Ecological Factors Affecting Rates of Spread in *Cytisus scoparius*, an Invasive Exotic Shrub

by

Ingrid Marie Parker

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1996

Approved by Douglas W. Schemske

(Chairperson of Supervisory Committee)

[illegible]

[illegible]

R. T. [illegible]

Roger del Moral

Program Authorized
to Offer Degree Botany

Date July 8, 1996

UMI Number: 9704532

University of Washington

Abstract

Ecological Factors Affecting Rates of Spread in *Cytisus scoparius*, an Invasive Exotic Shrub

by Ingrid Marie Parker

Chairperson of Supervisory Committee: *Professor Douglas W. Schemske*
Department of Botany

Invasions of exotic species are among our most daunting conservation challenges, and range expansion models provide us with a framework for modelling them. I have focussed on ecological factors contributing to variation in population growth and spread in *Cytisus scoparius* (Scotch broom), an exotic shrub invading western Washington.

The reproduction of *C. scoparius* is highly dependent on pollinators. Mean visitation rates (percent flowers tripped) varied from 3% to 30% among four populations over three years. Urban populations experienced greater visitation than prairie populations. Experimental pollen addition revealed significant pollinator limitation in all populations in two years. Fruit set was increased on average 280% to 2620%. No subsequent cost of reproduction was found, indicating that pollinators exert true population-level control over seed production.

The dual effects of seed number and safe-site limitation were investigated with an experiment crossing five seed densities (0-1000 seeds/m^2) with four surface treatments (control, "scalping" of the cryptogram layer, burning before seed addition, burning after seed addition). Seedling/seed decreased with seed density. Burning did not increase germination relative to controls, but seeds scarified by the burn had significantly higher germination rates than seeds added after the burn. Undisturbed plots had the highest germination levels, providing evidence that invasions are not always linked to disturbance.

The relative importance of all stages of the life cycle was evaluated using a matrix demographic approach. I followed marked individuals in six populations, three urban fields and three prairies, across three stages of invasion. Population growth was higher in prairie populations than urban populations and decreased as the invasion proceeded. Elasticity patterns revealed no "silver bullet" for population control in the form of a single dominant stage in early-invasion plots.

Finally, I modelled areal spread of the populations with a cellular automata model. By combining life history transition probabilities with dispersal parameters estimated from the field, I investigated the relative importance of dispersal and demographic variation. The difference in demographic rates between urban and prairie populations made a large difference in rate of spread, enough to swamp out variation in dispersal.

TABLE OF CONTENTS

List of Figures ... iii

List of Tables ... v

Introduction 1
- Demographic and spatial models: tools for synthesis ... 2
- Factors important to the ecology of exotic species ... 3

Chapter 1 Reproductive Ecology, Pollinator Limitation, and its Demographic Consequences 6
- Introduction to Chapter 1 ... 6
- Methods and materials ... 8
- Results ... 15
- Discussion ... 18

Chapter 2 Demography of Invasion in *C. scoparius* 34
- Introduction to Chapter 2 ... 34
- Methods ... 37
- Results ... 46
- Discussion ... 50

Chapter 3 Disturbance and the Cryptogamic Crust: Safe Site and Seed Limitation in the Establishment of *C. scoparius* 85
- Introduction to Chapter 3 ... 85
- Methods ... 87
- Results ... 90
- Discussion ... 91

Chapter 4 Dispersal and Rates of Spread in *C. scoparius*, a Modelling Approach 103
- Introduction to Chapter 4 ... 103
- Part 1: Dispersal ... 107
- The Frequency of Long-Distance Dispersal Events ... 107
- Ballistic Dispersal ... 108
- Relative Contribution of Ballistic Dispersal and Ant Dispersal to the Distribution of Seedlings ... 110
- Part 2: Construction and Results of a Spatial Model ... 114
- Spread of Populations from one Initial Founder: Variation in Dispersal vs. Demography ... 116
- Spread of Propagules from one Initial Founder: Variation in the Proportion of Long-Distance Propagules ... 118
- Spread of Populations from Varying Spatial Arrangements of Founders ... 119
- Conclusions ... 119

Bibliography ... 142

Appendix 1: Tripping Action of *Bombus* in the Act of Pollinating a *C. scoparius* Flower ... 158

Appendix 2: Transition Matrices for Each Population, Stage of Invasion, and Year ... 159

Appendix 3: List of Vascular Plant Species Found at each Site 169

Appendix 4: Demographic Transitions (in Matrix Form) Used for Spatial Simulation Model 172

LIST OF FIGURES

Number *Page*

1.1 Mean tripping rates in four populations over three years ... 30

1.2 Distribution of individual tripping rates ... 31

1.3 Fruit production in pollen-supplmented vs. control branches ... 32

1.4 Pollen limitation as a function of tripping rate ... 33

2.1 Life cycle graph ... 66

2.2 Biomass as a function of age ... 67

2.3 Box plot of age vs. stage ... 68

2.4 Stage-specific mortality in prairie and urban populations ... 69

2.5 Stage-specific fecundity in prairie and urban populations ... 70

2.6 Germination rates in prairie and urban populations ... 71

2.7 Box plot of biomass per square meter ... 72

2.8 Box plot of three measures of density ... 73

2.9 Increase in biomass over time ... 74

2.10 Change in densities over time ... 75

2.11 Finite rate of increase for each stage of invasion, population, and year ... 76

2.12 Lambda as a function of biomass ... 77

2.13 Actual stage distribution and stable stage distribution ... 78

2.14 Elasticities across stage classes ... 80

2.15 Elasticity for fecundity as a function of lambda ... 82

2.16 Simulation of population increase under natural and increased pollination, starting with ten seeds ... 83

2.17 Population increase under natural and increased pollination, starting with current stage distribution ... 84

3.1 Number of seeds germinating ... 100

3.2 Seedlings per seed for 100 to 1000 seeds 101

3.3 Number of seedlings originating from plots of different burn temperatures 102

4.1 Transect of patches along Rte. 26 on Mount St. Helens 127

4.2 Individual replicates from the ballistic dispersal experiment 128

4.3 Composite ballistic dispersal distribution 129

4.4 Individual replicates for "ant only" dispersal 130

4.5 Individual replicates for "ballistic + ant" dispersal 131

4.6 Composite distribution for ant dispersal only 132

4.7 Composite distribution for ballistic + ant dispersal 133

4.8 Schematic of the arrangement of dispersal "bins" 134

4.9 Example model output, including critical times 135

4.10 Number of bins filled under two different density criteria 136

4.11 Rate of spread for prairie and urban populations, three types of dispersal 137

4.12 Rate of spread as a function of lambda 138

4.13 Rate of spread under increasing proportions of ant-dispersed seeds 139

4.14 Design of model "experiment" to look at effect of multiple foci 140

4.15 Rate of spread as a function of the number of initial foci 141

LIST OF TABLES

Number *Page*

1.1 Fruit number per flower of control and hand-pollinated flowers 24

1.2 ANOVA of floral tripping rates 25

1.3 Pollen limitation in four populations in 1993 and 1994 26

1.4 Correlations between tripping rate and fruit production per plant 27

1.5 Cost of reproduction 28

1.6 Finite rates of increase with and without pollen limitation 29

2.1 Biomass as a function of diameter and branch number 58

2.2 Regression equations for biomass 59

2.3 Stage class criteria 60

2.4 ANOVA in fruit production 61

2.5 Correlations among lambda and four direct measures of invasion 62

2.6 Correlations between measures of invasion and measures of occupancy 63

2.7 Effect of habitat and stage of invasion on lambda 64

2.8 Time to "saturation" of plots under natural and increased pollination 65

3.1 ANOVA of seedlings germination 96

3.2 ANOVA of seedling survival 97

3.3 ANOVA of seedlings left in August 98

3.4 ANOVA of germination as a function of temperature of the burn 99

4.1 Summary data on dispersal distributions from "plant" and "ant" circles 121

4.2 Recursion equations for the spatial simulation 122

4.3 Comparison of eigenvalues for 7x7 and 4x4 matrices 123

4.4 Results from the simulation: space filled at critical times 124

4.5 Correlations between life history transitions and spread rate 125

4.6 ANOVA of spread rate on population type and number of foci 126

ACKNOWLEDGEMENTS

First I would like to thank my advisor, Doug Schemske, who with his great respect for the scientific endeavor, dedication to teaching and to mentoring, and extraordinary biological insight has provided me with an impossible role model. Doug's encouragement and friendship have been invaluable companions throughout my graduate career. His unique sense of humor keeps us all comfortably off-balance.

Second I am deeply indebted to Peter Kareiva for tireless attempts to teach me to take risks, to renounce my ineffecient ways, and to approach science as a cooperative and collegial enterprise. With his confidence, he has inspired me to bring confidence and joy to my research. This dissertation has benefitted from his critical comments, and also those of R.T. Paine, whose grand historical perspective on ecology has made a great contribution to my training. I thank Paine for six years of opinionated and enlightening banter. I would also like to thank Roger del Moral and Art Kruckeberg for providing me with a deeper understanding of the natural history and ecology of western Washington.

I am grateful for the scientific interaction, emotional support, warmth and fun shared with past and present members of both the Plant Experimental Drug Lab and the PinKo Lab and associates, especially: Carol Goodwillie, Mary Ruckelshaus, Denise Lello, John Bishop, Jane Wentworth, Brian Husband, Justin Ramsey, Kimiora Ward, Martha Groom, John Banks, Jennifer Ruesink, Bill Fagan, Ellen Gryj, Eli Holmes, Ellie Steinberg, Eli Meir, Cheryl Schultz, Claudia Jacobi, Gary Chang, and Miguel Pascual.

This research could not have been completed without huge amounts of help in the field. In addition to those named above, literally dozens of friends and family members have volunteered hours of their time, and I am eternally indebted to them all. Stephanie Madsen, Kimiora Ward and Heather Bonifield were excellent field assistants, rain or shine (or snow or hail). The personnell in the Fish and Wildlife and Forestry offices at Fort Lewis provided valuable logistic support, especially Joe Reasoner, Inger Schmidt, Dave Clouse, and Linda Adams. Don Varecamp and Lynn Catlin at Discovery Park were also very helpful. Modelling endeavors benefitted from the cheerful contributions and comments of Garrett Odell, Chris Jordan, Eli Meir, and the Mathematical Biology group at UW, and Jon Brasher graciously threw me a techno-paddle on several frantic occasions. My thoughts on invasion biology have been influenced over the years by long conversations with Sarah Reichard. I am also grateful for the generous hospitality extended to me at the University of Chicago, especially by Cathy Pfister, Tim Wootton, Joy Bergelson, and their labs. This research was funded by Sigma Xi, The Botany Graduate Research Fund, The Hardman Foundation, an NSF Dissertation Improvement Grant. and an NSF Training Grant in Mathematical Biology.

Finally, special thanks to Karen Goodell, Kent Koprowicz, Barb Best, Guy Parker, and my parents David and Hanne Booth for all their love and support.

For Mom and Dad,

the greatest gift I will ever know.

INTRODUCTION

Invasions of exotic species represent one of the major environmental challenges of this century (Hedgpeth 1993), and this realization has spawned a flood of books on the topic in recent years (Kornberg and Williamson 1986, Mooney and Drake 1986, Drake et al. 1989, Hengeveld 1989, Office of Technology Assessment 1993). Exotic species have become a serious concern for those charged with maintaining and protecting native communities, and in some regions the numbers of introduced plant species exceeds that of the native flora (Office of Technology Assessment 1993). Once an exotic pest becomes established, ecologists would like to know where it is likely to spread and when it will get there. Similarly, in order to allocate resources most effectively a manager of a preserve needs to know how fast an infestation will spread through a field once it is "infected." Thus the factors influencing rates of invasion are important both for understanding the dynamics of range expansion and to begin to address urgent questions of exotics management and control.

The pioneering work on invasive species by Charles Elton (1958) and Herbert Baker (1965) synthesized historical data and anecdotes of species introductions, and drew generalizations about the ecological characteristics of both invaders and invasible habitats. Since that time, several approaches have been taken to understanding what traits confer invasiveness. One common approach was to compile lists of characters that seem to show up in exotic weeds or pests (Baker 1965, Noble 1989). Many of the listed factors (e.g. non-restrictive germination requirements, rapid growth, high seed output, broad tolerance, self-compatibility) are characters that influence the intrinsic rate of increase or the degree to which it fluctuates in time or space. The quantitative extension of these verbal models was to extract patterns from databases of successful and non-successful introductions (Dritschilo et al. 1985, Lawton and Brown 1986, Roy 1990, Reichard 1994). Again, traits related to population growth were found to be important, such as high fecundity (O'Connor 1986, Bergelson and Crawley 1989), longevity (Crawley 1989), and length of the juvenile period or generation time (Bergelson and Crawley 1989, Reichard 1994). Broad tolerance or plastictiy, the ability to do well in many habitats (Forcella and Wood

1984, Moulton and Pimm 1986, Reichard 1994), and dispersal (Dritschilo et al. 1985) were also important in some cases.

Demographic and spatial models: tools for synthesis

Demography is the study of population growth and the factors that influence it throughout the life cycle. The response of vital rates (which describe the probabilities of moving through the life cycle) to the environment determines both population dynamics in the short-term and the evolution of life histories in the long-term (Charlesworth 1980, Caswell 1989, Schemske et al. 1994). As invasiveness is the result of a positive interaction between the traits of an introduced species and conditions in the new host habitat, evaluating the causes for success and spread of an invasive species is fundamentally a problem of demography (Kruger et al. 1986). A useful approach for analyzing demographic problems is matrix population models (Silvertown 1987, Caswell 1989). Because they integrate processes throughout the life cycle, such models sometimes demonstrate nonintuitive "emergent properties" of a population that cannot be inferred from studying individual life history stages (Werner and Caswell 1977). In the applied arena, matrix models have become common as tools in population viability analysis, which evaluates the demographic status of rare or sensitive species and can be used to compare the efficacy of different management strategies (Crouse et al. 1987, Menges 1990). The application of matrix models to invasive populations can similarly provide insights into the management of noxious species.

Not simply a stationary demographic process, invasions rely on the interplay of population dynamics and dispersal. At the most basic level, dispersal rates constrain the maximum speed with which a population may move in space. Dispersal and the resulting spatial distribution can also influence the velocity of spread through the production of "new foci" (Moody and Mack 1988, Hengeveld 1989). Mathematical treatment of the spatial spread of invading species has a rich history and has recently received renewed interest (Holmes et al. 1994). Range expansion models combine population growth with a measure of areal spread (Skellam 1951, Okubo 1988), and they have been remarkably successful in predicting rates of spread despite their simplicity (Ammerman and Cavalli-Sforza 1984, Okubo et al. 1989, Andow et al. 1990, Andow et al. 1993). When combined with empirical data, models of spread can provide insights into the relative importance of different aspects of the biology of an invasive species (Lubina and Levin 1988, Londsdale 1993).

Factors important to the ecology of exotic species

The dual importance of demography and dispersal is not unique to invasive species; it applies to native species as well, especially those such as early-successional colonizers for which metapopulation dynamics are likely to be important. However, an aspect that *is* unique to exotic invasions is the new ecological context in which introduced species find themselves. When an invader arrives in new territory it leaves behind the associates with which it has evolved, and so the character of interactions is, in a sense, fundamentally different. These novel species interactions can influence either population dynamics or dispersal, and thereby may play a role in determining the invasion process.

Darwin was one of the first to recognize the value of invasions for illustrating ecological principles. He used intercontinental introductions to support his ideas on the geometrical increase of populations and the importance of biotic interactions in determining range limits (1859, Ch.3). Because invasions are by definition non-equilibrial, they reveal underlying ecological forces that might otherwise be masked. For example, one "invasion dogma" is that exotics achieve their success by leaving behind natural pests (Dahlsten 1986, MacKauer et al. 1990), illustrating the importance of species interactions in regulating population growth.

Although there is a growing body of literature documenting interactions between invaders and native species (Roubik et al. 1986, Schofield 1989, Usher et al. 1992, Townsend 1996), mutualistic interactions have received almost no attention (but see (Valentine 1978, Kjellberg and Valdeyron 1990, Bossard 1991). As mutualisms are commonly thought to involve some degree of adaptation or coadaptation, there is an opportunity for exotic plants to suffer negative demographic effects from facing an entirely new guild of interacting species. In invading plants with specialist pollinators, the biology of the pollinator could constrain range expansion, or may result in an evolutionary shift to exploit a new species (Kjellberg and Valdeyron 1990).

Finally, there is an oft-noted relationship between exotic species and disturbed communities (Orians 1986, Hobbs 1989, Hobbs and Huenneke 1992); in some cases exotic species even appear to depend on disturbance to enter an ecosystem (Fox and Fox 1986, Parker et al. 1993). Hobbs and Huenneke (1992) suggest that disturbance usually acts to stimulate invasion by increasing the availability of suitable microsites for establishment. But is disturbance always a necessary condition for invasion? Can natural resource managers control exotic pests by using "ecosystem management" (LaRoe 1993, Noss et al. in press) to promote healthy plant communities resistant to invasion?

My dissertation is a case study of the invasion of *Cytisus scoparius* (Scotch broom) in western Washington. This aggressive, nitrogen-fixing shrub was introduced in the 1880's by early settlers of the Pacific Northwest as an ornamental (Gilkey 1957) and is now a noxious pest in rangelands and natural areas throughout the west coast of North America. *C. scoparius* is also a successful invader in several other parts of the world, including New Zealand, Australia, and Chile (S. Reichard, pers. com.). I focus on the population dynamics and ecology of *C. scoparius* in an attempt to shed light on what factors, both of the plant's autecology and its interactions with resident species, contribute to variation in rates of spread. Chapter One reports on a series of experiments and observational studies on reproductive ecology and plant-pollinator interactions. First I investigate the degree to which reproduction is dependent on the visitation of bees. Then I quantify the level of pollen limitation. Pollen limitation has been shown in many plant species (Schemske et al. 1978, Johnston 1991, Burd 1994), although it is generally not thought to be important in weed species (Baker 1965). By following subsequent demographic rates of hand-pollinated and control plants, I test for a "cost of reproduction" and evaluate the potential for pollinators to have a direct impact on the rate of population growth and spread of the invader.

Chapter Two details patterns of population growth rates in six populations of *C. scoparius*. Several thousand individuals in permanent plots were followed over three years (1993-95) to quantify how population dynamics depend on 1) the type of habitat being invaded and 2) the position relative to the front of the invasion wave. Three populations were in urban fields and three were in western Washington prairies. For each population there were plots of different "stages of invasion": early (few, scattered plants), intermediate (space beginning to fill with plants), and late (saturated with very large plants). Matrix analysis (e.g., the intrinsic rate of increase, elasticities and sensitivities, the stable and actual stage distributions) is used to gain insight into the differences among plots and among populations. Direct measures of invasion, such as changes in density and changes in plant biomass, are also presented.

Chapter Three describes an experiment evaluating the factors controlling rates of seedling establishment on the prairie. By manipulating both seed source and soil surface characteristics, I investigated the balance between seed and safe-site limitation (Harper

1977), and how human disturbance and management practices may affect this balance. The treatments included removal of the cryptogamic layer and control burning, either before or after the introduction of seeds. The timing of the burn is important in separating the effect of burning on the resident plant community from the scarifying effect on *C. scoparius* seeds themselves.

Chapter Four presents a collection of experiments designed to quantify the shape of the local seed dispersal distribution caused by ballistic dispersal and secondary ant dispersal, and also the frequency of long-distance dispersal events along roads. The dispersal information is then used in the construction of a spatial model of spread. By integrating dispersal with demography, the model provides a synthetic view of the invasion process and the relative importance of variation in different aspects of the ecology of *C. scoparius*.

CHAPTER 1. REPRODUCTIVE ECOLOGY, POLLINATOR LIMITATION, AND ITS DEMOGRAPHIC CONSEQUENCES.

INTRODUCTION TO CHAPTER 1

Introductions of exotic species provide a unique opportunity to study the demographic significance of species interactions. In fact, some of our classic examples of ecologically important interactions are cases of disruptive exotic predators or pathogens (von Broembsen 1989) or cases of spectacular invasions mitigated by biological control agents (Dodd 1957). Although there is a growing body of literature documenting interactions between invaders and native species (Roubik et al. 1986, Schofield 1989, Usher et al. 1992, Townsend 1996), mutualistic interactions have received almost no attention (but see (Valentine 1978, Kjellberg and Valdeyron 1990, Bossard 1991). When an invader arrives in new territory it leaves behind the associates with which it has evolved; as mutualisms are commonly thought to involve some degree of adaptation or coadaptation, there is an opportunity for exotic plants to suffer negative demographic effects from facing an entirely new guild of interacting species. It is important to ask whether a shortage of mutualists could limit the rate of population growth for an exotic species. In such a case, adaptation of the transplanted species to its new biotic environment could in fact exacerbate invasion problems. This scenario could explain the time lag that is often seen between the introduction of a new species and the manifestation of large-scale spread (Hengeveld 1989, Andow et al. 1993).

Pollination, in particular, is an example of a mutualism that has the potential to control important demographic attributes of populations. Limitation of seed production by insufficient pollinator visitation is common in plants (Schemske et al. 1978, Bierzychudek 1981, Galen 1985, Snow and Whigham 1989, Johnston 1991, Karoly 1992, Calvo 1993, Burd 1994). Burd (1994) found in a recent survey of the literature that 62% of 258 species experienced pollinator limitation in at least one population and year. However, assessing the importance of pollinator limitation in long-lived species is made difficult by the possibility of a cost of reproduction. That is, an increase in seed production may extract a subsequent cost in terms of survivorship or future reproduction, which may offset the benefit of that increase (Montalvo and Ackerman 1987, Zimmerman and Pyke 1988, Primack and Hall 1990, Ehrlén 1992). Therefore one must analyze later effects on the life cycle in order to translate pollinator limitation in a single season into a demographic impact of pollinators. The ecological importance of an absolute increase in seed set at the population level will depend on the role of seeds in population dynamics. This role is likely to be more important in invading populations. As life history theory predicts, fecundity (especially early in the life cycle) can have a large effect on rates of increase in rapidly growing populations (Lewontin 1965, MacArthur and Wilson 1967). Thus variation in pollinators may have greater consequences for invading species.

Many studies have shown that pollinator service can vary in both space (Campbell 1987, Johnston 1991, Murali 1993) and time (Horvitz and Schemske 1990, Dieringer 1992, Gomez 1993). By definition, pollinator limitation should decrease as levels of pollination increase, and empirical tests have shown this trend (Stanton et al. 1987, Widén and Widén 1990). However, for few species is there direct, detailed information on the relationship between natural variation in visitation and fruit set at the level of the individual (Zimmerman 1980, Schemske and Horvitz 1988, Real and Rathcke 1991). By combining experiments in pollen limitation with such detailed studies of natural patterns, phenomena such as pollination thresholds, the distribution of pollen limitation among individuals, and the shape of the response of pollen limitation to visitation rate can be investigated. Experiments provide a means of evaluating the consequences of natural patterns, while natural patterns provide a context for interpreting experimental results, such as the potential for evolution of the interaction between plants and pollinators.

The invasive shrub *Cytisus scoparius* (Leguminosae) has an unusual floral feature that makes it ideal for pollination studies. When flowers are successfully visited, they are "tripped" open by the pollinator and are easily distinguished from unvisited flowers. The research presented here takes advantage of this feature to quantify pollinator visitation to large numbers of individuals and to follow the demographic consequences of that visitation.

My approach involved a suite of field experiments designed to answer the following specific questions: 1) What is the range of variation in pollinator visitation to *C. scoparius* at the level of the population and of the individual? 2) To what extent is seed production pollinator limited in *C. scoparius* populations? 3) Is increased seed production within one season compensated by subsequent demographic costs? 4) How do fruit production and pollen limitation respond to natural variation in pollinator visitation in field populations? 5) What is the potential impact of pollinators on the population growth of this invader?

METHODS AND MATERIALS

Study plant:

Cytisus scoparius, Scotch broom, was introduced by early settlers of the Pacific Northwest as an ornamental (Gilkey 1957); the first recorded specimen was collected from a garden in Seattle in 1888. For the last four decades, *C. scoparius* has been regarded as a noxious pest in rangelands and natural areas throughout the west coast of North America from British Columbia to central California.

Cytisus scoparius is a large shrub, reaching a height of four meters or more in its introduced range. It has no form of vegetative reproduction and therefore relies entirely on seed set for reproduction. Plants begin reproducing in their third or fourth year and large, older individuals can produce several thousand flowers (unpubl. data). *C. scoparius* , which produces no nectar, has papilionaceous flowers with fused keel petals. An insect visitor must be large enough to push the keel down and split the petals, releasing the style and anthers which then spring up to contact the back of the pollinator in an explosive motion (Appendix 1). Once a flower is "tripped" in this way, it does not return to its original configuration. The fruits are pods (with an average of 7-8 seeds per pod) that dehisce explosively; seed dispersal is also furthered by ants (Bossard 1991).

Study sites:

Most of the experiments described here were performed in four populations split between two distinct habitats: native prairie and urban fields. Native prairie is found on the gravelly outwash plains of western Washington, which are characterized by shallow, coarse-textured soils and low levels of soil nutrients (Franklin and Dyrness 1988). Once covering great, park-like expanses (Kruckeberg 1991), these prairies have been reduced by development and agriculture to a few remnants, many of which are found on Fort Lewis, a 400,000 acre military base approximately 80 km south of Seattle. The prairies are dominated by *Festuca idahoensis* and include small herbaceous perennials such as *Cammassia quamash* and the state-threatened *Aster curtis*, with intervening space covered by a thick cryptogamic layer (Lang 1961). When invaded by *C. scoparius*, however, the prairies can be converted to monospecific stands of this exotic shrub. Aggressive efforts to control *C. scoparius* are in place in all managed prairie remnants. The two prairie populations primarily used in this study were Johnson Prairie and Thirteenth Division

Prairie, located approximately 20 km apart at opposite ends of the Fort Lewis reservation. I performed some of the auxiliary studies such as the autogamy experiments at Folsom Hill, another prairie site on Fort Lewis.

The two urban field populations were situated in large Seattle city parks; Magnuson Park and Discovery Park are on opposite sides of the city limits separated by 14 km. Both fields are in areas that had originally been forested but were subsequently used for land-fill and exhibit poorly developed soils. Dominant plants in these fields are primarily exotic species such as *Agrostis tenuis* and *Vicia villosa.*

*C. scoparius*flowers from April through June, although phenology differs considerably between urban and prairie sites. Urban sites begin and finish flowering more than two weeks earlier than prairie sites. This difference may be related to differences in the low temperatures of April, May and June, which average 6, 9, and 12 ^{o}C in Seattle versus 3, 6, and 9 ^{o}C at a site close to Fort Lewis (Sites 7468, 5224; Climatedata database).

Autogamy rates and consequences of selfing:

To establish the role of pollinators in seed production, in the spring of 1992 I marked forty flowers on each of twenty plants at Folsom Hill. I assigned ten flowers per plant to each of four treatments: 1) tripping the flower and adding outcross pollen collected from several individuals, 2) tripping the flower and adding self pollen, 3) tripping the flower without adding pollen, and 4) leaving the flower untripped (control). Pollinator visitation was so low in this population in 1992 that it was unnecessary to bag control flowers; controls were checked throughout the experiment to ensure that no natural pollination had occurred. On a subset of the plants, keel petals were removed from all the tripped flowers to prohibit secondary visitation from pollinators. However, results from these plants were not significantly different from unmanipulated plants, so data were combined. I recorded the number of fruits and the number of seeds for each fruit matured. The total number of fruits generated from 10 flowers and the mean number of seeds per fruit (with each replicate represented by a mean over all fruits produced) were compared among treatments using ANOVA and the Bonferroni-Dunn test.

To further investigate the importance of autogamy, I supplemented the tripping experiment described above by bagging entire branches of flowers in 1993. One branch on each of eight plants was enclosed in a long bag of bridalveil tied at the base. Once all flowers had dehisced and fruit production was initiated, I removed the bridalveil to avoid negative effects on fruit maturation.

Pollinator observations:

In 1994, pollinator observations were done whenever a pollinator was present. Bees were classified by field markings, and in 1995 reference bees were collected and identified. The extremely low frequency of pollinators prevented a formal observational study, so detailed records were kept of the number of hours spent in the field at each population during the flowering season to obtain relative abundances. In order to characterize pollinator behavior and evaluate the probability that flowers receive outcross pollen, for each pollinator I recorded the number of flowers tripped on a single plant, the distance flown between plants, and the number of plants visited before taking a long distance flight (>10m), after which the pollinator was lost from view.

Visitation rates:

In 1993 and 1994, I established a large-scale study to quantify visitation rates and pollinator limitation for two urban (Magnuson Park and Discovery Park) and two prairie (Johnson Prairie and 13th Division Prairie) populations of *C. scoparius*. In 1995 the same design was used to determine visitation rates only. In order to represent the average level of visitation and pollinator limitation at the level of the population, focal plants were selected randomly using transects through each site. Each population was represented by a different set of focal plants each year (n = 40 for Magnuson Park and Discovery Park in 1993, n = 30 for Johnson Prairie and 13th Division Prairie in 1993 and for all populations in 1994, and n = 20 for all populations in 1995). All plants were measured for diameter, stem number, height, and total fruits produced at the end of the season. Select branches on these plants and matched control plants (see below) were marked before flowering began, and I counted untripped and tripped flowers per branch through the season. Individual plants produce flowers continuously over 6-8 weeks; I consequently needed to perform multiple censuses per branch to estimate total flower number for the season. Due to the large number of flowers involved I could not mark each individual flower. The challenge was then to minimize the probability of missing flowers while also minimizing the probability of counting flowers more than once. The proper census interval depended on floral longevity, which was a function of environmental factors such as temperature and humidity. Therefore, at different points during the flowering season, I marked and followed several dozen individual flowers on several plants (separately in urban sites and prairie sites) and calibrated the census interval by the mean floral longevity. The average floral longevities (with a range representing separate flower censuses) for urban and prairie populations, respectively, were 12.0 and 5.7-9.7 in 1993, 5.4-8.2 and 4.2-10.4 in 1994, 6.2-8.7 and 5.9-6.6 in 1995. In 1993 the average census interval was 14.4 days in urban populations and 9.4 days in prairie populations, in 1994 the interval was 7.5 days in both urban and prairie populations, and in 1995 the interval was 7.2 days in urban populations and 6.7 days in prairie populations. Censuses were performed throughout the flowering season within a day or two of these intervals. Despite efforts to minimize the problem, some flowers were pollinated and developed into fruits between censuses, resulting in a few cases of individual fruit/flower ratios higher than one. Another concern is that tripped flowers tend to wilt and abscize before untripped flowers: on average, 1.4 days earlier. This is likely to affect results by somewhat inflating the fruit/flower ratio, deflating the tripping rate, and deflating the estimator for pollen limitation (see below) in plants experiencing higher visitation.

What is referred to here as "pollinator visitation rate" is the per-branch tripping rate, calculated by taking the ratio of tripped flowers to total flowers when these were summed over all censuses for each plant. All ratios were arcsine square-root transformed for analysis. Wherever the arcsine square-root transformation was used in this study, I replaced 0/n with 1/4n and n/n with 1 - 1/4n to improve the transformation at the extremes of the range (Zar 1984). Tripping rates were compared among sites using ANOVA and the Bonferroni/Dunn multiple comparisons test.

Pollinator limitation: experimental assessment

For each focal (i.e. "manipulated") plant described above, I identified two branches of similar size and randomly assigned them to either a hand-pollination or control treatment. Pollinations were done using glass slides containing pollen from three or more donors collected at least 10 m away from the recipient plant in order to minimize both donor-recipient interactions (Marshall and Ellstrand 1986, Schlichting and Devlin 1992) and bi-parental inbreeding. Observations of bee behavior in the field suggest that most flowers are likely to receive outcross pollen (see RESULTS); therefore my choice of donors was appropriate for this system. I tripped flowers by hand, then dragged the stigmatic surface across the slide of pollen. The number of pollen grains deposited by hand-pollination was well within the range of the natural distribution of grains deposited by bees (natural pollination, range = 10-102, MEAN = 40; hand-pollination, range = 22-107, MEAN = 51). In total, I hand-pollinated over 32,000 flowers during the two years of the study.

I censused developing fruits through the summer until they were mature, dry, and ready to dehisce. All analyses were done on final fruit counts. In 1993, I compared average seed number per fruit from hand-pollinated (p) and control (c) fruits on 15 individuals and found that pollen addition did not significantly increase seed number either in an urban population (Magnuson Park: 10 fruits per plant, $n = 15$, $X_c = 8.4 \pm 4.4$, $X_p = 8.6 \pm 3.8$, $t = 0.17$, $p > 0.68$) or a prairie population (Folsom Hill: 5 fruits per plant, $n = 15$, $X_c = 6.1 \pm 3.6$, $X_p = 7.1 \pm 3.7$, $t = 2.1$, $p > 0.15$). In addition, examination of total seed number per plant showed that fruit number explained 98% of the variance between plants, while seed number per fruit explained only 2% of the variance. For these two reasons I chose to approximate total seed output by fruit number.

With pollen limitation studies on large, multi-flowered species, there is a concern that reallocation between branches on a plant may cause the appearance of pollen limitation on a single branch even when the plant as a whole is limited by resources rather than by pollination (Stephenson 1981, Zimmerman and Pyke 1988). Therefore I included a second control for each experimental branch, a similar branch on a separate plant ("unmanipulated") near the experimental plant and close to it in size. If reallocation is important, one would predict the control branch on the unmanipulated plant to have a consistently higher rate of fruit maturation than the control branch on the manipulated plant. I tested for this reallocation using paired t-tests on 1) the log transformation of fruit number ($\log_{10}$[fruits + 1]) and 2) the arcsine square-root transformation (as described above) of the ratio of fruits to flowers, comparing the control branch on the manipulated plant to the second control branch on the unmanipulated plant.

The significance of pollinator limitation was assessed using paired t-tests on the fruit production of experimental and control branches in each population. In order to compare levels of pollinator limitation among populations, I constructed a composite measure equal to the difference between the fruit/flower ratios of the two branches. I then used ANOVA and the Bonferroni/Dunn test on this pollinator limitation measure. I also estimated the mean increase in fruit production under full pollination by taking the ratio of fruit number on the experimental branch to that on the control branch, substituting ones for zeros so that no replicates would be undefined. I calculated a separate mean for each population and year.

Many plants produce more flowers than fruits even when fully pollinated (Stephenson 1981). One interpretation is that the availability of resources places an absolute limit on fruit production. Therefore the mean fruit/flower ratio under conditions of maximum pollination can be used to examine variation in resource availability per flower. The ability of plants to mature fruits given maximum pollination was compared among populations by performing ANOVA on the (transformed) fruit/flower ratio for experimental branches.

Pollinator limitation: natural variation

Using tripped flowers again as a measure of visitation, I assessed the relationship between pollination and fruit set in natural populations in several ways. First, at the level of the branch, I regressed the proportion of flowers setting fruit against the visitation rate in 1993, 1994, and 1995. I used regression that does not estimate the intercept, thereby constraining the curve to pass through (0, 0), and included a quadratic term to look for significant "saturation" of the curve. Then I looked at how pollinator limitation, measured as [experimental fruit/flower - control fruit/flower], dropped off as a function of the tripping rate of the control branch using regression. Polynomial regression was used to test for a non-linear pattern.

To quantify the contribution of variation in pollinator visits to fruit production of the whole plant, I first regressed total fruit number of unmanipulated plants on their diameter to remove variation due to plant size. Fruit number was transformed as log (MEAN + 1) to achieve homoscedasticity. The residuals from this regression were then correlated with the tripping rate estimated from the control branch on that plant. Regressions and correlations were performed for each population individually and for the combined total for each year.

Cost of reproduction:

One concern about pollinator limitation studies on long-lived perennials is that pollen supplementation may not result in a life-time increase in seed production if plants experience a significant "cost of reproduction," compensating for increased reproduction with higher mortality, lower growth, or decreased seed production in future years. I tested for a cost of reproduction in *C. scoparius* by following the fates of the paired branches, comparing experimental, "manipulated control," and "unmanipulated control" branches for branch mortality and fruit production. I also compared manipulated (focal) and unmanipulated plants from the 1993 transects for the following whole-plant demographic characters in 1994: plant mortality, diameter growth ([diameter 1994 - diameter 1993]/diameter 1994), and total plant fruit production. In each case I used a G-test for mortality and paired t-test for growth and fruit production. Because pollination treatments augmented the reproduction of only a portion of the whole shrub, I also tested for whether detecting a cost of reproduction was dependent on the proportional increase of whole-plant fruit production. I calculated this proportional increase by substituting the number of fruits on the control branch for that on the experimental branch to get an estimated baseline per-plant fruit number (in the absense of hand-pollination). Then I divided the true (manipulated) per-plant fruit production by this baseline fruit production. I performed Spearman Rank correlations on the relationship between proportional increase in total fruit production and the difference between experimental and control 1) diameter growth and 2) total fruit production in the following year. Because the plants at 13th Division Prairie were lost in a control burn in 1994, and a subset of plants at Magnuson Park were pulled up by kite flying enthusiasts, these results represent only part of the original sample.

To quantify the potential for a cost of reproduction to counteract the effect of increased pollination, I constructed matrix models of the life cycle of *C. scoparius* based on extensive demographic studies in the four populations where pollination experiments were conducted (Chapter 2). Using data from sites at the front of the invasion (1993-94 for Johnson Prairie and Discovery Park, 1994-95 for all four populations), I calculated finite rates of increase (lambdas) for the populations under natural levels of pollinator visitation as a baseline. I then multiplied the fecundity values for all adult stages by the mean increase in fruit production for each population and year (see above) and recalculated lambdas. I had experimental pollination data only for the 1992-93 and 1993-94 seasons, but because pollinator visitation rates did not differ significantly between 1993 and 1995, I used pollination results from 1993 for the 1994-95 analyses. To see if a cost of reproduction could counteract the demographic effect of pollen supplementation, I then added a "cost" in mortality at two levels. First, an increase in mortality of 2.3%, as suggested by my data (Table 1.5), and second, an increase of 11.5%, five times the observed difference.

RESULTS

Autogamy rates and consequences of selfing:

Fruit production differed significantly among treatments of control, tripped, selfed, and outcrossed flowers (ANOVA, df = 3/76, F = 19.59, p < 0.0001; Table 1.1). Outcrossed flowers had a 40-fold higher probability of making a fruit than did untripped flowers and almost a four-fold higher probability than did selfed flowers. The outcrossed treatment was significantly different from all other treatments (Table 1.1). Mean number of seeds produced per flower also showed a significant treatment effect (ANOVA, df = 3/31, F = 3.47, p = 0.028), although multiple comparisons testing did not reveal any significant contrasts between individual pairs of treatments.

In 1993 eight bagged branches on separate plants, representing a total of 750 flowers, generated three mature fruits that together produced ten seeds. This equals 0.004 fruit/flower, in contrast to an open-pollinated population average of 0.196 fruit/flower for that population in 1993.

Pollinator observations:

The primary pollinators of *C. scoparius* in this study were workers of *Bombus vosnesenskii*, *B. melanopygus*, *B. mixtus*, *B. flavifrons*, and *B. occidentalis*, occasional queens of these *Bombus* species, and the introduced honeybee *Apis mellifera*. Sometimes the smaller bees, primarily *A. mellifera*, would visit flowers that had already been tripped, collecting pollen that had been left behind by the primary visitor from the base of the keel. These secondary visitors did not appear to contact the retracted stigmatic surface.

In 116 hours of observation in 1994, a total of 78 bees were seen pollinating *C. scoparius* plants. The rates of bee visitation followed the same pattern among populations as tripping rates gleaned from the flower censuses in 1994, with Magnuson Park and Discovery Park receiving 1.7 and 0.54 successful visits (i.e., tripping events) per hour, respectively, and Johnson Prairie and 13th Division Prairie receiving 0.29 and 0.26 visits per hour. The higher rate of bee visits in urban populations was due primarily to more visits from *Bombus* species: 1.37 and 0.32 per hour for Magnuson Park and Discovery Park, respectively, and 0.17 and 0.10 for Johnson Prairie and 13th Division Prairie. On average, bees visited 5.6 flowers per plant (median = 3.3) and flew 2.0 m between 2.4 plants in a localized area before taking a "long-distance" (>10m) flight.

Visitation rates:

Mean tripping rates ranged from 3.1% (13th Division Prairie, 1994) to 28.7% (Discovery Park, 1995); the two urban populations consistently received a higher proportion of visits than the two prairie populations (Fig. 1.1). Individuals varied in the proportion of flowers tripped from zero to over 70% (Fig. 1.2). When data from all years and sites were analyzed with ANOVA, the mean tripping rate varied significantly among populations (Table 1.2). Multiple comparisions revealed that Magnuson Park and Discovery Park were not significantly different from each other ($p > 0.50$), each was significantly different from both prairie populations ($p < 0.001$), and Johnson Prairie was significantly different from Thirteenth Division Prairie ($p < 0.05$).

Significant variation also occurred among years (Table 1.2), with multiple comparisons revealing no difference between 1993 and 1995 ($p = 0.5$), but significant differences between 1993 and 1994 ($p < 0.001$) and between 1994 and 1995 ($p < 0.001$). 1994 was a particularly poor year for pollinator visitation in all populations except for Magnuson Park (Fig. 1.1), and this anomaly was reflected in a significant population x year interaction (Table 1.2). In all years, visitation rates to individual plants spanned a range from < 1% to >70% of flowers (Parker, unpubl. data).

Pollinator limitation: experimental assessment

I found no evidence for reallocation of resources from under-pollinated to fully pollinated branches. The second control branch (on the unmanipulated plant) did not produce significantly more fruits than the first control (on the manipulated plant) in either 1993 ($n = 138$, $t = 0.53$, $p = 0.46$) or 1994 ($n = 115$, $t = 0.08$, $p = 0.78$). Similarly, the ratio of fruits to flowers was not significantly different between the two control branches for either 1993 ($t = 0.0001$, $p = 0.99$) or 1994 ($t = 0.0001$, $p = 0.99$). Because reallocation of resources did not occur, I have restricted all subsequent analyses on pollinator limitation to comparisons of the experimental branch and the control branch on the same plant.

Pollen addition significantly increased the number of fruits produced per flower in every population in both 1993 and 1994 (Fig. 1.3). The level of pollinator limitation (as represented by the difference in fruit/flower ratio between experimental and control branches) varied significantly among populations in both 1993 ($df = 3/132$, $F = 4.17$, $p = 0.007$) and 1994 ($df = 3/114$, $F = 24.57$, $p < 0.0001$). Multiple comparisons of means revealed that in 1993, only the difference between 13th Division Prairie and Discovery

Park was significant (Table 1.3). In 1994, neither the two urban populations nor the two prairie populations were significantly different from each other, while all comparisons between an urban and a prairie population were significant (Table 1.3).

The mean (± sd) proportional increase in fruit production under full pollination (experimental fruit number / control fruit number) for Johnson Prairie, 13th Division Prairie, Discovery Park, and Magnuson Park, respectively, was 5.3 (5.1), 6.2 (8.6), 2.8 (3.9), and 3.3 (5.1) in 1993, and 17.9 (21.6), 26.2 (21.0), 8.8 (14.7), and 4.6 (5.2) in 1994.

The mean fruit/flower ratio for fully pollinated branches showed no significant variation among populations in 1993 (pooled mean = 0.50, SD = 0.28; df = 3/134, F = 0.57, p = 0.63), but did vary among populations in 1994 (df = 3/114, F = 13.8, $p < 0.0001$). Multiple comparisons revealed no significant difference between Johnson Prairie and 13th Division Prairie (pooled mean = 0.59, SD = 0.18, p = 0.85), or between urban populations Magnuson Park and Discovery Park (pooled mean = 0.39, SD = 0.16, p = 0.86); all other comparisons were significant ($p < 0.001$). These data indicate that resources available to fruit production were the same in all populations in 1993, and higher in the two prairie populations than in the urban populations in 1994 (Fig. 1.3).

