N	10 W	11

Table A1.1 cont. Vegetation Sampling Plot (PMP) location.

Plot	Region	Locale	Township	Range	Section
74	Coast Range	Hoquiam, WA	20 N	9 W	30
75	Coast Range	Shelton, WA	21 N	3 W	33
76	Coast Range	Shelton, WA	21 N	3 W	13
77	Coast Range	Shelton, WA	21 N	3 W	10
78	Coast Range	Shelton, WA	19 N	5 W	2
79	Coast Range	Shelton, WA	19 N	5 W	13
80	Coast Range	Shelton, WA	20 N	4 W	27
81	Coast Range	Shelton, WA	20 N	6 W	31
82	Coast Range	Shelton, WA	19 N	6 W	13
83	Coast Range	Shelton, WA	19 N	6 W	12
84	Coast Range	Shelton, WA	20 N	5 W	24
85	Coast Range	Shelton, WA	20 N	6 W	23
86	Coast Range	Yachets, OR	12 S	11 W	23
87	Coast Range	Yachets, OR	12 S	11 W	23
88	Coast Range	Yachets, OR	12 S	11 W	23
89	Coast Range	Coos Bay, OR	24 S	10 W	14
90	Coast Range	Coos Bay, OR	26 S	12 W	28
91	Coast Range	Coos Bay, OR	24 S	11 W	35
92	Coast Range	Coos Bay, OR	24 S	9 W	32
93	Coast Range	Coos Bay, OR	25 S	9 W	2
94	Coast Range	Coos Bay, OR	24 S	9 W	35
95	Coast Range	Coos Bay, OR	24 S	9 W	26
96	Coast Range	Mary's Peak, OR	12 S	8 W	36
97	Coast Range	Roseburg, OR	26 S	8 W	10
98	Coast Range	Roseburg, OR	26 S	8 W	32

Table A1.1 cont. Vegetation Sampling Plot (PMP) location.

Plot	Region	Locale	Township	Range	Section
99	Cascades	Oakridge, OR	23 S	5 E	21
100	Cascades	Oakridge, OR	23 S	5 E	20
101	Cascades	Oakridge, OR	23 S	5 E	32
102	Cascades	Oakridge, OR	23 S	5 E	32
103	Cascades	Oakridge, OR	23 S	5 E	32
104	Cascades	Carson, WA	5 N	7 E	26
105	Cascades	Carson, WA	5 N	8 E	30
106	Cascades	Carson, WA	5 N	7 E	25
107	Cascades	Cougar, WA	5 N	7 E	34
108	Cascades	Cougar, WA	8 N	6 E	24
109	Cascades	Oakridge, OR	8 N	6 E	24
110	Cascades	Bucoca, WA	20 S	5 E	21
111	Cascades	Bucoca, WA	15 N	1 E	19
112	Cascades	Bucoca, WA	15 N	1 E	19
113	Cascades	Randle, WA	15 N	1 E	19
114	Cascades	Randle, WA	10 N	7 E	18
115	Cascades	Packwood, WA	11 N	7 E	6
116	Cascades	Packwood, WA	13 N	9 E	34
117	Cascades	Marcola, OR	13 N	9 E	7
118	Cascades	Marcola, OR	16 S	1 W	2
119	Cascades	Marcola, OR	16 S	1 W	2
120	Cascades	Marcola, OR	16 S	1 W	2
121	Cascades	Marcola, OR	16 S	1 W	1
122	Cascades	Marcola, OR	16 S	1 W	1
123	Cascades	Marcola, OR	16 S	1 W	1

Table A1.1 cont. Vegetation Sampling Plot (PMP) location.

Plot	Region	Locale	Township	Range	Section
124	Cascades	Marcola, OR	16 S	1 W	2
125	Cascades	Marcola, OR	16 S	1 W	2
126	Cascades	Marcola, OR	16 S	1 W	25
127	Cascades	Oakridge, OR	20 S	2 E	24
128	Cascades	Oakridge, OR	18 S	2 E	31
129	Cascades	Oakridge, OR	23 S	5 E	4
130	Cascades	Oakridge, OR	23 S	5 E	4
131	Cascades	Cottage Grove, OR	21 S	3 W	35
132	Cascades	Cottage Grove, OR	21 S	2 W	15
133	Cascades	Sedro Woolley, WA	37 N	8 E	35
134	Cascades	Sedro Woolley, WA	37 N	9 E	7
135	Cascades	Sedro Woolley, WA	37 N	9 E	7
136	Cascades	North Bend, WA	21 N	11 E	34
137	Cascades	North Bend, WA	20 N	11 E	2
138	Cascades	North Bend, WA	20 N	11 E	10
139	Cascades	Enumclaw, WA	18 N	9 E	17
140	Cascades	Mollalla, OR	7 S	3 E	14
141	Cascades	Mollalla, OR	7 S	2 E	11
142	Cascades	Cottage Grove, OR	21 S	3 W	25
143	Cascades	Mollalla, OR	6 S	3 E	28
144	Cascades	Cottage Grove, OR	20 S	2 W	19
145	Cascades	Cottage Grove, OR	23 S	3 W	1
146	Cascades	Scio, OR	7 S	1 E	23
147	Cascades	Oakridge, OR	20 S	4 E	25
148	Cascades	Lowell, OR	20 S	2 E	16

Table A1.1 cont. Vegetation Sampling Plot (PMP) location.