Pollinator limitation: natural variation

I found evidence for a relationship between natural visitation and fruit set both at the level of the individual branch and of the whole plant. In all three years, the regression of fruit/flower ratio on tripping rate was highly significant and explained a large proportion of the variance among branches in fruit/flower (1993: $R^2 = 0.62$, 1994: $R^2 = 0.80$, 1995: $R^2 = 0.81$, $p < 0.0001$). Only in 1993 was the quadratic term in the equation significant (1993: p = 0.003, 1994: p = 0.17, 1995: p = 0.11); that is, in 1994 and 1995 over the range of pollinator visitation seen by plants in the field, there was no saturation of the fruit/flower ratio. Regression of pollinator limitation (experimental fruit/flower - control fruit/flower) on the control branch tripping rate showed a significant linear relationship (Fig. 1.3; 1993: $R^2 = 0.17$, $p < 0.0001$; 1994: $R^2 = 0.30$, $p < 0.0001$). In both cases quadratic terms were non-significant (1993: p = 0.19, 1994: p = 0.32). The point at which pollinator limitation falls to zero (the X intercept) is approximately 0.65 in both years (Fig. 1.3; 1993 confidence interval 0.54-0.86; 1994 confidence interval 0.54-0.81), suggesting that fruit production may be saturated once about 65% of flowers are visited by pollinators.

At the whole-plant level, when variation in fruit number due to plant size (diameter) was removed, the residuals were significantly correlated with tripping rate in all three years (Table 1.4). When each population was taken separately, correlations were significant in 9/12 cases, and were positive in all cases. These significant correlations demonstrate that pollinator visitation, even when approximated by visitation rates to a single branch, is predictive of the reproductive output of individuals.

Cost of reproduction:

I was unable to find support for a cost to increased reproduction. On a per-branch basis, neither the experimental branch nor the control branch on the manipulated plant produced significantly fewer fruits than the control branch on the unmanipulated plant (Table 1.5). Similarly, branches on the unmanipulated plant were not more likely to senesce than those on the manipulated plant, nor were experimental branches more likely to senesce than control branches on the same plant. On a whole-plant level, there was no significant difference between manipulated plants and unmanipulated plants in mortality rate (8.5% for manipulated and 6.2% for unmanipulated), total fruit production, or growth in the year following the treatments (Table 1.5). The mean increase in total plant fruit production was 35% (sd = 103.7). Spearman rank correlations were not significant between proportional increase and either total fruit production ($r = -0.06$, $p = 0.60$) or relative growth in diameter ($r = 0.10$, $p = 0.38$), showing that plants that had a higher proportional increase in total fruit production were not more likely to exhibit a cost.

Matrix analysis of the four populations showed that even a very large cost of reproduction in terms of mortality (11.5%, five times the actual difference seen) could not counterbalance the increase in lambda brought about by pollen supplementation (Table 6).

DISCUSSION

Reproductive dependence on pollinators

The tripping experiment performed in 1992 and subsequent autogamy studies showed that *C. scoparius* plants are highly dependent on insect pollinators for reproduction. Floral structures thought to reduce autogamous self-fertilization are common in papilionid legume species (Ibraham and Coyne 1975, Tilton et al. 1984, Juncosa and Webster 1989), and the tripping mechanism of *C. scoparius* appears to act effectively to prohibit selfing. In addition, the difference in fruit maturation between selfed and outcrossed flowers indicates a large negative effect of inbreeding. This significant effect of pollen donor implies an important role for aspects of pollinator behavior such as the number of flowers visited per plant and the distance flown between successive plants. Interestingly, despite the availability of hundreds or sometimes even thousands of flowers on each individual, pollinators visit only about six flowers per plant and only 2-3 plants within a local area before moving on over longer distances. That is, observed patterns of pollinator visitation maximize the probability that flowers will receive outcross pollen. Augspurger (1980) also found that pollinators visited a limited number of flowers per plant in a mass-flowering shrub in Panama. *C. scoparius* provides more evidence against the hypothesis that mass-flowering is necessarily associated with low inter-plant pollinator movement.

Pollinator limitation, reallocation, and demographic compensation

Significant pollinator limitation of fruit production was found in all populations for both years in which it was measured (Fig. 1.3). Pollen or pollinator limitation is common in many plant species (reviewed in (Bierzychudek 1981, Young and Young 1992, Burd 1994). However, few studies have found pollinator limitation of the magnitude in this study, with hand-pollinations increasing fruit set up to 17-fold. That some individuals did experience high levels of visitation in the field in all years (Fig. 1.2) provides biological relevance for these experimental results.

Perhaps the greatest strength of this study is its ability to quantify pollinator limitation within the context of natural variation in visitation rates. As one would predict (Charlesworth 1989), natural fruit/flower ratios increased with visitation in all three years. Interestingly, this relationship was linear over the range of tripping rates seen in the field in 1994 and 1995. Evidence for saturation (apparently due to resource limitation) appeared only in 1993. The difference between years could be attributed to the fact that in 1993 more individuals had visitation rates greater than 50% (22, 6, and 7 individuals respectively in 1993, 1994, and 1995), providing better resolution of the saturating part of the curve. The composite measure of pollinator limitation (experimental fruit/flower - control fruit/flower) decreased with visitation rate, and this relationship was also linear (Fig. 1.4). Extrapolation from 1993 and 1994 regressions of pollinator limitation on tripping rate generates the prediction that plants should not be limited by pollinators when more than about 65% [0.54-0.86] of flowers are visited. This quantitative result would be expected to vary somewhat with resource levels, as resource limitation should result in pollen saturation at lower levels. Because of the difficulty of obtaining detailed information on pollinator visitation for a large sample of individuals in most systems, the shape of this relationship is not known for many plant species.

After variation in fruit production due to plant size was removed, significant correlations between tripping rate and the residuals demonstrated that pollinator visitation rate, even when extrapolated from a single branch, was predictive of the reproductive output of individuals in the field in most populations and years (Table 1.4). As the individuals in this study were a random sample from each population, this result demonstrates pollinator control over mean demographic rates of the four populations.

C. scoparius plants did not shunt resources within a season in response to pollination; that is, there was no significant difference in fruit number between the first and second (unmanipulated plant) control branches. Some studies have demonstrated reallocation from underpollinated to fully-pollinated inflorescences or branches (McCall and Primack 1985, Zimmerman and Pyke 1988), while others found no translocation of resources (Real and Rathcke 1991, Ehrlén 1992, Fox 1992). Reallocation may be more common in herbaceous species or in shrubs with sequentially developing shoots (Fox 1992), while in those woody species for which most growth occurs before the onset of flowering such as *C. scoparius*, branches may operate independently to meet their own carbon needs (Watson and Casper 1984). The large green fruits of this species may also provide their own photosynthate (Crookston et al. 1974, Bazzaz et al. 1979, Galen et al. 1993). That *C. scoparius* does not reallocate resources between branches suggests that the increase in fruit production seen under supplemental pollination represents true pollinator limitation at the level of the individual.

Studies demonstrating pollinator limitation for one season in a long-lived perennial do not necessarily indicate an increase in individual lifetime fitness or population-level seed production. There may be subsequent "costs of reproduction" to the plant such that an increase in fruit production in one year is offset by early mortality or a reduction in growth or fecundity the next year (Zimmerman and Aide 1989, Calvo and Horvitz 1990). Costs of reproduction have been suggested in several long-lived plant species (El Kassaby and Barclay 1992, Cipollini and Whigham 1994, Primack et al. 1994), but have not been found in other cases (Horvitz and Schemske 1988, Jennersten 1991, Piper 1992, Jackson and Dewald 1994, Lehtilä et al. 1994). When the magnitude of a cost of reproduction is known, quantitative analysis can be used to evaluate whether there is still a net demographic advantage of increased pollen receipt (Bierzychudek 1982, Calvo 1993, Ehrlén and Eriksson 1995). In *C. scoparius*, little evidence for a cost of reproduction was found for any demographic attribute. Both relative growth and fruit production in the following year were actually higher (although not significantly) for manipulated plants than unmanipulated plants. Mortality differed 2.3% in the expected direction, but this difference was not significant (Table 1.5). Although the largest plants in the study had thousands of flowers and only a small proportion of these were pollinated, the mean percent increase in whole-plant fruit production for manipulated plants was substantial (35%), and no relationship was found between the percent increase in whole-plant fruit number and the magnitude of "cost". However, it can not be stated with certainty that no cost would be seen if all flowers of all plants had been pollinated, or if pollen augmentation were continued for multiple seasons (Primack and Hall 1990). Matrix analysis shows that the magnitude of a cost would have to be extremely high to balance the large increase in fruit production generated by increased pollination in this study (Table 1.6). The 2.3% higher mortality rate seen in manipulated plants (although not significant) would have negligible ability to reduce lambda back to its current, under-pollinated levels in any of the four populations. Even a five-fold greater difference in mortality would not counterbalance full pollination, especially in the most rapidly growing populations.

Visitation of an invading plant by resident pollinators

Visitation rates were low in most sites and years, but varied significantly. Variation in mutualistic interactions is the rule rather than the exception (Thompson 1994), and numerous studies have shown variation in pollinator visitation between populations (Campbell 1987, Dieringer 1992, Murali 1993), between years in the same population (Horvitz and Schemske 1990, Gomez 1993), and between individuals (Zimmerman 1980, Widén and Widén 1990, Real and Rathcke 1991, Podolsky 1992). Two results that make this study particularly noteworthy are 1) the range of the variation, with population-wide averages in visitation from 3% to 29% and individual variation ranging from <1% to nearly 80% (Fig. 1.2), and 2) the relatively consistent pattern of variation between urban and prairie populations. Urban populations (Magnuson Park and Discovery Park) tended to receive higher visitation than prairie populations (Johnson Prairie and 13th Division Prairie), primarily due to an increase in the number of *Bombus* individuals. Several factors may explain the higher visitation in urban sites. First, there may simply be higher densities of *Bombus* colonies in urban areas, which could be due either to higher levels of food resources or to the availability of nest sites. In a similar case, (Darwin 1865 [1982])

#23] reasoned that because bumble bees use abandoned rat holes in urban areas, the local density of cats might effectively control populations of clover.

A second explanation for higher visitation rates in urban sites is pollinator competition from native species in the prairie sites. The potential for such competition has been shown in other systems (Waser 1978, Campbell 1985, Rathcke 1988, Feinsinger and Tiebout 1991). Because of its showy floral display and high densities, one might expect *C. scoparius* to be highly attrractive to pollinators; however, observations of bee behavior in prairie sites suggest that bees may prefer the native species available (pers. obs.). Under these conditions, one might expect to see long-term evolutionary changes in *C. scoparius* populations either to reduce flowering overlap with native species, to increase the reward presented to pollinators, or to keep flowers receptive for a longer period of time (Primack 1985, Rathcke 1988).

A third explanation for the shortage of pollinators in prairie populations is a poor match between plants and pollinators in terms of phenology. *C. scoparius* has been part of these prairie communities for a very short time in evolutionary terms, and may be in the process of shifting from traits that were more appropriate in its native range. Phenology has often been shown to be an important factor in mediating interactions between plants and pollinators (Schemske 1977, Augspurger 1981, Gross and Werner 1983, Gomez 1993). For *C. scoparius*, two pieces of evidence are suggestive. One unusual prairie site near 13th Division Prairie flowers several weeks after the end of flowering in other populations. In 1994, this site showed considerably higher tripping rates than the other populations, and many *Bombus* individuals were observed foraging there. Also, tripping rates tend to increase through the season (Parker, unpubl. data). Mismatches in phenology between plants and pollinators may occur when plants are responding to other selection pressures such as seasonal resources (Marquis 1988, Domínguez and Dirzo 1995), reviewed in (Rathcke and Lacey 1985) or the availability of seed dispersal agents or timing of florivores and seed predators (Schemske 1984, Petersson 1991, English-Loeb and Karban 1992). However, it is very possible that in the case of *C. scoparius*, the mismatch in phenology is due not to tradeoffs and stabilizing selection, but to a lack of equilibrium in phenological traits, with plants experiencing continued selection for later flowering.

Pollinators and the spread of invasive populations.

The finding that *C. scoparius* is incapable of autogamous reproduction did not meet our expectations for invading species. In his pioneering work, Baker (1965) declared that the capacity for autogamous self-pollination was one characteristic typical of successful invasive weeds for two reasons. First, when a propagule arrives at a site, there may be no conspecific individuals with which to mate, and second, in a new environment the necessary pollinators may not be present. Baker's views are in part corroborated by the results from *C. scoparius*: i.e., the inefficiency of its obligate relationship with pollinating mutualists is clearly a disadvantage. Yet this plant is a remarkably successful invader. Invasion biologists more recently have emphasized that the list of traits for an "ideal weed" does not define either necessary or sufficient conditions for invasion (Williamson 1994, Ruesink et al. 1995). Whether or not a species will invade a site is a fundamental question based on the integration of the entire life cycle. Populations of *C. scoparius* were increasing in all study sites despite significant pollinator limitation (Table 1.6; Chapter 2).

Although pollinator limitation has not precluded the success of *C. scoparius*, it may have a dramatic effect on its rate of spread. A simulation of newly-founded populations experiencing environmental conditions similar to those in 1993-94 and 1994-95 showed an increase of up to one or two orders of magnitude in the number of vegetative individuals present in ten years (Chapter 2). The effect was much more dramatic in prairie populations than in the slower-growing (and less pollinator-limited) urban populations.

So little is known about the pollination of most invasive species that it is hard at present to guess whether pollinator limitation of the invasion process could be a common phenomenon. With respect to Baker's generalizations, our picture of plant invaders as self-sufficient, vegetatively-reproducing or self-fertilizing, and removed from the vagaries of species interactions may be largely inaccurate. In an exhaustive study of woody plant species introduced in North America, Reichard (Reichard 1994) found that 59% of the successful invasive species for which information on breeding system was available are apparently outcrossing, and 57% of successful invaders do not reproduce clonally (Reichard, pers. comm.). Therefore, it may be common in woody invaders to be highly outcrossing and strongly dependent on local pollinating mutualists.

Table 1.1. Mean fruit number per flower (with standard deviation) and mean seed number per matured fruit (with standard deviation, sample size), averaged over 10 flowers per treatment and replicated on 20 plants, for four pollination treatments: untripped (control) flowers, tripped flowers to which no pollen was added, tripped flowers to which self pollen was added, and tripped flowers to which outcrossed pollen was added. ANOVA was performed on the raw number of fruits generated by ten flowers per plant. For seed number per fruit, the mean represents an average over all of the replicates that produced at least one fruit, with the value for each replicate derived as an average over all fruits produced. Treatments that are not significantly different by the Bonferroni-Dunn test ($p < 0.01$) share the same letter.

Measure	Treatment			
	Control	Tripped only	Self pollen	Outcross pollen
Fruits per flower	0.01[a] (0.031)	0.02[a] (0.041)	0.12[a] (0.19)	0.42[b] (0.33)
Seeds per fruit	1.00[a] (0.00, 2)	1.42[a] (0.51, 5)	1.79[a] (1.85, 11)	3.66[a] (2.14, 18)

Table 1.2. Analysis of variance of floral tripping rates over three years and four populations. Tripping rates were censused throughout the season (see text) on a different set of randomly-chosen plants each year. Data were transformed using the arcsine of the square-root of the proportion of flowers tripped.

	df	Sum of squares	Mean square	F-value	p-Value
Population	3	2.78	0.92	27.41	<0.0001
Year	2	0.57	0.39	8.50	0.0003
Population * year	6	0.66	0.11	3.27	0.0039
Residual	323	10.90	0.03		

Table 1.3. Mean and standard deviation of pollen limitation in four populations in 1993 and 1994. Pollen limitation is represented here as the difference in fruit/flower ratio between experimental and control branches. Treatments that are not significantly different by the Bonferroni-Dunn test share the same letter.

	Prairie		Urban	
Year	Johnson Prairie	13th Division Prairie	Magnuson Park	Discovery Park
1993	0.32^{ab}	0.35^{b}	0.21^{ab}	0.18^{a}
	(0.19)	(0.25)	(0.21)	(0.29)
1994	0.55^{b}	0.56^{b}	0.25^{a}	0.31^{a}
	(0.17)	(0.21)	(0.16)	(0.17)

Table 1.4. Correlations between tripping rate and the residual variation in fruit number per plant remaining from regressions of fruit number on plant diameter. Regressions were done for each population separately and for all populations pooled (Total), and utilized the log transformation for fruit number. "13th" = 13th Division Prairie, "Johnson" = Johnson Prairie, "Magnuson" = Magnuson Park, and "Discovery" = Discovery Park.

	Prairie		Urban		Total
	13th	Johnson	Magnuson	Discovery	
1993					
r	0.37	0.53	0.44	0.25	0.38
n	31	30	38	36	135
p	0.04	0.002	0.005	0.15	<0.0001
1994					
r	0.35	0.58	0.63	0.66	0.47
n	30	29	30	28	117
p	0.06	0.0006	<0.0001	<0.0001	<0.0001
1995					
r	0.67	0.72	0.61	0.09	0.32
n	20	20	20	20	80
p	0.0008	0.0002	0.003	0.71	0.004

Table 1.5. Tests for a cost of reproduction in *C. scoparius*. Comparisons are made 1) at the branch level between experimentally pollinated branches (E), control branches on the manipulated plant (C_{mp}), and control branches on the unmanipulated plant (C_{up}), and 2) at the whole-plant level between unmanipulated plants (up) and those receiving hand pollinations in 1993 (mp). Plant growth was measured as [1994 diameter - 1993 diameter]/1994 diameter, and plant fruit production was measured as [1994 fruit number - 1993 fruit number]. Means for mortality and branch fruit production represent data collected in 1994 for treatments imposed in 1993.

Measure	X_1*	X_2**	Test	df	Statistic	P
Branch mortality (C_{mp} vs. C_{up})	20/84	24/87	G-test	1	0.32	0.57
Branch mortality (E vs. C_{up})	24/82	24/87	G-test	1	0.06	0.81
Branch mortality (E vs. C_{mp})	24/82	20/84	G-test	1	0.64	0.42
Branch fruit production (C_{mp} vs. C_{up})	32.3	36.5	paired t	55	0.52	0.60
Branch fruit production (E vs. C_{up})	28.8	36.5	paired t	54	1.01	0.32
Branch fruit production (E vs. C_{mp})	28.8	32.3	paired t	60	0.37	0.71
Plant mortality (mp vs. up)	8/94	6/97	G-test	1	0.38	0.54
Plant fruit production (mp vs. up)	419	372	paired t	77	0.98	0.33
Plant growth in diameter (mp vs. up)	0.184	0.173	paired t	82	0.68	0.50

* Mean value for first treatment listed in pair.

** Mean value for second treatment listed in pair.

Table 1.6. Values for the finite rate of increase (lambda) in the four study populations at an early stage of invasion (i.e., the edge of the invading front, see Chapter 2). "F increase" is the proportional increase in fecundity per individual achieved by full pollination. Lambda is given for observed transition matrices, for matrices simulating full pollination, and for matrices simulating both full pollination and a cost of reproduction. Cost of reproduction was incorporated as an increase in mortality of all adult stages at one of two levels: the 2.3% increase suggested by the experiment as possible (although not statistically significant), and a 11.5% increase, five times larger than that observed.

Population	Year	λ_{obs}	λ_{poll}	$\lambda_{2.3\%\ Cost}$	$\lambda_{11.5\%\ Cost}$
Johnson Prairie	1994	1.84	3.24	3.24	3.21
	1995	1.93	2.53	2.53	2.50
13th Division Prairie	1995	1.76	2.34	2.33	2.30
Discovery Park	1994	1.22	1.51	1.50	1.46
	1995	1.08	1.16	1.15	1.09
Magnuson Park	1995	1.19	1.31	1.30	1.25

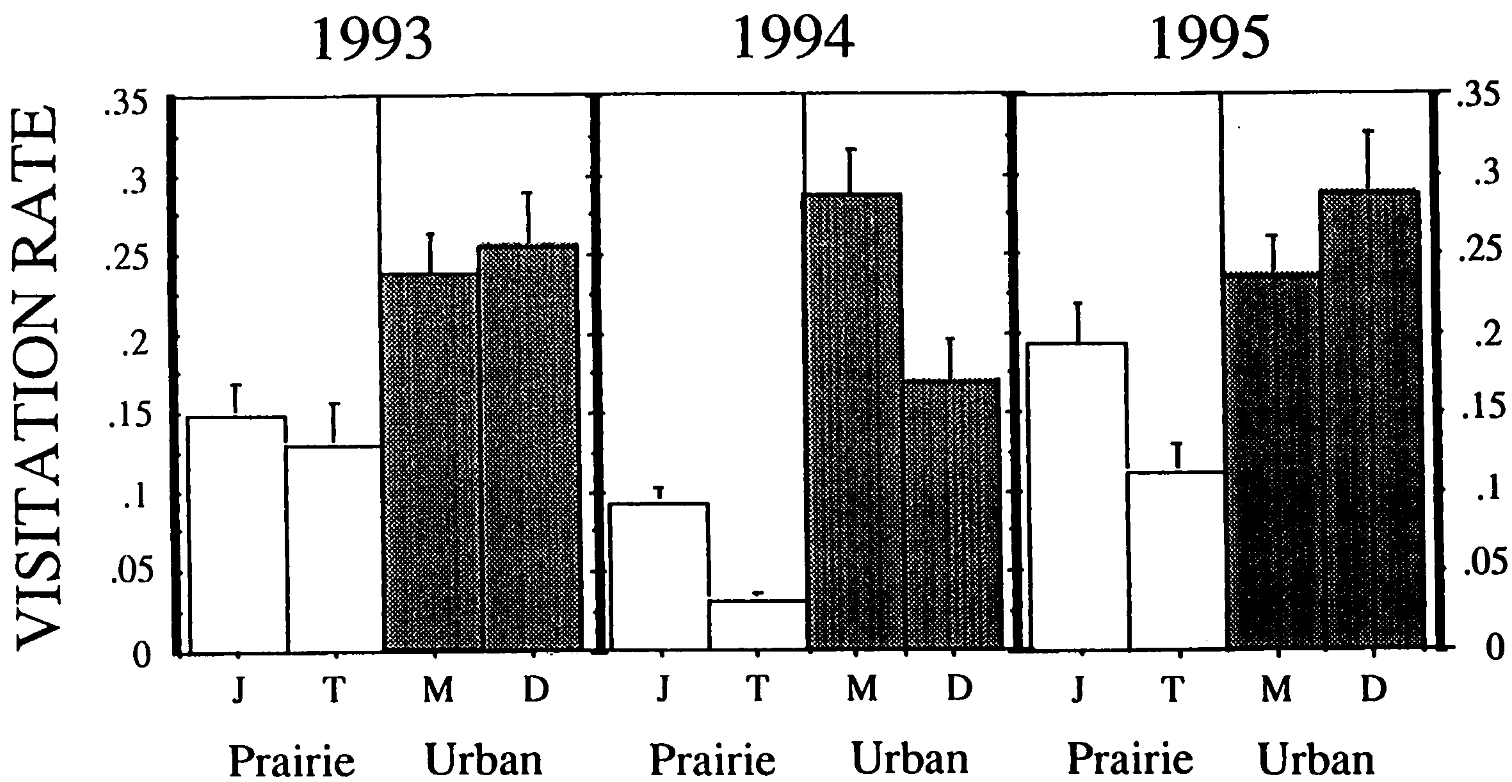


Figure 1.1. Mean visitation rate (tripped flowers/total flowers) measured in four populations in 1993, 1994, and 1995, based on censuses of a random sample of plants at each site. Sample sizes were: 1993, Magnuson Park (M) and Discovery Park (D): n = 40; 1993, Johnson Prairie (J) and 13th Division Prairie(T), n = 30; 1994, all populations: n = 30; 1995, all populations, n = 20. Vertical bars represent one standard error.

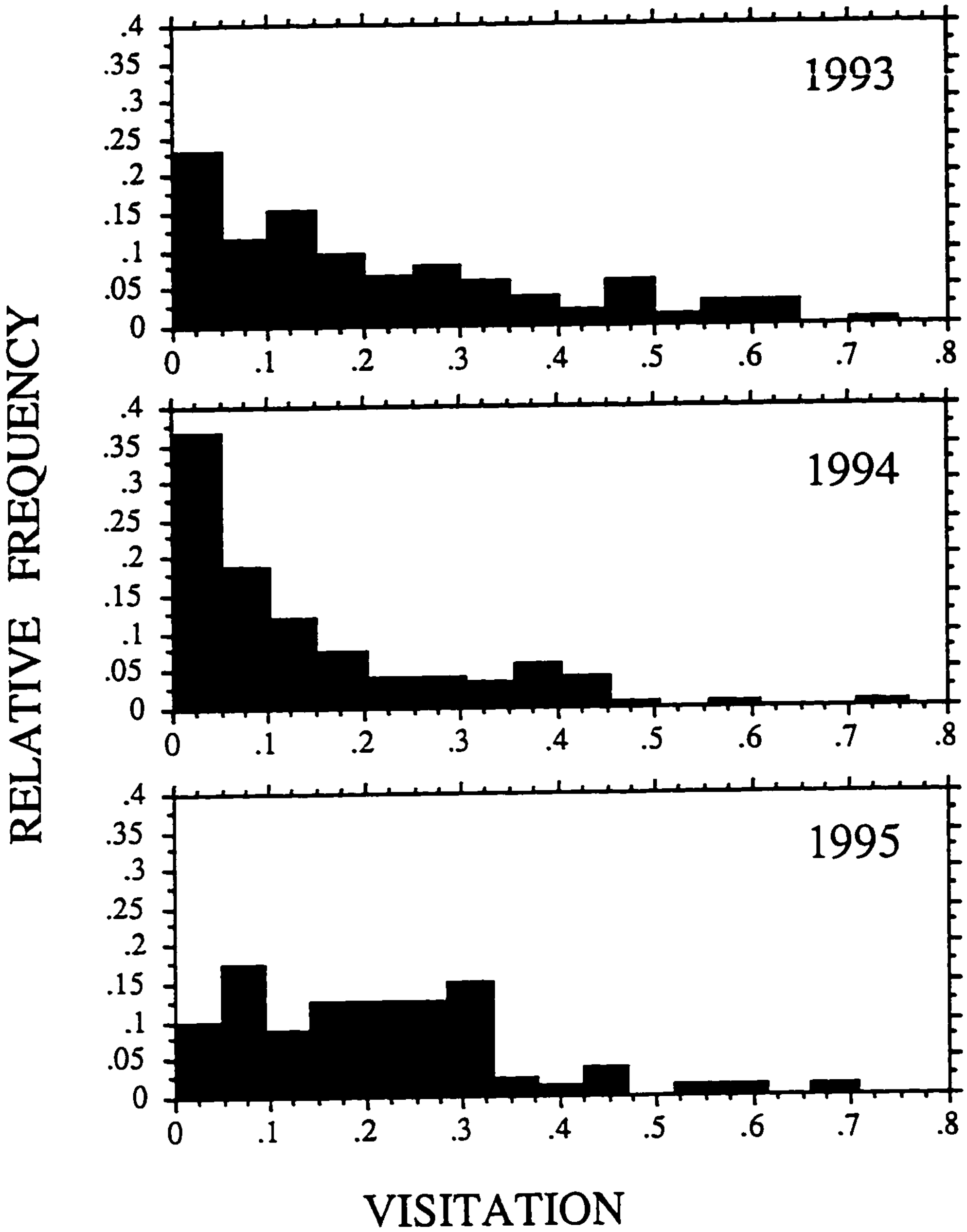


Figure 1.2. Histogram of the variation among individuals in visitation (tripping) rates. Within each year, data are pooled from all plants sampled from two urban fields and two prairies.

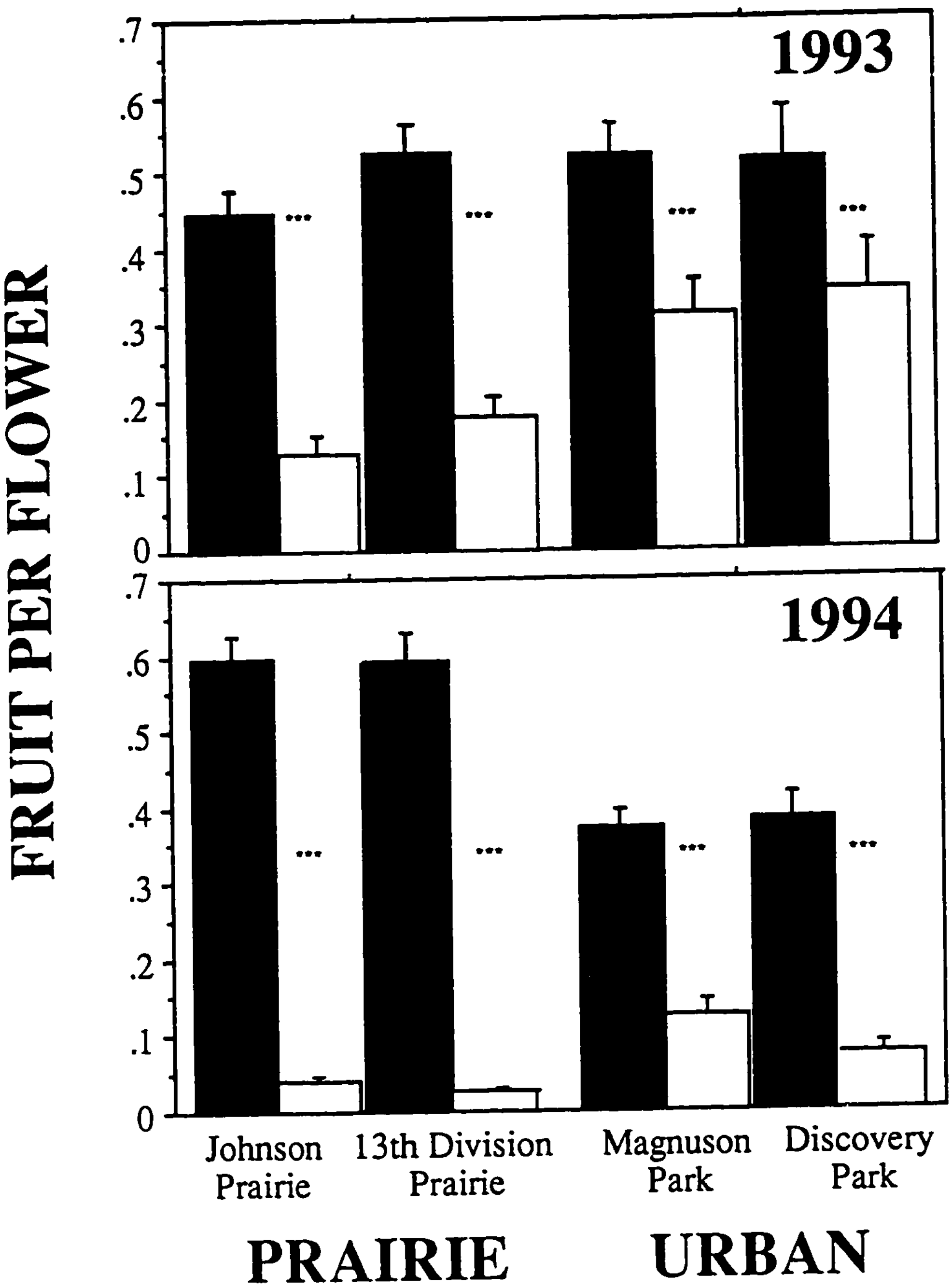


Figure 1.3. Fruit matured per flower for hand-pollinated branches (filled bars) and control branches (open bars) in 1993 and 1994 for four populations: two prairies, Johnson Prairie and 13th Division Prairie, and two urban fields, Magnuson Park and Discovery Park. N = 30 in all cases except for Magnuson Park and Discovery Park in 1993 (n = 40). Bars represent one standard error; *** denotes significance at the $P < 0.001$ level, with Bonferroni adjustment.

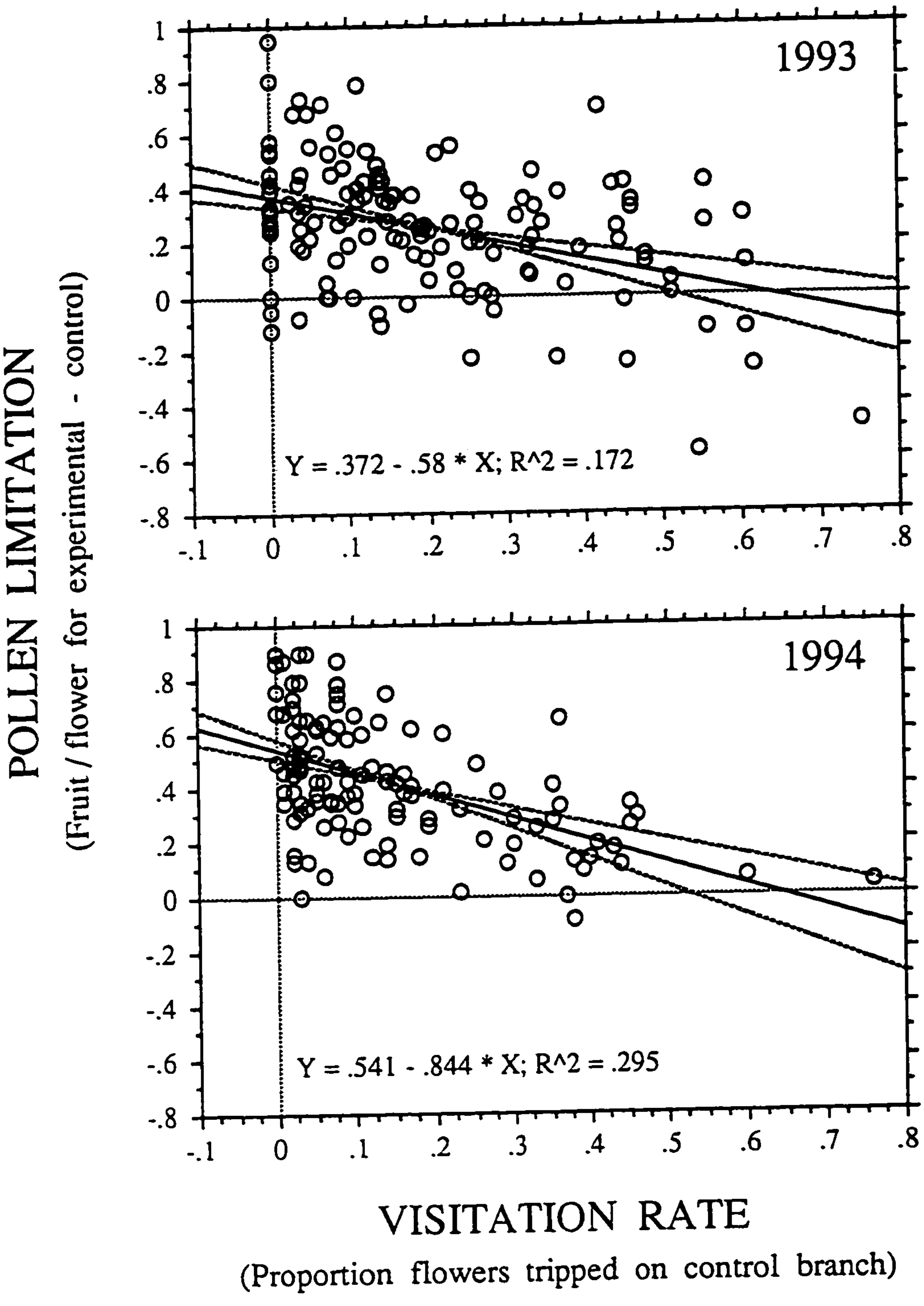


Figure 1.4. Regression of pollen limitation (fruit per flower of experimental branch minus control branch) on proportion of flowers tripped on the control branch, for all individuals pooled across populations in 1993 and 1994. Also shown are 95% confidence interval lines for the slope.

CHAPTER 2: THE DEMOGRAPHY OF INVASION IN *C. SCOPARIUS*:

> Cases could be given of introduced plants which have become common throughout whole islands in a period of less than ten years. Several of the plants now most numerous over the wide plains of La Plata, clothing square leagues of surface almost to the exclusion of all other plants, have been introduced from Europe; and there are plants which now range in India, as I hear from Dr. Falconer, from Cape Comorin to the Himalaya, which have been imported from America since its discovery. In such cases, and endless instances could be given, no one supposes that the fertility of these animals and plants has been suddenly and temporarily increased in any sensible degree. The obvious explanation is that the conditions of life have been very favourable, and that nearly all the young have been enabled to breed. In such cases the geometrical ratio of increase, the result of which never fails to be surprising, simply explains the extraordinarily rapid increase and wide diffusion of naturalised productions in their new homes.
>
> Charles Darwin
> The Origin of Species, 1859

INTRODUCTION TO CHAPTER 2

The population dynamics of invasive species is an area of great theoretical as well as practical interest (Mack 1985, Kruger et al. 1986). The intrinsic population growth rate of an invading organism in part determines its rate of spread (Skellam 1951, Hengeveld 1989, Andow et al. 1990, Andow et al. 1993). Population fluctuations of invading pest species can have important consequences for early detection and eradication efforts (Carey 1996). In addition, the densities reached by an invader in large part determines the impact of that species on the host community (Scorza 1983). Therefore the factors controlling both population growth and density regulation are critical to understanding the biology of invaders.

Speculation about the defining characteristics of invasive species has also emphasized population phenomena. For example, Baker (1965) suggested that successful invaders might show greater levels of phenotypic plasticity, allowing them to sustain consistently high population growth rates across many environments. In contrast, others have argued that invaders are strongly linked to disturbed sites and microsites (Orians 1986, Hobbs and Huenneke 1992, Parker et al. 1993). Little is currently known about spatial or temporal variation in growth rates for any plant species (Horvitz and Schemske 1995), let alone comparative information for native species and exotic pest species. Only by accumulating information from multi-population studies for many organisms will we be able to evaluate hypotheses about the factors controlling the demographic rates of invaders. It has also been suggested that problematic invasive species may experience positive density dependence at low densities, creating a positive feedback loop that allows population numbers to grow very rapidly to high levels (Kruger et al. 1986). More generally, an invading population by definition experiences a broad range of intraspecific densities at a single site. The demographic attributes of a population, as well as its interactions with other species, are likely to be strongly influenced by where plants are located relative to the front of the invasion wave.

Despite the apparent importance of taking a population dynamics approach to the study of invasive species, few workers have done so for plant invaders. Matrix demographic analysis, now a common tool in population biology, is uniquely suited to understanding how factors influencing population-level processes may contribute to overall dynamics. Demographic analysis has been useful in many different contexts. The asymptotic rate of population growth is equivalent to fitness, which enables its use in life history theory (Caswell and Werner 1978, Charlesworth 1980) and in making predictions about the way selection should act in a given environment (Horvitz and Schemske 1995). Demographic analysis is also useful in comparing the lifetime effects of different experimental treatments (Crawley et al. 1993, Parker and Kareiva 1996), and in a similar vein, is an important tool for conservation biologists and resource managers as a way to explore the consequences of management options (Schemske et al. 1994). By evaluating the contribution of different stages of the life cycle to population growth, conservation biologists have identified stages and biological processes critical to the viability of threatened or endangered species (Menges 1986, Crouse et al. 1987, Menges 1990). The same analysis can be done for exotic pest species, with the intention of identifying stages and processes most promising for reducing the viability of these species. The modelling effort in its more naive form is a hopeful quest for the "Achilles heel" of the pest; a more sophisticated view is that even if the model does not reveal one critical stage of the life cycle, it can be used to quantify the effectiveness of different management options, particularly those focussed on altering the vital rates such as biological control.

Finally, demographic analysis allows one to quantify the population-level effects of interspecific interactions, utilizing the natural range of variation in density of the interacting species (Ehrlén 1992, Ehrlén and Eriksson 1995). I have shown that pollinators have a very strong effect on seed reproduction in *C. scoparius* (Chapter 1), but to what extent do pollinators control population dynamics? A persistent controversy in plant population ecology rests on the question: "Does seed number really matter?" (Harper 1977, Louda 1982, Andersen 1989, Hoffman and Moran 1991). Many have argued that seedling recruitment is limited not by the seed source but by the availability of safe sites (Harper 1965) or other factors. However, life history theory predicts that reproduction should be most important in rapidly growing or colonizing populations (MacArthur and Wilson 1967), and others have argued that seed number is most likely to affect population dynamics in invading populations--where safe-sites are least occupied and seed input is most limited (Kruger et al. 1986, Wood and Anderson 1990, McEvoy et al. 1992).

The goal of this chapter is to take a synthetic view of the life cycle and population dynamics of Scotch broom (*Cytisus scoparius*), an invasive shrub on the west coast of North America. I derive a simplified, 7-stage life cycle to present stage-specific demographic rates. Following individuals in several populations in two distinct habitats, and sampling across the range of variation represented by the advancing front of each population, I quantify variation in demography. I compare direct measures of invasion (increase in density, increase in plant biomass) with results from matrix population models. Then focussing on the analytical results, I investigate the questions: 1) What is the magnitude of population growth rates in this species, and how much do they vary between populations and among common habitats? 2) Which life history transitions contribute the most to population growth rates? 3) What is the importance of pollinator-driven variation in fecundity to population growth? 4) How are demographic rates affected by where a plant is relative to the front of the local invasion wave, and what controls the response to increasing intraspecific density?

METHODS

Study plant:

Cytisus scoparius, Scotch broom, was introduced from Europe or the British Isles by early settlers of the Pacific Northwest as an ornamental (Gilkey 1957) the first preserved specimen was collected from a garden in Seattle in 1888. For the last four decades, *C. scoparius* has been regarded as a noxious pest in rangelands and natural areas throughout the west coast of North America from British Columbia to central California.

C. scoparius is a large shrub, reaching a height of four meters or more in its introduced range. It has no form of clonal growth and therefore relies entirely on seed set for reproduction. Plants begin reproducing in their third or fourth year (unpubl. data). Flowering occurs from April through June, and seeds are dispersed from late July to September by ballistic dispersal and secondarily by ants. Seeds begin to germinate in early March, and some germination occurs throughout the summer (see Chapter 3).

Study Sites

Preliminary studies suggested that there might be important ecological and demographic differences between populations in two major types of *C. scoparius* habitat: native prairies and urban fields or roadsides. In 1993, I established permanent plots in two populations, Johnson Prairie and Discovery Park, representing these two types of habitat. In 1994, four more populations were added to the study: prairie sites Thirteenth Division Prairie and Weir Prairie, and urban fields Magnuson Park and Montlake Fill. All three prairies are located on the gravelly outwash plains of western Washington, which are characterized by shallow, coarse-textured soils and low levels of soil nutrients (Franklin and Dyrness 1988) Once covering great park-like expanses (Kruckeberg 1991), these prairies have been reduced by development and agriculture to a few remnants, many of which are found on the Fort Lewis military base approximately 80 km south of Seattle. The prairies are dominated by *Festuca idahoensis*, and include small herbaceous perennials such as *Cammassia quamash* and the state threatened *Aster curtis*, with intervening space covered by a thick cryptogamic layer (Lang 1961). When invaded by *C. scoparius*, however, the prairies can be converted to monospecific stands of this exotic shrub. Thirteenth Division Prairie is located in the northeast corner of the base, While Johnson and Weir Prairies are 20 km away in the Southwest corner. Two of the urban field populations (Magnuson Park and Discovery Park) were situated in large Seattle city parks separated by 14 km. Both fields are in areas that had originally been forested but were subsequently used for land-fill and exhibit poorly developed soils. The third urban population is on the Montlake Fill, an area reclaimed from Lake Washington by landfill. Dominant plants in these fields are primarily exotic species such as *Agrostis tenuis* and *Vicia villosa.*

In each population, I chose plots that represented different stages on the continuum of the invasion wave. In the 1993 populations I had early, intermediate, and late stage plots, but in the 1994 populations I had only early and intermediate stage plots. Early stage plots were at the outer edge of the broom populations, where most space was "open" and *C. scoparius* individuals were scattered. Intermediate plots were just behind the front, where space was beginning to fill up but the "canopy" was still quite open. Late stage plots were areas of very high *C. scoparius* density toward the center of the infestations. To be able to compare among populations, I based plots of the same stage on informal plant density criteria. Potential sites were identified by sight, then the number of small and large plants per square meter was censused to be sure the plant density was within a certain range. To be sure that equivalent numbers of plants were included in the demographic analysis for each plot, early stage plots covered a greater area (96 - 316 m^2) than intermediate-stage (24 - 60 m^2) or late-stage (20 - 24 m^2) plots. This range in plot sizes could affect both the mean and variance of demographic rates due to genetic and ecological factors. Smaller plots will include a more limited sample of (probably related) genotypes, and will also experience a smaller range of environmental conditions. Thus one would expect greater demographic stochasticity in smaller plots. Splitting the plots into subplots over an equal area was considered, but logistics and the patchy nature of broom stands ruled out this approach.