Plot	Region	Locale	Township	Range	Section
149	Cascades	Lowell, OR	20 S	2 E	8
150	Cascades	Dexter, OR	20 S	1 W	11
151	Cascades	Dexter, OR	19 S	1 W	35
152	Cascades	Scio, OR	7 S	1 E	23
153	Cascades	Lowell, OR	20 S	2 E	15
154	Cascades	Vida, OR	17 S	1 E	13
155	Cascades	Vida, OR	17 S	1 E	13
156	Cascades	Vida, OR	17 S	1 E	13
157	Cascades	Vida, OR	17 S	1 E	13
158	Cascades	Vida, OR	16 S	2 E	5
159	Cascades	Mollalla, OR	5 S	3 E	25
160	Cascades	Mollalla, OR	6 S	4 E	15
161	Cascades	Mill City, OR	11 S	1 E	27
162	Cascades	Longview, WA	8 N	1 E	20
163	Cascades	Longview, WA	8 N	1 E	20
164	Cascades	Longview, WA	8 N	1 E	20
165	Cascades	Longview, WA	8 N	1 E	20
166	Cascades	Randle, WA	11 N	7 E	5
167	Cascades	Packwood, WA	13 N	9 E	18
168	Cascades	Sedro Woolley, WA	36 N	6 E	36
169	Cascades	Sedro Woolley, WA	36 N	6 E	35
170	Cascades	Sedro Woolley, WA	36 N	7 E	32
171	Cascades	Vida, OR	16 S	2 E	5
172	Cascades	Mill City, OR	8 S	3 E	25
173	Cascades	Sweet Home OR	11 S	4 E	25

Table A1.1 cont. Vegetation Sampling Plot (PMP) location.

Plot	Region	Locale	Township	Range	Section
174	Cascades	Detroit, OR	10 S	7 E	27
175	Cascades	Detroit, OR	9 S	6 E	28
176	Cascades	Randle, WA	11 N	7 E	32
177	Cascades	Kid Valley, WA	10 N	2 E	16
178	Cascades	Mossy Rock, WA	11 N	3 E	7
179	Cascades	Mossy Rock, WA	11 N	3 E	11
180	Cascades	Kid Valley, WA	10 N	2 E	16
181	Cascades	Mollalla, OR	7 S	3 E	16
182	Cascades	Puyallup, WA	18 N	5 E	10
183	Cascades	Puyallup, WA	18 N	5 E	23
184	Cascades	Puyallup, WA	18 N	5 E	29
185	Cascades	Puyallup, WA	18 N	5 E	29
186	Cascades	Enumclaw, WA	19 N	10 E	16
187	Cascades	Cottage Grove, OR	23 S	2 W	11
188	Cascades	Detroit, OR	9 S	7 E	15
189	Cascades	McKenzie Bridge,	14 S	7 E	33
190	Cascades	Randle, WA	10 N	6 E	14
191	Cascades	Morton, WA	11 N	6 E	9
192	Cascades	Morton, WA	11 N	6 E	9
193	Cascades	Morton, WA	11 N	3 E	3
194	Cascades	Morton, WA	11 N	3 E	3
195	Cascades	Morton, WA	11 N	3 E	9
196	Cascades	Sweet Home OR	11 S	5 E	29

Table A1.2. Occurrence frequency of species used in multivariate analysis. PSME (Douglas-fir) measurement plot (PMP) frequency indicates the number of times each species occurred the data analyzed and has a maximum of 196 for the initial sampling and 195 for the final sampling. Quadrant (Quad) frequency indicates the number of times the species was observed in each quadrant of the subplots and has a maximum of 3136 for the initial sampling and 3120 for the final sampling. Initial sampling was conducted as each plot was installed and the final sampling was made two years later on the same plot. Species that were included only in the final sampling are indicated (*) and those only in the initial sampling are indicated (†). RVMM codes are modified from Garrison *et al.* 1977.