Stage classification

Three size measurements were taken in the field: the height, the number of branches at soil surface, and the diameter of the largest branch at 5cm above ground level. Three measures were taken because it was not clear which would provide the best indicator of stage or size class. The morphology of plants differed among populations, and particularly among invasion-stage plots within populations, with late-stage plots having taller, lankier plants, and some populations having higher numbers of branches (at soil surface level) than others. I decided the best way to circumvent this problem would be to approximate biomass as closely as possible for each of the populations and plots. In

September of 1995, I measured height, branch number and diameter on a sample of plants outside of the permanent plots in each population (200 plants total). I then pulled these plants out by the roots with a Weed Wrench (TM) and weighed them to the nearest 25g using a spring balance. I weighed each plant three times and took the average. I regressed biomass on the various size measures in each population, using the square root of biomass as the dependent variable for the regression. Height did not significantly increase my ability to predict biomass, therefore I dropped height from the model and retained diameter and branch number. I then tested for significant differences between the slopes of the regression lines using analysis of covariance, with population as a factor and diameter and number of branches as covariates. The population * diameter and population * branch# interaction terms were highly significant, indicating differences in the relationship between populations (Table 2.1). In converting my field measurements of diameter and branch number to biomass, therefore, I used separate regressions for the different populations (Table 2.2).

Stage classes were assigned using a mixture of size criteria and simple "biological" criteria (Table 2.3). Biological criteria delimited 1) seeds, 2) seedlings, defined as plants no larger than the maximum size I had ever observed first-year germinants to attain, and 3) juveniles, plants larger than the biggest first-year germinants, but below the minimum size apparently required to produce a fruit. Because pollinator visitation levels could affect the size at first reproduction, I was careful to define the maximum juvenile size (or conversely, minimum adult size) consistently across all populations. Since the biomass regressions were not very accurate for small plants (the scale was unreliable below 100g), diameter measures were used to define seedlings and juveniles. Reproductive *C. scoparius* plants obviously form a continuum across a wide range of sizes and, consequently, "fates" (especially fecundity). Therefore adults were split into four size categories, a number chosen to balance the greatest accuracy in representing the average behavior of individuals against the problem of having smaller sample sizes in each cell. The process of defining classes was complicated by the fact that the analyses required stage classes to remain consistent across all populations and stages of invasion. Regression equations of biomass on diameter and branch number provided an "estimated biomass" for each plant, and adults were assigned to size class based on their estimated biomass.

In order to test the correspondence of stage classification and age classification, I took circular stem samples from each of the plants used in the biomass correlations and submitted them to dendrochmonological analysis. I used a belt sander with 220 grit sandpaper, and then hand-sanded each sample with consecutively finer paper, finishing with 600-1000 grit. I was then able to count growth rings under a dissecting microscope. I regressed diameter and biomass on age (N = 168), and also compared the distribution of ages comprised in each stage class.

Direct measures of invasion

I tracked the progression of *C. scoparius* invasion directly using 1) measurements of biomass accumulation and 2) measurements of plant density. I calculated the plant biomass per square meter by estimating the biomass of each plant in the plot using the abovementioned regression equations, excluding plants for which the regression yielded a negative mass (some seedlings and juveniles), and then summing over all plants in a plot and dividing by the area. I compared early, intermediate, and late invasion stages for biomass per square meter, as well as a) the total number of vegetative plants per square meter, b) the number of adult plants (all plants exclusive of seedlings and juveniles) per square meter, and c) the number of x-large plants per square meter, using ANOVA and the post-hoc Bonferroni-Dunn test.

I tracked the increase of biomass in each plot over time, and the proportional increase in biomass was calculated by dividing all values by the initial (1993 or 1994) biomass in the plot. I took the difference of the logs of biomass (log[1995]-log[1994]) as one estimate of the rate of invasion--that is, the speed at which *C. scoparius* fills up space and increases its draw on the local resources. I then correlated this change in biomass with initial biomass using Spearman rank correlations. The 14 plots served as replicates. I did the same set of analyses (increase over time, difference in logs, correlation with original value) for the three density measures described above. In addition, I asked how well each of the four measures of invasion (change in biomass, change in each of three density measures) could be explained by each of the remaining measures of current occupancy (biomass, density), again using Spearman rank correlations.

Demographic analysis: Transition rules

Matrix elements were determined from the probability of passing from one stage class to each of the other stage classes. Because *C. scoparius* is a shrub, its size as measured by diameter could only increase monotonically; however, whole plants could shrink by losing branches. The frequency of shrinking was generally quite low

(Appendix 1). In a few cases, sample sizes were too small to observe a transition that biological intuition dictated must occur. For example, of the 132 plants alive in the intermediate-stage plot at Discovery Park in 1994 there were only three seedlings and four juveniles, and all of these died before the 1995 census. Rather than adding in an arbitrary value, as is done in some studies (e.g. Boeken and Canham 1995), I dealt with these "problem transitions" in the following manner. Sampling from a binomial distribution, I calculated the "true" transition probability that would yield a zero value 50% of the time, given the sample size. This protocol took advantage of the information provided by the sample size itself. In Appendix 1, I provide both the original value as well as the estimated value for all problem transitions.

Fecundity. The generation of fecundities (top row elements) depends on the timing of the census (Horvitz and Schemske 1995). Because censuses were done at the time of fruit production (late summer), and fecundities were estimated as the probability of producing *next* year's seed for a plant in a particular stage class, juveniles had a non-zero entry. I calculated fecundity as follows: The average number of fruits per plant at the t + 1 census was found for each stage class at time t. Then this number was multiplied by the average number of seeds per fruit in that population/plot. That is, mean fecundity for small adults for the 1993-94 matrix was the mean number of seeds produced in 1994 by a plant that was a small adult in 1993. This calculation took into account plants that died between the censuses, as well as those that grew or shrank into different stage classes in the following year.

Seed dormancy. A great challenge is posed by the need to estimate the fraction of seeds remaining dormant from year to year. *C. scoparius* seeds have the potential to live many years under controlled conditions (Youngman 1951) and in the field as well (R. Lande, pers. com.). The seed stage is therefore made up of seeds of many different ages. Seed age could affect dormancy both by changes in characteristics of the seed coat over time and by random variation among seed cohorts (Kalisz and McPeek 1992, McPeek 1993). The ideal seed bank study would include many years of data, in which fresh seeds were put out every year and subsets of each cohort were sampled every year. However, the seed bank estimates presented here were necessarily based on information from a limited time scale. I set up experiments to estimate dormancy probabilities for three types of seeds: seeds produced in 1993 and analyzed at the 1994 census (1993 0-yr olds), seeds produced in 1993 and analyzed at the 1995 census (1994 1-yr olds), and seeds produced in 1994 and analyzed at the 1995 census (1994 0-yr olds). Details of the experimental design are described below.

In the fall of 1993, freshly-collected seeds (combined from many donors at the appropriate site) were placed out in the field in mesh envelopes; each envelope contained 50 seeds and a tablespoon of autoclaved soil collected from that site. I removed whatever litter or surface material was present (including moss), nailed the envelope to the soil surface, and replaced the surface material to simulate the microenvironment experienced by seeds lying on the soil at each location. A subsequent experiment (see below) showed that placing the seeds in envelopes did not introduce a systematic bias relative to scattering seeds directly on the soil (number germinated: paired Wilcoxon Signed Rank Test, $N = 11$, $Z = 1.6$, $P = 0.11$). Twenty-seven seed envelopes were placed at 1m intervals along transects adjacent to each demography plot (in early, intermediate, and late invasion stages) at Discovery Park, Magnuson Park, Johnson Prairie, and 13th Division Prairie. I used the transects to increase the range of microsites sampled in each population. At each demography census, 8 envelopes from each transect were randomly selected and collected from the field, and the seeds remaining were counted and tested for viability using tetrazolium (Moore 1973). Seeds were scarified by hand using a triangular file, left in petri dishes on moist filter paper for 5-12 hours until they were fully imbibed, and then soaked in 1% tetrazolium solution in a dark incubator for 3-4 hours. I sliced each seed open with a razor blade and inspected the embryo and endosperm under a dissecting microscope. Viable seeds showed a fairly uniform, dark red color. Dead or damaged seeds did not stain. I generated a mean proportional viability for each population from the 27 replicates of 50 seeds each.

In the fall of 1994, again seeds were set out in envelopes, in the way described above with 50 seeds per envelope. 18 envelopes per population were divided among 3 rectangular stainless steel insect exclosures. Each exclosure was sunk 3 cm into the ground and extended 10cm above the ground, with a bevelled edge pointing inward to discourage ants or seed predators such as carabid beetles from removing the seeds. The bevelled edge was thickly coated with "Tanglefoot" (TM). Then the exclosures were divided in half, with one half used for envelopes and the other for an open-ground "control". At the time of the1995 demography census, three envelopes per exclosure or 9 envelopes total per population were collected and their seeds tested for viability.

Mean dormancy estimates differed for these three seed cohorts, so I used the mean of all three estimates for the seed -> seed transition probabilities. I also explored with matrix analysis the consequences of using each of the various dormancy estimates. Fortunately, which estimate was used made very little difference in the basic outcomes of the analysis.

Demographic Analysis: analytical results

The life cycle of *C. scoparius* is represented in Figure 1. Transitions between stages of the life cycle were summarized in a transition matrix model of the form

$$\mathbf{n}(t + 1) = \mathbf{A} \cdot \mathbf{n}(t)$$

where $\mathbf{n}(t)$ is a vector of stage classes at time t, and **A** is the matrix which describes how each stage class contributes to the number of individuals in all other stage classes at the next time step. The model can be solved to give the expected stable stage distribution (corresponding to the right eigenvector of A), and the population growth rate or finite rate of increase at that stage distribution (corresponding to the dominant eigenvalue λ).

I used transition matrices to calculate the finite rate of increase for each combination of year, population, and invasion stage. Discovery Park and Johnson Prairie were followed for three years yielding two transitions, and the other four populations were followed for two years yielding one transition. Using analysis of variance with plots as replicates, I tested for significant temporal variation in lambda for Discovery Park and Johnson Prairie. I also tested for a significant effect on lambda of habitat type (urban, prairie) and stage of invasion (early, intermediate, late) in 1994-95.

I tested for a correspondence between lambda and each of the direct measures of invasion (increase in biomass, increase in total plant density, density of adults, and density of x-large adults) using Spearman rank correlations. I also generated correlations between lambda and each of the four measures of current occupancy.

I calculated the predicted stable stage distribution from the 1994-95 transition matrices for each plot and compared it to the actual stage distribution in 1995. I quantified the magnitude of the correspondence using percent similarity (Horvitz and Schemske 1995), calculated as follows:

$$PS = \sum_{i=1}^{n} \min(a_i, s_i) \times 100$$

where a is the value from the actual stage distribution and s is the value from the stable stage distribution, and n is the number of stages. I then tested for a significant difference between the actual and stable stage distributions with a Kolmogorov-Smirnoff test (Siegel 1956), using the stable stage distribution as an expected distribution.

There are two common ways to quantify the contribution of each entry in a matrix to the population growth rate: sensitivity and an elasticity (Caswell 1989). Sensitivities are more direct in that they measure how a small change in the magnitude of the entry translates into lambda.

$$\partial\lambda / \partial a_{ij} = v_i w_j / \langle \mathbf{w}, \mathbf{v} \rangle$$

One difficulty in interpreting sensitivities is that they are affected by the scale of each transition, which is particularly a problem when comparing changes in growth or mortality (by definition bounded by 0 and 1) with changes in fecundity (ranging into the thousands). Because of this difficulty, the use of sensitivities has been displaced in many recent studies by elasticities, which are *proportional* sensitivities. Elasticities measure the proportionate change in lambda with a given proportionate change in each entry.

$$a_{ij} / \lambda \times \partial\lambda / \partial a_{ij}$$

Elasticities have two special advantages: 1) they can be directly compared between different entries and different matrices, and 2) because they always sum to one, different individual elasticities can be combined to evaluate the influence of changes in all transitions having to do with growth, for example, or fecundity.

To simplify conceptualizing the elasticity structure, I summed the elasticities down each column excluding the top row (seed production), generating elasticities for the fate of seedlings, juveniles, and small, medium, large and x-large adults. Then I summed the top row (excluding dormancy, a_{11}) to get an elasticity for fecundity.

Fecundity, pollination, and population growth

I used regression to explore the relationship between elasticity for fecundity and lambda. However, because lambda appears in the denominator of the equation for elasticity, and because all elasticities are constrained to sum to one, artifactual relationships between lambda and elasticities might be expected. Although I present the results for elasticities in order to conform to related published research (Silvertown et al. 1993), I also calculated Spearman rank correlations between lambda and the sensitivity for fecundity of each life-history stage. Sensitivities do not suffer from the same artifactual relationship with lambda.

In addition to its theoretical implications, the relationship between population growth and the influence of reproduction is also of interest in the context of *C. scoparius* because it can be used to address the question "When does the interaction between the plant and its pollinators matter on a population level?" However, elasticities and sensitivities are not necessarily the best way to ask this question because 1) they are only valid for small changes relative to the value of the transition entry (and are therefore dependent on the value of the entry itself), and 2) they follow from analyses that assume an aymptotic (stable) rate of growth, stable stage distribution, etc. To ask the question more directly, I simulated the growth of *C. scoparius* populations in the four sites where I had experimental data on seed production under natural levels of pollination and full pollination (Chapter 1). I used the matrix for each population--Johnson Prairie and 13th Division Prairie, and Discovery Park and Magnuson Park, with two separate transitions for Johnson Prairie and Discovery Park. Then I altered the fecundities in the top row by multiplying seed production by the proportional increase obtained through pollen supplementation. For the 1993-94 transition, I used 1994 experimental data. However, I had matrices for the 1994-95 transition but no experimental data for 1995. Because pollinator visitation rates were not significantly different in 1995 from those in 1993 (Chapter 1), I made the assumption that pollen supplementation would have the same effect on fecundity in 1995 as it did in my 1993 experiments. Therefore, for the 1994-95 transition I inserted proportional increases based on 1993 results. The simulation assumed that there was no demographic "cost" of the added reproduction (Chapter 1).

I used the models to do two different types of thought experiment. First was to ask "Given current levels of pollination vs. ideal levels of pollination, how fast would a newly colonized site accumulate *C. scoparius* individuals?" I started each empty site with ten seeds and iterated the matrices over 20 years. I plotted the buildup of individuals over time. Second, I asked "Given current densities of plants in the early-stage plots for each population, what would be the effect of an instantaneous change in the pollination environment at each site?" I started with the existing stage distributions and densities (per m^2), iterated the matrices, and again plotted the buildup of individuals over time. Because the initial population vectors in this simulation were in terms of plants per square meter, unrestricted growth into the hundreds or thousands was unrealistic. A more relevant response variable was how many years it took the plots to fill up with plants. I chose the density of x-large adults as the best indicator of "filled" plots (see Fig. 2.8), and counted the number of iterations to reach x-large >= 1.5.

RESULTS

Stage, age, and demographic traits.

Diameter and biomass both increased with age (diameter vs. age, $N = 168$, $r^2 = 0.48$, $P < 0.0001$; biomass vs. age, $N = 168$, $r^2 = 0.33$, $P < 0.0001$); However, the large range of sizes shown by plants of any particular age (Fig. 2.2) makes age a poor predictor of size, supporting the argument for using stage- or size-based (Lefkovitch matrix) rather than age-based (Leslie matrix) demography for this plant species. The mean age of each stage did vary significantly (ANOVA $F = 20.4$, $P < 0.0001$, Fig.2.3), although a Bonferroni-Dunn test revealed significant differences in mean age only between x-large adults and each other stage.

Over the course of the three years of this study, I marked, mapped, and followed the fate of 3046 plants; each plot had between 135 and 312 individuals, with a mean of 218. The stage classification based on biomass was predictive of fate, i.e., demographic rates varied with stage class. Seedlings, juveniles, and small adults in general showed the highest mortality rates (Fig. 2.4), with the exception of early-invasion plots at Montlake Fill and Magnuson Park, which had high mortality rates in 1995 for extra large and large adults, respectively (see Appendix). Fruit production increased with stage class (Fig. 2.5), and the F value for the effect of stage class was five times larger than for any other effect (Table 2.4). Variance in fruit production also increased dramatically in the larger stage classes.

Urban populations differed from prairie populations in their demographic rates. Mortality rates were almost always higher for individuals of the same stage in urban populations than they were in prairie populations (Fig. 2.4). Establishment rates were much lower in urban populations than prairie populations (Fig. 2.6). Patterns of fecundity in the different populations reflected a balance between 1) the increased vigor and growth of plants in prairie sites and 2) the low level of pollinator visitation in those same populations (see Chapter 1). This is seen by comparing the fruit production of the various stage classes within the same year (year t), to the fruit production values used in the matrix (year t+1) which incorporate growth and survival (Fig. 2.5). The first measure primarily reflects the pollination environment, and in all cases but the late-invasion plots for small and medium adults, plants in urban populations had higher fecundity than those in prairie populations. The second measure reflects the fact that prairie plants growing in the early-invasion stage plots were more likely to grow into larger, more fecund plants in the next year (Fig. 2.5). Invasion stage had a significant direct effect on fecundity (Table 2.4), and the interaction between population and invasion stage, and the three-way interaction population x stage of invasion x stage class, were significant (Table 2.4).

Stage of invasion, biomass, and density.

In terms of biomass, the original delineation of early, intermediate, and late-invasion plots was consistent and comparable among populations; total estimated biomass was significantly different (and non-overlapping) among density categories (Fig. 2.7), with post-hoc tests showing all comparisons to be significant at $P < 0.0001$ in both 1994 and 1995. The medium density plots showed the greatest scatter (Fig. 2.7).

Other measures of density provide a different picture of the differences among plots (Fig. 2.8). The number of x-large plants (i.e., all plants > 900g) followed the same pattern as total estimated biomass, with significant variation among stages of invasion (ANOVA, 1994: $F = 41.0$, $P < 0.0001$, 1995: $F = 40.0$, $P < 0.0001$) and all plot comparisons being significant (Bonferroni-Dunn test, $P < 0.001$). Likewise, analysis of the number of adult plants varied significantly among invasion stages (1994: $F = 22.1$, $P < 0.0001$; 1995: $F = 12.2$, $P < 0.002$), but only the post-hoc comparison between early invasion and mid-invasion plots was significant in 1995, and betweetn early and the other two in 1994 ($P < 0.001$). When the comparison is done for all vegetative plants including juveniles and seedlings, the F-values are much lower, although significant, in 1994 ($F = 6.8$, $P = 0.012$) and are not significant in 1995 ($F = 2.7$, $P = 0.11$). In both cases the mean is highest for intermediate plots, and in 1994 only early and intermediate plots are significantly dfferent. An interesting comparison can be made between total density and biomass (or the density of x-large adults) for the variation among late-stage plots. The late plots at Discovery Park and at Johnson Prairie are widely different in terms of total numbers, but nearly identical for biomass, suggesting a "maximum occupancy" for *C. scoparius* that remains constant over very different habitats.

Direct estimates of invasion (change over time).

Estimated biomass increased in all plots between the first and last years of the study (Fig. 2.9). High density plots rose in biomass between 1993 and 1994, but appeared to lose biomass between 1994 and 1995. These were the only cases in which biomass did not increase monotonically. The difference of the logs of biomass (log[1995] - log[1994]) was negatively correlated with initial biomass ($N = 14$, $\rho = -0.74$, $P = 0.0015$), indicating a biomass-equivalent of density-dependence in invasion.

Plant densities showed a much less consistent pattern over time (Fig. 2.10). From 1994 to 1995, the total plant density increased in 10/14 plots, but decreased in Discovery Park intermediate and late, Magnuson Park early, and Montlake Fill intermediate plots. The density of just adult plants increased in 9/14 plots, but decreased in a slightly different set of plots: Johnson Prairie late, Montlake Fill intermediate, and all Discovery Park plots. The density of x-large plants did not decrease in any of the populations, but did remain constant in three plots, again a different set: Johnson Prairie intermediate, Weir Prairie intermediate, and Discovery Park late plots. The change over time for each of these density measures was calculated as the difference in the logs, and there were no significant correlations among the three measures (Table 2.5). However, the difference in logs of x-large plants and of adult plants were both significantly correlated with the difference in logs of biomass (Table 2.5). Correlations between the four different measures of occupancy and those for change over time (difference of logs) revealed that total density and density of adults are both uncorrelated with any measure of invasion rate (Table 2.6). The density of x-large plants shows an effect identical to biomass; it is negatively correlated with change in biomass, change in adults, and change in x-large plants.

Analytical results of the demographic model

Lambda, the finite rate of increase, was greater than one (population increasing) in early-stage plots for both populations for the 1993-94 transition and for all six populations for the 1994-95 transition (Fig. 2.11). The magnitude of lambda in all plots varied between 0.88 and 1.93, and was lower in urban populations than prairie populations (Table 2.7). The two populations for which three years of data were available showed no significant temporal variation in lambda (Paired t, $DF = 5$, $t = 1.26$, $P = 0.26$).

In six of eight cases, lambdas decreased as the stage of invasion increased. The two exceptions were Discovery Park 1993-94, for which the late stage plot had a higher lambda than the intermediate-stage plot, and Magnuson Park 1994-95, for which the intermediate-stage plot had a higher lambda than the early stage plot. The effect of invasion stage was significant, as was the interaction between habitat and invasion stage (Table 2.7). Consistent with this result was a significant negative regression of lambda on biomass, but only for prairie populations (Fig. 2.12).

Lambda also decreased significantly with higher standing biomass and with higher densities of x-large adults (Table 2.6). It was not correlated either with density of all adult plants or with total density. In comparisons with direct measures of invasion, Lambda was significantly correlated with the change in biomass over time (difference of logs) and with change in the density of adults (Table 2.5), but was not correlated with either of the remaining two direct measures of invasion, change in total plant density or change in the density of extra-large plants.

In every case, the observed stage distribution in 1995 was significantly different from the stable stage distribution predicted from the model using 1994-95 transitions (Fig. 2.13). However, in 11 of 14 cases, the percent similarity exceeded 70%. The two cases with percent similarity < 50% were mid- and late-stage plots at Discovery Park. There was no apparent relationship between stage of invasion and percent similarity.

Elasticities provide a way to compare the relative importance of demographic stages. Overall patterns in the elasticity structure were similar between years and across populations (Fig. 2.14), but differed among plots in different stages of invasion. Elasticities were fairly even across life history stages at the early stage of invasion, but were completely dominated by the fate of x-large plants at the late stage of invasion (Fig.2.14). Interestingly, plots at the intermediate stage of invasion differed in their elasticity structure depending on whether they were in urban or prairie habitats. The elasticities of intermediate plots in prairies were more like early plots, while in urban fields the elasticity of x-large individuals was more dominant as in late stage plots (Fig. 2.14).

The elasticity for fecundity (summed across all adult stages) is tightly linked to the magnitude of lambda (Fig. 2.15). However, the tightness of this relationship is suspect because of 1) the constraint of all elasticities to sum to one, and 2) the appearance of lambda in the denominator of the equation for elasticity. Sensitivities for fecundity are also strongly linked with lambda; Spearman rank correlations ($N = 20$) between lambda and sensitivity was highly significant for juveniles ($\rho = 0.86$, $P = 0.0002$), small adults

(ρ = 0.79, P = 0.0006), medium adults (ρ = 0.79, P = 0.0005), large adults (ρ = 0.84, P = 0.0003), and x-large adults (ρ = 0.87, P = 0.0001).

Simulation of pollinator limitation

I ran two types of simulations combining matrices with the experimental results presented in Chapter 1. The first explored a scenario of the founding of a new population under current pollination conditions vs. favorable (full) pollination conditions. In this case, pollen limitation has a major effect on the rate at which individuals accrue in prairie populations, but not in the slower-growing urban populations (Fig. 2.16). Already within five years, full pollination resulted in an order of magnitude higher number of plants in prairie populations.

The second type of simulation explored the consequences of an instantaneous change in the pollination environment, starting with conditions currently present in the populations. There is a time-lag built into this use of the model, because the extra seeds produced in the first generation under new pollination conditions do not contribute new individuals to the population until several generations later. Thus the "natural" and "altered" trajectories do not diverge until about year four (Fig. 2.17). Although the build-up of plant numbers shows the same pattern as in the previous case (Fig. 2.17), the response variable of interest here is at what point the density reaches the maximum level, i.e., when the plots are "filled". Because the prairie populations are already growing so fast, additional pollination has essentially no effect on the time to fill space in the prairie populations (Table 2.8). In contrast, urban populations are growing more slowly and increasing pollination there does make a difference in how fast the current populations would be projected to reach maximum density (Table 2.8).

DISCUSSION

The demographic models presented here synthesize a great deal of information about the ecology and life history of *C. scoparius*, a weedy exotic shrub invading along the West Coast. After some general comments, I will discuss the findings presented in this chapter in three parts: first, I will explore the demography of invasion--focussing on what happens at the edge of the expanding front (the early invasion-stage plots), considering temporal and spatial variation. Second, I will discuss the importance of pollinators to rates of population growth in invading populations. Third, I will consider the demographic consequences of the increase in density and biomass that occurs through the course of an invasion.

General

Size/stage based (Lefkovitch) models were appropriate in this system because size was not well correlated with age (Fig. 2.2). The relationship between size and age is likely to differ under different circumstances, with older plants being much smaller in poor environments than in the best environments. Therefore having a size-based stage classification was particularly critical in this study because of the need to compare characteristics and performance of populations experiencing very different conditions. The use of estimated biomass to define life stages allowed me to compensate for differences in morphology, particularly branchiness, among populations. Choosing the number and definition of size classes was a difficult compromise between 1) obtaining sufficient representation in each class for all 14 population/invasion-stage plots, and 2) dividing up the life cycle of a large, long-lived plant into reasonably homogeneous subsets. The size classification chosen was successful in that stage classes were predictive of fate; that is, stages were significantly different in terms of survivorship and fecundity. An alternative stage structure using only one adult stage is presented in Chapter 4 (Table 4.3). Analytical results are quite consistent between the two models.

The greatest shortcoming of the matrices is that my estimates of seed viability do not include post-dispersal seed predation. It was not possible to get direct estimates of seed predation because ants readily moved seeds around, and therefore the dormancy rates presented here represent an upper limit. However, the ant exclosures from 1994-95 can be used to get an idea of the possible magnitude of seed predation. Assuming that "extra" seedlings in the exclosures came from seeds that would have been eaten outside, one can compare the seedling/seed ratios in the enclosures to those in adjacent demography plots to estimate the proportion of seeds escaping predation. Averaged over the four populations, the ratio of germination rate in demography plots to exclosures was 0.108 (sd = 0.039), meaning that 90% of seeds may possibly be eaten in these populations. Because of the limited nature of these data, and because other factors may be responsible for the difference in seedling number seen between the enclosures and the plots, I did not try to incorporate seed predation in the matrices. I did explore the consequences of the possible error with matrix analysis, however, and found that reduction of the seed-to-seed transition made very little difference except in 1) reducing the elasticity for dormancy, and 2) reducing lambdas between one and eight percent.

Demography of invasion

Details of the demography of invasive species are not well known. In the early plots located at the edge of the invading front of *C. scoparius* populations, population growth rates were always greater than one (ranging from 1.06 to 1.93); that is, all six populations were increasing. There was little temporal variation in the two populations that were followed over three years, supporting Baker's hypothesis about buffering and consistent growth rates in invasive exotic species (Baker 1965). Of course, one must use caution when making generalizations about temporal variation over a limited time scale. Additional years of data may reveal greater fluctuations over time.

In contrast, there was significant variation between urban and prairie populations, with prairie populations growing more rapidly. The difference between urban and prairie populations appeared not to be controlled by a single life-history stage, but rather was exhibited throughout the life cycle (Fig. 2.4, Fig.2.5, Fig. 2.6). The only case in which vital rates were higher in urban sites was for fecundity, which was controlled in part by the more favorable pollinator environment in urban populations (Chapter 1). In the prairies' fastest-growing, early-stage plots, the higher survivorship and growth of individuals still overcame the effect of pollination, resulting in greater fecundities for the top row of prairie matrices (Fig. 2.5).

Spatial or habitat-based variation in population growth rate is the norm rather than the exception (Werner and Caswell 1977, Horvitz and Schemske 1986, Menges 1990). However, the pattern seen here is particularly interesting in light of theoretical predictions from invasion biology. It is commonly stated that exotic species are tightly linked to disturbed habitats and habitats dominated by human influences (Orians 1986, Hobbs and Huenneke 1992, Parker et al. 1993, Ruesink et al. 1995). Much of *C. scoparius* habitat falls in this category--urban fields, highway rights-of-way, abandoned lots, landfills, etc. Some have even maintained that invasions are dependent on disturbance, and that undisturbed ecosystems are perfectly "resistant" to invaders (Fox and Fox 1986). My data do not support such a view. In fact, the most rapid rates of spread occurred in the most pristine habitats. Natural disturbances also can not explain this pattern; some have suggested that *C. scoparius* establishes in small patches of bare ground such as gopher mounds, but I found no evidence for high levels (or even normal levels) of establishment on the small disturbances in my demography plots (see also Chapter 3). In a project coordinated with this dissertation work, UW undergraduates Stan Harpole and Diana Dionne found the highest plant species diversity, as well as the highest native species diversity, in Johnson Prairie--where *C. scoparius* reached its highest population growth rate (Appendix 2). It appears as if "biotic resistance" (Elton 1958, Simberloff 1986) is not a factor limiting the spread of this particular invader.

In all cases except one, the actual stage distribution was significantly different from the stable stage distribution, and percent similarity varied from 32.7 to 96.8 %. Interestingly, although one might predict that populations in later stages of invasion would resemble their predicted stable stage distribution more closely, this was not the case.

Elasticity analysis did not yield any suggestions for an "Achilles heel" for *C. scoparius*--that is, no life stage or transition overwhelmingly dominated population growth in rapidly invading populations. Rather, elasticity was fairly uniformly distributed throughout the life cycle in early invasion-stage plots.

Demographic impacts of pollinators

My experimental work on pollen limitation in *C. scoparius* showed that autogamy was rare and seed production was highly dependent on the frequency of pollinator visits--which varied among populations and among individuals (Chapter 1). The matrix models presented here demonstrate that this pollinator control over reproduction can in fact have a population-level effect. The importance of pollinators will increase in populations with higher growth rates for two reasons. First, when lambda is higher, a small increase in lambda will result in a much more rapid divergence in numbers due to exponential growth. Second, as lambda increases, the elasticity or sensitivity of fecundity increases (Fig. 2.15). That means that factors affecting fecundity will have a disproportionately larger effect on changes in lambda at high growth rates.

Others have found a similar relationship between lambda and the importance of fecundity. For *Calathea ovandensis*, the second largest correlation with lambda was that for elasticity of the fecundity of the largest stage class (Horvitz and Schemske 1995). The pattern has also found over a broader taxonomic scale; in a survey of 66 demographic studies, Silvertown et al. (1993) found a similar positive correlation between lambda and the combined elasticity of fecundity.

These analytical arguments were corroborated by the simulation I used to estimate the actual effect of pollinators in the populations I studied. Incorporating pollinationinduced increases in seed production, with parameters estimated from natural pollination levels and pollen supplementation experiments, I found that prairie populations started from 10 seeds would be an order of magnitude larger within 10 years if maximum pollination were occurring relative to natural 1995 pollination levels. Relative to natural 1994 pollination levels, the population at Johnson Prairie would be two orders of magnitude larger. As predicted above, pollinators only had an important effect on plant numbers for the prairie populations, where growth rates were high. In addition to their higher lambdas, prairie populations had lower natural levels of pollination (Chapter 1) resulting in a bigger overall effect of variation in pollinator visitation.

A different way to use the model is to ask questions about the effect of increasing pollination in the current populations rather than imagining the founding of a new population. Could a sudden change in pollinator availability affect the speed with which the current early invasion-stage plots fill to maximum density? The time-lag associated with this use of the model basically obscures any effect of increased seed production in the fast-growing prairie populations (Fig. 2.17). However, full pollination in urban sites makes a large difference, decreasing time to saturation by as much as one-third (Table 2.8). This result points to the fact that the assessment of where and when pollination "makes a difference" depends on what part of the process, and what spatial scale, one is most interested in.

Others have also used matrix analysis to evaluate the effects of variation in species interactions. Ehrlén and Eriksson studied the pollination of *Lathyrus vernus*, comparing matrices for fully-pollinated plants and for plants experiencing natural levels of pollen limitation (Ehrlén and Eriksson 1995). In *L. vernus*, unlike *C. scoparius* (Chapter 1), plants showed a significant cost of reproduction, and the primary motivation for Ehrlén and Eriksson's analysis was to explore whether that cost compensated for the demographic benefit of added pollinator visitation. They found that full pollination did *not* have an overall positive effect on population growth. Two other studies that have estimated population dynamics consequences of pollen limitation also have failed to find a significant overall effect (Bierzychudek 1982, Calvo and Horvitz 1990). In contrast, workers who have looked for population-level effects of negative plant-insect interactions have found them. Doak (1992) demonstrated long-term effects of insect damage on the population dynamics of *Epilobium angustifolium*. Ehrlén (1995) simulated different levels of meristem damage from molluscs, grazing by vertebrates, and seed predation; natural levels of herbivore damage reduced lambda, primarily through meristem damage, while seed predation did not have a large effect (Ehrlén 1995). Bishop (1996) also found that a stem-miner had a large effect on lambda of *Lupinus lepidus* while a seed predator did not. In contrast, a specialist seed predator did reduce lambda in *Ardisia escallonioides* (Pascarella and Horvitz In Review). In this case the importance of the effect varied with the degree of canopy closure.

The biology of density-dependence

The invasion of *C. scoparius* involves an impressive increase in plant density, from scattered individuals to a near monoculture involving several kilograms of plant material per square meter. Such a range in density is characteristic of many noxious invasive pests, and the final densities reached in part determine the ecological impact of a weed. In addition to defining the demographic character of the invasion process, the increase in density over time within single populations provides an excellent system with which to examine mechanisms of density dependence.

Different measures of occupancy provide different pictures of what was happening to plots over time. Total density of vegetative plants and density of adult (flowering) plants actually peaked in plots that were at the intermediate stage of invasion, whereas the density of extra-large plants increased from early- to intermediate- to late-stage plots (Fig. 2.8). Total estimated biomass increased monotonically with invasion stage. The different measures of invasion rate--lambda, the change over time (difference of logs) of biomass, total density, adult density, and x-large adult density--were not well correlated (Table 2.5), nor did they show consistent negative correlations with different measures of density (Table 2.6). Of particular interest is the fact that total plant numbers, which is the traditional density measure in population biology, was entirely uncorrelated with all other measures of occupancy, and, for that matter, with all estimates of invasion rate including lambda.

In terms of the overall importance of broom in the biotic community or its impact on the host ecosystem, biomass may a better measure than simple numerical density because it integrates the relative ability of each plant to deplete local resources (soil nutrients, water, light, etc.). Given the well-studied phenomena of self-thinning and compensatory growth in plants (Harper 1977), it is perhaps not surprising that it was biomass, and not simple numbers, that generated the functional responses we expect from density dependence. Estimated biomass increased from year to year in all plots except for high density plots from 1994-95. The magnitude of the change in biomass was highly negatively correlated with biomass itself. Population growth rate was also negatively correlated with biomass, but when population types were split the correlation was significant only for prairie populations (Fig. 2.12).

There was little evidence for an intermediate density at which population growth rate or any of the vital rates actually increased, except in the case of the intermediate plot at Magnuson Park, which showed a higher lambda than the corresponding early plot. Although the representation of densities was rather crude and therefore may not have provided enough resolution to see such an effect, there does not appear to be consistently positive density dependence in this invasive species. In contrast, in the invasive exotic *Cereus peruvianus*, recruitment rate was positively correlated with population density (Taylor and Walker 1984), and Richardson obtained similar results for three other invasive species (Kruger et al. 1986).

The elasticity structure changed dramatically as the invasion progressed and total plant biomass increased. In the late invasion plots, elasticity was overwhelmingly dominated by the survival of x-large plants. This was not an artifact attributable to having sample sizes too small to see mortality in that stage class, because survivorship equal to one was not allowed under the protocol used here for "problem transitions". Rather, the populations are stable because x-large adults live a long time and dominate the population dynamics. One should be cautious in interpreting the elasticity pattern of late invasion plots from a conservation perspective; cutting down all the extra-large adults in late-stage plots would of course not result in a local extinction of *C. scoparius*. This illustration underscores the well-known concept that matrix models only describe a single set of conditions under which the matrix was built and should not be interpreted as "predictions" (Caswell 1989).

In conclusion, this study revealed some expected patterns for invading populations, such as the decrease in lambda as an invasion proceeds and the greater importance of early life history stages in the most rapidly colonizing plots (Lewontin 1965). However, using a demographic approach I have also discovered some unexpected aspects of the biology of *C. scoparius*. For one, its rates of increase are greatest in the most undisturbed open habitats, and it is in no way dependent on agents of disturbance for its success. Second, its dependence on resident pollinators for reproduction (Chapter 1) has important reverberations through the life cycle. Third, although vital rates and population growth are strongly influenced by stage of invasion and standing biomass, these are not closely correlated with simple numerical density. The usefulness of these matrix models as a management tool for exotic species is yet to be proven. Although no "Achilles heel" was found for *C. scoparius*, in future work I hope to apply the models to current and projected biological control efforts, to define the degree of efficacy required of particular insect agents to have a lasting impact on *C. scoparius* populations in Western Washington.

Table 2.1. Analysis of covariance for the square-root of biomass, as a function of diameter and number of branches, with population as a factor. A significant interaction with population means that the relationship between branch number, diameter, and biomass differs among populations.

source	df	sum sq.	mean sq.	F	P
population	5	670.6	134.1	4.6	0.0006
diameter	1	58,980.5	58,980.5	2021.1	0.0001
branch #	1	3486.0	3486.0	119.4	0.0001
pop*diam	5	445.1	89.0	3.0	0.011
pop*branch	5	2040.6	408.1	14.0	0.0001
residual	182	5311.3			

Table 2.2. Regression equations used to estimate the square root of biomass for each individual based on its diameter and number of branches. The relationship was calculated separately for each population.

Population	N	Equation	Adjusted R^2
Johnson Prairie	50	-16.2 + 8.0 * br# + 2.0 * diam	0.946
13th Division Prairie	30	-6.0 + 2.6 * br# + 1.7 * diam	0.918
Weir Prairie	29	-8.4 + 2.0 * br# + 1.6 * diam	0.881
Discovery Park	40	-18.8 + 8.6 * br# + 1.9 * diam	0.965
Magnuson Park	26	-11.3 + 6.8 * br# + 1.6 * diam	0.949
Montlake Fill	25	-8.1 + 2.7 * br# + 1.6 * diam	0.953

Table 2.3. Stage class criteria for seven stages of the *C. scoparius* life cycle. (I) Seeds: Both newly produced seeds and those in the seed bank (Fecundities were calculated as seed production at time $t + 1$). (II) Seedlings: Plants no larger than the size attainable by first-year (one-year-old) plants. (III) Juveniles: Plants larger than the largest first-year plant, but smaller than the minimum size at which reproduction occurred. (IV) Small adults: Plants large enough to produce fruits (even if no reproduction occurred in a particular year), plus (V) Medium adults, (VI) Large adults, and (VII) Extra-large adults, defined according to their estimated biomass.

Stage	Definition
I. Seed	
II. Seedling	diameter $\leq$ 1.8 mm
III. Juvenile	1.8 mm $<$ diameter $\leq$ 5 mm
IV. Small adult	diameter $>$ 5 mm; biomass $\leq$ 100 g
V. Medium adult	100 g $<$ biomass $\leq$ 400 g
VI. Large adult	400 g $<$ biomass $\leq$ 900 g
VII. Extra-large adult	biomass $>$ 900 g

Table 2.4. Analysis of variance for fruit production in 1994, including stage class in 1994 as a factor. Other factors include stage of invasion (early, intermediate, late), and population (Johnson Prairie and Discovery Park). Only two populations were included in this analysis in order to represent the full range of invasion stages (only these populations had late-invasion plots).

Source	DF	Sum of Squares	F	P
Population	1	201,529	7.4	0.0068
Stage Class	3	4,534,452	55.4	0.00005
Invasion Stage	2	153,496	2.8	0.0001
Pop * Stage Class	3	611,354	7.5	0.061
Pop * Invasion	2	131,962	2.4	0.090
Stage Class * Invasion	6	473,858	2.9	0.0086
Pop * Stage Class * Invasion	6	518,013	3.2	0.0046
Error	596	16,254,289		

Table 2.5. Spearman rank correlations among lambda (the finite rate of increase) and four direct measures of invasion: change in ($\log_{10}$) 1) biomass, 2) total density of vegetative plants, 3) density of adult plants, 4) density of x-large plants.

	Lambda	Δ Biomass	Δ Total	Δ Adults	Δ X-Large
Lambda	1				
Δ Biomass	0.83 (0.003)	1			
Δ Total plants	0.41 (0.14)	0.11 (0.70)	1		
Δ Adult plants	0.73 (0.008)	0.60 (0.031)	0.33 (0.24)	1	
Δ X-Large	0.34 (0.22)	0.64 (0.020)	-0.29 (0.30)	0.17 (0.53)	1

Table 2.6. Spearman rank correlations between five measures of invasion--change in ($\log_{10}$) estimated biomass, change in ($\log_{10}$) total plant density, change in ($\log_{10}$) adult plant density, change in ($\log_{10}$) extra-large plant density, and lambda (finite rate of increase)--and four measures of occupancy. Invasion measures were estimated between 1994 and 1995, occupancy was based on plant numbers in 1994.

Measure of Occupancy	Measure of invasion				
	Δ Biomass	Δ Total	Δ Adults	Δ X-Large	Lambda
Biomass	- 0.75	0.11	-0.61	-0.61	-0.62
	(0.0067)	(0.70)	(0.028)	(0.028)	(0.026)
Total plants	-0.16	0.47	-0.31	-0.48	0.19
	(0.56)	(0.09)	(0.76)	(0.08)	(0.49)
Adult plants	-0.38	0.18	-0.52	-0.20	-0.40
	(0.16)	(0.52)	(0.06)	(0.46)	(0.15)
X-Large plants	-0.74	0.11	-0.67	-0.67	-0.58
	(0.0081)	(0.70)	(0.016)	(0.016)	(0.037)

Table 2.7. Test for significant effects of invasion stage (early, intermediate, late) and habitat (prairie vs. urban field) on lambda generated from the 1994-95 transition matrices. Data from 1993-94 were not used in this analysis.

Source	DF	Sum squares	Mean square	F	P
Invasion Stage	2	0.447	0.224	8.32	0.0111
Habitat	1	0.200	0.200	7.45	0.0259
Stage*habitat	2	0.212	0.106	3.95	0.0642
Residual	8	0.215	0.027		

Table 2.8. The time (in years) until early invasion stage plots reach occupancy saturation (i.e., the density of x-large adults reaches that of late-stage plots, which is 1.5 per square meter). Each site was started with a vector that represented the density and stage structure found in that population in 1994. Then the vector was iterated through successive transitions using matrix multiplication.

	Time to saturation under Current natural pollination	Time to saturation under Full pollination
1994		
Johnson Prairie	4	4
Discovery Park	13	9
1995		
Johnson Prairie	6	5
13th Division Prairie	7	7
Discovery Park	29	19
Magnuson Park	13	11

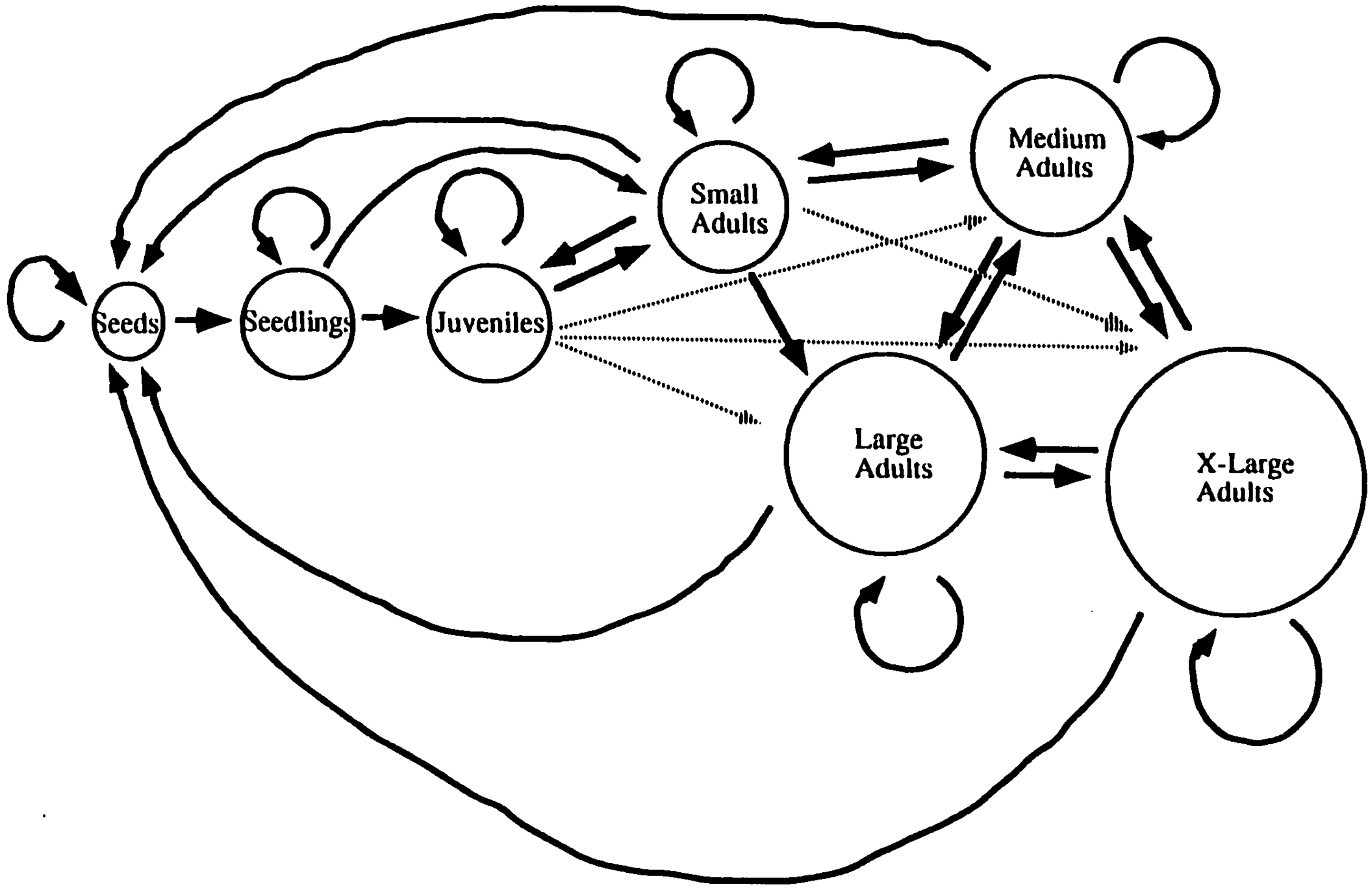


Figure 2.1. Graph of life cycle for C. scoparius, showing all possible transitions (those with non-zero matrix entries in at least one plot and year). Dotted lines represent transitions that were only seen in one or two plot*year combinations.

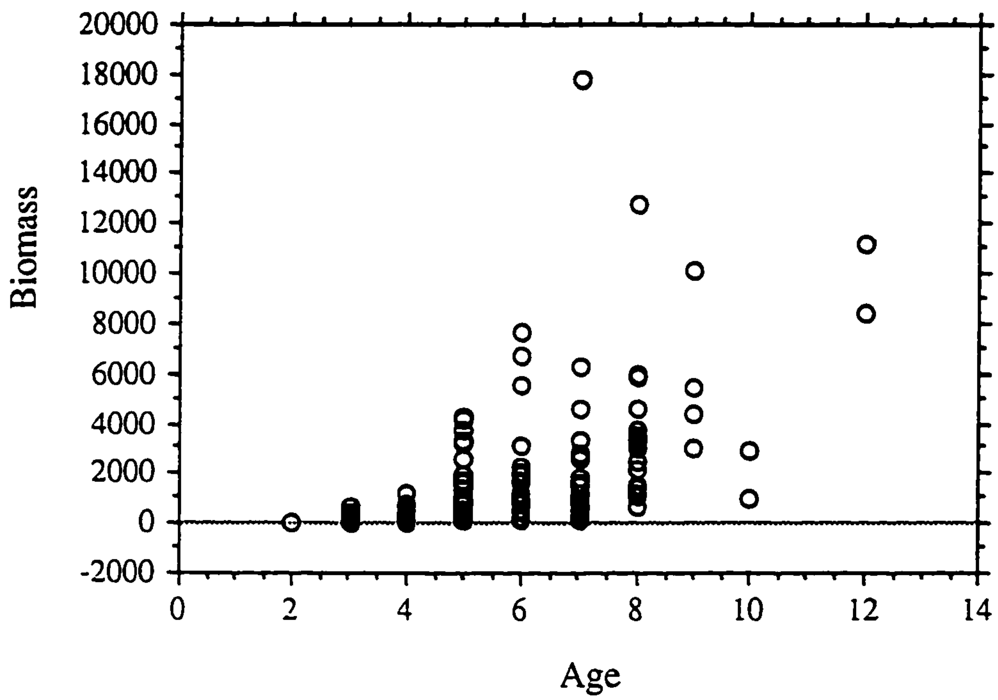


Figure 2.2. Plant biomass as a function of age. This sample (N=168) includes plants taken from all six populations involved in the study, with subsets from early, intermediate, and late stages of invasion.

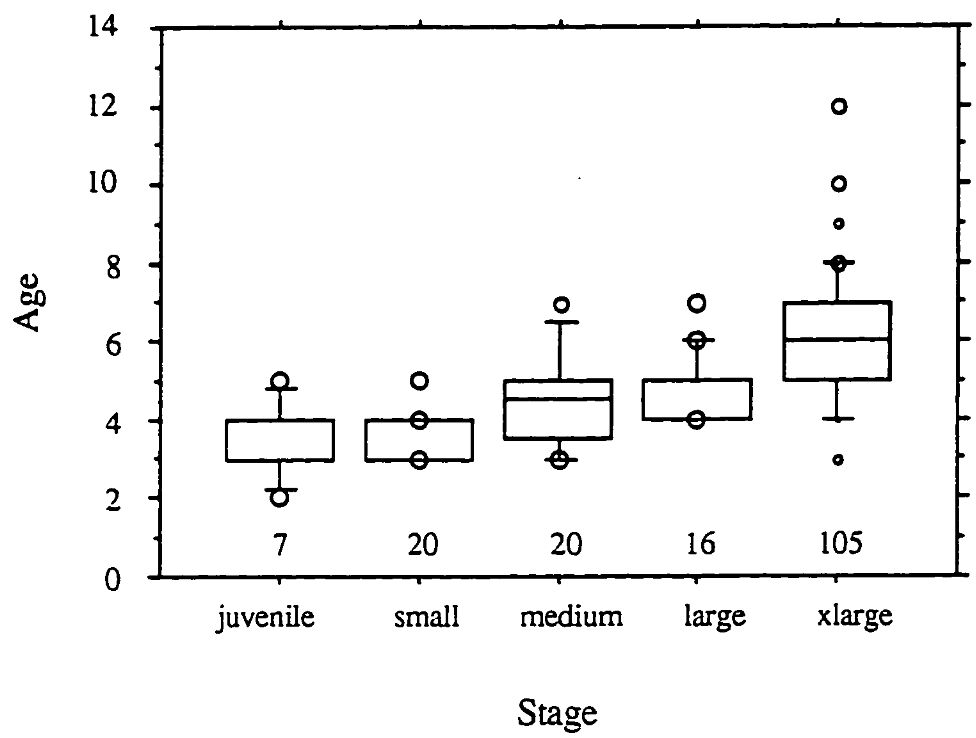


Figure 2.3. Box plot of the distribution of ages in each stage class, as defined in Table 3.stagedef. Boxes surround the central 50% of the data, with the middle line representing the median, and outer lines at 10% and 90%. Sample sizes are presented for each stage class. Analysis of variance indicates a significant effect of stage (DF = 4, Mean square = 46.3, F = 20.4, P < 0.0001), but a post-hoc Bonferroni-Dunn test reveals significant differences only between the extra-large class and each other class (P < 0.0001).

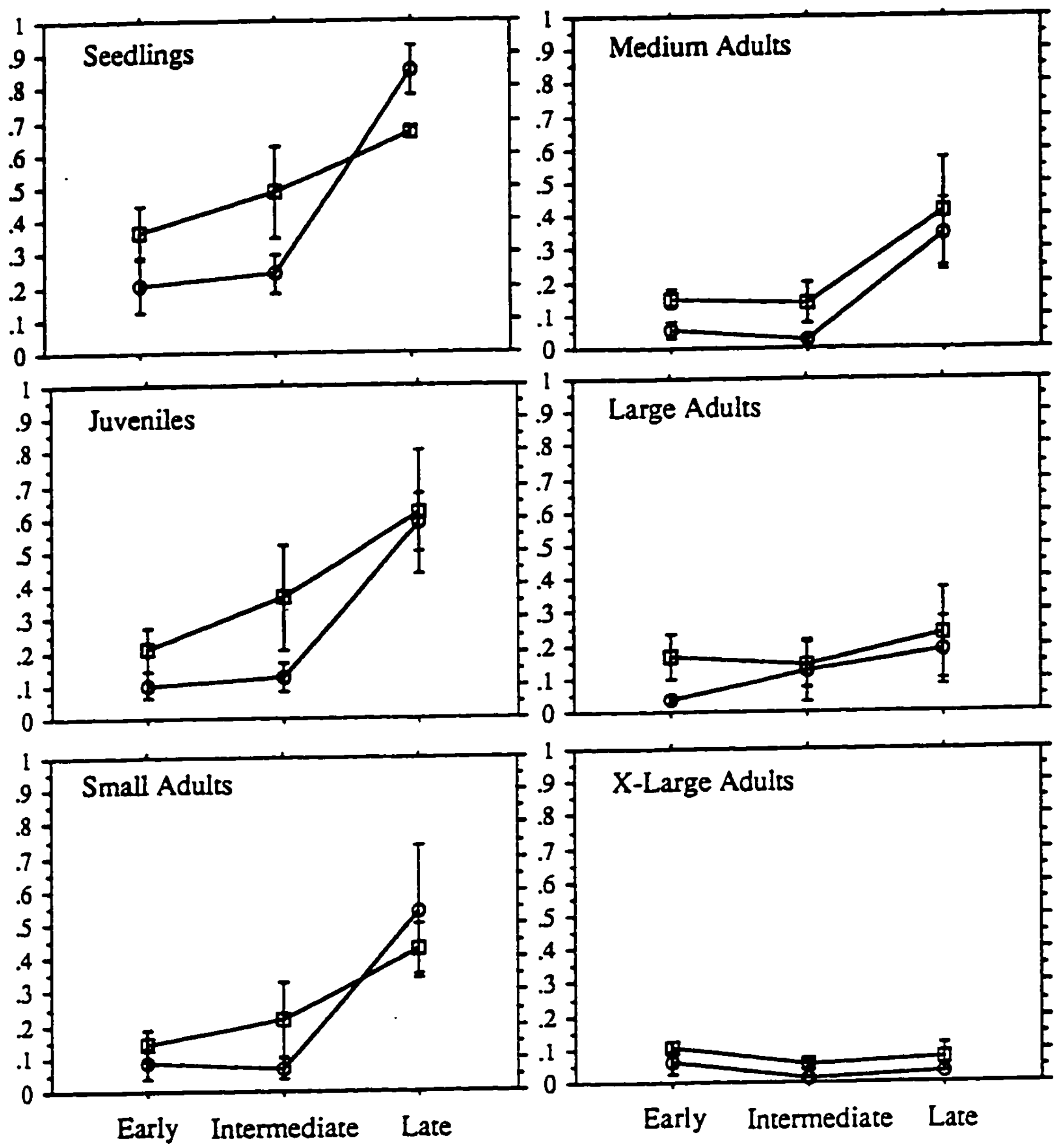


Figure 2.4. Mean mortality rates of plants of different life history stages, in prairie populations (circles) and urban populations (squares) and across stages of invasion (early, intermediate, late). Means are across three populations, with two separate transitions for Johnson Prairie and Discovery Park. Bars represent +/- one standard error.

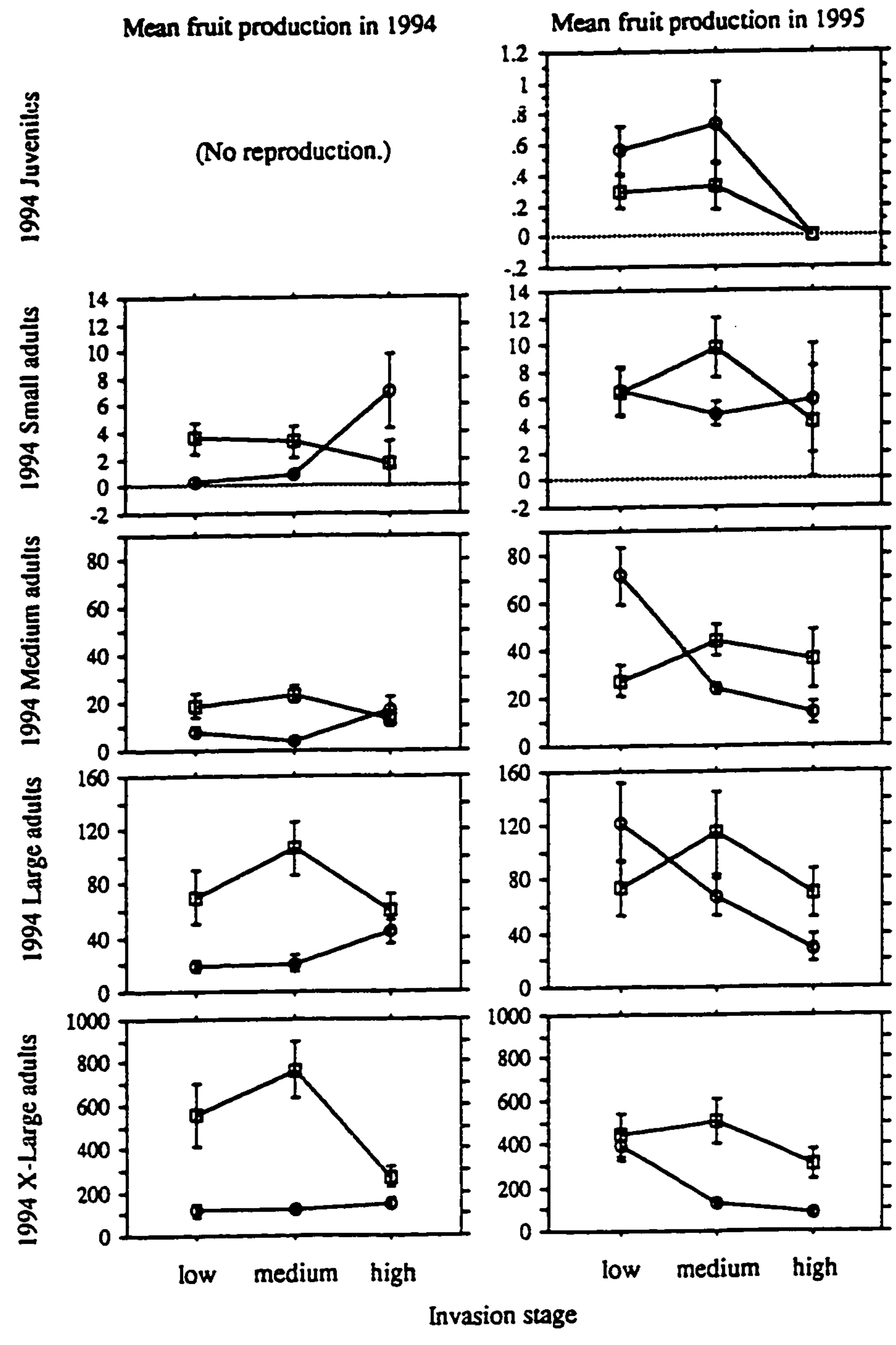


Figure 2.5. Mean stage-specific fruit production in prairie populations (circles) and urban populations (squares) across stages of invasion. Two types of fecundity are presented: the mean current (1994) reproduction of plants within a given stage in 1994, and the mean reproduction in the following year (1995) of plants within a given stage in 1994. The second measure is used in transition matrices and incorporates mortality and growth.

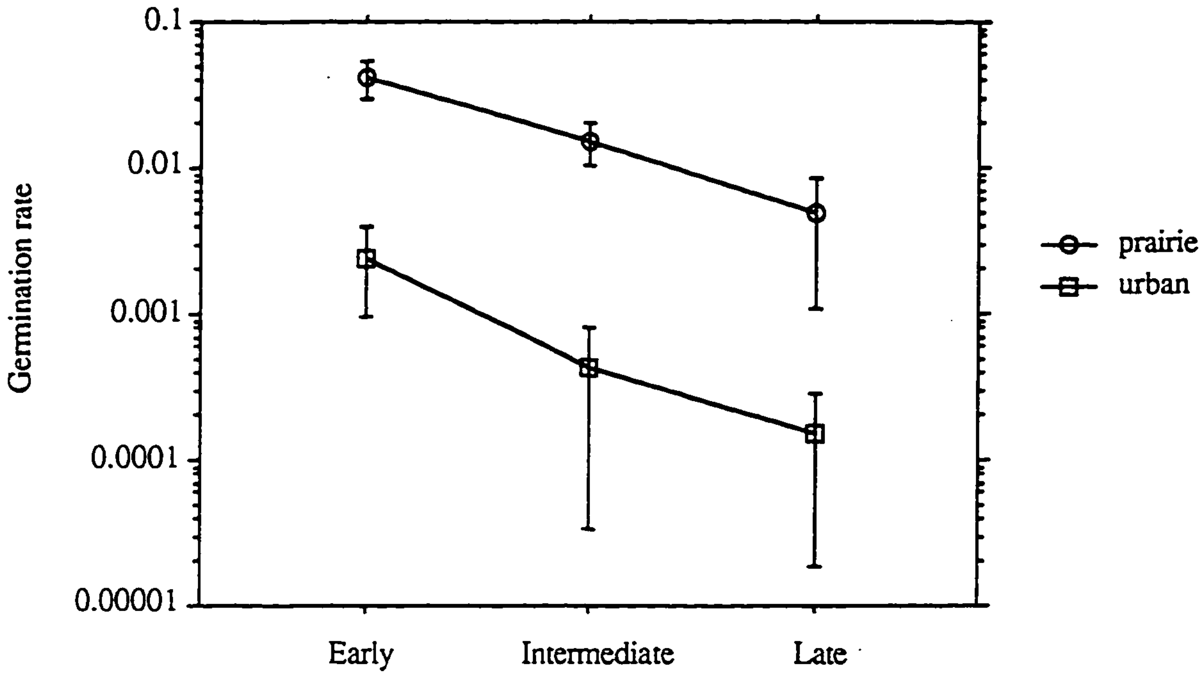


Figure 2.6. Mean germination rates (seedlings per seed) in prairie populations (circles) and urban populations (squares), across three stages of invasion (early, intermediate, late). Note log10 scale.

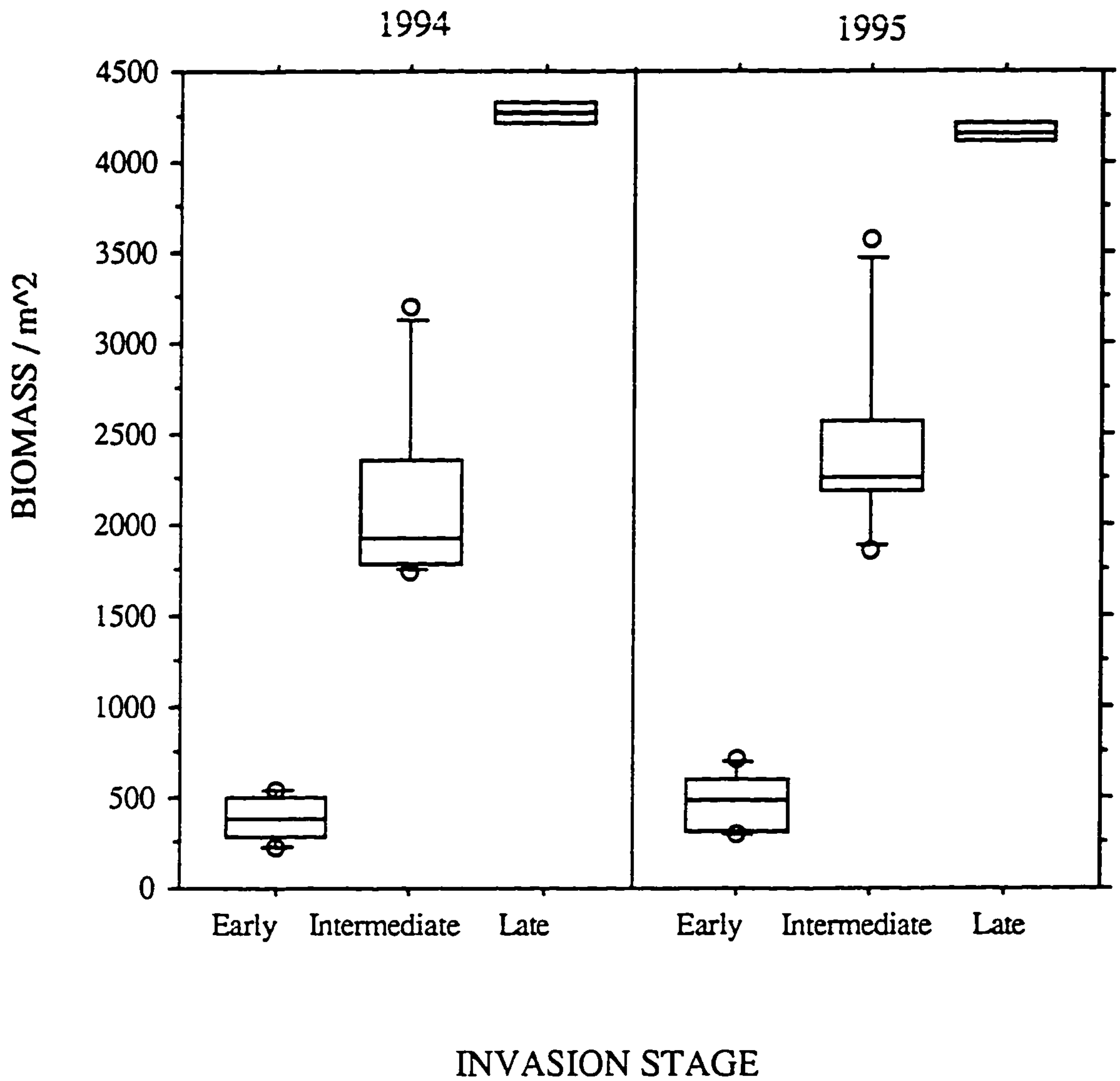


Figure 2.7. Box plot of mean estimated *C. scoparius* plant biomass per square meter in plots at different stages of invasion in 1994 and 1995. Early and intermediate invasion stages had six replicates (three urban and three prairie populations); the late stage had two replicates (one urban and one prairie population). Boxes surround the central 50% of the data, with the middle line representing the median, and outer lines at 10% and 90%. Analysis of variance showed highly significant variation for biomass among invasion stages (1994: $DF = 2$, $F = 82.7$, $P < 0.0001$; 1995: $DF = 2$, $F = 68.8$, $P < 0.0001$).

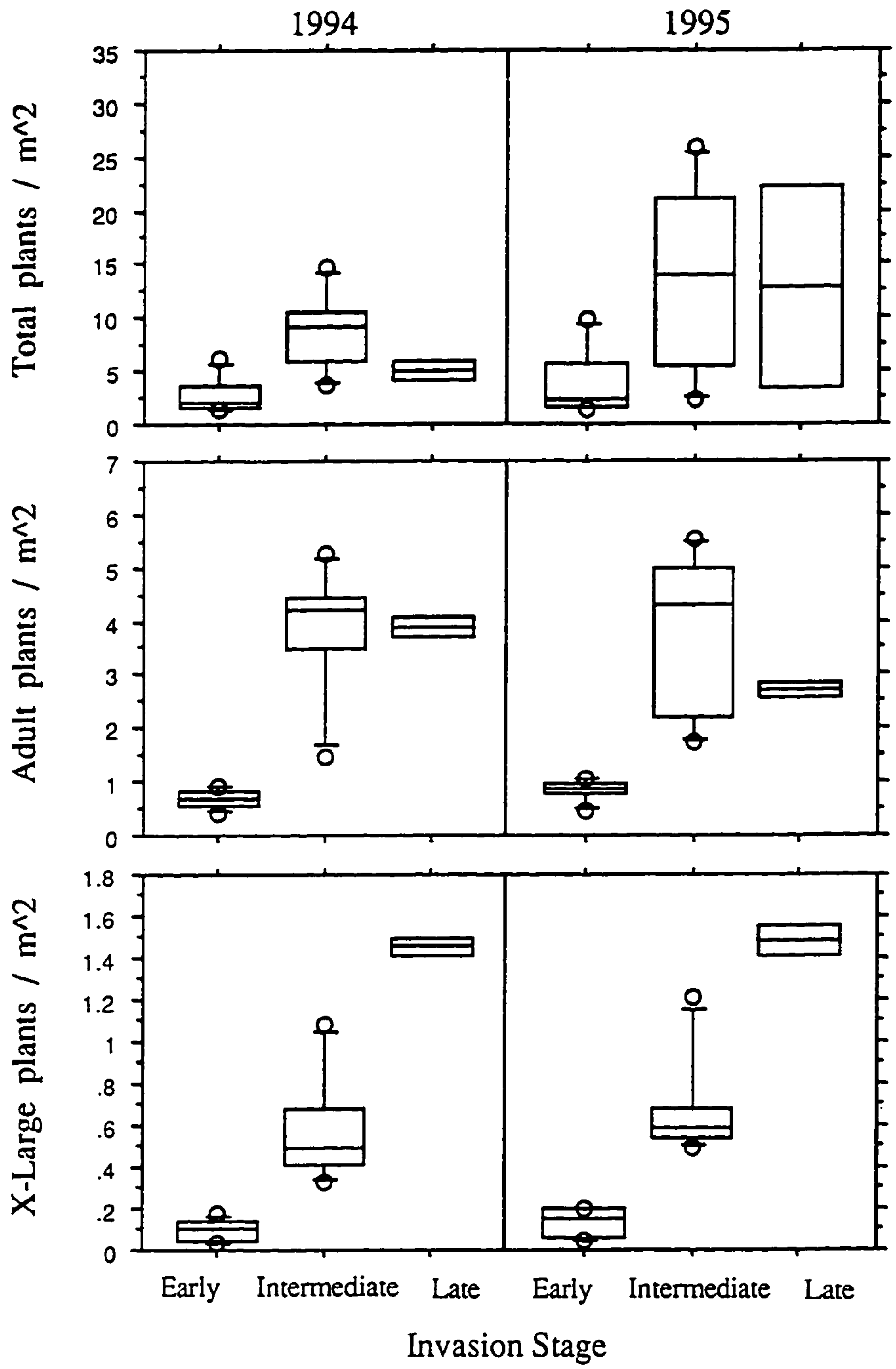


Figure 2.8. Box plots of three measures of density across invasion stages. Boxes surround the central 50% of the data, with the middle line representing the median, and outer lines at 10% and 90%.

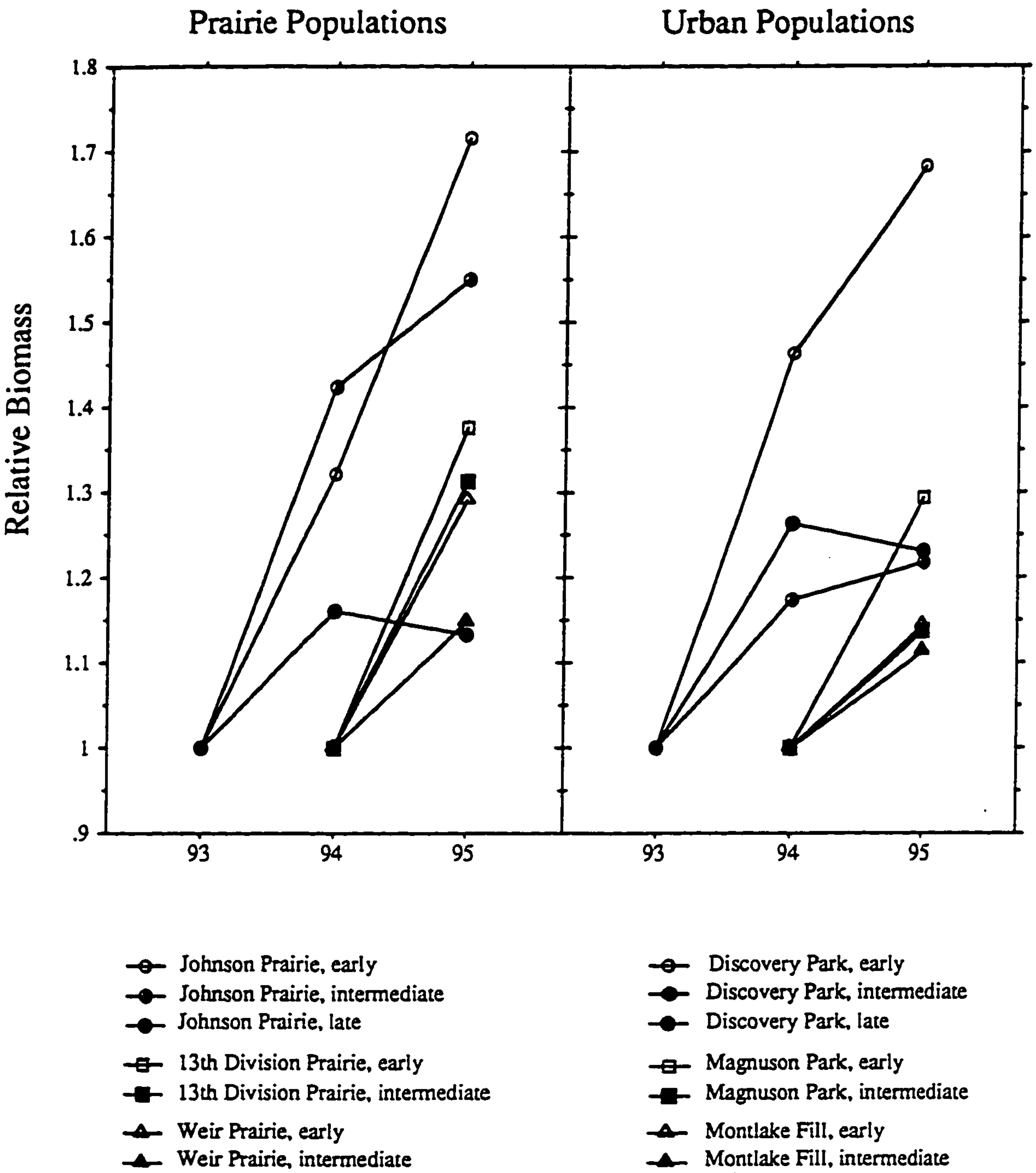


Figure 2.9. The increase of total estimated *C. scoparius* plant biomass per square meter from 1993 to 1995, standardized to the initial amount of biomass (1993 levels). Open symbols represent early invasion stage plots; half-filled and filled symbols of the same shape represent intermediate and late stage plots in the same populations.

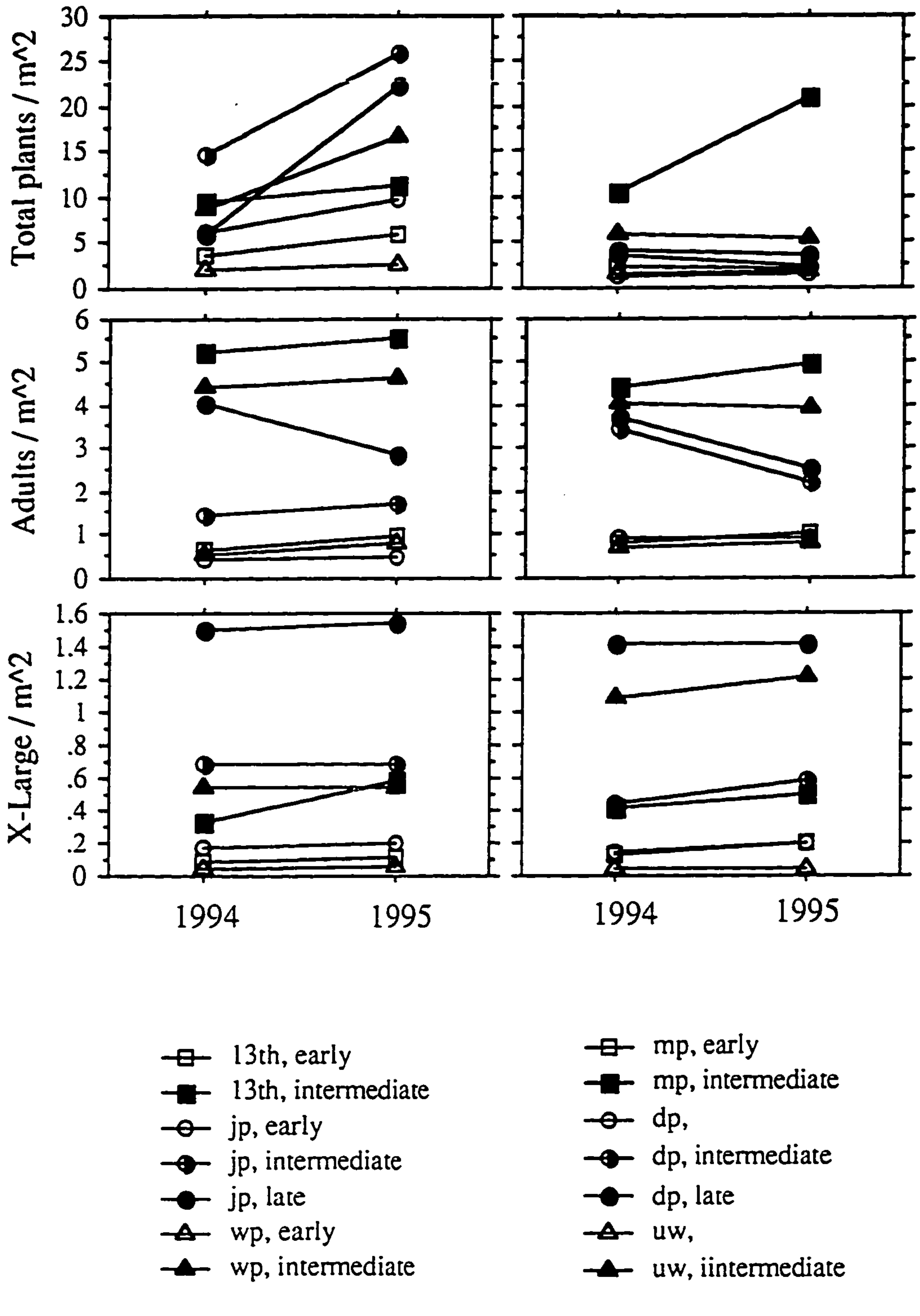


Figure 2.10. Densities of C. scoparius (plants per square meter) over time, measured for total plants, just adult plants, and just x-large adult plants.

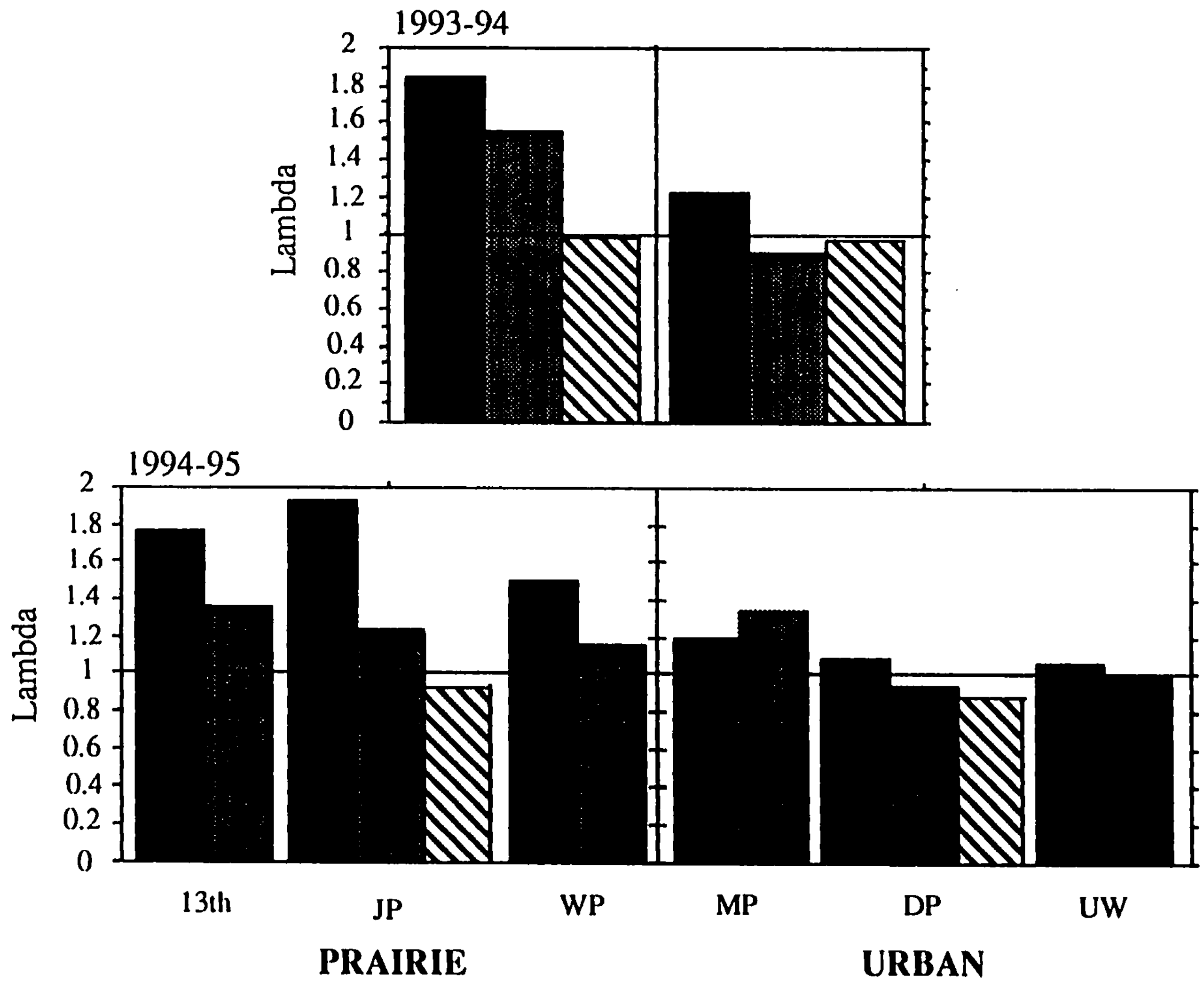


Figure 2.11. The finite rate of increase (lambda) calculated for two populations (one prairie and one urban) for 1993-1994 and six populations (three prairie and three urban) for 1994-1995. Each population wasrepresented by plots of different stages of *C. scoparius* invasion. Black bars = early stage, gray bars = intermediate stage, striped bars = late

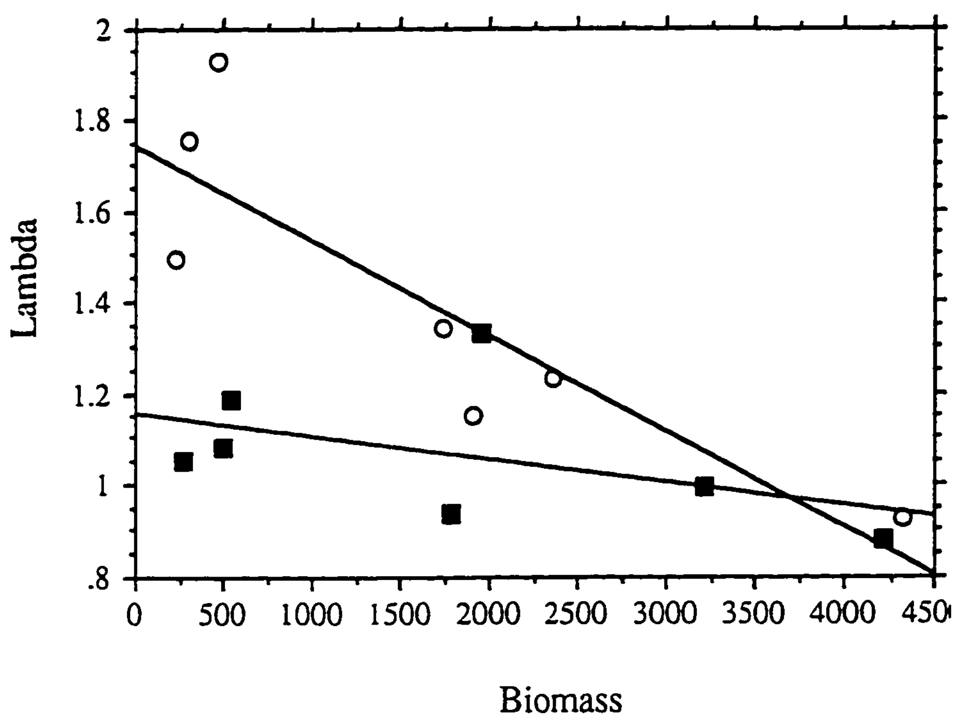


Figure 2.12. Lambda as a function of estimated biomass per square meter, for prairie populations (open circles) and urban populations (dark squares). Regression of lambda on biomass is significant for prairie populations ($F = 16.2$, $P = 0.01$, $R^2 = 0.76$ [Spearman rank $Z = 2.5$, $p = 0.014$]) but not for urban populations ($F = 1.5$, $P = 0.29$, $R^2 = 0.23$ [Spearman rank $Z=1.5$, $p = 0.13$]).

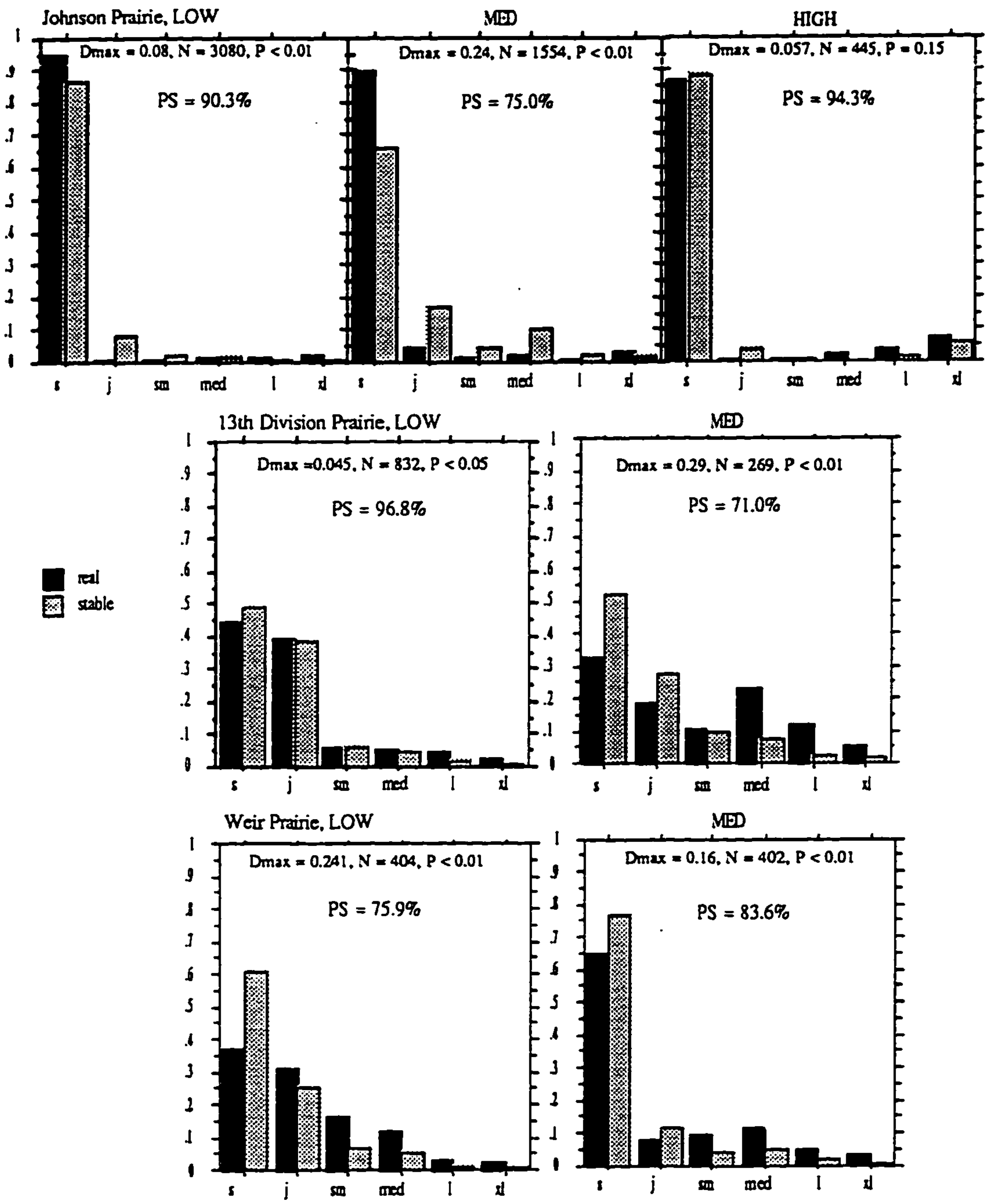


Figure 2.13a. Actual stage distribution in 1995 (black bars) and the stable stage distribution (grey bars: calculated from matrix analysis using 1994-95 transition matrices) for all plots. The degree of correspondence is expressed with percent similarity (PS; see text), and the significance of the deviation of the actual distribution from the expected is calculated using a Kolmogorov-Smirnoff one-sample test (Siegel 1956). s=seedlings, j=juveniles, sm=small adults, med=medium adults, l=large adults, xl=extra large adults. Prairie populations.