RVMM Code	Common Name	Specific Epithet	Initial PMP	Initial Quad	Final PMP	Final Quad
ACTR*	Vanilla-leaf	*Achlys triphylla*	3	6	4	12
ANMA	Pearly Everlasting	*Anaphalis margaritacea*	64	262	52	227
ARCO*	Hairy Manzanita	*Arctostaphylos columbiana*	3	9	7	32
ARPA	Green-leaf Manzanita	*Arctostaphylos patula*	4	18	6	17
ARUV	Kinnikinnick	*Arctostaphylos uva-ursi*	7	27	5	20
ARVI	White-leaf Manzanita	*Arctostaphylos viscida*	5	21	1	5
BARE	Bare Ground	N/A	115	753	111	704
BENE	Oregon-grape	*Berberis nervosa*	103	769	104	785
CARE	Sedge	*Carex* spp.	5	18	17	69
CEVE	Snowbrush	*Ceanothus velutinus*	13	127	16	125
CHLE*	Ox-eye Daisy	*Chrysanthemum leucanthemum*	3	4	10	57
CIAR	Canada Thistle	*Cirsium arvense*	26	136	25	114
CIVU	Bull thistle	*Cirsium vulgare*	20	99	15	51
COCA*	Bunchberry	*Cornus canadensis*	3	5	7	30
CYSC	Scotch Broom	*Cytisus scoparius*	2	14	4	16
DIFO	Pacific Bleeding Heart	*Dicentra formosa*	2	14	7	15
DIPU	Foxglove	*Digitalis purpurea*	31	126	34	143
EPAN	Fireweed	*Epilobium angustifolium*	39	197	48	237
EPIL	Willowherb	*Epilobium* spp.	16	112	10	44
EQUI	Horsetail	*Equisetum* spp.	2	12	2	6

Table A1.2 cont. Occurrence frequency of species used in multivariate analysis.

RVMM Code	Common Name	Specific Epithet	Initial PMP	Initial Quad	Final PMP	Final Quad
FERN	Fern	N/A	3	9	9	22
FRVE	Strawberry	*Fragaria* spp.	18	38	18	53
GALI	Bedstraw	*Galium* spp.	9	25	16	37
GASH	Salal	*Gaultheria shallon*	115	1208	114	1261
GRAS	Grasses	N/A	92	652	78	576
HODI	Oceanspray	*Holodiscus discolor*	39	117	41	138
HYPE	Common St. John's-wort	*Hypericum perforatum*	9	30	5	16
HYRA	Hairy Cat's-ear	*Hypochaeris radicata*	29	254	37	228
IRIS	Iris	*Iris* spp.	17	133	21	107
LACT*	Wild Lettuce	*Lactuca* spp.	1	2	3	16
LATH*	Pea	*Lathyrus* spp.	4	9	25	120
LIBO	Twinflower	*Linnaea borealis*	16	113	20	121
LILY	Lily	*Lily* spp.	4	11	2	3
LOMI	Small-flowered Lotus	*Lotus micranthus*	2	20	2	2
LOTU*	Lotus	*Lotus* spp.	3	4	2	10
LUPI	Lupine	*Lupinus* spp.	6	20	6	10
MADI*	Tarweed	*Madia* spp.	1	4	3	12
MONT*	Montia	*Montia* spp.	3	25	4	25
ORGA	Organic Debris	N/A	196	3127	195	3099
OXOR	Redwood Sorrel	*Oxalis oreganum*	16	65	18	90
PAMY	Oregon Boxwood	*Pachistima myrsinites*	6	12	7	29
POMU	Swordfern	*Polystichum munitum*	129	804	123	825
PTAQ	Bracken Fern	*Pteridium aquilinum*	113	1068	116	113
RHMA	Pacific Rhododendron	*Rhododendron macrophyllum*	19	164	19	168

Table A1.2 cont. Occurrence frequency of species used in multivariate analysis.

RVMM Code	Common Name	Specific Epithet	Initial PMP	Initial Quad	Final PMP	Final Quad
RIBE	Currant	*Ribes* spp.	15	42	9	20
RISA	Red-flowering Currant	*Ribes sanguineum*	19	75	20	85
ROGY	Baldhip Rose	*Rosa gymnocarpa*	30	60	33	73
RUDI	Himalayan Blackberry	*Rubus discolor*	22	94	25	125
RULA	Evergreen Blackberry	*Rubus laciniatus*	18	57	21	50
RULE	Black Raspberry	*Rubus leucodermis*	36	124	29	89
RUPA	Thimbleberry	*Rubus parviflorus*	48	291	56	353
RUSP	Salmonberry	*Rubus spectabilis*	54	461	57	428
RUUR	Trailing Blackberry	*Rubus ursinus*	116	983	133	1236
SAMB	Elderberry	*Sambucus* spp.	16	27	22	35
SENE	Groundsel	*Senecio* spp.	4	29	11	54
SESY†	Woodland Groundsel	*Senecio sylvaticus*	15	114	0	0
SMRA	False Solomon's-seal	*Smilacina racemosa*		13	10	43
SOOL†	Common Sowthistle	*Sonchus oleraceus*	4	12	0	0
STAC*	Hedgenettle	*Stachys* spp.	2	1	7	13
SYAL[8]	Common Snowberry	*Symphoricarpus albus*	8	26	0	0
SYMO	Trailing Snowberry	*Symphoricarpus mollis*	13	54	20	106
TRIF	Clover	*Trifolium* spp.	9	13	8	16
VAAL	Alaskan Blueberry	*Vaccinium alaskaense*	7	39	8	72
VACC†	Huckleberry	*Vaccinium* spp.	5	11	0	0
VAHE	Inside-out Flower	*Vancouveria hexandra*	4	15	7	12
VAME	Black Huckleberry	*Vaccinium membranaceum*	9	34	4	19
VAOV	Evergreen Huckleberry	*Vaccinium ovatum*	21	118	23	134
VAPA	Red Huckleberry	*Vaccinium parvifolium*	70	268	71	280
VICI	Vetch	*Vicia* spp.	12	59	2	12

[8]Combined with trailing snowberry in the final sampling.

Table A1.2 cont. Occurrence frequency of species used in multivariate analysis.

RVMM Code	Common Name	Specific Epithet	Frequency			
			Initial		Final	
			PMP	Quad	PMP	Quad
WHMO	Yerba de Selva	*Whipplea modesta*	19	110	14	96
XETE	Bear-grass	*Xerophyllum tenax*	9	43	7	42

Appendix 2: Allometric Relationships for Target Species.

Woodland Groundsel Shoot Biomass (g) - Experiment 1:

$$\ln(shoot\ biomass) = -11.3 + 3.3\ln(ht) - 0.17(d) - 0.9(l) \tag{28}$$

($R^2 = 0.77$, P = 0.0001, 0.0001, 0.0001, 0.0019, and 0.002 for the model and parameters, respectively).

Woodland Groundsel Root Biomass (g)- Experiment 1:

$$\ln(roots\ biomass) = -10.5 + 2.7\ln(ht) - 0.12(d) - 0.5(l) \tag{29}$$

($R^2 = 0.65$, P = 0.0001, 0.0001, 0.0001, 0.040 and 0.047 for the model and parameters, respectively).

Woodland Groundsel Achene Production·plant^{-1} - Experiment 1:

$$\ln(achenes/plant) = -1.6 + 2.7\ln(ht) - 0.22(d) - 1.25(I) \qquad \textbf{(1)}$$

($R^2 = 0.44$, P = 0.0001, 0.24, 0.0001, 0.01 and 0.001 for the model and parameters, respectively). For each equation, ht is height (cm), d is woodland groundsel density (plants·m^{-2}), and I is an indicator variable for the presence of interspecific competition. Plant height was found to be the dominant independent variable in all three relationships having partial R^2 of 0.72, 0.62, and 0.36, shoot biomass, root biomass, and achene production, respectively.

Woodland Groundsel Height (cm) - Experiments 1 & 3:

$$(ht)^{\frac{1}{2}} = 2.4 + 0.27(d) + 0.71(I) + 0.22(N) + 5.31(T) - 0.19(N*T), \qquad \textbf{(2)}$$

($R^2 = 0.56$, P=0.0001, 0.009, 0.0001, 0.056, 0.0001, 0.0001, and 0.006 for the model and parameters, respectively).

Woodland Groundsel Canopy Diameter (cm) - Experiments 1 & 3:

$$\ln(dia) = 1.6 + 0.22(d) - 0.4(I) + 0.04(N) + 0.9(t), \qquad \textbf{(3)}$$

($R^2 = 0.35$, P=0.0001, 0.0001, 0.0001, 0.002, 0.004, and 0.0001 for the model and parameters, respectively). In each equation, d is woodland groundsel density (plants·m^{-2}),

Woodland Groundsel Canopy Diameter (cm) - Experiments 1 & 3:

$$\ln(dia) = 1.6 + 0.22(d) - 0.4(I) + 0.04(N) + 0.9(t), \qquad (32)$$

($R^2 = 0.35$, P=0.0001, 0.0001, 0.0001, 0.002, 0.004, and 0.0001 for the model and parameters, respectively). In each equation, d is woodland groundsel density (plants·m^{-2}), I is an indicator variable for interspecific competition, N is the added nitrogen level (0 for ambient, 5 for 62.5 kg·ha^{-1}, and 10 for 125 kg·ha^{-1}), and T is an indicator variable for data from Experiment 1.

$\ln(\text{Seeds/Plant}) = 5.46 + 1.85 \ln(\text{Plant Diameter})$
$R^2 = 0.2879$