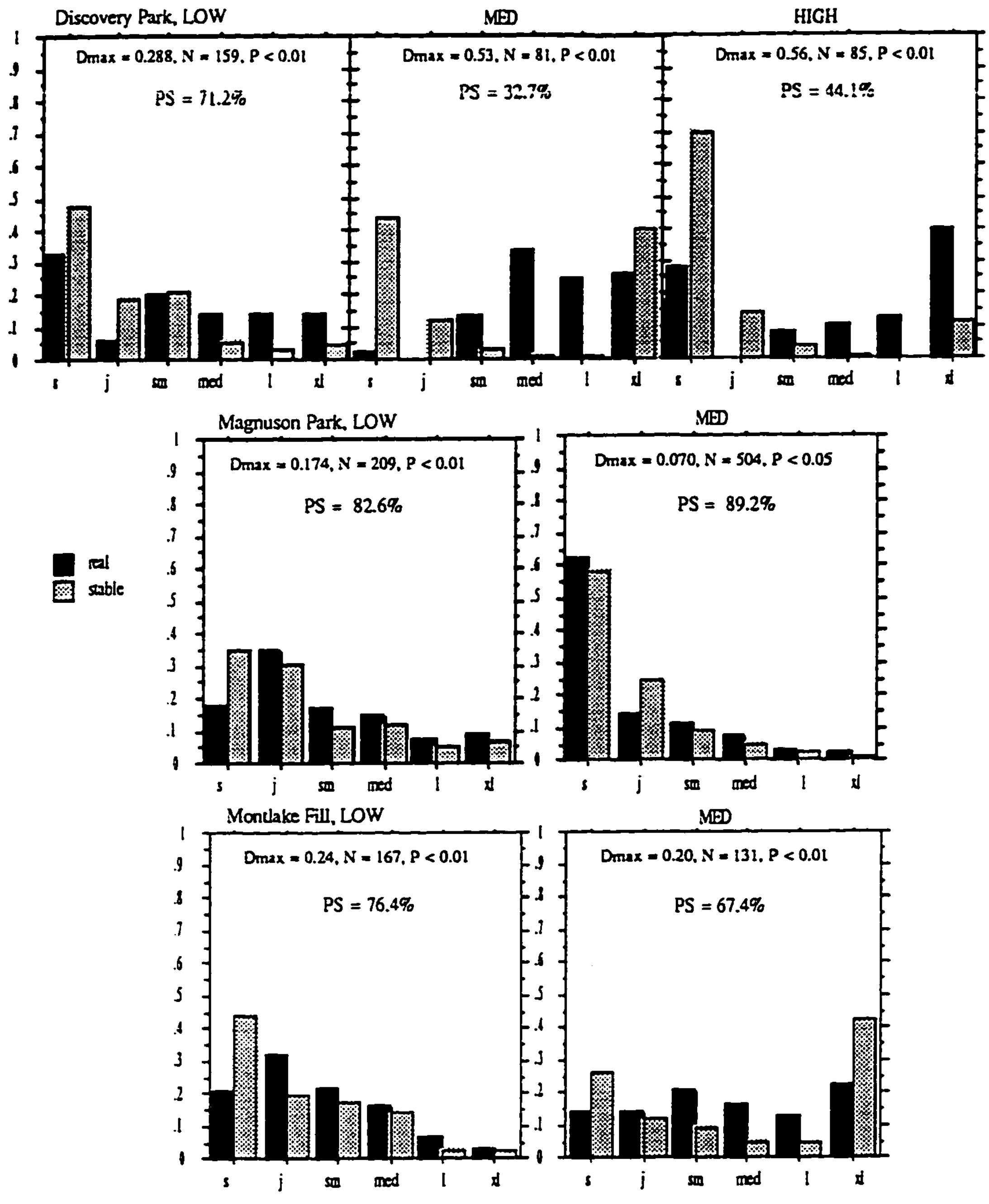


Figure 2.13b. Actual stage distribution in 1995 (black bars) and the stable stage distribution (grey bars: calculated from matrix analysis using 1994-95 transition matrices) for all plots. The degree of correspondence is expressed with percent similarity (PS; see text), and the significance of the deviation of the actual distribution from the expected is calculated using a Kolmogorov-Smirnoff one-sample test (Siegel 1956). s=seedlings, j=juveniles, sm=small adults, med=medium adults, l=large adults, xl=extra large adults. Urban populations.

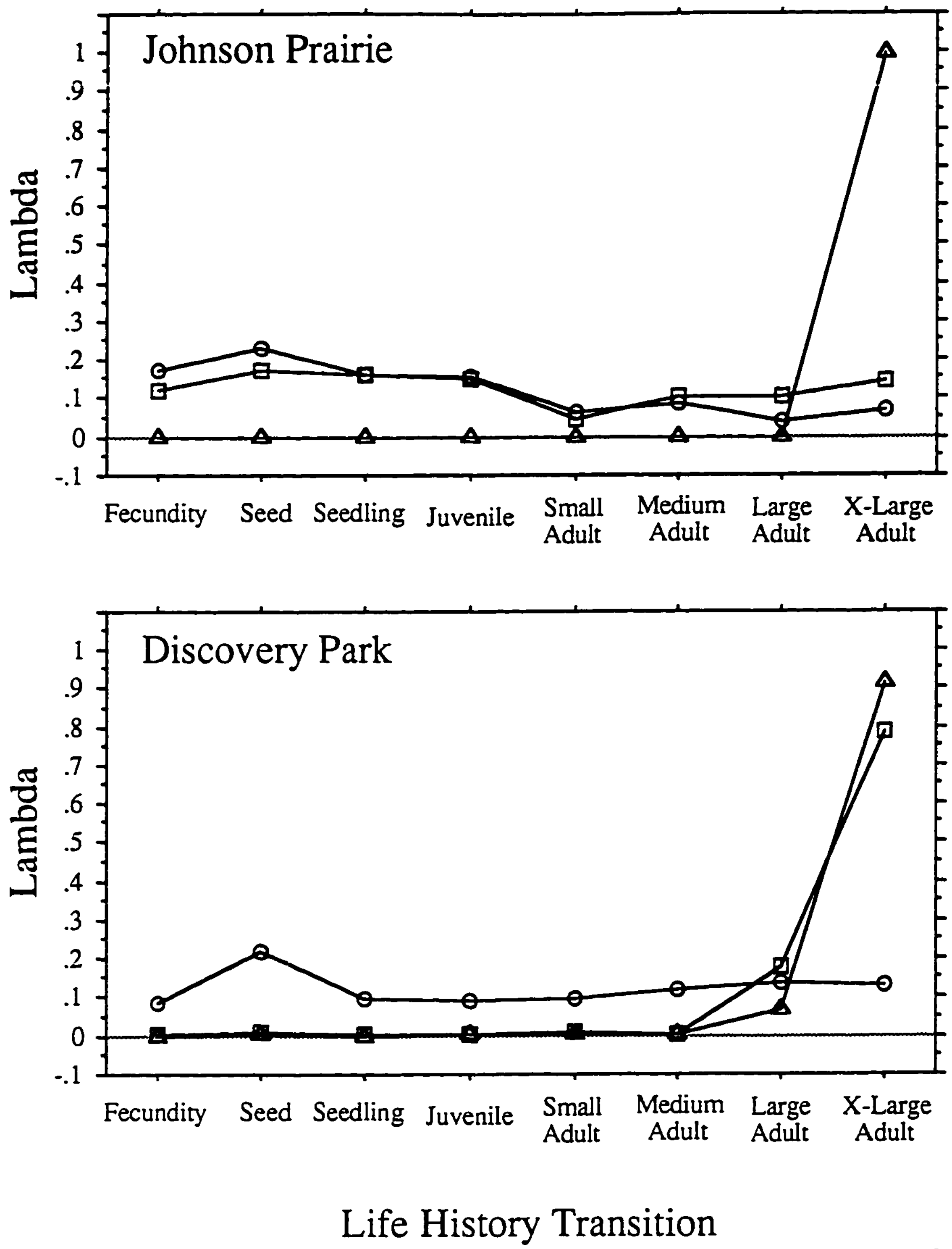


Figure 2.14a. Combined elasticities for the fates of seven different life-history stages for the 1993-94 transition, Johnson Prairie and Discovery Park. Different symbols represent early- (circles), intermediate- (squares), and late- (triangles) stages of invasion for each population.

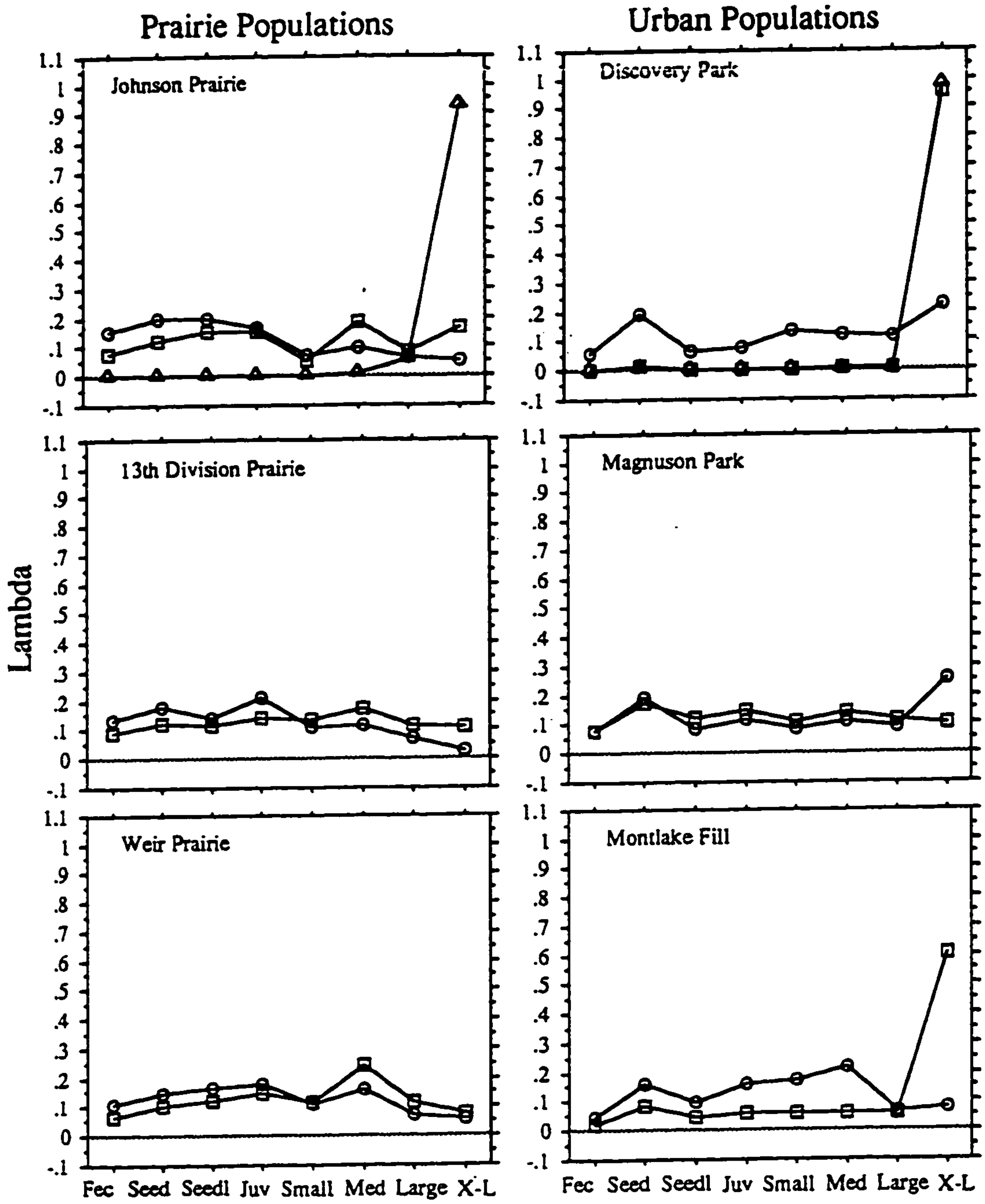


Figure 2.14b. Combined elasticities for the fates of seven different life-history stages for the 1994-95 transition, all six populations. Different symbols represent early- (circles), intermediate- (squares), and late- (triangles) stages of invasion for each population. Elasticities were combined by summing down each column, excluding fecundites.

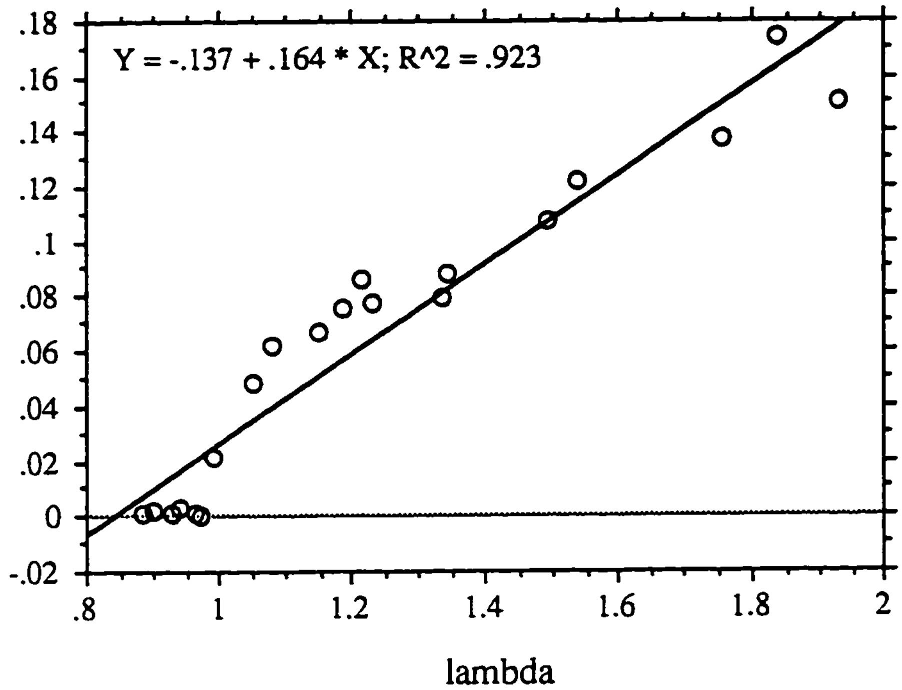


Figure 2.15. Combined elasticity for fecundity as a function of lambda, the finite rate of increase. Each replicate represents one density plot in a population (N=14); only data from 1994-95 are included.

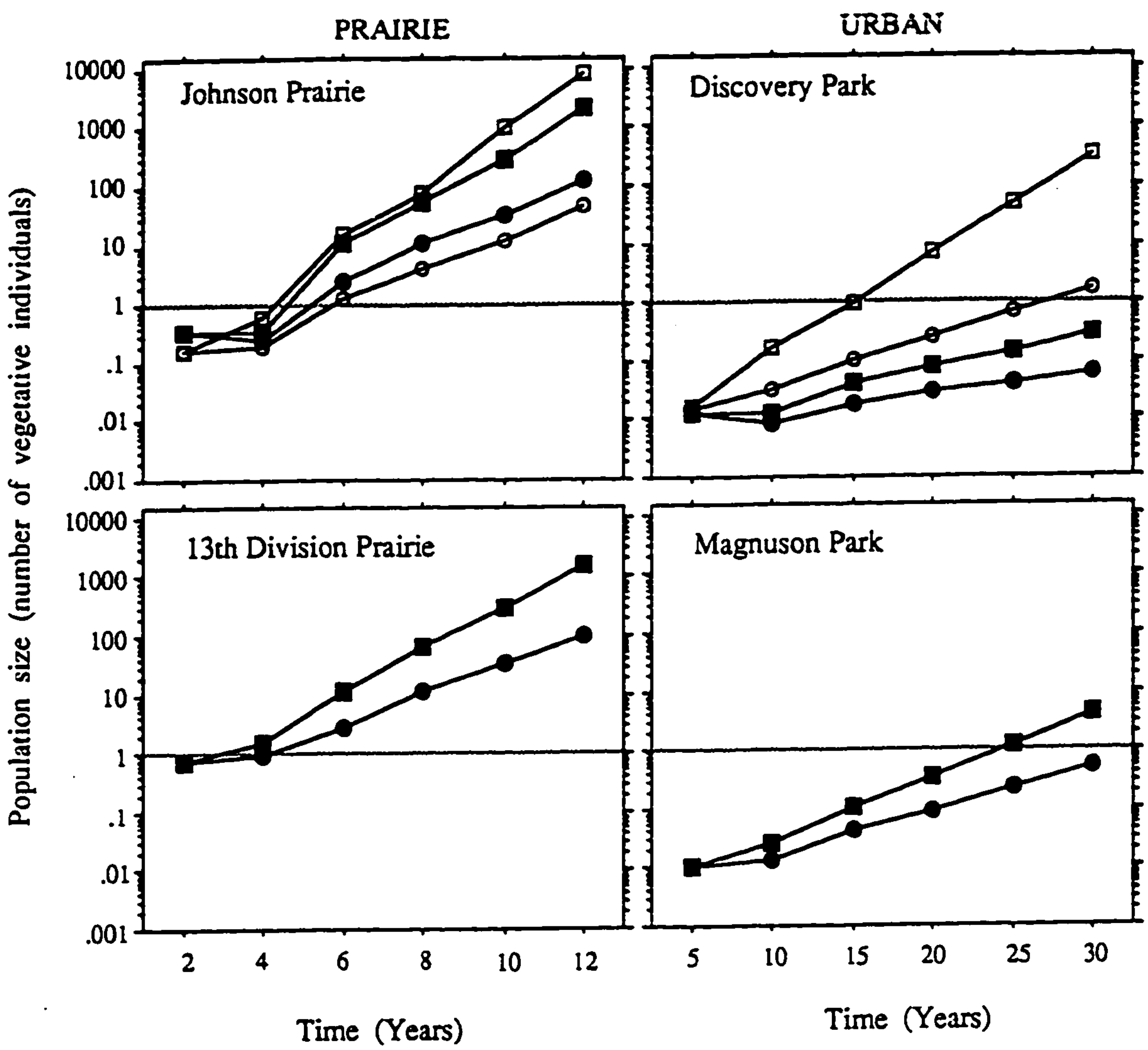


Figure 2.16. Results of a simulation of 20 of population growth of *C. scoparius* started from 10 seeds. The simulation is based on matrices with fecundity values incorporating either natural levels of pollination (circles; e.g., Appendix 1) or experimental pollen supplementation (squares). Note log scale and difference in the time scale for prairie populations (12 years) and urban populations (30 years).

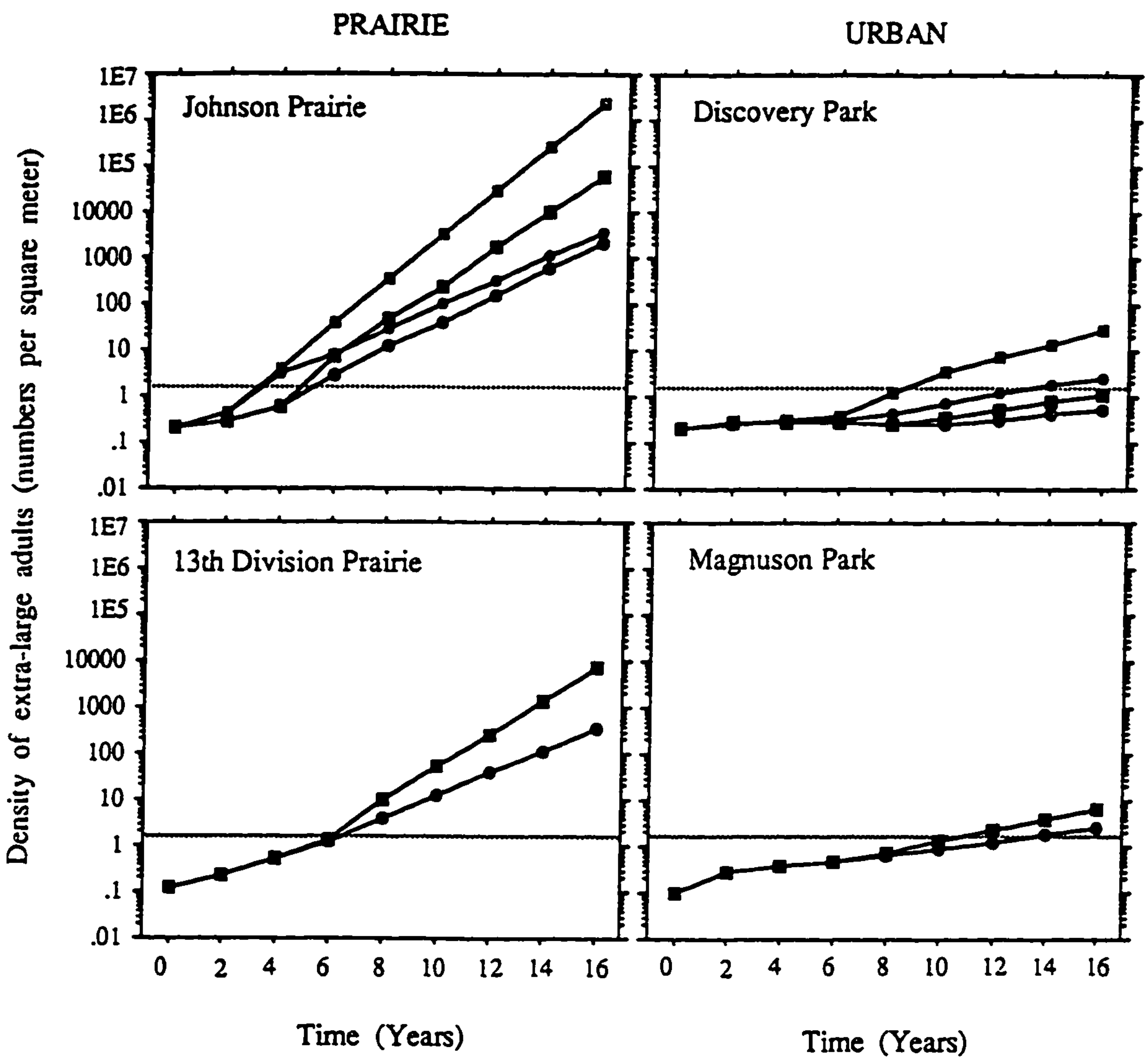


Figure 2.17. Results of a simulation of 16 years of population growth of *C. scoparius* populations projected from their current density and stage distribution. The simulation is based on 1994 densities, and matrices with fecundity values incorporating either natural levels of pollination (circles; e.g., Appendix 1) or experimental pollen supplementation (squares). Note log scale.

CHAPTER 3:
DISTURBANCE AND THE CRYPTOGAMIC CRUST: SAFE SITE AND SEED LIMITATION IN THE ESTABLISHMENT OF *C. SCOPARIUS*

INTRODUCTION TO CHAPTER 3

A prominent issue in invasion theory has been the relationship between the degree of disturbance of a host ecosystem and the spread of exotic species (Ewel 1986, Orians 1986, Hobbs 1989, Hobbs and Huenneke 1992). Taking an extreme position, Fox and Fox (1986) suggested that all invasions are dependent on disturbance. Theoretical approaches to this issue have shown a relationship between species richness and the invasibility of a community (Case 1990, Case 1991, Drake 1991)); similarly it has been postulated that species-poor island communities are more invasible than mainland communities (Elton 1958, Carlquist 1965) but see (Simberloff 1986). The term "biotic resistance" was coined to describe the idea that species-rich communities should be more resistant to invasions. Disturbance is connected to biotic resistance because heavily disturbed communities are assumed to have simplified, less resistant species assemblages (Elton 1958, Sharples 1983).

Other investigations have focussed on the role of specific types of disturbance in ecosystems (reviewed in (Hobbs and Huenneke 1992), defining disturbance as everything from simply a reduction of standing biomass (Grime 1979), to "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985). Empirical work has shown a role in the success of various exotic species for such diverse agents of disturbance as gophers (Hobbs and Mooney 1985), grazing (Cross 1981), rooting by introduced pigs (Kotanen 1993), and roads (Parker et al. 1993). Management actions themselves can sometimes represent a disturbance, and in these cases resource managers are faced with tradeoffs regarding the potential or predicted responses of different species of concern (Hobbs and Huenneke 1992). A common example is the use of control burning in grassland ecosystems; while it is a very useful tool for eliminating certain target species, burning can also produce incidental undesired effects--both negative effects on sensitive native plants or animals and positive effects on nontarget exotic populations.

From an extensive review of the literature, Hobbs and Huenneke (1992) concluded that disturbance usually acts to stimulate invasion by increasing the availability of suitable microsites for establishment. This suggestion is related to the assertion that most plant populations are limited by their access to "safe sites" (Harper 1977). The relative importance of seed limitation and safe-site limitation in natural populations has long been a matter of controversy in plant ecology (Harper 1965, Louda 1982, Andersen 1989, Hoffman and Moran 1991). Invading or colonizing species are perhaps different because newly founded populations are by definition seed-limited. However, one may think of all populations as going through colonizing and post-colonizing phases (Lewontin 1965), and the relative importance of seeds and safe-sites should change between these phases. The functional response of seedling number to seed number should show density dependence and saturation. For few species, however, do we have information on the shape of this response, and how it may be altered by factors affecting the availability of safe sites.

The weedy shrub Scotch broom (*C. scoparius*) invades the glacial outwash prairies of western Washington, which are considered rare ecosystems and are an important priority for conservation. These prairies are characterized by the presence of a cryptogamic crust, often dominated by the moss *Racomitrium* (Franklin and Dyrness 1988). Cryptogamic (also called cryptobiotic or microphytic) crusts are assemblages of mosses, algae, lichens, and liverworts that have been shown to play a large role in plant community dynamics in areas such as polar deserts (Gold and Bliss 1995), alpine zones (Gold, Glew and Dickson, unpubl. ms.), and especially semiarid desert (Harper and Marble 1988, Metting 1991), where they have been well-studied. It has been suggested that the invasion of *C. scoparius* might be linked to disturbance of this cryptogamic layer (J. Reasoner, pers. com.), and for this reason the enhancement of *C. scoparius* spread is considered one of the potential environmental impacts of soil disturbance. In addition, burning is used routinely to control *C. scoparius*, in Washington as well as other areas where *C. scoparius* is a pest species. While it kills adult plants, burning has also been implicated in the stimulation of seed germination in *C. scoparius* by disrupting the hard seed coat (Mobley, 1954). Burning also affects cryptogamic crusts, which can be entirely killed by a hot burn (Johansen et al. 1993), and it is sometimes followed by the establishment of large numbers of *C. scoparius* seedlings.

Here I describe an experiment designed to evaluate the importance of both seed limitation and safe-site limitation in determining *C. scoparius* establishment, and to measure how common human impacts on the prairie plant community may influence germination through their influence on safe-site availability. Disturbance treatments were designed to address two types of questions; first, what is the role of the cryptogam layer in *C. scoparius* establishment--does it inhibit or encourage germination? Second, does burning stimulate *C. scoparius* germination, and is the effect of burning due to the removal of competition and release of nutrients, or is it primarily a direct effect on seed germination through scarification of the seed coat?

METHODS

Study plant:

Cytisus scoparius, Scotch broom, was introduced by early settlers of the Pacific Northwest as an ornamental (Gilkey 1957) the first recorded specimen was collected from a garden in Seattle in 1888. For the last four decades, *C. scoparius* has been regarded as a noxious pest in rangelands and natural areas throughout the west coast of North America from British Columbia to central California.

Cytisus scoparius is a large shrub, reaching a height of four meters or more in its introduced range. It has no form of clonal growth and therefore relies entirely on seed set for reproduction. Plants begin reproducing in their third or fourth year (unpubl. data). Seed production per plant varies over four orders of magnitude and is strongly dependent on plant size (see Chapter 2). The diaspore is a seed about a milimeter in diameter and an attached eliasome. Seeds are dispersed from late July through September, by ballistic dispersal and secondarily by ants; germination begins in early March.

Study Site:

A site was chosen for the experiment at the northeast corner of Weir Prairie on the Fort Lewis Military Base, Thurston County, WA. Weir Prairie is one of the better examples of glacial outwash prairies left in western Washington (Kruckeberg 1991), and it is home to such common prairie natives as *Festuca idahoensis*, *Camassia quamash*, and *Panicum occidentale*. Weir prairie supports a population of *C. scoparius*, which must be controlled by regular burning there. Burns are generally done in early spring (February-April) or in fall (September-October) (J. Reasoner, pers. com.). Experiments were conducted on a section of prairie approximately 35m x 15m that was nearly free of *C.*

scoparius with no fruiting adults nearby. I laid out a rectangular grid of 160 square plots (8 x 20). Each square plot was 1.5m on a side and had within it a circle of area 1m^2, with the exterior square acting as a "buffer zone" for the treatments, which were contained within the circles. The *C. scoparius* seedbank was almost nonexistent at this site; before imposing the treatments I removed a total of nine seedlings from 360 square meters.

The experiment was a two-factor factorial design, with a series of disturbance treatments and a series of seed treatments. The disturbance treatments were: 1) control, 2) "scalped" (Belnap 1993): the cryptogam layer was scraped to soil surface while leaving other plant species intact, 3) "burned before": vegetation was burned before adding seeds, and 4) "burn after": vegetation was burned after adding seeds. Seed treatments were designed to approximate an exponential decay in seed densities as one goes farther from the front of invading seed-dispersing *C. scoparius* plants, which accurately reflects a translation of the probability density function (Chapter 4) into seeds per m^2. The only exception to the exponential series was the highest seed density treatment, which was constrained by the amount of time available for collecting the large numbers of seeds required. Seed treatments were: 1) control (zero seeds), 2) 20 seeds, 3) 100 seeds, 4) 500 seeds, 5) 1000 seeds. In all, 51,840 seeds were collected, counted, and used in this experiment. Treatments were randomly assigned to each plot, with 8 replicates for each of the 20 treatment combinations (4 surface x 5 seed).

On July 28, 1994, I censused the vegetation in all plots, using the point cover method with a nine-point grid in each plot. The proper conditions for a good burn occurred on September 22, 1994, from 1 pm to 3 pm. The burning itself was done by the fire crew at Fort Lewis, using the same techniques that are used for routine control burns. Fires were started with a match when possible, with a drip torch if fuels would not light with a match. Each plot was burned separately using a welded circle of sheet metal 45cm tall to contain the flames. In order to quantify the range of temperatures in the burned plots and compare the experiment as a whole to typical control burns, I placed metal plates containing heat-sensitive paint in four replicates with different fuel levels. The plates revealed that temperatures varied from 288°F to 475°F, well within the range of typical control burns (J. Reasoner, pers. comm.). To guage the relative temperature of the burn in each plot, on September 23 I visually assessed the color and appearance of each replicate and noted it as a cool, medium, hot, or very hot burn.

The scalping treatment was imposed on September 23. I used a hoe to scrape the cryptogam layer off of the soil surface, leaving the topsoil intact and taking care not to disturb the vascular plants. Seeds were scattered haphazardly into the plots, using a circular cardboard barrier to keep them within the boundaries of the plot. Seeds for the "burn after" treatment were scattered the morning of September 22, seeds for the rest of the treatments were scattered on September 23.

I began censusing seedling emergence on March 24, 1995. To estimate germination and mortality of all seedlings and to obtain information about the relative schedule of emergence for different treatments I randomly subsampled three replicates of each treatment to be censused six times through the spring and summer (4/13, 5/6, 5/26, 6/18, 7/9, 8/7). Time constraints prohibited a full census of all plots at every date, and the remaining five replicates were censused on only two dates (5/19, 8/7). Each new seedling was marked with a colored toothpick, with a different color pattern for each census. If a seedling had died by a certain census, its color was recorded and the toothpick removed.

I decomposed the success of *C. scoparius* in each plot into germination and early establishment (defined as survival through the first summer). I used analysis of variance to test for the effects of surface treatment, seed input, and the interaction between surface treatment and seed input on total number of seedlings germinating (regardless of their fate). I then did the same analysis on the proportion of germinated seedlings surviving to the last census. I looked for evidence of density dependence by plotting the functional response of seedlings per seed input as seed number increased, and performing a similar two-factor analysis of variance on this measure.

Two comparisons of interest were examined in more detail: burning before *vs.* after seed input, and scalping of the cryptogam layer *vs.* no disturbance. Using ANOVA, I compared germination rates for different burn temperatures and examined the relationship between temperature and the cover of cryptogams or *Agrostis*. I used Spearman rank correlation to inspect the cover data from undisturbed plots for a relationship between the relative cover of cryptogams and the germination rate.

I used the subsample of plots for which I had six censuses to ask how much information was lost from the remainder of the plots. That is, because some seedlings germinated and then immediately died within unsampled intervals, a proportion of seedlings went undetected. For the subsample, I compared results from the full set of censuses with a reduced dataset that eliminated seedlings that had germinated and died before or between the 5/26 and 8/7 census dates. Mortality was significantly underestimated by this short-cut (paired t-test DF = 43, $t = 5.3$, $P < 0.0001$), but the mean difference between the six-census and two-census mortality rates was only 8.1%. To remain consistent, when calculating mean survivorship rates and germination rates I used the two-census estimates for all replicates, with the caveat that they slightly overestimate the true survivorship and underestimate germination rate.

A complicating factor in this study is that *C. scoparius* seeds have eliasomes and are dispersed by ants. It was not feasible to remove the eliasomes from the 51,840 seeds used in this experiment, and despite the paucity of warm and dry weather in the Northwest between October and March, some ant dispersal did occur. Evidence for this is found in the non-zero seedling emergence from control plots (see Fig. 3.1). Plots receiving 20 seeds consistently had more seedlings than control plots across surface treatments, but this difference was not significant (ANOVA, seed treatment DF = 1, mean square = 1.2, F = 0.24, P = 0.62). It follows that most seedlings in 20-seed plots probably originated from "alien" seeds, and therefore I chose to remove this treatment from the consideration of how seedling#/seed changes with seed density. I included the 20-seed plots in the rest of the analyses, however, because in no other case did the polluting effects of ant dispersal substantially change the interpretation of the data.

RESULTS

The experiment yielded a total of 1050 seedlings (from the two-census approximation) with a mean of 6.6 seedlings per m^2 plot, giving an overall germination percentage of 2.0%, or 2.2% with adjustment. These numbers correspond nicely with germination rates estimated from the demography plots at Weir Prairie (Chapter 2), which were 1.7% for the intermediate invasion stage and 6.9% for early invasion stage. The total number of seeds germinating varied significantly with both surface treatment and seed input and with the interaction between the two factors (Fig. 3.1, Table 3.1).

Germination rate as expressed as seedling per seed also declined with increasing seed number, from 100 to 1000 seeds (Fig. 3.2). The difference among seed classes was significant (ANOVA, DF = 2, F = 11.2, P < 0.0001), as was the difference among surface treatments (DF = 3, F = 20.95, P < 0.0001). There was no significant interaction between surface treatment and seed number (DF = 6, F = 0.83, P = 0.55), suggesting that density dependence does not differ among surface treatments over this range of seed densities.

Seedling survival to August did not vary among surface treatments (Table 3.2). Seed number also did not have a significant effect on survival; that is, there was no evidence for density-dependent mortality of seedlings across the observed densities (Table 3.2). Therefore the final number of seedlings alive in August was dominated by patterns in the germination rates, and showed significant effects of both surface treatment and seed number (Table 3.3).

The undisturbed community was overwhelmingly dominated by the cryptogamic crust and the grass *Agrostis tenuis*, which when combined occupied a mean of 94% of the points. The mean cover of cryptogams was 67.5%, ranging from 22% to 100%; the mean cover of *Agrostis* was 35.5%, ranging from 11% to 78%. The cover of cryptogams and of *Agrostis* were negatively correlated ($N = 31$, $r = -0.92$, $P < 0.0001$), and the hottest burns occurred in plots with the highest cover of *Agrostis* (Mean cover for cool, medium, hot, and very hot, respectively = 2.2, 2.5, 2.2, and 3.8; ANOVA, $DF = 3$, $F = 4.6$, $P = 0.005$) and least cover of cryptogams (Mean cover for cool, medium, hot, and very hot, respectively = 7.1, 5.9, 6.5, and 4.9; ANOVA, $DF = 3$, $F = 5.1$, $P = 0.003$). Seeds that were added before burning produced more seedlings than those added after burning (Table 3.4, significant main effect of timing), and for plots in which seeds were added before burning, intermediate temperatures seemed to yield the most seedlings (Fig. 3.3, Table 3.4, marginally significant effect of temperature), although the interaction between timing and temperature was not significant (Table 3.4).

Although plots with intact cryptogams had much higher levels of germination than scalped plots (Fig. 3.1), there was no correlation between cryptogam cover and number of seedlings within the control plots ($r = -0.16$, $P = 0.39$).

DISCUSSION

I found a significant effect of surface treatment on germination rate (Fig.3.1) and on final seedling density (Table 3.3), with the highest number of seedlings in the control plots and the fewest seedlings in plots where the cryptogamic crust had been scalped. This finding was surprising in that it suggests that disturbance inhibits, rather than enhances, the establishment of this invasive species in western Washington prairies.

Several mechanisms could explain the lower number of seedlings in disturbed plots. One is that seed predation is higher in disturbed plots because seeds are easier to find. In a similar experiment, Bossard (Bossard 1990) found that plots in which the soil was turned over to 15cm did not differ from control plots in *C. scoparius* establishment at one site, but had significantly more seedlings at the other site. She showed that the lack of differences at the first site could be attributed to avian seed predation. Although seed predation by birds was not observed at my sites in Washington, seeds may be taken by rodents or invertebrates such as carabids (B. Semsrott, pers. obs.). Without seed predator exclosures fine enough to exclude invertebrates, it is not possible to evaluate this hypothesis directly; however, one piece of information argues against it as the primary explanation for reduced germination rates in disturbed plots. If seed predation and apparency were the primary factors controlling the difference between treatments, one would expect treatments to also differ in the number of seeds left dormant in the plots. Therefore, at the final census I counted not only seedlings but also seeds left. I recovered a total of 138 seeds, and found that seed number did not differ significantly between control and scalped plots (ANOVA, DF = 1, F = 1.7, P = 0.20).

Another explanation for the lower germination rate in disturbed plots is that the structure of the intact community actually fosters *C. scoparius* germination and early growth. Cryptogam layers are common in high-stress environments, particularly in semiarid deserts (Harper and Marble 1988, Metting 1991), in the arctic (Gold and Bliss 1995) and at high altitudes (Gold, Glew and Dickson, unpublished ms.). They increase infiltration and protect soils, decreasing erosion of silt and clay and consequently the loss of important nutrients (Eldridge 1993). In addition, the components of the crust themselves are involved in fixing nitrogen (Reifner and Bowler 1995, Gold, Glew and Dickson, unpublished ms.), and are secondarily involved in increasing the availability of other nutrients to plants (Harper and Pendleton 1993). Cryptogamic crusts can also moderate temperature extremes (Gold, personal communication). Crusts also increase surface roughness (Anderson et al. 1982), and they have been implicated in the establishment of vascular plant species (St. Clair et al. 1984). Lichens on the coastal bluffs and cliffs of California increase the water available to seeds and seedlings of species such as *Dudleya* through fog capture (Reifner and Bowler 1995). Soil moisture may be a key abiotic factor influencing *C. scoparius* germination, as Bossard (1990) found a significant correlation between soil moisture and seedling establishment in both of two widely differing sites.

One puzzling result from this experiment is that despite the lower seedling density found in scalped plots as compared to those with cryptogams intact, seedling number was not correlated with estimated percent cryptogam cover. Such a relationship may have been obscured by the crudeness of the nine-point cover estimate or by variation due to other factors, or it may indicate that the processes fostering *C. scoparius* germination in undisturbed plots are complex and not simply related to the overall coverage of the cryptogam layer. Mechanisms having to do with seed predation and stimulation of germination are not mutually exclusive, and may have interacted to produce the observed pattern. Seeds in moist, protected mossy sites may germinate earlier, removing them from the risk of predation. If seeds in disturbed sites remain dormant longer, they may increase their risk of predation.

There was a significant effect of seed number on seedling number, with all surface treatments showing a monotonic increase (Fig. 3.1); however, the ANOVA also revealed a significant interaction between surface treatment and seed number, suggesting differences in how fast seedling number increased (Table 3.1). The seedling/seed ratio illustrated density dependence with a decline across seed input levels from 100 to 1000/m^2 (Fig. 3.2). All treatments showed this decline, and although it appeared to be most pronounced in the control plots, the interaction term in the ANOVA was not significant. The movement of seeds among plots by ants could contribute to this pattern; however, it can not be wholly responsible for it, as can be shown by a simple example. Just focussing on the undisturbed plots, one can generate a summary germination rate across all seed densities, MEAN = 0.078. The null hypothesis is that all plots share this germination rate and that the estimated seedling/seed ratios were simply products of seed immigration and emigration. In order for the 1000-seed plots to show their 0.033 germination rate under a "true" rate of 0.078, approximately 58% of all seeds would have to be redistributed among the other plots. If ants were moving 58% of the seeds in the 1000- and 500-seed plots randomly into other plots, each control plot would be receiving on average 218 seeds. Under the null hypothesis, 0.078 of these should be germinating, yielding 17 seedlings. In actuality, controls among the undisturbed plots had a mean of only 2.6 seedlings, so it is extremely unlikely that the pattern of density dependence could be caused simply by ant dispersal. The mechanism for density dependence is not clear. Given the low densities of realized seedlings in the experiment (the maximum being 80/m^2), it seems unlikely that safe sites were saturated. In a separate experiment (see Chapter 2), I added 300 seeds to 25cm x 25cm metal exclosures covered with Tanglefoot$_{TM}$, and found up to 140 seedlings growing through September at a density of 2240 seedlings per square meter. Therefore it is possible that seed predation was again responsible for the pattern, with denser aggregations of seeds attracting more predators.

Unlike germination, survivorship of germinated seedlings did not vary significantly either among surface treatments or among seed input levels. The overall mean survivorship was 62.5% from March to August. This high survivorship (albeit overestimated somewhere between 5 and 10%) is rather remarkable given the hot, dry conditions in the Northwest during the summer months.

The burn treatments in this experiments were motivated by the common observation that control burning of *C. scoparius* populations often results in dense stands of seedlings (Mobley 1954). However, I found no evidence that burning increased the success of *C. scoparius* seeds to establish in intact (uninvaded) prairie. Burning did not result in higher numbers of seedlings than in control plots. This result argues against any mechanism of "nutrient release" or release from competitors. However, the comparison of seedling establishment in plots where the seeds were added before burning to that in plots where seeds were added after burning does show a positive effect of burning on seed germination itself (Fig. 3.2). Legumes are well known for their tough seed coat and long-lived seeds (Youngman 1951), and various rigorous treatments have been shown to stimulate germination in *C. scoparius* without killing the seeds: for example, alternate immersion in liquid nitrogen and boiling water (Bossard 1990). The temperature of a burn varies with many factors, including humidity and water content of the substrate, and, as I found, with fuel levels. The estimated temperature of the burn in each individual plot was positively associated with cover of the introduced grass *Agrostis tenuis* and negatively associated with cryptogam cover. Because germination appeared to respond most to intermediate temperatures (Fig. 3.3), however, it is not possible to posit either a positive or negative indirect effect of the introduced grass on *C. scoparius* invasion.