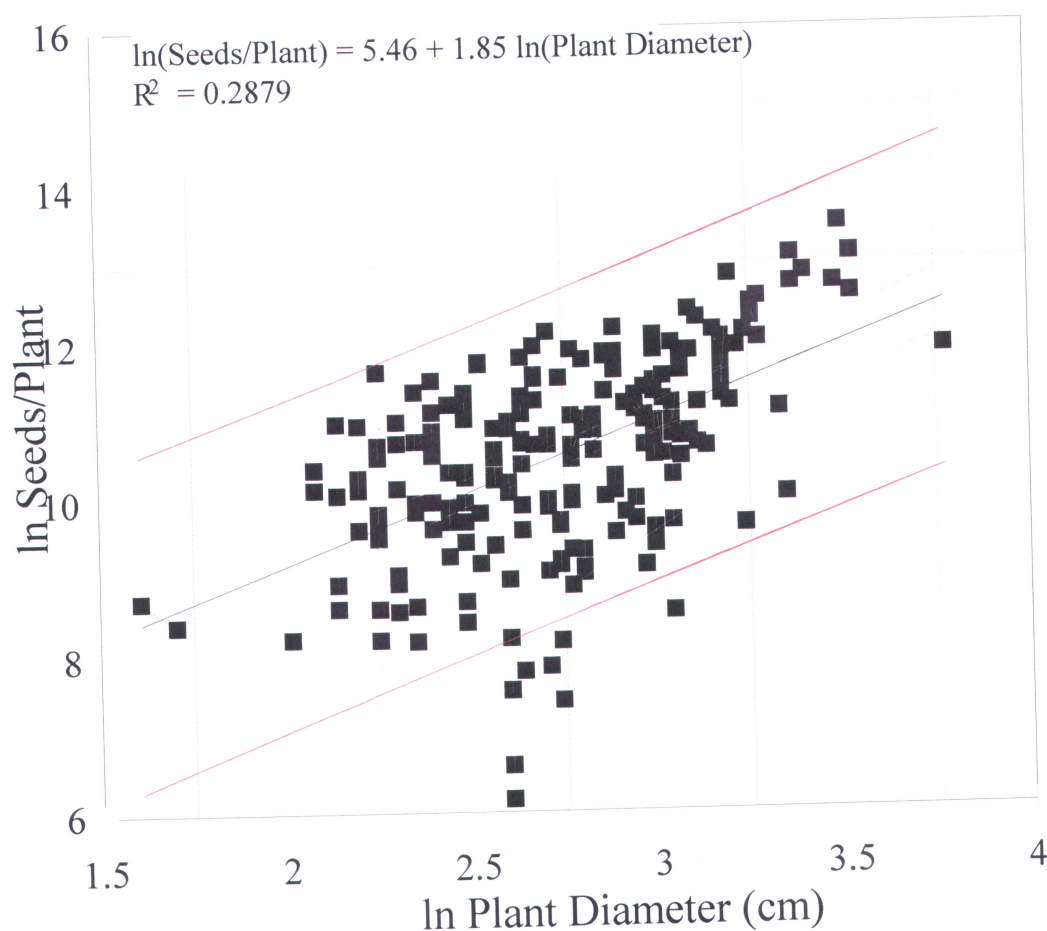**Figure A2.1**. Allometric relationship between foxglove rosette diameter (cm) and seed production (ln seeds·plant^{-1}). The data is represented (■) and the regression relationship is indicated (—). The 95% confidence intervals for the model are represented (– –). The 95% prediction interval are indicated (–). The models and the parameters used for these relationships are significant (p=0.0001 for all except intercept where p=0.0045).

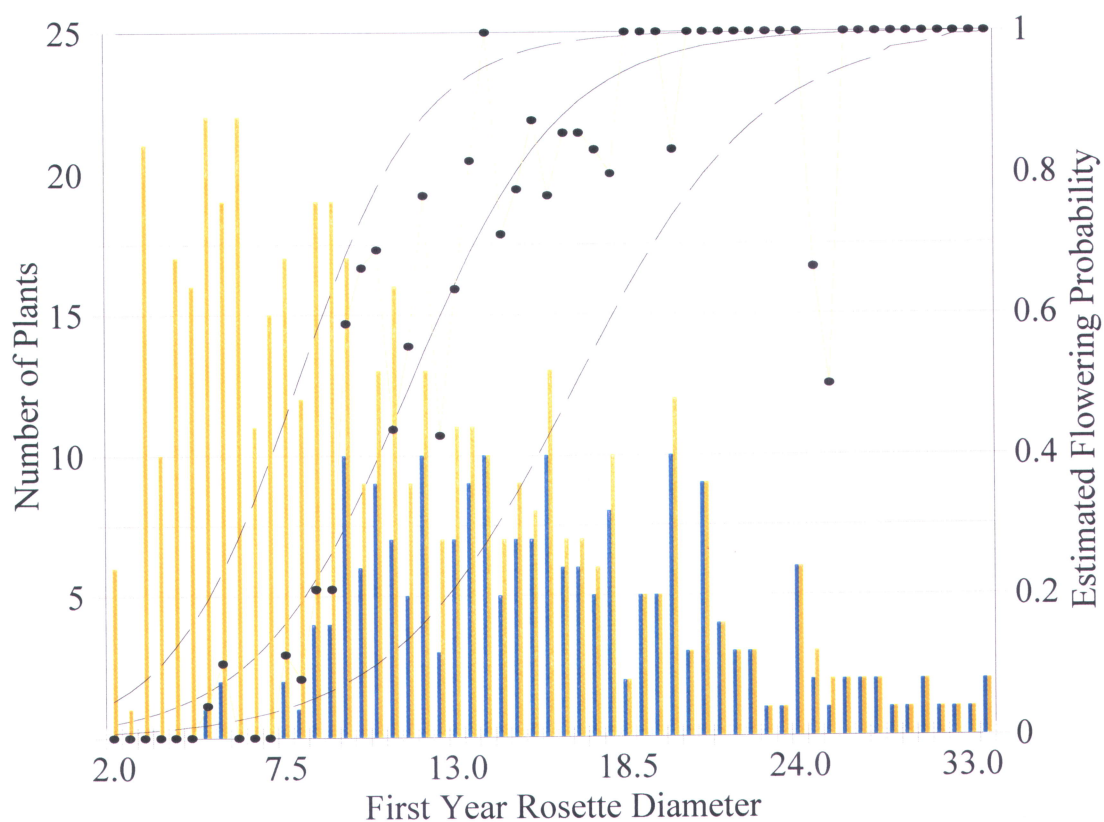**Figure A2.2**. Relationship between foxglove rosette diameter (cm) and flowering. The total number of plants in each diameter class is indicated (|), while the number of flowering plants is represented (|). The actual and estimated probability of flowering are indicated (●) and (- -), respectively, while (—) are the 95% confidence intervals for the estimated probability model. The parameters used for this relationship are significant (p=0.0001).
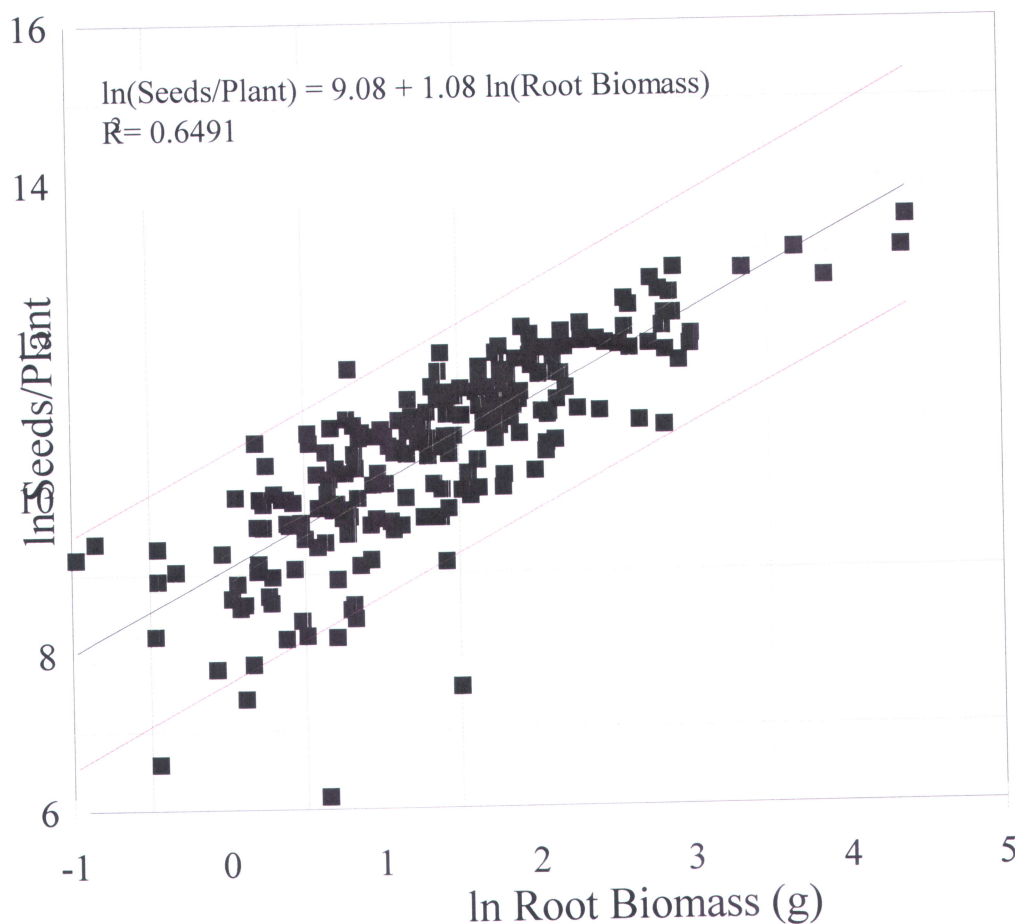
Figure A2.3. Allometric relationship between foxglove root biomass (g) and seed production (seeds·plant^{-1}). The data is represented (■) and the regression relationship is indicated (—). The 95% confidence intervals for the model are represented (– –). The 95% prediction interval are indicated (–). The model and the parameters used for this relationship are significant (p=0.0001 for all).

Fireweed Shoot Biomass (g) - Experiments 1 & 3:

$$\ln(SB) = -0.91 + 0.25 \ln(Dia),$$

$(R^2 = 0.5239)$.