Management implications.

The message that undisturbed prairie is most favorable for *C. scoparius* establishment is discouraging for land managers in that reducing disturbance will not solve the invasion problem. At Fort Lewis, one of the environmental impacts of tracked vehicles (e.g., tanks) in training areas was considered to be the enhancement of *C. scoparius* spread; although tracked vehicles may increase spread by moving seeds over long-distances, they are not likely to be increasing the sucess of established spreading populations. However, if seed predators are primarily responsible for reduced seedling numbers in scalped plots then the response of *C. scoparius* populations to disturbance may be scale-dependent, and one should be careful when extrapolating these results to landscape-scale disturbances. Rather than reducing the density of *C. scoparius* seeds and consequently *C. scoparius* populations, large-scale community or soil disturbances may first reduce the density of seed predators, negating their positive effects.

The finding that disturbance is not driving *C. scoparius* invasion helps to eliminate some concerns, such as whether disturbance caused by the rare pocket gopher (*Thomomys mazama*) plays a role in establishment of the pest plant (E. Steinberg, pers. com.). The results of this experiment are consistent with observations I have made in the prairie demographic plots (Chapter 2), where I have marked and mapped all new seedlings and have rarely found seedlings in disturbances such as mole or gopher mounds.

It is important to keep in mind that these findings are specific to the cryptogam-dominated prairies of western Washington, and in particular, areas that are not already fully infested with *C. scoparius*. Bossard (1990) found at one site that germination increased when soil was turned over relative to controls, the opposite result from that found here. Sites dominated by strongly competitive, turf-forming grasses, such as the urban fields used in my demography plots (Chapter 2), might be expected to show a more positive effect of soil disturbance or removal of surrounding vegetation. However, these rare and sensitive prairie ecosystems appear to be unfortunately well-suited to assisting the invasion of *C. scoparius*.

Where it is logistically possible, burning has become more and more prevalent as a control measure for *C. scoparius*. This experiment showed that burning does not make prairies more "invasible"--rather, seedlings are less likely to establish in burned plots than in undisturbed plots. However, burning does have a direct effect on seeds by stimulating germination. Although this effect on germination can result in thick monocultures of plants for the unwary manager (Don Varecamp, pers. com.), burning can also be used as a tool to flush out the seed bank and reduce the number of years of follow-up needed to eradicate a population.

Table 3.1. Analysis of variance on the total number of germinated seedlings per square meter plot, with surface treatment and seed number input as main effects.

Source	DF	Sum of Squares	F-value	P-value
Surface Treatment	3	3969.0	23.0	<0.0001
Seed Number	4	4673.6	20.3	<0.0001
Surface * Seed	12	3356.2	4.9	<0.0001
Residual	140	8052.2		

Table 3.2. Analysis of variance of seedling survival from March to August with surface treatment and seed number input as main effects.

Source	DF	Sum of Squares	F-value	P-value
Surface Treatment	3	0.093	0.287	0.83
Seed Number	4	0.211	0.485	0.75
Surface * Seed	12	0.935	0.718	0.73
Residual	140	10.64		

Table 3.3. Analysis of variance of the final number of seedlings remaining in August, with surface treatment and seed number input as main effects.

Source	DF	Sum of Squares	F-value	P-value
Surface Treatment	3	1435	21.9	0.0001
Seed Number	4	1663	19.0	0.0001
Surface * Seed	12	1280	4.9	0.0001
Residual	140	3055		

Table 3.4. Analysis of variance on the number of seeds germinating per square-meter plot, in plots of different temperatures (estimated *a posteriori*).

Source	DF	Sum of Squares	F-value	P-value
Temperature	3	228.4	2.22	0.094
Timing of burn	1	138.4	4.03	0.048
Temp * Timing	3	101.1	0.98	0.406
Residual	70	2403.5		

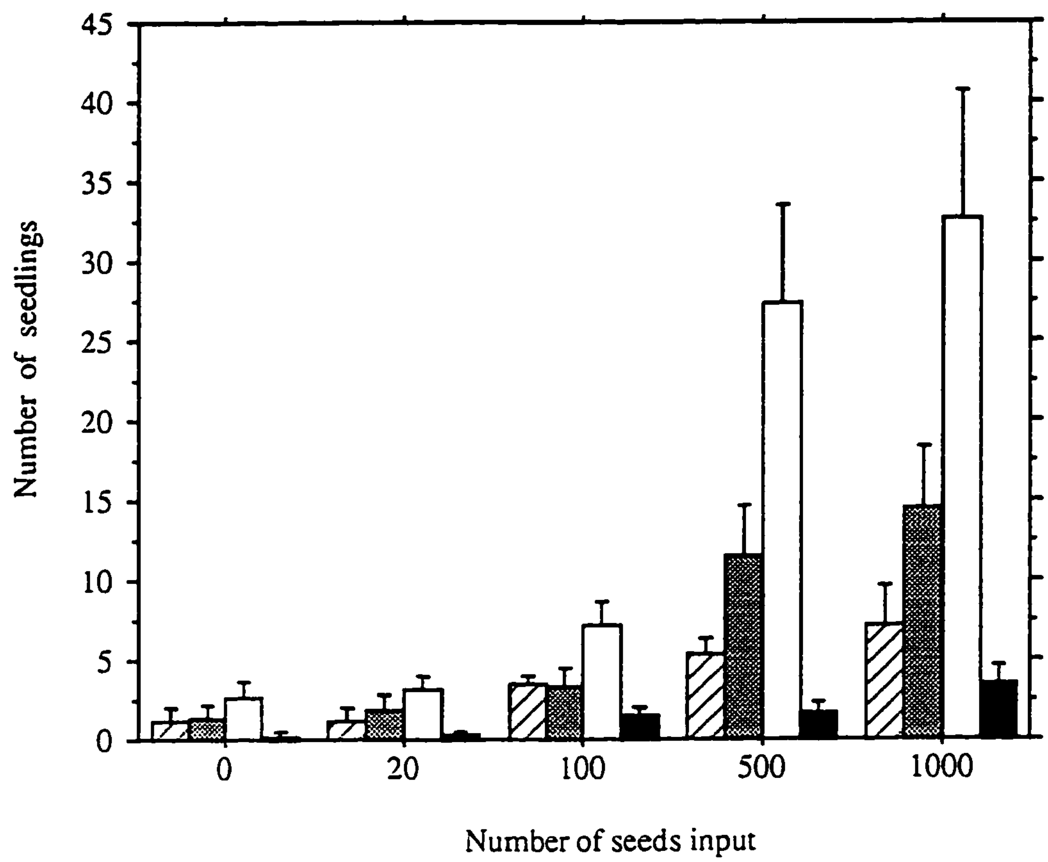


Figure 3.1. Total number of seedlings germinating in each square meter plot as a function of seed input (0, 20, 100, 500, 1000) and surface treatment. Open bars = control (undisturbed), black bars = cryptogam layer scraped off, striped bars = burned with seeds added after (unscarified), gray bars = burned with seeds added before burning (scarified).

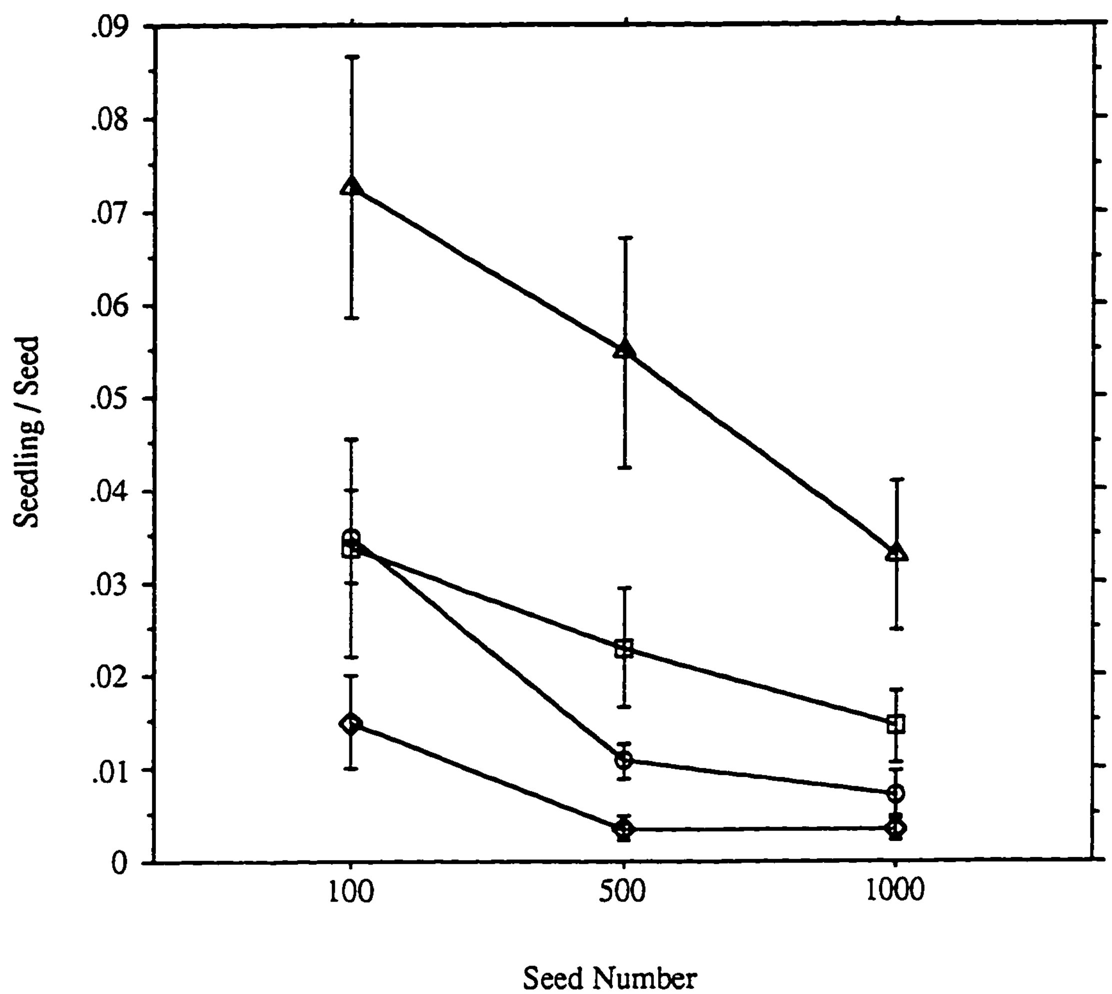


Figure. 3.2. The number of seedlings germinating per seed number at different levels of seed inputs (100, 500, 1000 seeds), for four surface treatments. Triangles = control, squares = burned with seeds added before, circles = burned with seeds added after, diamonds = removal of the cryptogam layer.

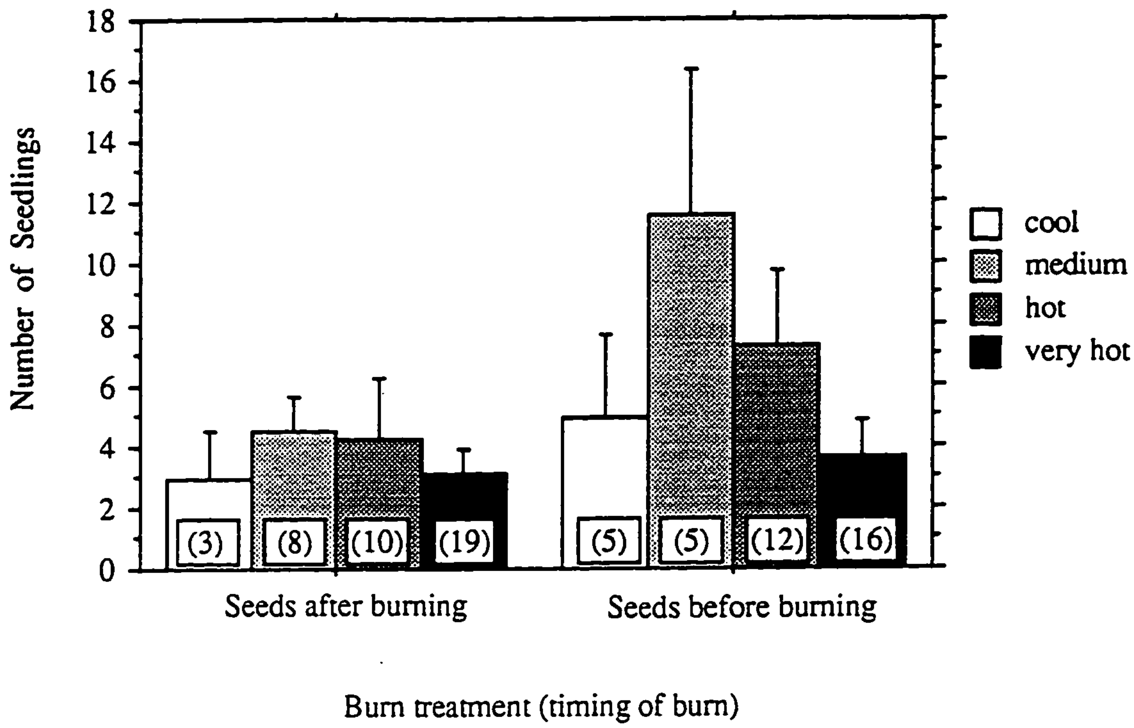


Figure 3.3. Number of seedlings arising from burns of different temperatures, split by two treatments: seeds added before burning (scarified), and seeds added after burning (unscarified). Burn temperatures were estimated visually *a posteriori*, based on color and appearance of the plots. Numbers in parenthesis are the number of plots in each temperature category.

CHAPTER FOUR:
DISPERSAL AND RATES OF SPREAD IN *C. SCOPARIUS*, A MODELLING APPROACH

INTRODUCTION TO CHAPTER FOUR

The rate of spread of a population is a function of two processes: an increase in population numbers, and a simultaneous increase in the amount of area covered by the population. The former is described by demographic rates, and the latter is dominated by dispersal.

Invasion theory and range expansion

The mathematical theory exploring invasion biology has a rich history, and it has recently seen a resurgence of interest. Fisher (1937) developed the initial invasion model to describe the spread of an advantageous gene in a population; he used "reaction-diffusion" equations, coupling a growth term with simple diffusion to describe the spatial movement of alleles. Skellam (1951) adapted a mathematically identical model to the movement of organisms across a landscape, and used it to analyze the spread of muskrats in Europe. The form of the model, in one dimension, is:

$$(1) \qquad \partial N/\partial t = rN\,(1 - N/K) + D\,\partial^2 N/\partial x^2 .$$

where N is the population size, K is the carrying capacity of the environment, D is a constant dispersal rate, and r is the intrinsic rate of increase. One basic result from Fisher-type models is that a constant speed of invasion (a "travelling wave") is ultimately attained, with that speed (c) given by the expression

$$(2) \qquad c = 2\sqrt{(rD)}$$

(Fisher 1937). When this model is expanded to two dimensions, waves still form and expand, but there is no rigorous travelling wave solution. Rather, the wave speed is slower at first and accelerates to an asymptotic speed, which is given by the one-dimensional travelling wave speed in (2).

Since the pioneering work of Fisher and Skellam, models of invasion have become increasingly realistic and complex (Kareiva 1990, Goldwasser et al. 1994, Holmes et al. 1994). For example, some have looked at the behavior of invading populations that show Allee effects (Lewis 1993, Kot, in press #208), directed as opposed to random (diffusive) dispersal (Holmes 1993), and density-dependent dispersal (Pablo and Vasquez 1991). While the theory has advanced rapidly, so have studies analyzing empirical records of spread. Most simply, these studies use observed range expansion rates to fit Skellam's model; this has been done for the European starling, English sparrow, and house finch (Okubo 1988), the collared turtle dove (Hengeveld 1989), the Himalayan thar (Caughley 1970), California sea otter (Lubina and Levin 1988), cholla (Allen et al. 1991), and *Mimosa pigra* (Londsdale 1993). The calculated rate of spread was used in some cases to gain insights into processes that may not be amenable to direct empirical study. For example, Caughley (1970) asked whether the spread of the Himalayan thar could have been explained by random dispersal or was more likely driven by population pressure. Lubina and Levin (1988) evaluated the relative importance of behavior and mortality in the spread of the sea otter. Londsdale (1993) quantified the role of dispersal by water in the invasion of *Mimosa pigra*, a floodplain weed.

Others have used direct data on demography and dispersal to make independent estimates of predicted rates of spread, and then compared these estimates to observed rates. Such a comparison has been made for organisms as diverse as Grey squirrels (Okubo et al. 1989), cereal leaf beetles (Andow et al. 1990), and neolithic farmers (Ammerman and Cavalli-Sforza 1984). The results in the majority of cases correspond rather well--surprisingly well when one considers the level of variation that might be expected in demographic and dispersal parameters, and the level of simplicity in the models. In one case, Andow (1990, 1993) found that the predicted rate of spread for the cereal leaf beetle were much slower than the observed rate of spread. From this incongruency they concluded that long-distance dispersal events that were not included in the model must be important in this system.

Two recent theoretical advances are particularly pertinent to the study of ecological range expansion. First, the differential equations of the model above (equation 1) have two flaws for the study of plant populations. First, they are continuous in time and therefore do not apply very well to organisms with discrete seasonal growth and pulse reproduction and a distinguishable dispersal phase. In contrast, integro-difference equations were developed to model time as discrete and the population growth phase as separate from the dispersal phase (Weinberger 1978, Kot and Schaffer 1986, Hardin et al. 1990, Kot 1992). These models have generated a whole new set of predictions and results having to do with invasion rates and patterns (e.g., Kot and Schaffer 1985, Kot 1992, Neubert 1994).

Second, it has been shown using the basic Fisher equation, that the distribution of dispersal distances (as opposed to just the mean) can have profound effects on the velocity of the wave front, with occasional long-distance propagules contributing disproportionately to increasing the speed of invasion (Goldwasser et al. 1994, Cook in review). Earlier simulation models have suggested similar results (Auld and Coote 1980, Moody and Mack 1988, Hengeveld 1989). The significance of this work is that it suggests that the details of dispersal can be extremely important in the process of invasion.

Quantifying the details of dispersal in an invasive exotic plant

Dispersal can occur on two scales, regional and local. The first determines the frequency of founder events, or how often new populations are formed and sites are colonized. Simulations have suggested that in terms of regional spread, the distribution and frequency of founder events may dominate the spread of an invader at the landscape scale (Auld and Coote 1980, Moody and Mack 1988). These founder events in the spread of weeds are most likely to be controlled by patterns of human transportation and commerce (Forcella and Harvey 1988). Because of the extreme difficulty involved in observing low-probability and long-distance processes, we know almost nothing about the details of these occurrences--their frequency or the causes of their success or failure (Silvertown 1991).

On the local scale, the result from theoretical work that the outer limits of the dispersal distribution are important still holds. However, the processes contributing to variation in dispersal are probably quite different at this scale, and unlike the colonization events discussed above may be quite independent of human dispersal agents (e.g. (Londsdale 1993). The invasive shrub that forms the focus of this dissertation, *Cytisus scoparius*, has two forms of local dispersal: ballistic dispersal and ants.

Local dispersal has long been viewed as influencing plant fitness by removing seeds from close contact with both the parent plant and siblings and therefore from high concentrations of seed predators (Janzen 1970, Connell 1971, Howe and Smallwood 1982), reviewed in (Dirzo and Domínguez 1986). Explosive or ballistic dehiscence specifically has been suggested as a strategy for avoiding seed predation, because it removes a large proportion of the seeds away from the parent plant (Janzen 1969, Beattie and Lyons 1975). Ballistic dispersal occurs in at least 23 plant families, is represented among a wide diversity of plant guilds (annuals and perennials, herbs, shrubs and trees), and is found in all kinds of habitats (Stamp and Lucas 1983). The ballistic propulsion of seeds is an interesting biomechanical problem and has received some theoretical attention (Beer and Swaine 1977, Swaine and Beer 1977). It has also drawn the attention of applied mathematicians (Neubert 1994), because it often leads to interesting probability density functions that have a maximum some distance away from the center (Stamp and Lucas 1983, Carey and Watkinson 1993). Ballistic dispersal is also often coupled with secondary dispersal mechanisms such as water (e.g., Impatiens capensis) or ants (e.g., *Crotalaria rotundifolia*, (Stamp and Lucas 1990)).

Mutualistic interactions in which plants exploit animals for seed dispersal are extremely common (Estrada and Fleming 1986), and more than 3000 plant species in 60 families are specialized to use ants as dispersal agents (Handel and Beattie 1990). The seeds of ant-dispersed plants are attached to specialized structures called eliasomes, which contain nutrients such as fats and fatty acids (Beattie 1985). It is most often carnivorous ants, not seed-harvesting species, that perform this benefit for the plant, and eliasomes may contain chemical attractants that mimic animal tissue or elicit corpse-carrying behavior (ref). Ant-dispersal is thought to benefit the plant by ensuring germination under improved conditions (safe-site effect) and/or by increasing the distance from the parent. Some have found large safe-site effects of ant dispersal (Hanzawa et al. 1988, Hughes and Westoby 1992), while others have not (Heithaus 1986, Rice and Westoby 1986). Depending on the distribution of safe sites, the simple distance effect of dispersal can represent a benefit to the plant even if ant nests themselves do not provide safe sites (Green 1983, Andersen 1988). As emphasized above, during a range expansion dispersal itself is a key element of population dynamics, making invasive species a special case in which the importance of dispersal mechanisms is heightened.

This chapter is divided into two parts. The first describes a series of empirical studies designed to quantify both the frequency of long-distance founder events and the local dispersal distribution, decomposing the latter into the relative contributions of ballistic dispersal and ant dispersal. Each experiment or study is described with methods, results, and a brief discussion. The second part of the chapter incorporates information on dispersal with demographic data in a modelling approach that is the discrete-space simulation analog of integro-difference equations. The model structure is described in detail, and then results from the models are presented and discussed.

PART I. DISPERSAL

1) THE FREQUENCY OF LONG-DISTANCE DISPERSAL EVENTS.

Although theory and common sense argue for their importance, long-distance dispersal events are extremely difficult to quantify and predict (Silvertown 1991), especially in areas where the study species is already established. I took advantage of an ecological "clean slate" in the form of the volcanic eruption of Mount St. Helens to get a rough estimate of the frequency of colonization and establishment of new *C. scoparius* populations along roadways.

Methods.

Mount St. Helens erupted in May of 1980, leaving behind a blast zone and blow-down zone in which nearly all plant life was killed and buried in ash. A 16-mile, one-lane road (Rte. 26) was built on the east side of the volcano, ending above Spirit Lake at Windy Ridge, and was opened to tourists in 1984. *C. scoparius* had been observed colonizing along the road, although it was not yet a common plant on the volcano.

On September 8, 1995, I mapped every patch of Scotch broom along the road to Windy Ridge to the nearest tenth of a mile. When the patch consisted of just a few individuals, I collected every individual; for large patches, I collected a sample of the largest and oldest-looking individuals. I cut them down and used loppers or a handsaw to extract a segment of the main stem, including the top of the root. I sanded the cross-section using a belt sander with 220 grit sandpaper and then consecutively finer grit sandpaper by hand, finishing with 600-1000 grit. I estimated the age of each plant by counting the growth rings under a dissecting microscope. Assuming that plants would not flower and reproduce until three years old (Parker, pers. obs.), I could then estimate the *minimum* number of independent founder events caused by long-distance (from off the mountain) dispersal.

Results and Discussion.

I found eight patches of Scotch broom along the road to Windy Ridge (Fig.4.1). The oldest plant was 10 years old and was located at mile 14.2. This plant could not give rise to any new patches seven years or older; under this assumption, there were at least six separate colonizations (mile points: 9.1, 9.6, 10.0, 12.4, 14.2, 14.5). The remaining two patches (mile points: 10.6, 14.6) were six years old and very probably also independent colonizations.

The age structure of three of the patches (mile points 9.1, 10.0, and 14.2) followed a pattern one would expect if one founder plant had given rise to all other plants in the patch. In the other five patches, from four to more than a dozen separate individuals must have been introduced as seed simultaneously, because no single plant could have been the parent of the others. This pattern suggests that seeds are often dispersed in groups, as opposed to singly, along roadways.

One possible mechanism for this pattern of *C. scoparius* colonization is that the seeds could have been brought in originally during the road construction itself, with "dirty gravel" taken from *C. scoparius*-infested gravel pits. If this is primarily the agent of dispersal, then the frequency of long-distance dispersal due simply to ordinary vehicle traffic might be considerably lower than presented here. One piece of evidence for a large "pulse" of founding events is that all eight patches were six years or older, whereas if vehicle traffic were solely responsible for dispersal at this scale one would expect an even distribution of patch ages. However, the1990 paving of Rte. 99, a two-lane road parallel to Rte. 26, may also have reduced the frequency of tourist-vectored colonization. Because of the potential importance of individual founding events, the use of dirty gravel in road building may have been extremely important in the historical spread of *C. scoparius* across western Washington.

2) BALLISTIC DISPERSAL.

The initial form of dispersal in *C. scoparius* is explosive dehiscence from the pods (ballistic). The "explosion" is made possible by perpendicular fibers in the fruit, which dry and finally cause the fruit to split open rapidly in a twisting motion. The force of the fruit popping open thrusts the seeds out away from the plant. Ballistic dispersal is a fairly common form of dispersal in plants (Stamp and Lucas 1983).

Methods.

In order to characterize the dispersal distribution of *C. scoparius* seeds due to ballistic dispersal, I chose an isolated individual more than 20m from any other adult plant. In the early morning, I rolled out a 1m-wide and 8m-long plastic sheet marked off in 50cm segments from the base of the target plant. A 10cm edge around each segment was painted with Tanglefoot$_{TM}$ to catch any seeds that rolled after landing on the sheet. At the end of the day, I counted the number of seeds in each distance segment. I replicated the study 8 times with different plants, locations, and compass directions. I pooled the replicates to give one summary distribution. The data were analyzed by first translating from the rectangular segments to an estimate of total seeds landing in each annulus, using the equation:

$$\frac{\text{total \# seeds landing in annulus}}{\text{between x and x+ 0.5 meters}} = \frac{\text{\# in segment}}{0.5\ m^2} \times \frac{\pi\ [(x+0.5)^2 - x^2]\ m^2}{\text{annulus}}$$

These numbers were then again adjusted to obtain the probability density function (Silverman 1986) for ballistic dispersal. A curve was fitted to the data assuming an underlying gamma distribution (Hastings and Peacock 1974),

$$y = \beta\, e^{(-\beta x)} * (\beta x)^{(\alpha - 1)}$$

and the parameters of that curve were determined by minimizing the overall Chi-Square value using a routine written in Excel 5.0.

Results.

In the eight replicates, I recovered a total of 618 seeds, with individual replicates varying from 16 to 231 seeds (Fig. 4.2). The maximum distance travelled was between 5.5m and 6.0m, and the mean calculated directly from the data was 1.08m, std = 1.10.

The probability distribution did not fall monotonically but peaked between 0.5 and 1.0 meters (Fig. 4.3). When fitted with a gamma distribution, alpha = 1.88 and beta = 0.78 ($\chi^2 = 0.071$), and the expected value and variance of the distribution, respectively, were 2.40 and 3.08. Alpha controls whether or not the distribution has a "hump" in the middle, while beta controls the steepness of the curve. For alpha equal to one the gamma distribution collapses to an exponential distribution. The alpha of 1.88 found here shows that the curve is considerably different from exponential, peaking away from the center point of release. The fit curve overestimates the mean generated directly from the (discontinous) data; this is because the tail of the fit distribution is much longer than that for the true distribution. Ballistic dispersal in *C. scoparius* shows a very short and abrupt tail, a pattern that is consistent with other ballistically-dispersed plants (Stamp and Lucas 1983).

The maximum and average found from the direct measurement correspond well with those found for *C. scoparius* in California (Bossard 1991). Bossard calculated an average distance of 0.96m and a maximum of 5.4m. This suggests that the biomechanics of seed pod dehiscence are constant from place to place. Beer and Swaine (Beer and Swaine 1977, Swaine and Beer 1977) coupled a theoretical exploration of ballistic dispersal with an empirical study of dehiscence in *Hura crepitans*, a woody euphorb, and concluded that the orientation of the fruits on a plant was a very important factor in determining dispersal distance. They also found that plant height was not an important factor (Beer and Swaine 1977). That height contributes little to dispersal distance has consequences for the invasion biology of *C. scoparius*; the dispersal distribution of individual plants due to ballistic dispersal should be fairly constant across adult stage classes. What will not remain constant, however, is the mean dispersal distribution across stages of invasion, as increased plant density should result in the increased interference of branches etc., decreasing the mean dispersal distance. Because dispersal is only critical to the invasion process at the edge of the front, however, this change with density should not have a biologically imporant effect.

3) RELATIVE CONTRIBUTION OF BALLISTIC DISPERSAL AND ANT DISPERSAL TO THE DISTRIBUTION OF SEEDLINGS.

Scotch broom seeds have eliasomes which are attractive to ants. In California, Bossard (Bossard 1990) found that ants carried the seeds at one site 96cm on average (maximum = 5.25m). Using a similar technique, B. Semsrott (unpublished data) studied the ant-dispersal of 50 broom seeds at one urban site (Magnuson Park) and one prairie site (Thirteenth Division Prairie) in western Washington. At Magnuson Park, most dispersal was accomplished by *Myrmica incompleta*, with a mean distance of 79cm (n = 32). At 13th Division Prairie, *Aphaenogaster occidentalis* carried most of the seeds, with a mean distance of 93cm (n = 29). Although the means of these two distributions are quite similar, their shapes were very different. At Magnuson Park, the great majority of seeds had their eliasomes removed and were left at the original release site, while a few seeds were carried a long distance (maximum distance = 4.65m). In contrast, most of the seeds at 13th Division Prairie were carried an intermediate distance, creating an almost normal distribution around the mean (maximum = 1.70m).

These studies showed that ant behavior can vary in different locations, and could potentially have a large effect on the local dispersion of the next generation of Scotch broom seedlings. I designed an experiment to decompose the contributions of two dispersal mechanisms, ballistic dispersal and ant dispersal, to the distribution of seedlings in the following year.

Methods.

This experiment was performed in the Fort Lewis Artillery Impact Area, a prairie used for artillery practice, which as a result of bombing during the dry summer months burns nearly every year (J. Reasoner, pers. comm.). Because of the frequent burning there is no viable population of Scotch broom inside the Artillery Impact Area (although there is a large population across the road). Each replicate of the experiment consisted of three randomly-assigned, 10m-radius circles: one control, one "plant" circle, and one "ant" circle. For each plant circle I collected a large adult plant with mature fruits from across the road, counted the fruits, counted the number of seeds in a subsample of fruits, and lashed the plant to rebar using plastic cable ties. I estimated the total number of seeds produced by each plant, then placed that number of previously-collected seeds in a pile at the center of each "ant" circle. Six replicates were set up on 7/28/93, and four more replicates, with two extra "plant" circles, on 8/7/94.

The following spring, I searched the 314m^2 of each circle intensively for seedlings, measuring the distance of each from the center of the circle. For the first round of replicates, I performed two censuses where I marked seedlings, 4/25/94 and 6/22/94, and then I mapped all seedlings on 8/3/94. For the second round of replicates, I marked and mapped all seedlings from 4/30 to 5/14/95, and censused a second time from 6/10 to 6/23/95.

As above, a curve was fitted to the data assuming an underlying gamma distribution (Hastings and Peacock 1974), and the parameters of that curve were determined by minimizing the overall Chi-Square value using a routine written in Excel 5.0.

Results and Discussion.

The number of seedlings recovered per circle varied from 7 to 101 (Table 4.1). The overall germination rate was 3.2% for ant replicates, and 3.6% for plant replicates, falling nicely within the range of prairie germination rates presented in Chapter 2. The germination rates for individual replicates ranged from 1% to 14%. Germination rate did not differ between ant and plant replicates (Mann-Whitney U test, $N = 22$, $Z = 0.165$, $p = 0.87$). Control circles produced no seedlings.

The mean distance travelled, calculated directly from the data, ranged from 9.8cm to 161.3cm in ant replicates (Table 4.1, Fig. 4.4) and from 70.4cm to 226.9cm in plant replicates (Table 4.1, Fig. 4.5). The mean of the mean distances for ant replicates was 79.0 (SD = 61.7, Max = 760cm) , while the mean for plant replicates was 153.3 (SD = 40.5, Max = 955cm). The mean distance for plants was significantly greater than that for ants (Mann-Whitney U, $N = 22$, $Z = 2.44$, $P = 0.015$). The mean of the means is higher than the mean of the composite distribution (all seedlings pooled within a treatment), which was 92.6 (SD = 125.1) for the ant treatment and 155.2 (SD = 105.1) for the plant treatment (Fig. 4.6, Fig. 4.7).

The gamma distribution is well-suited to fitting the data for both ant and plant treatments, as it can produce either a monotonic dropoff or a "humped" distribution, depending on the value of alpha (see above). I fit the composite distributions to gamma functions using the Chi-Square criterion. For the ant treatment, alpha = 0.323 and beta = 0.418 ($\chi^2 = 0.120$) (Fig. 4.6), and the expected value and variance of the fit distribution were 0.77 and 1.84, respectively. For the plant treatment, alpha = 1.84 and beta = 1.05 ($\chi^2 = 0.072$) (Fig. 4.7), and the expected value and variance were 1.75 and 1.66, respectively.

When one tries to synthesize the results of the ballistic dispersal study with the results of this experiment, there are both satisfying consistencies and puzzling inconsistencies. First, it is clear that the general shape of the distribution caused by the ballistic dispersal (Fig. 4.3) also dominates the shape of the distribution of seedlings in the experimental plant plots, where both ballistic and ant dispersal contribute to the distribution (Fig. 4.7). In addition, the maximum dispersal distance in the plant plots (955cm) is considerably greater than that for either ballistic dispersal (575cm) or ant dispersal (760cm) alone. However, the mean dispersal distance for the seeds in the first study (240cm) is actually greater than that for the composite "ballistic + ants" plant experiment (153cm), which is not what one would expect. Because on average ants should be moving seeds in all directions without specific reference to the placement of the plant, the mean would not be expected to change although the variance might increase. One explanation for a smaller mean dispersal in the second study is that seeds beyond 1.5 m might experience proportionally greater mortality, through predation or disease, than seeds close to the source. This pattern is the reverse of what we would predict based on the theory that either proximity to the parent plant or negative density-dependence should increase the establishment rates of plants dispersing farther (Connell 1971, Janzen 1971, Howe and Smallwood 1982). In this experimental system, there is no natural "parent environment" to act as an attractant or source of natural enemies, but sibling density effects might still be expected (Dirzo and Domínguez 1986). Perhaps rather than being disproportionately damaging to high densities of seeds or seedlings, predators are satiated on a fine scale, leading to a greater establishment rate at higher densities (Augspurger and Kitajima 1992, Burkey 1994). A second explanation for the contrast between the two distributions is that the reduced dispersal distance in the second case is an artifact of the experimental design. Although fruits were fully mature when the plants were placed in the field, the removal of the plant from its root base may have changed the turgor pressure in the fruits and consequently the force of the exploding pod. Alternatively, the plants may have been "sagging" more than normal, thereby changing the angle of presentation of the fruit, which would also have reduced the average distance travelled by the seed.

One aspect of the biology of ant dispersal is not captured very well by using any continuous distribution like the gamma distribution to fit the data. Not only is there a great deal of spatial variation in how many seeds are moved and how far they go, but because of the behavior of ants and the placement of ant nests (Semsrott, unpublished data), ant dispersal results in occasional long-distance jumps--often of not just one seed, but several in close proximity. This commonly results in a discontinuous distribution for individual replicates, even those with large sample sizes (Fig. 4.4). Therefore, although the great majority of seeds remain within a meter and a half of the release point and ant dispersal would not seem to change the main part of the dispersal distribution by very much (e.g., compare Fig. 4.3 and Fig. 4.7), ants can move seeds or groups of seeds out to isolated points in the tail of the distribution. The primary effect of ants, then, may reside in these discontinuous jumps.

PART II. CONSTRUCTION AND RESULTS OF A SPATIAL MODEL

Model Structure.

The models of spatial spread of *C. scoparius* are discrete-space simulations based on the concept of integro-difference equations (Kot and Schaffer 1986, Kot 1992, Neubert 1994), which couple discrete-time population dynamics with a discrete dispersal phase. Such a model is appropriate for plants such as *C. scoparius* which have fairly discrete generations in the form of growing seasons, at the end of which propagules are produced and dispersed. The simulations had the form of cellular automata models, which are defined by a regular lattice of cells or bins each of which has a "state" that is determined by local rules consistent for all cells (Wolfram 1983, Wolfram 1984). The state of cells in a lattice are often described as "occupied", or "unoccupied", or perhaps contain a density. However, it is also possible to include stage structure in such models. Cellular automata models have become a popular tool for modelling a variety of processes in plant population biology, including clonal growth (Inghe 1989), plant competition (Weiner and Conte 1981, Crawley and May 1987, Czárán 1989, Silvertown et al. 1992), and succession (Hogeweg et al. 1985, van Tongeren and Prentice 1986, Czárán and Bartha 1989). Auld and Coote (1980) used cellular automata models to investigate the spread of a weeds from farm to farm. Their model had a simple expression for density within farms, three population growth rates, and three categories of "mobility": 10% of seeds dispersing 5 farms away, 5% of seeds dispersing 3 farms away, and 1% of seeds dispersing 1 farm away. They found that increasing population growth increased the effect of "mobility" on spread, but increasing mobility decreased the effect of population growth on spread. They did not however separate the effect of distance from that of the proportion of dispersers.

I incorporated stage structure by translating the demographic transitions (Chapter 2) directly into recursion equations describing the density of individuals in each stage at time t as a function of the density of individuals in all stages at time t-1 (Table 4.2). For logistic and computational reasons I simplified the 7x7 matrix used in Chapter 2 to a 4x4 matrix with seeds, seedlings, juveniles, and adults. The two types of matrices differed in lambda from -4.6% to 12.9%, but the rank ordering of the populations and years was identical except for one case (Table 4.3). Fractional individuals were allowed in this model, so that rather than probabilities of plants growing from one stage to another, transitions were simply multipliers representing the average demographic change.

I simulated a prairie or field as a grid of $1m^2$ "bins" each of which held a density of plants of each stage class. At each time step, the production of new adults, juveniles, seedlings and seeds was calculated for each bin, then the seeds were redistributed among neighboring bins with a dispersal function. The construction of neighborhoods in cellular automata models can have a large effect on the outcome (Holmes 1995). Three common methods are 1) to have hexagonal bins, 2) to use a single distance for all eight neighbors touching a focal bin, or 3) to use one distance for the four bins sharing a side with the focal bin and a greater distance for the four bins sharing only a corner point with the focal bin. All of these methods had important disadvantages, and I therefore chose a different method using concentric circles drawn around the focal bin. Each circle carved out an annulus of one bin width, and I counted a bin as within that annulus if it fit within the annulus or spanned that annulus and the previous one (Fig. 4.8). Every time seeds were redistributed, the surrounding bins were assigned a distance based on which annulus they were in relative to the dispersing bin. Then the number of seeds going that distance was divided by the number of bins in the annulus, and that number was placed in each bin. Again fractional numbers of seeds were allowed in the model, so seeds were distributed evenly and continuously across bins.

The dispersal curves used for this redistribution function were the probability density functions generated from the field studies described above. I used the actual data for "explode", "ant", and "plant" distributions. Because the "home bin" should receive all the seeds travelling between 0 and 0.5 m (not 0 and 1), distributions were recalculated to reflect this arrangement (bins equal to 0-0.5, 0.5-1.5, 1.5-2.5, etc.). The edges of the lattice had absorbing boundaries--that is, the lattice was modelled as a field or prairie surrounded by uninhabitable land, such as forest, agricultural field, or asphalt.

Density-dependence was included in this model to preclude the "explosion" of the population from the center out. That is, if biologically unrealistic densities are allowed to develop in the bins that are filled early on, those bins will dominate the dynamics of the entire lattice by flooding it with seeds. The density-dependence in this model is very simple, yet tied to the biology of *C. scoparius*. Individuals in each bin are allowed to survive and grow according to the recursion equations until the number of adults reached a certain maximum level, after which the densities of seedlings, juveniles, and adults are constrained to stay below their set limits. Seeds, however, continue increasing in the seed bank indefinitely. Density-dependence in the model was controlled solely by adult plants because it was adult density or biomass that best represented the progression of invasions in the field (Chapter 2). The maximum number of adults per bin was set at 5 m^{-2}, close to the average number of adults found in the late invasion-stage plots at both Discovery Park and Johnson Prairie.

The output of the model was the change in the number of bins occupied over time. I kept track of several different measures of occupancy, or stage-specific plant density per bin: greater than zero seedlings, greater than one seedling, greater than one juvenile, greater than zero adults, greater than one adult, five adults (saturated). For each of these "counters", I kept track of the number of bins "filled" at each time step. From this I could calculate 1) the time to reach each of a series of critical points in areal extent (time to $1000m^2$, time to $5000m^2$, etc., see Fig. 4.9), and 2) the rate of spread, defined as the increase in the square root of the filled area over time (Fig. 4.9). Counters of greater than one (as opposed to those greater than zero) had an initial lag time while the number of filled bins stayed at zero (Fig. 4.9). In addition, as the lattice became filled and plants reached the edge, the rate decreased because some of the seeds were being dispersed off the lattice and there were no new bins to reach. I did not include either the initial or the final phase of spread in my calculation of the rate. The lag time was quantified, however, in T100, the time to fill 1% of the area of the lattice.

I used the model to investigate the relative importance of dispersal and demography under three scenarios: 1) spread from a single founder, contrasting the three empirically-derived dispersal distributions, 2) spread from a single founder, varying the proportion of long-distance propagules, and 3) spread from varying spatial arrangements of founders. In each case I submitted the results of the model to a series of statistical tests.

1) Spread of populations from one initial founder: variation in dispersal *vs.* demography.

The grid was set as empty except for one adult plant (the "founder") in the center bin. I simulated the spread of all six populations, with two different transition years for Discovery Park and Johnson Prairie, giving eight different sets of demographic parameters: four for prairies and four for urban fields. Each set of demographic parameters was run for the three different dispersal distributions, giving a total of 24 runs.

The conclusions drawn from the model depend on the "counter" used. Because fractional individuals were allowed, bins could be "filled" with seedlings >0 at infinitesimally small densities. Therefore these >0 measures were entirely driven by the dispersal distribution. The result is a pattern in which a whole set of bins are "filled", then three years pass in order for plants to grow to seed-producing adults, and then a second whole tier of bins are instantaneously filled (Fig. 4.9). Because of the artificiality of these measures, I do not emphasize them here. However, they do illustrate that where dispersal is the only process driving spread, ballistic dispersal results in the slowest spread, ant dispersal is the next-slowest, and ballistic + ant ("plant") dispersal results in the most rapid spread. What is interesting about this result is that it does not follow from the relative means of the three dispersal distributions, which increase from ant, then ballistic, finally to ballistic + ant (Fig. 4.6, Fig. 4.3, Fig. 4.7). Rather, the maximum distance of the three distributions is the important factor, once again illustrating the critical nature of the tails of dispersal distributions in invasion studies.

When a more biologically reasonable measure is used, such as >1 adult, the patterns become more complicated and more tied to demography. The four measures like this used, >1 seedling, >1 juvenile, >1 adult, and Max Adult, all produced identical results separated only by a matter of a few years (Fig. 4.10). I will focus only on Max Adult, which can be readily interpreted as the conversion of open prairie or field into closed *C. scoparius* thicket.

Prairie populations filled up space faster than urban populations (Table 4.4). The difference between prairie and urban was significant at all four critical times (ANOVA, $n = 24$, $DF = 1$: for T100, $F = 60.8$, $P < 0.0001$; for T500, $F = 66.6$, $P < 0.0001$; for T1000, $F = 68.3$, $P < 0.0001$; for T5000, $F = 72.5$, $P < 0.0001$). These same ANOVA's revealed no significant effect of dispersal type (F values = 0.16, 0.47, 0.49, 0.51, for T100, T500, T1000, T5000, respectively, all $P > 0.60$).