Fireweed Plant Volume (cc) - Experiments 1 & 3:

$$\ln(RB) = -0.85 + 0.24 \ln(Vol),$$

$(R^2 = 0.4796)$.

Fireweed Buds Per Plant:

$$\ln(B/P) = 0.29 + 0.31 \ln(SB),$$

$(R^2=0.8565)$. where SB is shoot biomass, Dia is plant diameter, RB is root biomass, Vol is plant volume and B/P is the number of buds per plant. All variables were log-transformed.

Appendix 3: Population model matrices. The transition matrices are for stochastic population models. These matrices were developed from transition probabilities derived from Experiments 1, 2, and 3.

Woodland groundsel population vectors and transition matrices.

Creation of the woodland groundsel population vector, n_t, required iteratively multiplying the transition matrix and a vector containing elements of the population. The first vector, **n1**, contained only the number of achenes produced off-site. When the transition matrix, **S1** was multiplied by this vector, **n1**, the vector, **n2**, was produced as indicated below:

$$
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.9 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.96 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.02 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.95 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 4{,}155 & 0
\end{pmatrix}
\cdot
\begin{pmatrix}
190{,}400 \\
0 \\
0 \\
0 \\
0 \\
0 \\
0
\end{pmatrix}
=
\begin{pmatrix}
190{,}400 \\
14.25 \\
0 \\
0 \\
0 \\
0 \\
0
\end{pmatrix}
(n2)
$$

The vector **n2** contains the values for off-site achene production and the early seed bank. By repeatedly multiplying the transition matrix and the product vector until all the cells are filled produces the first-year population vector, n_t, as shown below:

$$
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.9 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.96 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.02 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.95 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 4{,}155 & 0
\end{pmatrix}
\bullet
\begin{pmatrix}
190{,}400 \\
14.25 \\
0 \\
0 \\
0 \\
0 \\
0
\end{pmatrix}
=
\begin{pmatrix}
190{,}400 \\
14.25 \\
13.68 \\
0 \\
0 \\
0 \\
0
\end{pmatrix}
\quad \textbf{(n3)}
$$

$$
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.9 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.96 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.02 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.95 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 4{,}155 & 0
\end{pmatrix}
\bullet
\begin{pmatrix}
190{,}400 \\
14.25 \\
13.68 \\
0 \\
0 \\
0 \\
0
\end{pmatrix}
=
\begin{pmatrix}
190{,}400 \\
14.25 \\
13.68 \\
0.27 \\
0 \\
0 \\
0
\end{pmatrix}
\quad \textbf{(n4)}
$$

$$
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.9 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.96 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.02 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.95 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 4{,}155 & 0
\end{pmatrix}
\bullet
\begin{pmatrix}
190{,}400 \\
14.25 \\
13.68 \\
0.27 \\
0 \\
0 \\
0
\end{pmatrix}
=
\begin{pmatrix}
190{,}400 \\
14.25 \\
13.68 \\
0.27 \\
0.26 \\
0 \\
0
\end{pmatrix}
\quad \textbf{(n5)}
$$

$$
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.9 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.96 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.02 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.95 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 4{,}155 & 0
\end{pmatrix}
\bullet
\begin{pmatrix}
190{,}400 \\
14.25 \\
13.68 \\
0.27 \\
0.26 \\
0 \\
0
\end{pmatrix}
=
\begin{pmatrix}
190{,}400 \\
14.25 \\
13.68 \\
0.27 \\
0.26 \\
1080 \\
0
\end{pmatrix}
\quad (n6)
$$

$$
\begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.9 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.96 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.02 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.95 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 4{,}155 & 0
\end{pmatrix}
\bullet
\begin{pmatrix}
190{,}400 \\
14.25 \\
13.68 \\
0.27 \\
0.26 \\
1080 \\
0
\end{pmatrix}
=
\begin{pmatrix}
190{,}400 \\
14.25 \\
13.68 \\
0.27 \\
0.26 \\
1080 \\
972
\end{pmatrix}
\quad (n_t)
$$

The rows and columns in the matrices below represented the same stages as for the deterministic woodland groundsel transition matrix, S1 (see Chapter 3, Page 79). The reduced matrices have the same structure as S1' (see Chapter 3, Page 80).

Model 1 (reduced matrix only):

$$
S2' = \begin{pmatrix} 1 & 0 \\ 0.000075 & 37.3 \end{pmatrix}.
\qquad (37)
$$

Model 2, Year 1 (full and reduced matrices, respectively):

$$
S3 = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.76 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.01 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.30 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.81 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 29800 & 0
\end{pmatrix}, \quad
S3' = \begin{pmatrix}
1 & 0 \\
0.000075 & 52.3
\end{pmatrix} . \quad (38)
$$

Model 2, Year 2 (full and reduced matrices, respectively):

$$
S3 = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.76 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.01 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.25 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.81 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 29800 & 0
\end{pmatrix}, \quad
S3' = \begin{pmatrix}
1 & 0 \\
0.000075 & 43.6
\end{pmatrix} . \quad (39)
$$

Model 2, Year 3 (full and reduced matrices, respectively):

$$
3 = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0.000075 & 0 & 0 & 0 & 0 & 0 & 0.76 \\
0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.01 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.05 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.81 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 29800 & 0
\end{pmatrix}, \quad
S3' = \begin{pmatrix}
1 & 0 \\
0.000075 & 8.7
\end{pmatrix} (40)
$$

Model 3, Year 1 (full and reduced matrices, respectively):

$$S4 = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.000075 & 0 & 0 & 0 & 0 & 0 & 0.76 \\ 0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.01 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.30 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.81 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 44600 & 0 \end{pmatrix}, \quad S4' = \begin{pmatrix} 1 & 0 \\ 0.000075 & 78.2 \end{pmatrix} .(41)$$

Model 3, Year 2 (full and reduced matrices, respectively):

$$S4 = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.000075 & 0 & 0 & 0 & 0 & 0 & 0.76 \\ 0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.01 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.25 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.81 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 24100 & 0 \end{pmatrix}, \quad S4' = \begin{pmatrix} 1 & 0 \\ 0.000075 & 35.2 \end{pmatrix} .(42)$$

Model 3, Year 3 (full and reduced matrices, respectively):

$$S4 = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.000075 & 0 & 0 & 0 & 0 & 0 & 0.76 \\ 0 & 0.95 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.01 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.05 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.81 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 8300 & 0 \end{pmatrix}, \quad S4' = \begin{pmatrix} 1 & 0 \\ 0.000075 & 2.4 \end{pmatrix} .(43)$$

Foxglove transition matrices.

For Years 1, 2, and 3 to 6, respectively. The rows and columns represented the same stages as for the deterministic foxglove transition matrix, **D** (see Chapter 4, Page 118).

No added nitrogen fertilizer in Experiment 1:

$$
\mathbf{D}_{1-0} = \begin{pmatrix} 1 & 0 & 54153 \\ 0 & 0.106 & 0.947 \\ 0 & 0.476 & 1.004 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 17328 \\ 0 & 0.135 & 0.510 \\ 0 & 0.399 & 1.000 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 10350 \\ 0 & 0.885 & 0.413 \\ 0 & 0.055 & 1.000 \end{pmatrix}. \quad (44)
$$

62.5 kg·ha^{-1} nitrogen in Experiment 1:

$$
\mathbf{D}_{1-5} = \begin{pmatrix} 1 & 0 & 54153 \\ 0 & 0.210 & 3.384 \\ 0 & 0.540 & 1.024 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 17328 \\ 0 & 0.26 & 0.477 \\ 0 & 0.461 & 1.002 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 10350 \\ 0 & 0.946 & 0.133 \\ 0 & 0.069 & 1.001 \end{pmatrix}. \quad (45)
$$

125 kg·ha^{-1} nitrogen in Experiment 1:

$$
\mathbf{D}_{1-10} = \begin{pmatrix} 1 & 0 & 54153 \\ 0 & 0.180 & 4.804 \\ 0 & 0.571 & 1.036 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 17328 \\ 0 & 0.225 & 0.594 \\ 0 & 0.493 & 1.003 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 10350 \\ 0 & 0.935 & 0.184 \\ 0 & 0.078 & 1.001 \end{pmatrix}. \quad (46)
$$

No nitrogen fertilizer in Experiment 3:

$$\mathbf{D}_{3-0} = \begin{pmatrix} 1 & 0 & 22510 \\ 0 & 0.268 & 0.351 \\ 0 & 0.353 & 0.17 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 7092 \\ 0 & 0.268 & 0.104 \\ 0 & 0.611 & 0.17 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 2454 \\ 0 & 0.268 & 0.098 \\ 0 & 0.299 & 0.17 \end{pmatrix} \qquad (47)$$

62.5 kg·ha^{-1} nitrogen in Experiment 3:

$$\mathbf{D}_{3-5} = \begin{pmatrix} 1 & 0 & 22510 \\ 0 & 0.106 & 1.568 \\ 0 & 0.353 & 0.17 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 7092 \\ 0 & 0.106 & 0.211 \\ 0 & 0.611 & 0.17 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 2454 \\ 0 & 0.106 & 0.122 \\ 0 & 0.299 & 0.17 \end{pmatrix} . \qquad (48)$$

125 kg·ha^{-1} nitrogen in Experiment 3

$$\mathbf{D}_{3-10} = \begin{pmatrix} 1 & 0 & 22510 \\ 0 & 0.044 & 1.856 \\ 0 & 0.353 & 0.17 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 7092 \\ 0 & 0.044 & 0.272 \\ 0 & 0.611 & 0.17 \end{pmatrix}, \begin{pmatrix} 1 & 0 & 2454 \\ 0 & 0.044 & 0.134 \\ 0 & 0.299 & 0.17 \end{pmatrix} . \qquad (49)$$