Similarly, the rate of spread (of "saturated" bins) was significantly higher for prairie populations (Fig. 4.11, ANOVA, $F = 96.0$, $P < 0.0001$). The ranking of the three dispersal types changes between prairie and urban. Ballistic dispersal consistently resulted in the fastest spread in urban populations, while ballistic + ants resulted in the fastest spread in prairie populations.

With only one mode of dispersal included, the regression of spread rate on lambda was significant (Fig. 4.12, $r^2 = 0.89$, $P = 0.0003$). Perhaps more interesting than the existence of the significant relationship is the fact that there is scatter about the line. I correlated the residuals of the regression with different individual life history transitions to see if there was one phase of the life cycle that might be responsible for this variation in spread rate, but found no significant correlations (Table 4.5). The largest values of r were 0.596 ($P = 0.12$) and 0.498 ($P = 0.22$) for juvenile survivorship and adult fecundity, respectively. I also correlated individual transitions with spread rate itself (Table 4.5), and found significant correlations for juvenile fecundity (positive), adult survivorship (positive), and dormancy (negative). One should be particularly careful not to equate correlation with causation here; these transition probabilities are simply ones that are consistently larger (or smaller) in the faster growing populations.

The main result from this use of the model is that the addition of the dispersal tail by ants, and more generally, the contrast among dispersal distributions that are quite different in both mean and shape, has little effect on the rate of spread relative to the large differences in demographic parameters among habitats.

2) Spread of populations from one initial founder: variation in the proportion of long-distance propagules.

To move away from the specifics of a single experiment, I asked more generally how varying the proportion of seeds going relatively longer-distances (presumably due to ants) might affect rates of spread. I was also interested in the potential of ant-behavior to create new, randomly-located points of high concentration of seeds or seedlings that might act as local scale "foci" for invasion (Moody and Mack 1988).

The grid was set as empty except for one adult plant (the "founder") in the center bin. Again I simulated the spread of all six populations, but included only 1994-95 runs for Johnson Prairie and Discovery Park. Instead of using the three empirical dispersal distributions, I systematically varied the proportion of seeds being taken by "ants" beyond the reach of ballistic dispersal. First seeds were redistributed according to the ballistic distribution; then a given proportion of them (0, 0.00001, 0.0001, 0.001, 0.01, 0.02, or 0.05) was placed in a randomly-chosen bin between 5 and 10m away from the source, simulating a nest site or seed cache.

Again the difference in rate of spread between prairie and urban populations was much greater than differences among runs due to the variance in proportion of seeds going out to the tail of the distribution (Fig 4.13). Even with 5% of seeds (equivalent to as many as 200 seeds from every filled bin in each time step) going relatively long distances, urban populations do not approach the spread rates achieved by prairie populations with no long-distance dispersal. Similar to Auld and Coote's (1980) "mobility" measure, rather than masking differences due to demography, increasing dispersal intensifies those differences.

3) Spread of populations from varying spatial arrangements of founders.

Taking the concept of "new foci" to a larger, landscape scale, I asked how much the distribution of founders affected subsequent rates of spread, or the occupation of space. In other studies the spatial arrangement of founding events has been shown to have a large impact on spread (Moody and Mack 1988).

For each population, using only the composite "ballistic + ants" dispersal curve, I did three runs each of which was started with four adult individuals. The "one focus" case placed all four plants in the center bin, the "two foci" case place two plants in each of two bins, and the "four foci" case placed one plant in each of four bins (Fig 4.14).

The number of foci did significantly affect spread rate (Table 4.6), and even with the same initial number of founding adults, the spread rate was almost twice as fast for four foci as it was for a single focus (Fig. 4.15). However, again the variance due to population type was much greater than that due to number of foci (Table 4.6). Although the effect of additional foci appeared to be more important in the fast-growing prairie populations (Fig. 4.15), the proportional increase was about the same, and analysis of variance revealed no significant population type * foci interaction term (Table 4.6).

Conclusions.

The results presented here both provide insight into the specifics of *C. scoparius* invasion and illuminate the factors important to invasion processes in general. As expected, both population growth rate and dispersal can contribute to variation in rates of spread. Increasing the number of independent sources for population growth (foci) can greatly increase the rate of spread, as has been suggested previously both in models (Moody and Mack 1988) and empirical case histories (Selleck et al. 1962).

Although these generalizations did not furnish any big surprises, applying the models to the particular case of *C. scoparius* did result in some unexpected patterns. Specifically, although recent theory has shown that the details of dispersal can be very important in determining rates of spread (Goldwasser et al. 1994, Kot et al. in press, Cook in review), local variation in dispersal that I measured in the field, even artificial variation meant to evaluate the importance of different dispersal mechanisms, had a negligible effect on how fast space was filled. The proportion of seeds going beyond the primary dispersal distribution also had a surprisingly small effect. Possibly this would have increased in importance if the tail had been much longer, similar to the effect of having multiple foci. However, even in the case of multiple foci, variation in demographic parameters such as that observed between prairie and urban populations completely dominated variation in rates of spread. Although the simple finite rate of increase (λ) did not explain 100% of the variation in spread rate (Fig 4.12), I was unable to attribute the remaining variation to any particular life history stage or transition. Future work will focus on explaining this variation, seeking an understanding of how life history variation may affect invasion rates.

Table 4.1. Summary data from individual replicates of the Artillery Impact Area dispersal experiment. N = number of seedlings found, X = mean distance (cm), STD = standard deviation of distance (cm), MAX = maximum distance.

		Ant Treatment				Plant Treatment			
Replicate	Seed #	N	X	STD	MAX	N	X	STD	MAX
1	910	16	9.8	7.0	25	34	70.4	59.5	293
2	770	16	12.7	16.5	68	28	133.7	69.7	335
3	1050	20	18.8	21.4	66	26	154.6	86.4	380
4	1610	22	161.3	247.6	556	33	134.5	84.7	376
5	700	52	15.4	17.4	81	49	137.7	84.1	364
6	770	7	88.1	49.2	144	41	125.4	98.2	457
7	700	88	137.3	150.5	740	50	173.6	97.1	400
8	600	40	161.6	103.0	500	26	226.9	195.6	955
9	700	101	91.5	91.4	760	28	157.8	52.2	340
10	1200	91	93.0	125.6	585	91	182.8	124.1	590
11	2800					69	139.1	81.3	345
12	2450					42	203.3	89.2	395

Table 4.2. Recursion equations used to generate plant densities at time t+1; these equations form the basis of the population growth phase in the spatial models. t = time step.

$adults_{t+1}$ = (**SuperGrowth** * $seedlings_t$) + (**JuvGrowth** * $juveniles_t$) + (**AdultSurvival** * $adults_t$)

juveniles[x][y][t+1] = (**Establishment** * $seedlings_t$) + (**JuvSurvival** * $juveniles_t$)

seedlings[x][y][t+1] = (**Germination** * $seeds_t$) + (**SeedlingSurvival** * $seedlings_t$)

seeds[x][y][t+1] = (**JuvFecundity** * $juveniles_t$) + (**AdultFecundity** * $adults_t$) + (**Dormancy** * $seeds_t$)

Table 4.3. Comparison of the dominant eigenvalues generated from the 7x7 matrices presented in Chapter 2 with those generated from the 4x4 matrices used in the spatial simulations. Only matrices from the early stage of invasion were used, for two populations in 1993-94 and six populations in 1994-95.

	λ 7x7	λ 4x4	% Difference
1993-94			
Johnson Prairie	1.838	1.888	2.7
Discovery Park	1.217	1.161	- 4.6
1994-95			
Johnson Prairie	1.930	2.179	12.9
13th Division Prairie	1.758	1.859	5.7
Weir Prairie	1.497	1.552	3.7
Discovery Park	1.085	1.117	2.9
Magnuson Park	1.189	1.170	- 1.6
Montlake Fill	1.056	1.079	2.2

Table 4.4. Summary of the results of a spatial simulation of *C. scoparius* spread over time. Numbers here are for Max Adult, the point at which bins reach the maximum allowed plant density. T100 = time to fill 100 bins (1% of lattice), T500 = time to fill 500 bins (5% of lattice), T1000 = time to fill 1000 bins (10% of lattice), T5000 = time to fill 5000 bins (50% of lattice), RATE = rate of spread, increase in square-root of area over time. Numbers given for all sets of demographic parameters, but only for the "plant" dispersal distribution (see text).

	T100	T500	T1000	T5000	RATE
1993-94					
Johnson Prairie	15	22	29	52	1.66
Discovery Park	58	85	104	183	0.49
1994-95					
Johnson Prairie	13	19	25	45	1.68
13th Division Prairie	16	24	30	55	1.57
Weir Prairie	22	33	41	75	1.14
Discovery Park	74	107	130	227	0.39
Magnuson Park	54	81	99	174	0.52
Montlake Fill	34	51	63	114	0.78

Table 4.5. Correlations between individual life history transitions and 1) the rate of spread (increase in the square root of bins filled to Max Adult over time) and 2) the residuals of a regression between rate of spread and lambda. The transitions are taken from the 4x4 matrices used in the model (see Tables 4.2 and 4.3).

	with rate of spread		with residuals	
Transition	ρ	P	ρ	P
Juvenile fecundity	0.722	0.04	0.110	0.80
Adult fecundity	0.328	0.44	-0.504	0.22
Dormancy	-0.922	0.0003	-0.221	0.62
Germination	0.605	0.12	0.215	0.62
Seedling survival	0.171	0.70	0.230	0.60
Establishment	0.125	0.78	0.054	0.90
Supergrowth (seedling->adult)	0.290	0.50	0.243	0.58
Juvenile survivorship	0.001	0.99	0.595	0.12
Growth (juvenile->adult)	0.349	0.42	-0.248	0.57
Adult survivorship	0.740	0.03	0.420	0.32

Table 4.6. Analysis of variance of the effect of populations type (prairie/urban) and the number of initial foci (1, 2, 4) on rate of spread (the increase in square-root of bins filled over time).

Source	DF	Sum Sq.	F	P-Value
Population Type	1	9.9	52.2	0.0001
# Foci	2	3.2	8.5	0.0044
Pop Type * Foci	2	0.8	2.2	0.15
Residual	13	2.5		

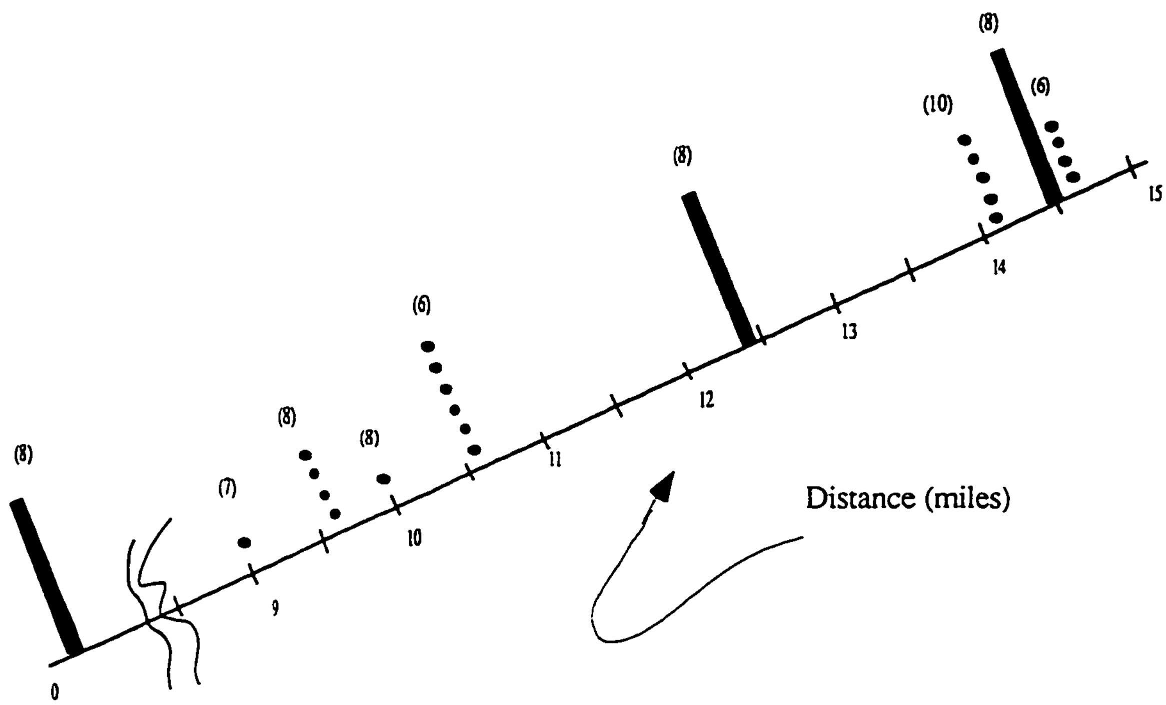


Figure 4.1. Pattern of *Cytisus scoparius* distribution along Route 26 at Mount St. Helens. Dots represent individual plants, bars represent large groups of plants. Number in parentheses is the estimated age of the oldest plant in the patch. The numbers below the line represent (uphill) distances in miles from the start of Rte 26, where there is a large patch of *C. scoparius*.

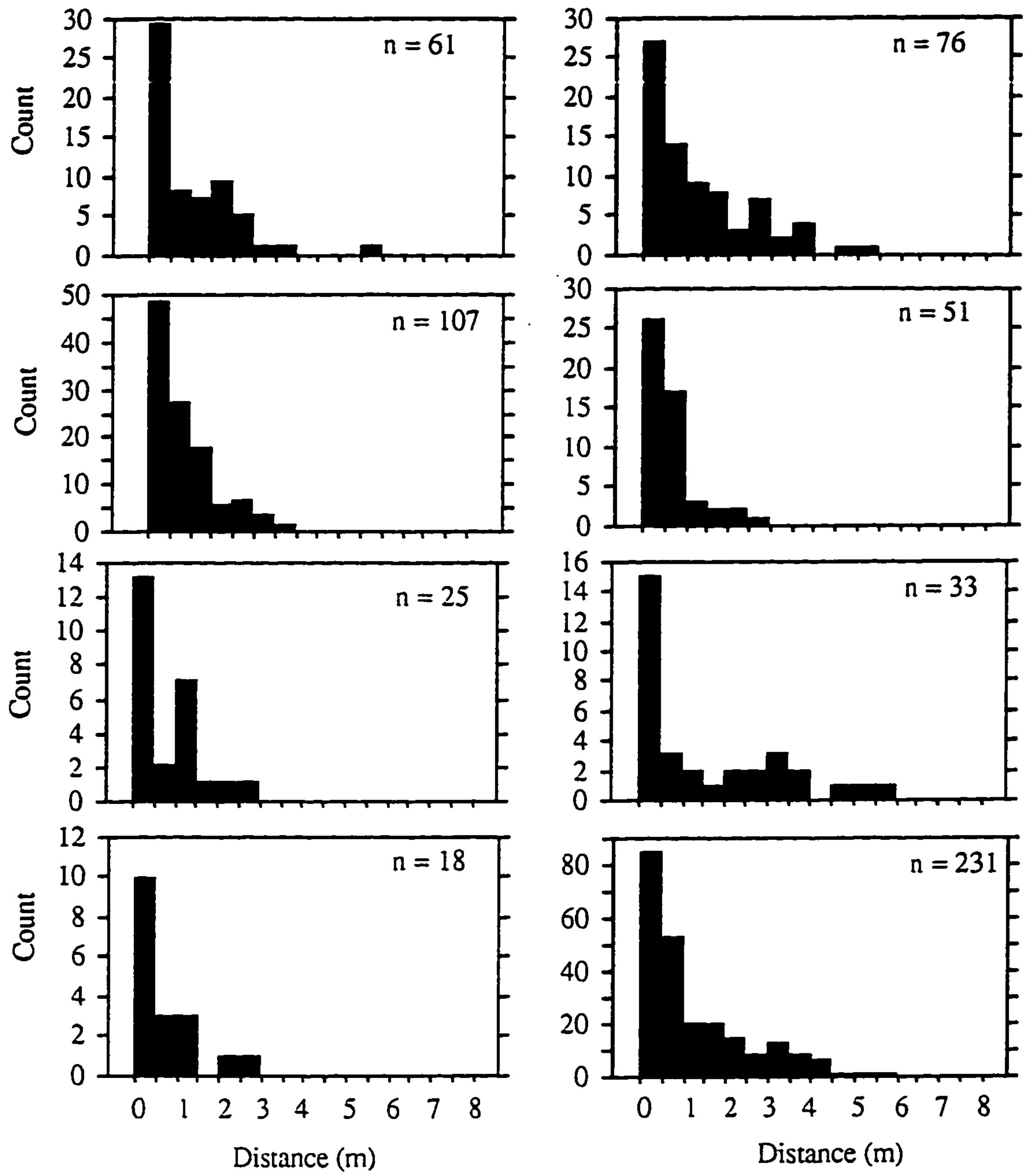


Fig. 4.2. Individual replicates of the ballistic dispersal experiment. These are not probabilitydensity functions, but raw data from linear strips radiating out from each plant. A composite of the converted distributions (accounting for relative area at each distance) is presented in Fig. 4.3.

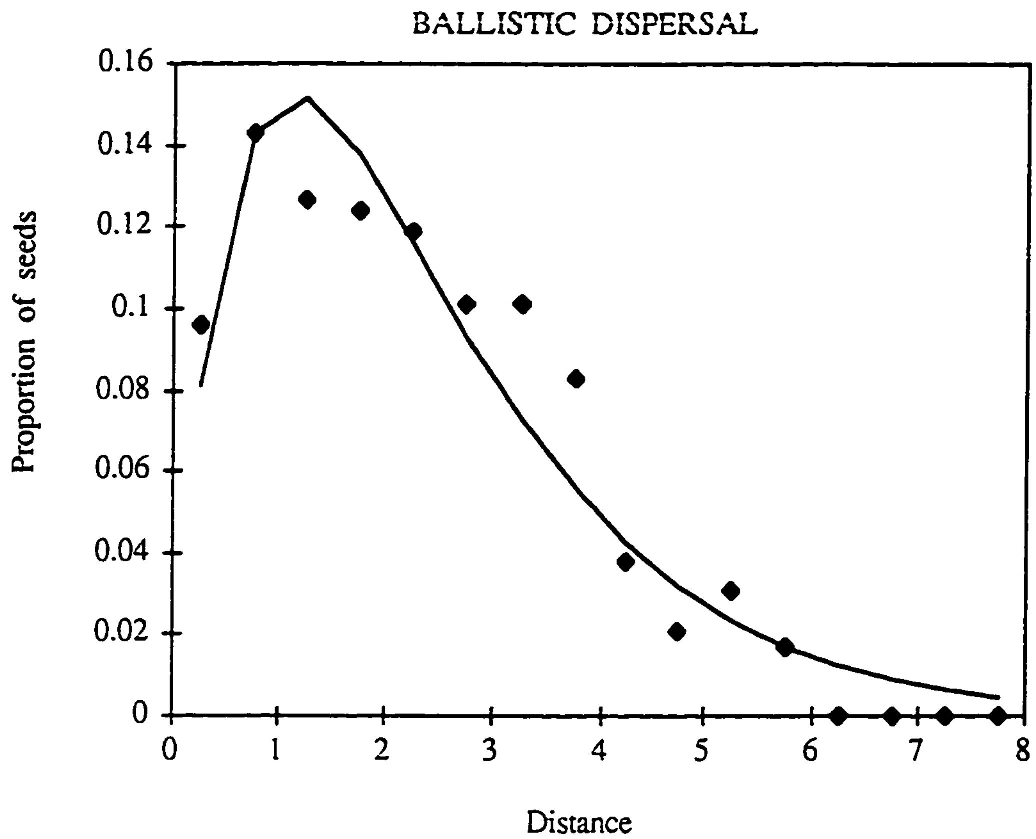


Fig. 4.3. The probability density function for seeds dispersed by ballistic dispersal. Mean = 1.08m, standard deviation = 1.10, maximum between 5.5 and 6.0m. The curve was fit with a gamma distribution (minimizing Chi-Square): alpha = 1.88, beta = 0.78.

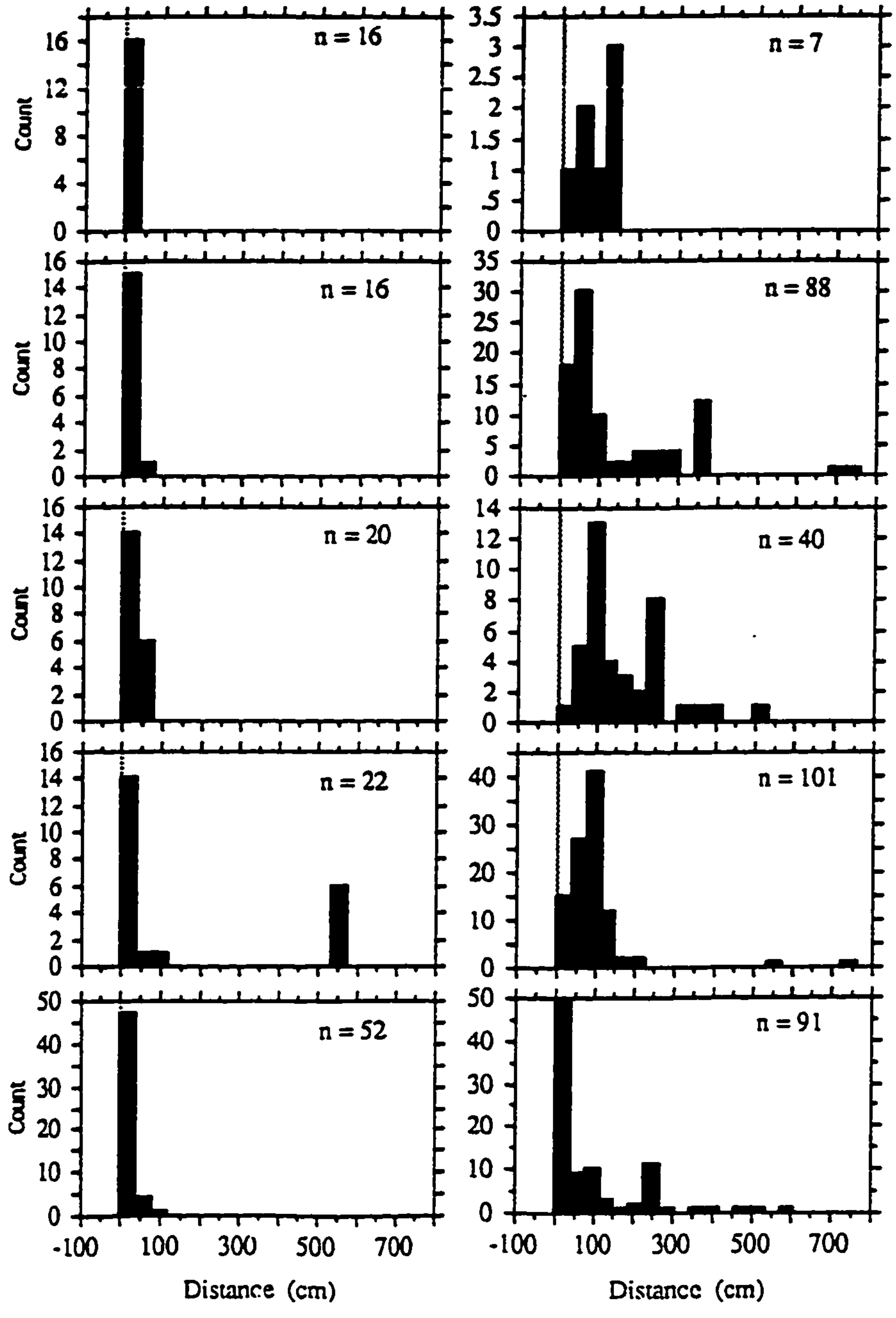


Figure 4.4. The dispersal distribution for individual replicates of the ant-dispersal-only treatment in the artillery impact area. Composite distribution is shown in Fig. 4.6.

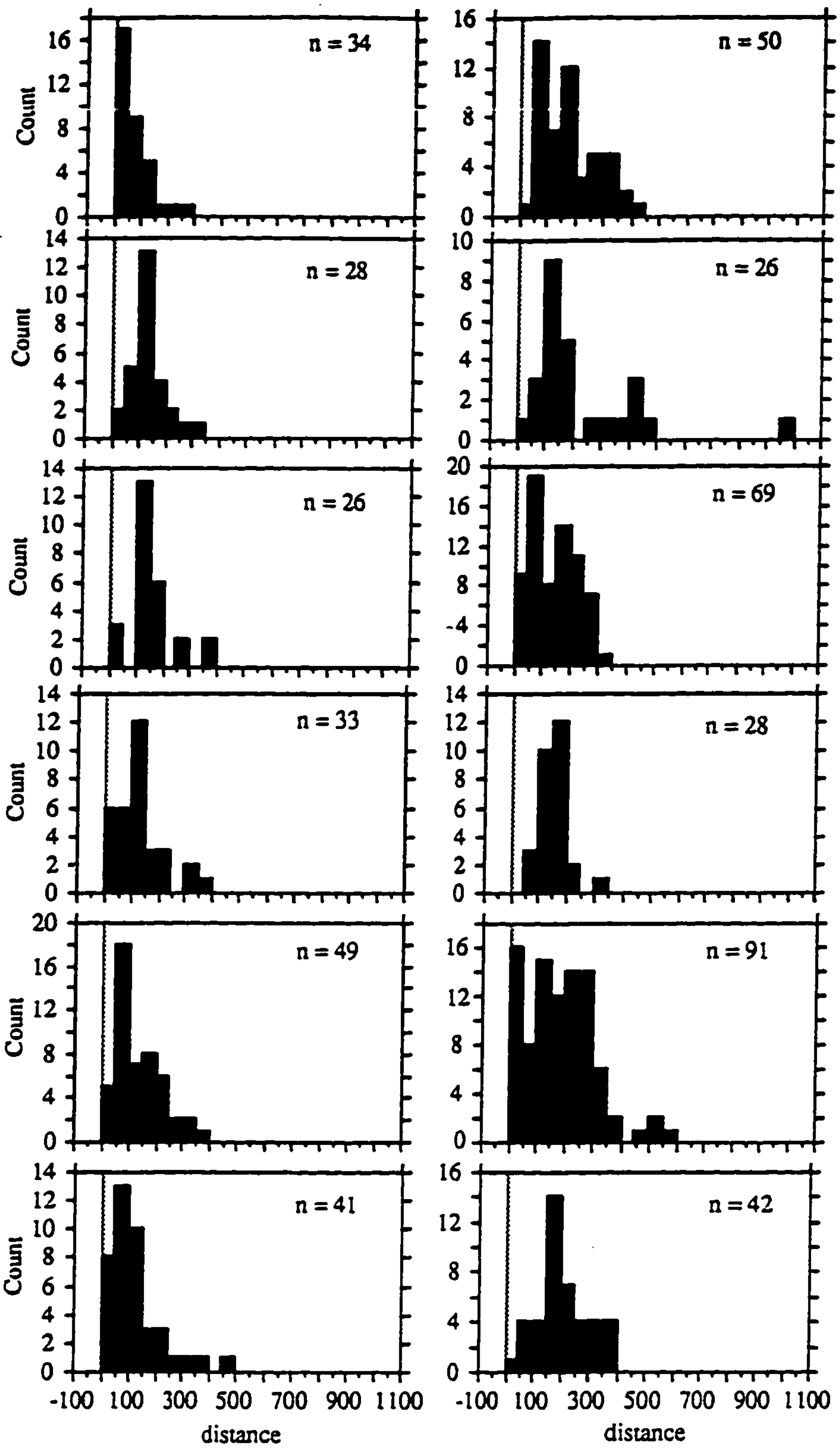


Figure 4.5. The dispersal distribution for individual replicates of the plant-dispersal (ballistic + ants) treatment in the artillery impact area. Composite distribution in Fig. 4.7.

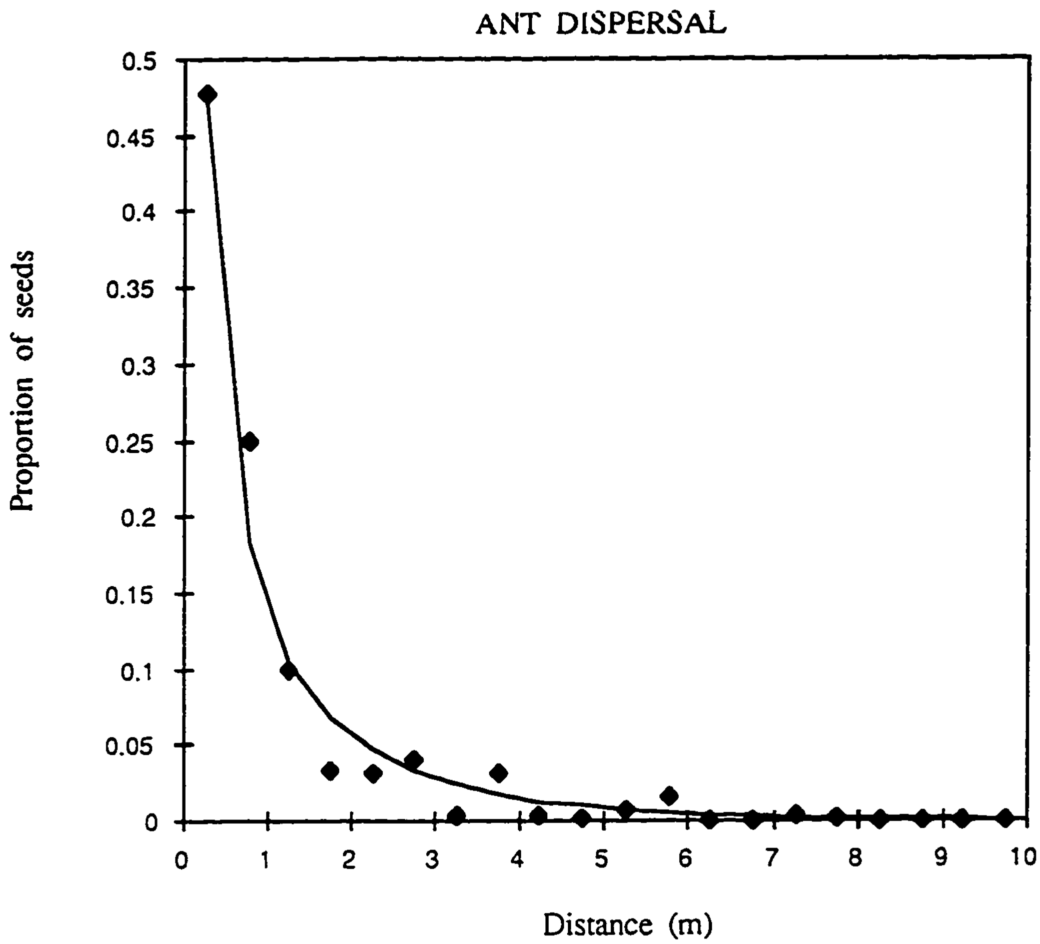


Fig. 4.6. The probability density function for seeds dispersed by ants, from experimental source depots in the artillery impact area. Mean = 0.93m, standard deviation = 1.25, maximum = 7.60. The curve was fit with a gamma distribution(minimizing Chi-Square): alpha = 0.32, beta = 0.42.

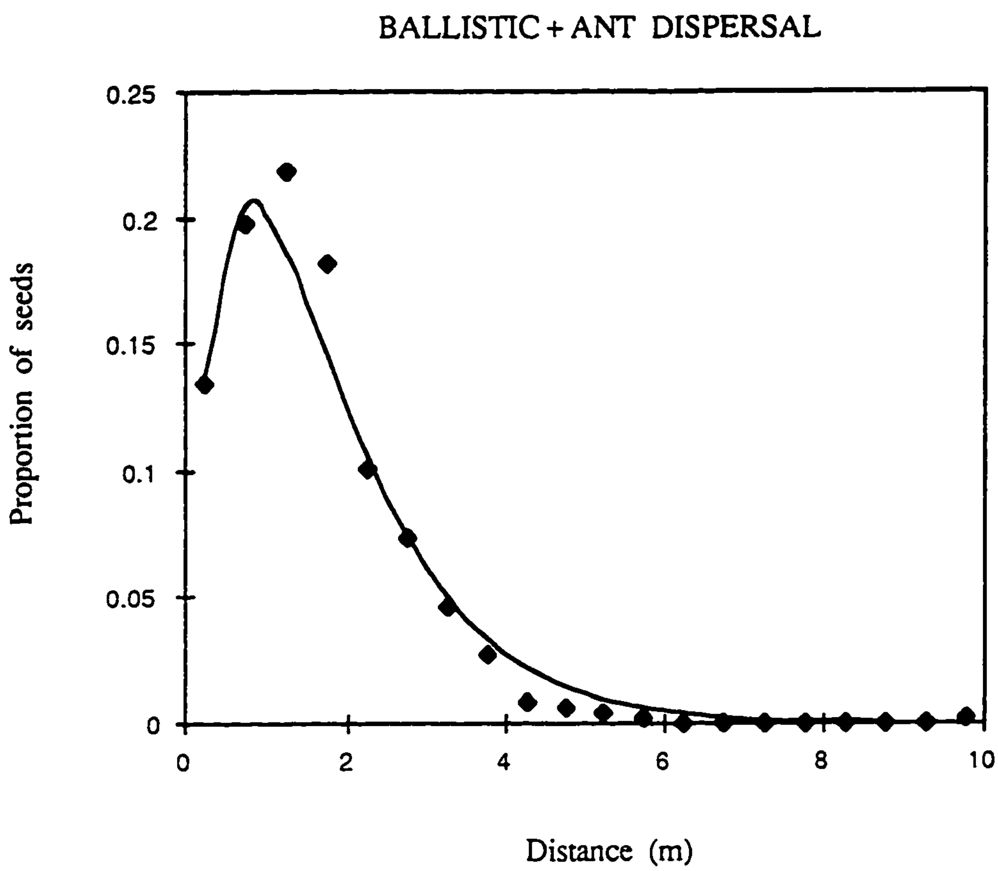


Fig. 4.7. The probability density function for seedlings germinating from seeds dispersed by experimental plants in the artillery impact area. Mean = 1.55m, standard deviation = 1.05, maximum = 9.55. The curve was fit with a gamma distribution (minimizing Chi-Square): alpha = 1.84, beta = 1.04.

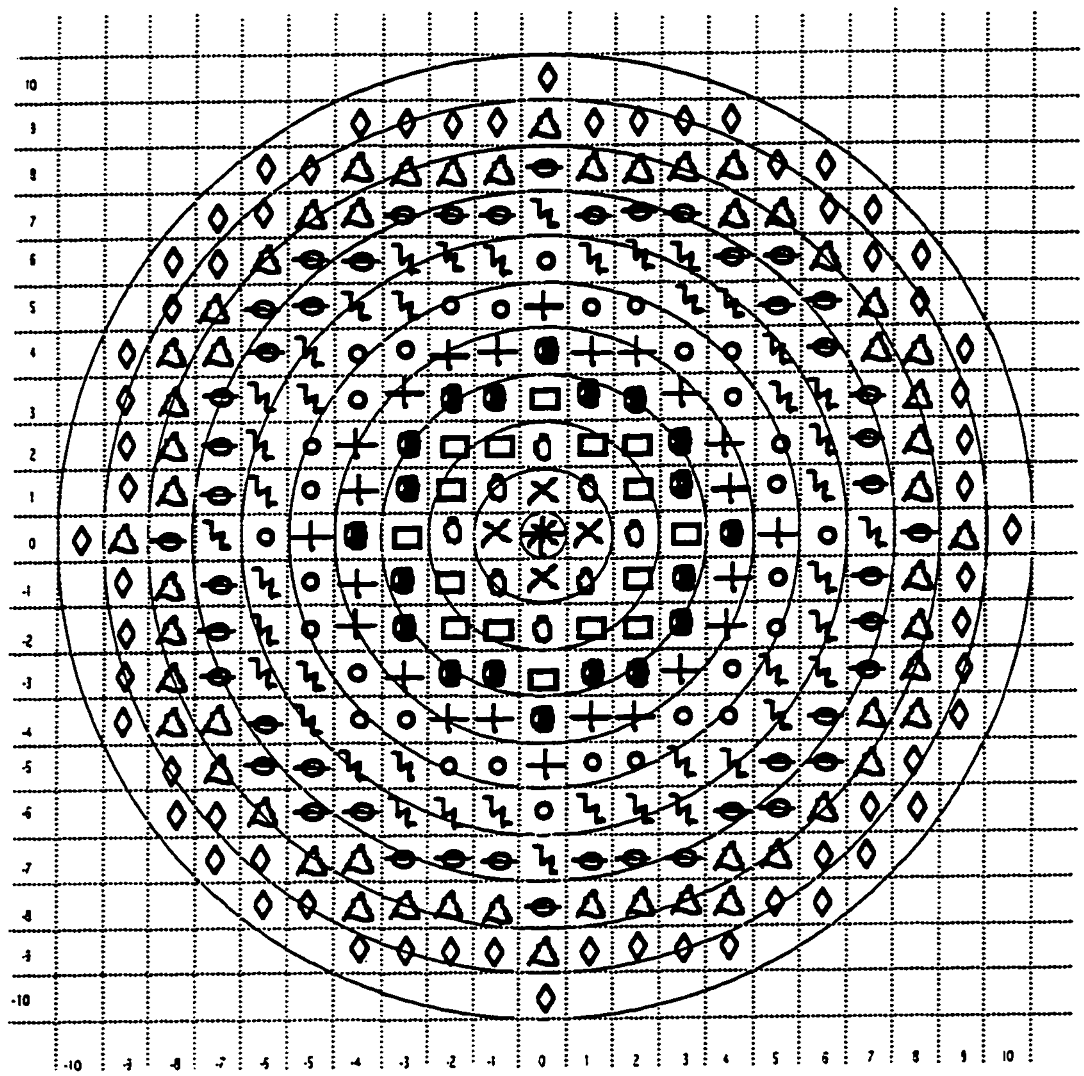


Figure 4.8. Schematic of the arrangement of dispersal "bins", i.e., the way distance between a receiving bin and the dispersing focal bin was determined. Bins carrying the same symbol were counted as the same distance.

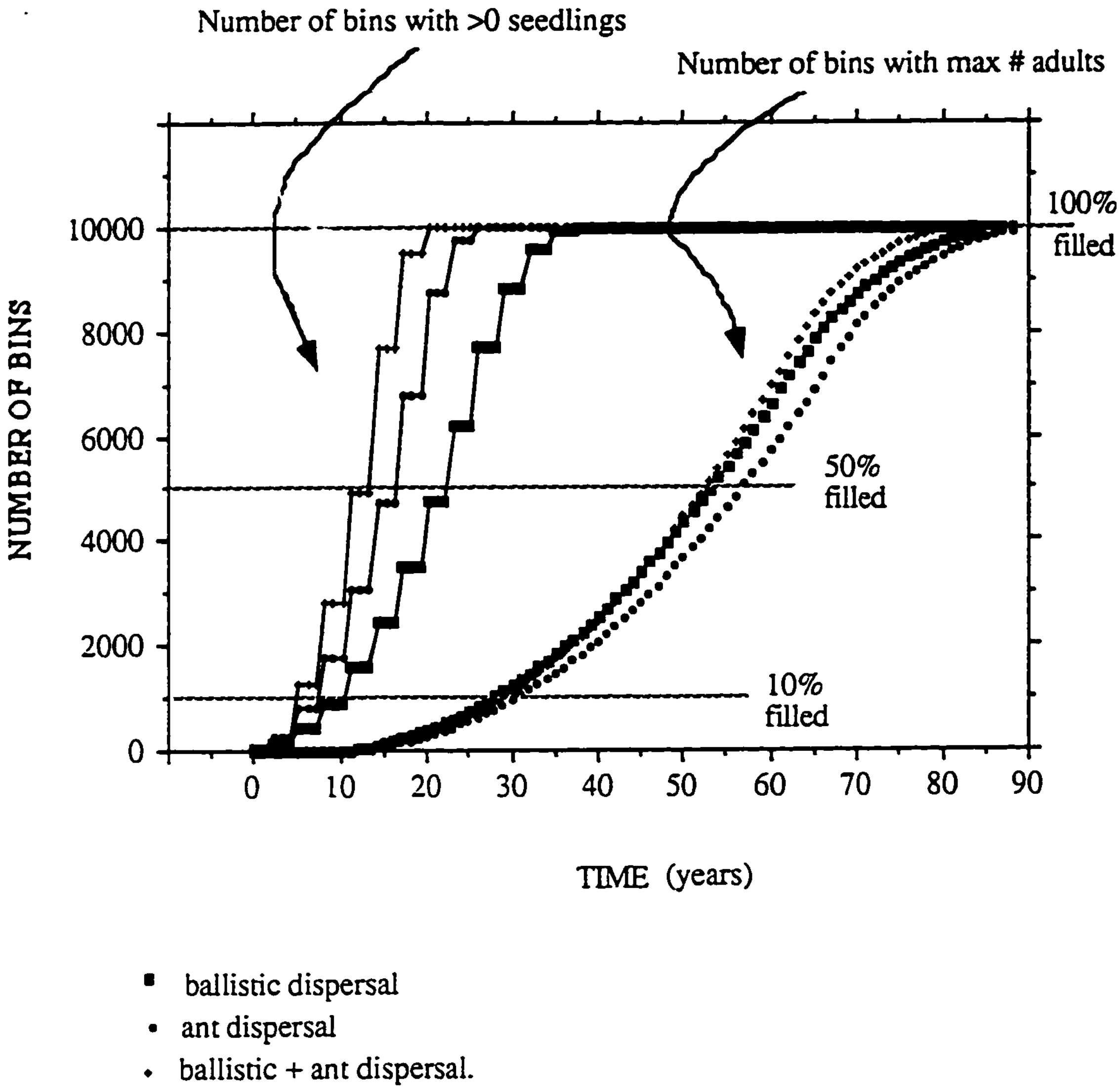


Figure 4.9. An example of the output of one run of the model for each of three dispersal types. The results shown are for one set of demographic parameters, Johnson Prairie 1993-94.

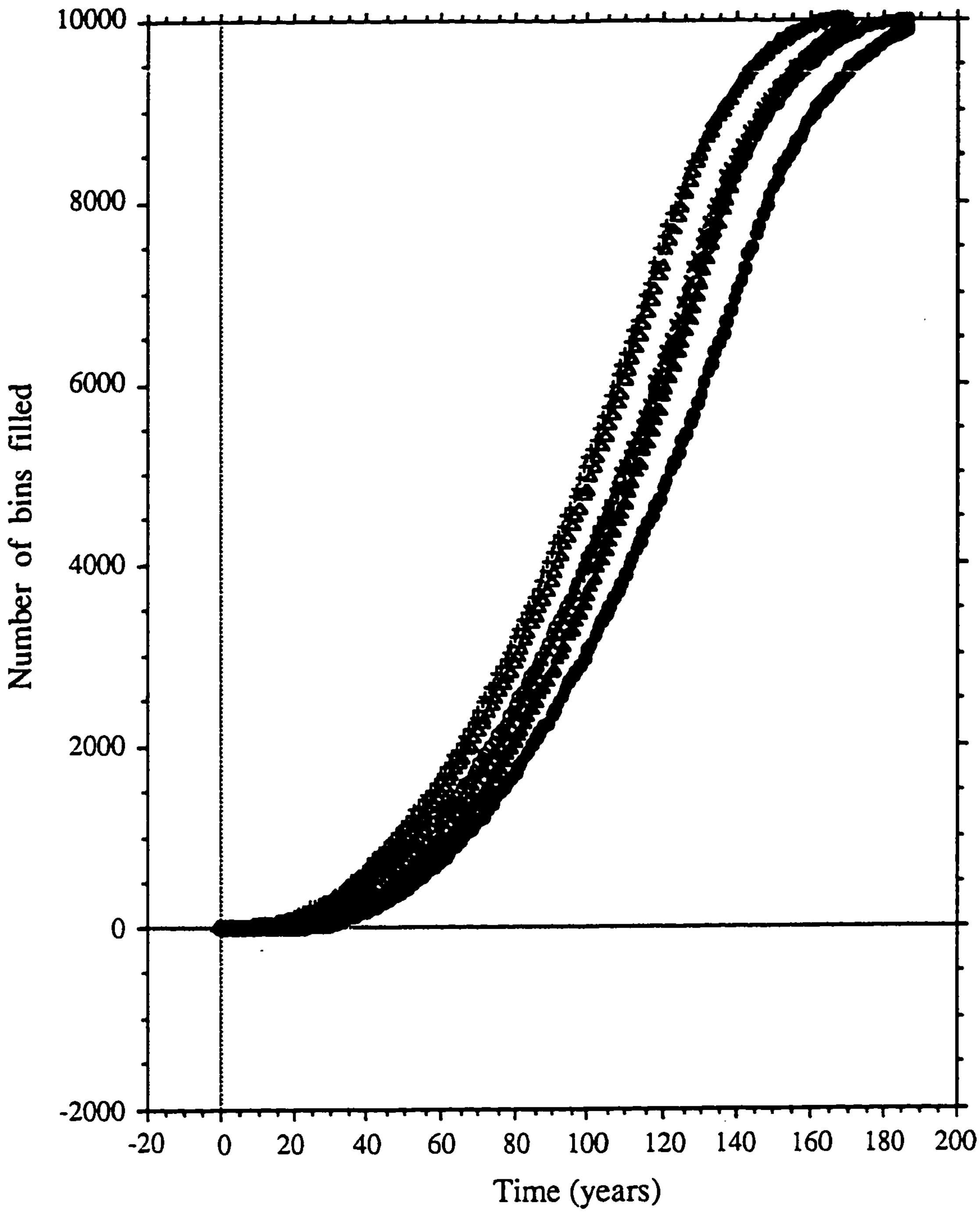


Figure 4.10. Trajectory of the number of bins filled over time for a representative population (Montlake Fill 1994-95). Shown are results using two different density criteria, greater than one seedling and maximum possible adult density, for ant dispersal only (open and filled circles, respectively), for ballistic dispersal only (+ and x, respectively), and for ballistic plus ant dispersal (open and filled triangles, respectively).

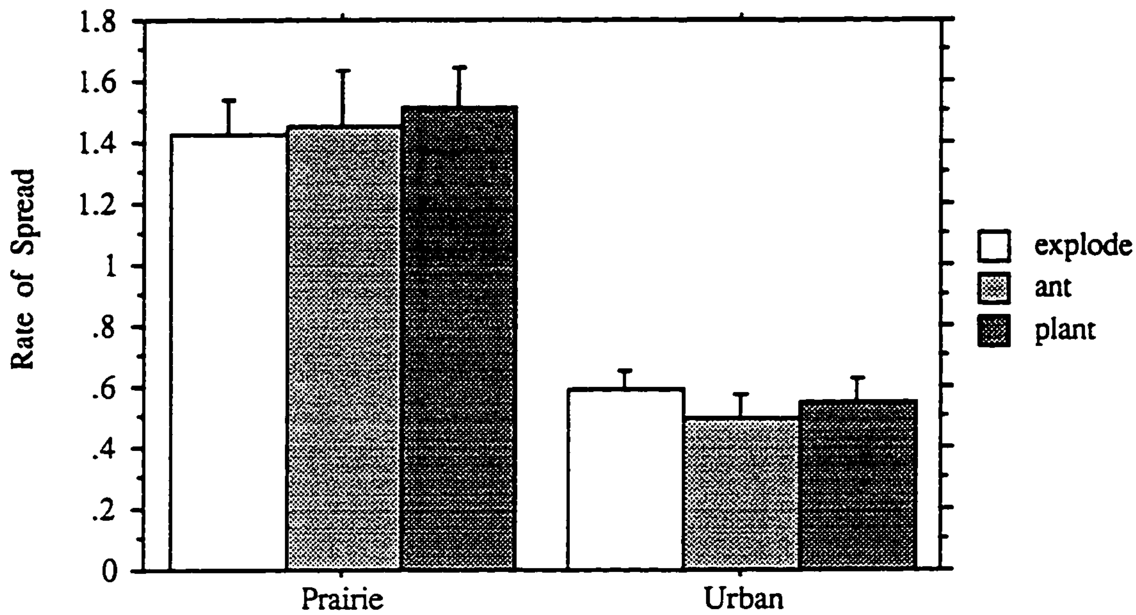


Figure 4.11. Rate of spread (increase in the square root of bins filled to the maximum density of adults, over time) for prairie and urban populations. The simulations utilized one of three empirically-derived dispersal distributions: ballistic dispersal, ant dispersal, or ballistic + ant ("plant").

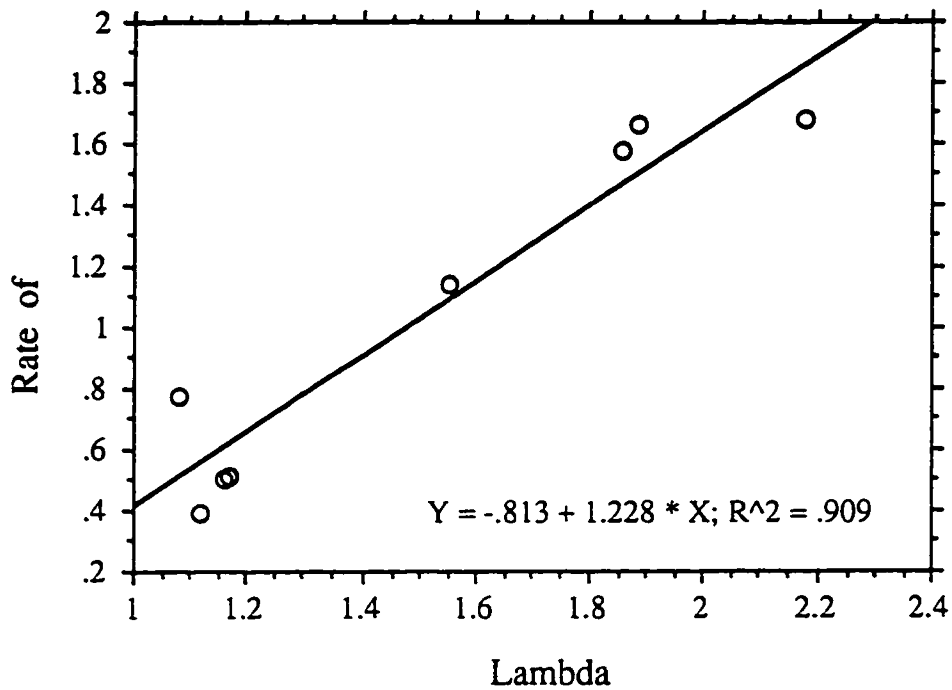


Figure 4.12. Regression of the rate of spread, calculated as the increase in the square-root of number of bins filled over time, on lambda, the finite rate of increase, for four sets of demographic parameters. Only included here are spread rates for ballistic + ant dispersal.

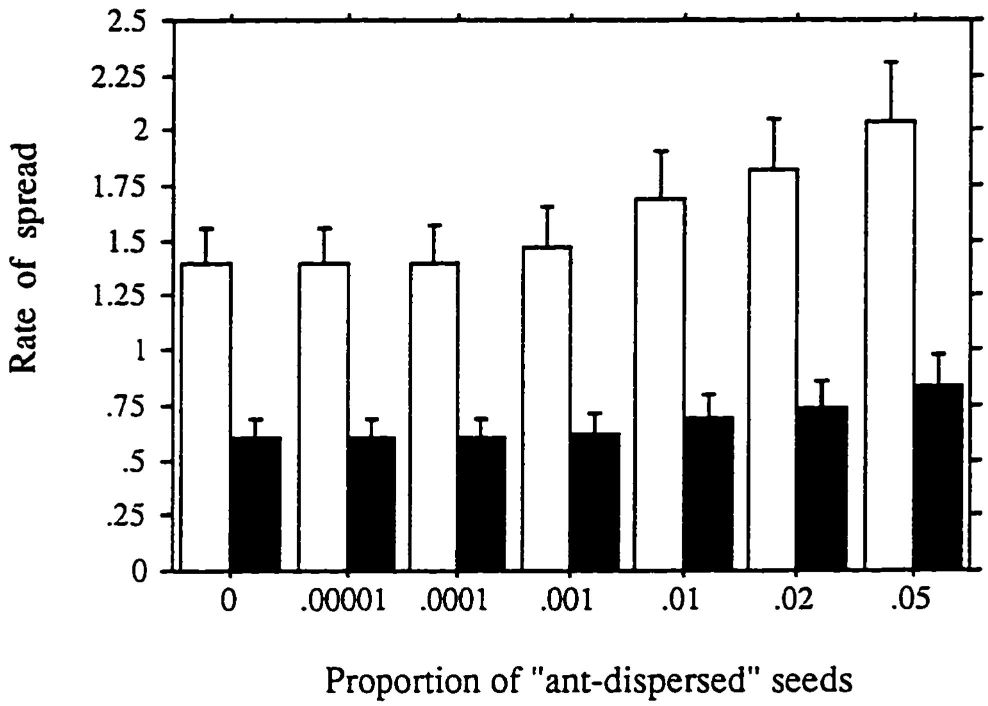


Figure 4.13. The effect on rate of spread of systematically increasing the proportion of seeds being dispersed between 5 and 10 meters (extending the maximum dispersal distance beyond the 6m achieved by ballistic dispersal), for prairie populations (open bars) and urban populations (filled bars).

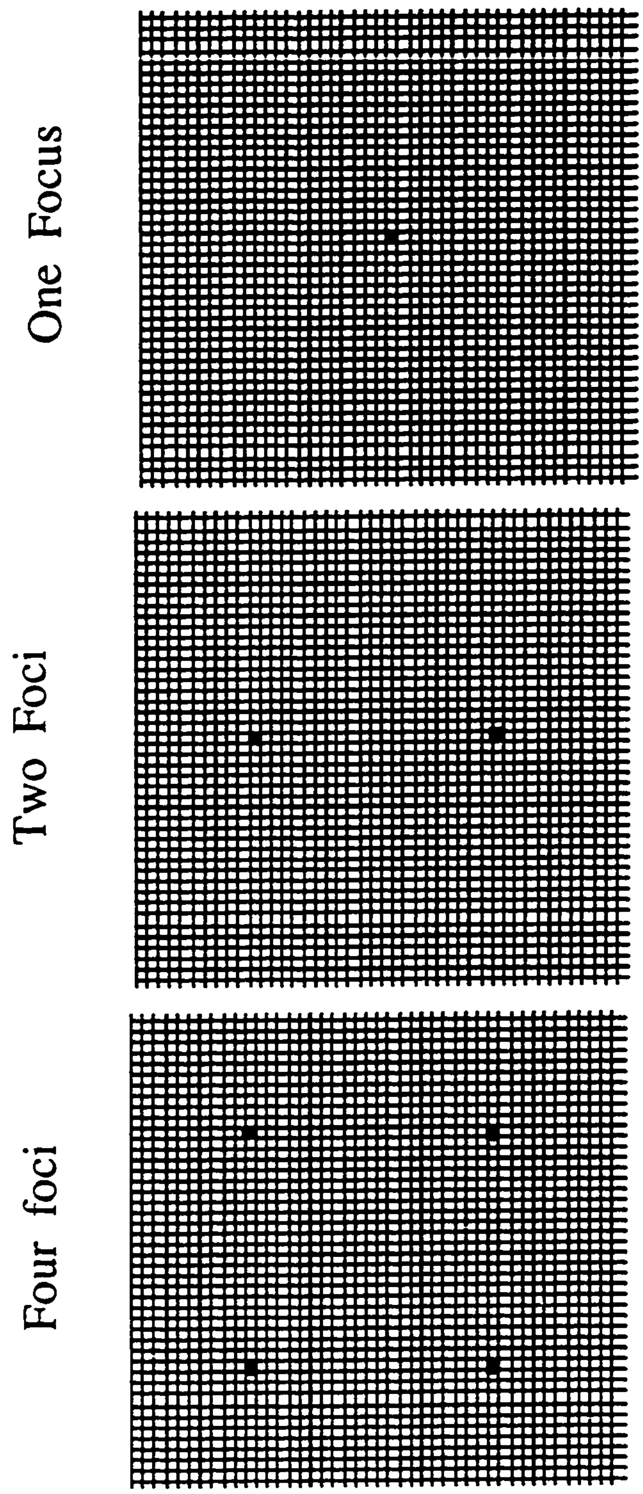


Figure 4.14. Design of model to quantify the effect of the distribution of founders on rate of spread.

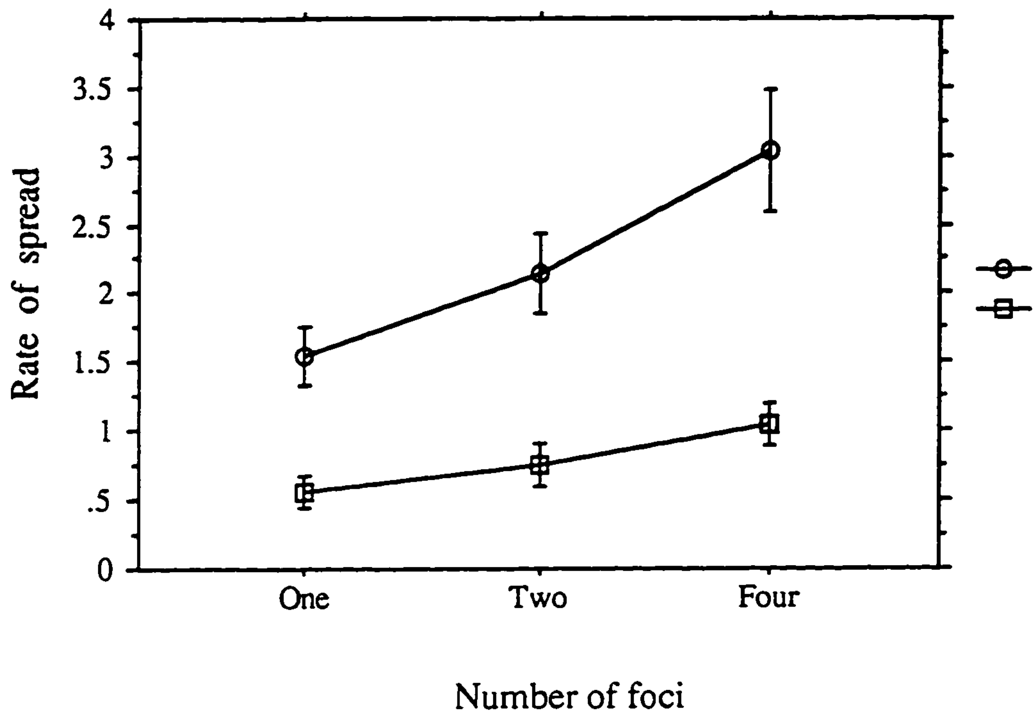


Figure 4.15. The effect of the number of initial foci, or founder patches, on rate of spread for prairie populations (circles) and urban populations (squares).

BIBLIOGRAPHY

Allen, L. J. S., E. J. Allen, C. R. G. Kunst and R. E. Sosebee. 1991. A diffusion model for dispersal of *Opuntia imbricata* (cholla) on rangeland. Journal of Ecology **79**:1123-1135.

Ammerman, A. J. and L. L. Cavalli-Sforza. 1984. The neolithic transition and the genetics of populations in Europe. Edited by Princeton University Press, Princeton, NJ.

Andersen, A. N. 1988. Dispersal distance as a benefit of myrmecochory. Oecologia **75**:507-511.

Andersen, A. N. 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? Oecologia **81**:310-315.

Anderson, D. C., K. T. Harper and R. C. Holmgren. 1982. Factors influencing development of cryptogamic soil crusts in Utah deserts. Journal of Range Management **35**:180-185.

Andow, D., P. Kareiva, L. S. and A. Okubo. 1990. Spread of invading organisms. Landscape Ecology **4**:177-188.

Andow, D. A., P. M. Kareiva, S. A. Levin and A. Okubo. 1993. Spread of invading organisms: patterns of spread. pp. 219-242 *in* K. Kim and B. A. McPheron eds. Evolution of Insect Pests: Patterns of Variation. John Wiley and Sons, New York.

Augspurger, C. K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). Ecology **62**:775-788.

Augspurger, C. K. and K. Kitajima. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. Ecology **73**:1270-1284.

Auld, B. A. and B. G. Coote. 1980. A model of a spreading plant population. Oikos **34**:287-292.

Baker, H. G. 1965. Characteristics and modes of origin of weeds. pp. 147-168 *in* H. G. Baker and G. L. Stebbins eds. The Genetics of Colonizing Species. Academic Press, New York.

Bazzaz, F. A., R. W. Carlson and J. L. Harper. 1979. Contribution to reproductive effort by photosynthesis of flowers ad fruits. Nature **279**:554-555.

Beattie, A. J. 1985. The evolutionary Ecology of Ant-Plant Mutualisms. Edited by Cambridge University Press, Cambridge.

Beattie, A. J. and N. Lyons. 1975. Seed dispersal in *Viola* (Violaceae): adaptations and strategies. American Journal of Botany **62**:714-722.

Beer, T. and M. D. Swaine. 1977. On the theory of explosively dispersed seeds. New Phytologist **78**:681-694.

Belnap, J. 1993. Recovery rates of cryptobiotic crusts: inoculant use and assessment methods. Great Basin Naturalist **53**:89-95.

Bergelson, J. and M. Crawley. 1989. Can we expect mathematical models to guide biological control programs?: a comment based on case studies of weed control. Comments on Theoretical Biology **1**:197-216.

Bierzychudek, P. 1981. Pollinator limitation of plant reproductive effort. American Naturalist **117**:838-840.

Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs **52**:335-351.

Bossard, C. 1991. The establishment and dispersal of *Cytisus scoparius* (Scotch broom) in California Sierra Nevada Foothill and northern coastal habitats. National Park Service Technical Report 91/06,

Bossard, C. C. 1990. Secrets of an ecological interloper: ecological studies on *Cytisus scoparius* in California. Ph.D. University of California, Davis.

Bossard, C. C. 1990. Tracing of ant dispersed seeds: a new technique. Ecology **71**:1370-1371.

Bossard, C. C. 1991. The role of habitat disturbance, seed predation and ant dispersal on establishment of the exotic shrub *Cytisus scoparius* in California. American Midland Naturalist **126**:1-13.

Burd, M. 1994. Bateman's principle and plant reproduction: The role of pollen limitation in fruit and seed set. Botanical Review **60**:83-139.

Burkey, T. V. 1994. Tropical tree species diversity: a test of the Janzen-Connell model. Oecologia **97**:533-540.

Calvo, R. N. 1993. Evolutionary demography of orchids: intensity and frequency of pollination and the cost of fruiting. Ecology **74**:1033-1042.

Calvo, R. N. and C. C. Horvitz. 1990. Pollinator limitation, cost of reproduction, and fitness in plants: A transition-matrix demographic approach. Am. Nat. **136**:499-516.

Campbell, D. R. 1985. Pollinator sharing and seed set of *Stellaria pubera*: competition for pollination. Ecology **66**:544-553.

Campbell, D. R. 1987. Interpopulational variation in fruit production: The role of pollinator-limitation in the Olympic Mountains. American Journal of Botany **74**:269-273.

Carey, P. D. and A. R. Watkinson. 1993. The dispersal and fates of seeds of the winter annual grass *Vulpia ciliata*. Journal of Ecology **81**:759-767.

Carlquist, S. 1965. Island Life. Edited by Natural History Press, Garden City, NY.

Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities.

Case, T. J. 1991. Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. Biological Journal of the Linnean Society **42**:239-266.

Caswell, H. 1989. Matrix Population Models. Edited by Sinauer Assoc., Sunderland.

Caswell, H. and P. A. Werner. 1978. Transient behavior and life history analysis of teasel (*Dipsacus sylvestris* Huds.). Ecology **59**:53-66.

Caughley, G. 1970. Liberation, dispersal and distribution of Himalayan thar (*Hemitragus jemlahicus*) in New Zealand. New Zealand Journal of Science **13**:220-239.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge Studies in Mathematical Biology. Edited by Cambridge University Press, Cambridge.

Charlesworth, D. 1989. Evolution of low female fertility in plants: pollen limitation, resource allocation, and genetic load. Trends in Ecology and Evolution **4**:289-292.

Cipollini, M. L. and D. F. Whigham. 1994. Sexual dimorphism and cost of reproduction in the dioecious shrub *Lindera benzoin* (Lauraceae). American Journal of Botany **81**:65-75.

Connell, J. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. pp. 298-310 *in* P. J. den Boer and G. R. Gradwell eds. Dynamics of Populations. Centre for Agricultural Publishing and Documentation, Wageningen.

Cook, J. in review. Biological invasions: the effect of long-range dispersal. Ecology

Crawley, M. J. 1989. Chance and timing in biological invasions. pp. 407-423 *in* J. A. Drake, H. A. Mooney, F. d. Castri, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson eds. Biological Invasions: A Global Perspective. Wiley & Sons, New York.

Crawley, M. J., R. S. Hails, M. Rees, D. Kohn and J. Buxton. 1993. Ecology of transgenic oilseed rape in natural habitats. Nature **363**:620-623.

Crawley, M. J. and R. M. May. 1987. Population dynamics and plant ccommunity structure: competition between annuals and perennials. Journal of Theoretical biology **125**:475-489.

Crookston, R. K., J. O'Toole and J. L. Ozbun. 1974. Characterization of the bean pod as a photosynthetic organ. Crop Science **14**:708-712.

Cross, J. R. 1981. The establishment of *Rhododendron ponticum* in the Killarny oakwoods, S.W. Ireland. Journal of Ecology **69**:807-824.

Crouse, D. T., L. B. Crowder and H. Caswell. 1987. A stage based population model for loggerhead sea turtles and implications for conservation. Ecology **68**:1412-1423.

Crouse, D. T., L. B. Crowder and H. Caswell. 1987. A stage based population model for loggerhead sea turtles and implications for conservation. Ecology **68**:1412-1423.

Czárán, T. 1989. Coexistence of competing populations along an environmental gradient: a simulation study. Coenoses **4**:113-120.

Czárán, T. and S. Bartha. 1989. The effect of spatial pattern on communit dynamics: a comparison of simulated and field data. Vegetatio **83**:229-239.

Dahlsten, D. L. 1986. Control of Invaders. pp. 275-302 *in* H. A. Mooney and J. A. Drake eds. Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York.

Darwin, C. 1865 [1982]. The Origin of Species by Means of Natural Selection. Edited by Penguin Books, New York.

Dieringer, G. 1992. Pollinator limitation in populations of *Agalinis strictifolia* (Scrophulariaceae). Bulletin of the Torrey Botanical Club **119**:131-136.

Dirzo, R. and C. A. Domínguez. 1986. Seed shadows, seed predation, and the advantages of dispersal. pp. 237-249 *in* A. Estrada and T. H. Fleming eds. Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht.

Dodd, A. P. 1957. The biological control of prickly pear in Australia. pp. *in* A. Keast, R. L. Crocker and C. S. Christian eds. Biogeography and Ecology in Australia.

Domínguez, C. A. and R. Dirzo. 1995. Rainfall and flowering synchrony in a tropical shrub: variable selection on the flowering time of Erythroxylum havanense. Evolutionary Ecology 9:204-216.

Drake, J. A. 1991. Community assembly mechanics and the structure of an experimental species ensemble. American Naturalist **137**:1-26.

Drake, J. A., H. A. Mooney, F. d. Castri, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson. 1989. Biological Invasions: A Global Perspective. Edited by Wiley & Sons, New York.

Dritschilo, W., D. E. Carpenter, J. L. Hastings, O. Meyn, D. Moss and M. N. Weinstein. 1985. Implications of data on introduced species in California for field releases of recombinant DNA organsims. School of Public Health, UCLA, Ehrlén, J. 1992. Proximate limits to seed production in a herbaceous perennial legume, *Lathyrus vernus*. Ecology **73**:1820-1831.

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

Ehrlén, J. and O. Eriksson. 1995. Pollen limitation and population growth in a herbaceous perennial legume. Ecology **76**:652-56.

El Kassaby, Y. A. and H. J. Barclay. 1992. Cost of reproduction in Douglas-fir. Canadian Journal of Botany **70**:1429-1432.

Eldridge, D. J. 1993. Cryptogams, vascular plants, and soil hydrological relations: some preliminary results from the semiarid woodlands of eastern Australia. Great Basin Naturalist **53**:48-58.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Edited by Methuen, London.

English-Loeb, G. M. and R. Karban. 1992. Consequences of variation in flowering phenology for seed head herbivory and reproductive success in *Erigeron glaucus* (Compositae). Oecologia 588-595.

Estrada, A. and T. H. Fleming. 1986. Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht.

Ewel, J. J. 1986. Invasibility: lessons from south Florida. pp. 214-249 *in* H. A. Mooney and J. A. Drake eds. Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York.

Feinsinger, P. and H. M. Tiebout. 1991. Competition among plants sharing hummingbird pollinators: laboratory experiments on a mechanism. **72**:1946-1952.

Fisher, R. A. 1937. The wave of advance of advantageous genes. Ann. Eugen. **7**:355-369.

Forcella, F. and S. Harvey. 1988. Patterns of weed migration in Northwestern USA. Weed Science **36**:194-201.

Forcella, F. and J. Wood. 1984. Colonization potentials of alien weeds are related to their native distributions: implications for plant quarantine. Journal of the Australian Institute of Agricultural Science 35-41.

Fox, J. F. 1992. Pollen limitation of reproductive effort in willows. Oecologia **90**:283-287.

Fox, M. D. and B. J. Fox. 1986. The susceptibility of natural communities to invasion. pp. 57-66 *in* R. H. Groves and J. J. Burdon eds. Ecology of Biological Invasions: An Australian Perspective. Australian Academy of Sciences, Canberra.

Franklin, J. F. and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Edited by Oregon State University Press, Corvallis.

Galen, C. 1985. Regulation of seed-set in *Polemonium viscosum*: floral scents, pollination, and resources. Ecology **66**:792-797.

Galen, C., T. E. Dawson and M. L. Stanton. 1993. Carpels as leaves meeting the carbon cost of reproduction in a alpine buttercup. Oecologia **95**:187-193.

Gilkey, H. M. 1957. Weeds of the Pacific Northwest. Edited by Oregon State College, Corvallis.

Gold, W. and L. C. Bliss. 1995. Water limitations and plant community development in a polar desert. Ecology **76**:1558-1568.

Goldwasser, L., J. Cook and E. D. Silverman. 1994. The effects of variability on metapopulation dynamics and rates of invasion. Ecology **75**:40-47.

Gomez, J. M. 1993. Phenotypic selection on flowering synchrony in a high mountain plant, *Hormathophylla spinosa* (Cruciferae). Journal of Ecology **81**:605-613.

Green, D. S. 1983. The efficacy of dispersal in relation to safe site density. Oecologia **56**:356-358.

Grime, J. P. 1979. Plant strategies and vegetation processes. Edited by Wiley, Chichester, U.K.

Gross, R. S. and P. A. Werner. 1983. Relationships among flowering phenology, insect visitors, and seed set of individuals: experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). Ecological Monographs **53**:95-117.

Handel, S. N. and A. J. Beattie. 1990. Seed dispersal by ants. Scientific American **263**:76-83.

Hanzawa, F. M., A. J. Beattie and D. C. Culver. 1988. Directed dispersal: Demographic analysis of an ant-seed mutualism. American Naturalist **131**:1-13.

Hardin, D. P., P. Takac and G. F. Webb. 1990. Dispersion population models discrete in time and continuous in space. Journal of Mathematical Biology **28**:1-20.

Harper, J. L. 1965. The nature and consequences of interference amongst plants. Genetics Today, Hague.

Harper, J. L. 1977. Population Biology of Plants. Edited by Academic Press, New York.

Harper, K. T. and J. R. Marble. 1988. A role for nonvascular plants in management of arid and semiarid rangelands. pp. 135-169 *in* P. T. Tueller eds. Application of Plant Sciences to Rangeland Management and Inventory. Kluwer Academic Publishers, Boston.

Harper, K. T. and R. L. Pendleton. 1993. Cyanobacteria and cyanolichens: can they enhance availability of essential minerals for higher plants? Great Basin Naturalist **53**:59-72.

Hastings, N. A. J. and J. B. Peacock. 1974. Statistical Distributions. Edited by Butterworths, London.

Hedgpeth, J. 1993. Foreign invaders. Science **261**:34-35.

Heithaus, E. R. 1986. Seed dispersal mutualism and the population density of Asarum canadense, an ant-dispersed plant. pp. 199-210 *in* A. Estrada and T. H. Fleming eds. Frugivores and Seed Dispersal. W. Junk Publishers, Dordrecht.

Hengeveld, R. 1989. Dynamics of Biological Invasions. Edited by Cambridge University Press, Cambridge.

Hobbs, R. J. 1989. The nature and effects of disturbance relative to invasions. pp. 389-405 *in* J. A. Drake, H. A. Mooney, F. d. Castri, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson eds. Biological Invasions: A Global Perspective. Wiley & Sons, New York.

Hobbs, R. J. and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: Implications for conservation. Conservation Biology **6**:324-337.

Hobbs, R. J. and H. A. Mooney. 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbances. Oecologia (Berlin) **67**:342-351.

Hoffman, J. H. and V. C. Moran. 1991. Biocontrol of a perennial legume, *Sesbania punicea,* using a florivorous weevil, Trichapion lativentre--weed population dynamics with a scarcity of seeds. Oecologia **88**:574-576.

Hogeweg, P., B. Hesper, C. P. v. Schail and W. G. Beeftink. 1985. Patterns in vegetation succession, an ecomorphological study. pp. 637-666 *in* J. White eds. The Population Structure of Vegetation. W. Junk, Dordrecht.

Holmes, E. E. 1995. Spatial models in ecology: explorations into the impact of spatial behavior on population dynamics. Ph.D. University of Washington.

Holmes, E. E., M. A. Lewis, J. E. Banks and R. R. Veit. 1994. Partial differential equations in ecology: Spatial interactions and population dynamics. Ecology **75**:17-29.

Horvitz, C. C. and D. W. Schemske. 1986. Seed dispersal and environmental heterogeneity in a neotropical herb: a model of population and patch dynamics. pp. 169-186 *in* A. Estrada and T. H. Fleming eds. Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht.

Horvitz, C. C. and D. W. Schemske. 1988. Demographic cost of reproduction in a neotropical herb: an experimental field study. Ecology **69**:1741-1745.

Horvitz, C. C. and D. W. Schemske. 1990. Spatiotemporal variation in insect mutualists of a neotropical herb. Ecology **71**:1085-1097.

Horvitz, C. C. and D. W. Schemske. 1995. Ecological Monographs

Howe, H. and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics **13**:201-228.

Hughes, L. and M. Westoby. 1992. Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. Ecology **73**:1285-1299.

Ibraham, A. M. and D. P. Coyne. 1975. Genetics of stigma shape, cotyledon position, and flower color in reciprocal crosses between *Phaseolus vulgaris* L. and *Phaseolus coccineus* Lam. and implications in breeding. Journal of the American Society of Horticultural Science **100**:622-626.

Inghe, O. 1989. Genet and ramet surviorship under different mortality regimes--a cellular automata model. Journal of Theoretical Biology **138**:257-270.

Jackson, L. L. and C. L. Dewald. 1994. Predicting evolutionary consequences of greater reproductive effort in *Tripsacum dactyloides*, a perennial grass. Ecology **75**:627-641.

Janzen, D. H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. Evolution **23**:1-27.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist **104**:501-528.

Janzen, D. H. 1971. Seed predation by animals. Ann. Rev. Ecol. Syst. **2**:465-492.

Jennersten, O. 1991. Cost of reproduction in Viscaria vulgaris (Caryophyllaceae): a field experiment. Oikos **61**:197-204.

Johansen, J. R., J. Ashley and W. R. Rayburn. 1993. Effects of rangefire on soil algal crusts in semiarid shrub-steppe of the Lower Columbia Basin and their subsequent recovery. Great Basin Naturalist **53**:73-88.

Johnston, M. O. 1991. Pollen limitation of female reproduction in *Lobelia cardinalis* and *L. siphilitica*. Ecology **72**:1500-1503.

Juncosa, A. M. and B. D. Webster. 1989. Pollination in Lupinus nanus subsp. latifolius (Leguminosae). American Journal of Botany **76**:59-66.

Kalisz, S. and M. A. McPeek. 1992. Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. Ecology **73**:1082-1093.

Kareiva, P. 1990. Using models of population spread to analyze the results of field releases. University of California at Davis.

Karoly, K. 1992. Pollinator limitation in the facultatively autogamous annual, *Lupinus nanus* (Leguminosae). American Journal of Botany **79**:49-56.

Kjellberg, F. and G. Valdeyron. 1990. Species-specific pollination: a help of a limitation to range extension? pp. 371-378 *in* F. di Castri, A. J. Hansen and M. Debussche eds. Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers, Dordrecht.

Kornberg, H. and M. H. Williamson. 1986. Quantitative Aspects of the Ecology of Biological Invasions. Philos. Trans. R. Soc. Lond.,

Kot, M. 1992. Discrete-time travelling waves: ecological examples. Journal of Mathematical Biology **30**:413-436.

Kot, M., M. A. Lewis and P. van den Driessche. in press. Dispersal data and the spread of invading organisms.

Kot, M. and W. M. Schaffer. 1986. Discrete-time growth-dispersal models. Mathematical Biosciences **80**:109-136.

Kotanen, P. M. 1993. Revegetation of meadows disturbed by feral pigs (*Sus scrofa* L.) in Mendocino County, California. Ph.D. University of California, Berkeley.

Kruckeberg, A. R. 1991. The Natural History of Puget Sound Country. Edited by University of Washington Press, Seattle.

Kruger, F. J., D. M. Richardson and B. W. v. Wilgen. 1986. Processes of invasion by alien plants. pp. *in* I. A. W. MacDonald, F. J. Kruger and A. A. Ferrar eds. The Ecology and Management of Biological Invasions in Southern Africa. Oxford University Press, New York.

Lang, F. A. 1961. A study of the vegetation change in the gravelly prairies of Pierce ad Thurston Counties, western Washington. M.S. University of Washington.

LaRoe, E. T. 1993. Implementation of an ecosystem approach to endangered species conservation. Endangered Species Update **10**:3-12.

Lawton, J. and K. Brown. 1986. The population and community ecology of invading insects. Philosophical Transactions of the Royal Society of London **B 314**:607-617.

Lehtilä, K., J. Tuomi and M. Sulkinoja. 1994. Bud demography of the mountain birch *Betula pubescens* spp. *tortuosa* near tree line. Ecology **75**:945-955.

Lewis, M. A. a. P. K. 1993. Allee dynamics and the spread of invading organisms. Theoretical Population Biology **43**:141-158.

Lewontin, R. C. 1965. Selection for colonizing ability. pp. 588 *in* H. G. Baker and G. L. Stebbins eds. The Genetics of Colonizing Species. Academic Press, New York.

Londsdale, W. M. 1993. Rates of spread of an invading species--*Mimosa pigra* in northern Australia. Journal of Ecology **81**:513-521.

Louda, S. 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. Ecological Monographs **52**:25-41.

Lubina, J. A. and S. A. Levin. 1988. The spread of a reinvading species: Range expansion of the California sea otter. American Naturalist **133**:526-543.

MacArthur, R. H. and E. O. Wilson. 1967. The Theory of Island Biogeography. Edited by Princeton University Press, Princeton, N. J.

Mack, R. N. 1985. Invading plants: their potential contribution to population biology. pp. 127-142 *in* J. White eds. Studies on Plant Demography: A Festschrift for John L. Harper. Academic Press, London.

MacKauer, M., L. Ehler and J. Roland. 1990. Critical Issues in Biological Control. Edited by Intercept Press, Andover, UK.

Marquis, R. J. 1988. Phenological variation in the neotropical understory shrub Piper arieianum: causes and consequences. Ecology **69**:1552-1565.

Marshall, D. L. and N. C. Ellstrand. 1986. Effective mate choice in wild radish: evidence for selective seed abortion and its mechanism. American Naturalist **131**:739-756.

McCall, C. and R. B. Primack. 1985. Effects of pollen and nitrogen availability on reproduction in a woodland herb, Lysimachia quadrifolia. Oecologia **67**:403-410.

McEvoy, P., N. T. Rudd, C. S. Cox and M. Huso. 1992. Disturbance, competition, herbivory effects on ragwort *Senecio jacobaea* populations: a biological control case study. Ecological Monographs

McPeek, M. A. 1993. Population sampling and bootstrapping in complex designs: demographic analysis. pp. 232-252 *in* S. M. Scheiner and J. Gurevitch eds. Design and Analysis of Ecological Experiments. Chapman & Hall, New York.

Menges, E. S. 1986. Predicting the future of rare plant populations: demographic monitoring and modeling. Natural Areas Journal **6**:13-25.

Menges, E. S. 1990. Population viability analysis for an endangered plant. Cons. Biol. **4**:52-62.

Metting, B. 1991. Biological surface features of semiarid lands and deserts. pp. 257-293 *in* J. Skujins eds. Semiarid Lands and Deserts: Soil Resource and Reclamation. Marcel Dekker, inc., New York.

Montalvo, A. M. and J. D. Ackerman. 1987. Limitations to fruit production in *Ionopsis utricularioides* (Orchidaceae). Biotropica **19**:24-31.

Moody, M. E. and R. N. Mack. 1988. Controlling the spread of plant invasions: the importance of nacent foci. Journal of Applied Ecology **25**:1009-1021.

Mooney, H. A. and J. A. Drake. 1986. Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York.

Moore, R. P. 1973. Tetrazolium staining for assessing seed quality. pp. 347-366 *in* W. Heydecker eds. Seed Ecology. Butterworths, London.

Moulton, M. and S. Pimm. 1986. Species introduction to Hawaii. pp. 231-249 *in* H. A. Mooney and J. A. Drake eds. Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York.

Murali, K. S. 1993. Differential reproductive success in Cassia fistula in different habitats--A case of pollinator limitation? Current Science **65**:270-272.

Neubert, M. G. 1994. The nonlinear dynamics of predator-prey growth and dispersal. Ph.D. University of Washington.

Noble, I. R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. pp. 301-313 *in* J. A. Drake, H. A. Mooney, F. d. Castri, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson eds. Biological Invasions: A Global Perspective. Wiley & Sons, New York.

Noss, R. F., E. T. L. III and J. M. Scott. in press. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation.

O'Connor, R. J. 1986. Biological characteristics of invaders among bird species in Britain. Philosophical Transactions of the Royal Society of London **B 314**:583-598.

Office of Technology Assessment. 1993. Harmful Non-Indigenous Species in the United States. U.S. Congress,

Okubo, A. 1988. Diffusion-type models for avian range expansion. pp. 1038-1049 *in* H. Queslet eds. Acta XIX Congressis Internationalis Ornithologici. University of Ottowa Press, Ottowa, Canada.

Okubo, A., P. K. Maini, M. H. Williamson and J. D. Murray. 1989. On the spatial spread of the grey squirrel in Britain. Proceedings of the Royal Society of London B **23B**:113-125.

Orians, G. H. 1986. Site characteristics favoring invasions. pp. 133-148 *in* H. A. Mooney and J. A. Drake eds. Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York.

Pablo, A. P. and J. L. Vasquez. 1991. Travelling waves and finite propagation in a reaction-diffusion equation. Journal of Differential Equations **93**:19-61.

Parker, I. M. and P. Kareiva. 1996. Assessing the risks of genetically engineered organisms: acceptable evidence and reasonable doubt. Biological Conservation

Parker, I. M., S. K. Mertens and D. W. Schemske. 1993. Distribution of seven native and two exotic plants in a tallgrass prairie in southeastern Wisconsin: The importance of human disturbance. The American Midland Naturalist **130**:43-55.

Pascarella, J. B. and C. C. Horvitz. In Review. Environmental variation and the population dynamics of a tropical shrub: projection matrix analysis. Ecology

Petersson, M. W. 1991. Pollination by a guild of fluctuating moth populations: option for unspecialization in *Silene vulgaris*. Journal of Ecology **79**:591-604.

Piper, J. K. 1992. Size structure and seed yield over 4 years in an experimental *Cassia marilandica* Leguminosae population. Canadian Journal of Botany **70**:1324-1330.

Podolsky, R. D. 1992. Strange floral attractors: Pollinator attraction and the evolution of plant sexual systems. Science **258**:791-793.

Primack, R. B. 1985. Longevity of individual flowers. Annual Review of Ecology and Systematics **16**:15-38.

Primack, R. B. and P. Hall. 1990. Costs of reproduction in the Pink Lady Slipper orchid: a four-year experimental study. American Naturalist **136**:638-656.

Primack, R. B., S. L. Miao and K. R. Becker. 1994. Costs of reproduction in the pink lady's slipper orchid (Cypripedium acaule): Defoliation, increased fruit production, ad fire. American Journal of Botany **81**:1083-1090.

Rathcke, B. 1988. Interactions for pollinations among coflowering shrubs. Ecology **69**:446-457.

Rathcke, B. and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics **16**:179-214.

Real, L. A. and B. J. Rathcke. 1991. Individual variation in nectar production and its effect on fitness in *Kalmia latifolia*. Ecology **72**:149-155.

Reichard, S. E. 1994. Assessing the potential of invasiveness in woody plants introduced to North America. PhD. University of Washington.

Reifner, R. E. and P. A. Bowler. 1995. Cushion-like fruticose lichens as Dudleya seed traps and nurseries in coastal communities. Madrono **42**:81-82.

Rice, B. and M. W. Westoby. 1986. Evidence against the hypothesis that ant-dispersed seeds reach nutrient-enriched microsites. Ecology **67**:1270-1274.

Roubik, D. W., J. E. Moreno, C. Vergara and D. Wittman. 1986. Sporadic food competition with the African honey bee: projected impact on neotropical social bees. Journal of Tropical Ecology **2**:97-111.

Roy, J. 1990. In search of the characteristics of plant invaders. pp. 335-352 *in* F. d. Castro, J. Hansen and M. Debussche eds. Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers, Netherlands.

Ruesink, J., I. M. Parker, M. J. Groom and P. Kareiva. 1995. Reducing the risks of nonindigenous species introductions: guilty until proven innocent. Bioscience **45**:465-477.

Schemske, D. W. 1977. Flowering phenology and seed set in Claytonia virginica (Portulacaceae). Bulletin of the Torrey Botanical Club **104**:254-263.

Schemske, D. W. 1984. Population structure and local selection in *Impatiens pallida* (Balsaminaceae), a selfing annual. Evolution **38**:817-832.

Schemske, D. W. and C. C. Horvitz. 1988. Plant-animal interactions and fruit produciton in a neotropical herb: a path analysis. Ecology **69**:1128-1137.

Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, C. Goodwillie, I. M. Parker and J. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. Ecology **75**:584-606.

Schemske, D. W., M. F. Willson, M. N. Melampy, L. J. Miller, L. Verner, K. M. Schemske and L. B. Best. 1978. Flowering ecology of some spring woodland herbs. Ecology **59**:351-366.

Schlichting, C. D. and B. Devlin. 1992. Pollen and ovule sources affect seed production of *Lobelia cardinalis* (Lobeliaceae). American Journal of Botany **79**:891-898.

Schofield, E. K. 1989. Effects of introduced plants ad animals on island vegetation: examples from the Galápagos archipelago. Conservation Biology **3**:

Scorza, R. 1983. Ecology and genetics of exotics. pp. 219-238 *in* Wilson and Graham eds. Exotic Plant Pests and North American Agriculture.

Selleck, G. W., R. T. Coupland and C. Frankton. 1962. Leafy spurge in Saskatchewan. Ecological Monographs **32**:1-29.

Sharples, F. E. 1983. Spread of organisms with novel genotypes: thoughts for an ecological perspective. Recombinant DNA Technical Bulletin **6**:43-56.

Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. Edited by McGraw-Hill, New York.

Silverman, B. W. 1986. Density Estimation for Statistics and Data Analysis. Edited by Chapman and Hall, New York.

Silvertown, J. 1991. Dorothy's dilemma and the unification of plant population biology. Trends in Ecology and Evolution **6**:346-347.

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. Journal of Ecology **81**:4465-476.

Silvertown, J., S. Holtier, J. Johnson and P. Dale. 1992. Cellular automaton models of interspecific competition for space--the effect of pattern on process. Journal of Ecology **80**:527-534.

Silvertown, J. W. 1987. Introduction to Plant Population Ecology. Edited by Longman, London.

Simberloff, D. 1986. Introduced insects: a biogeographic and systematic perspective. pp. 3-26 *in* H. A. Mooney and J. A. Drake eds. Ecology of Biological Invasions of North American and Hawaii. Springer-Verlag, New York.

Skellam, J. 1951. Random Dispersal in Theoretical Populations. Biometrika **38**:196-218.

Snow, A. A. and D. F. Whigham. 1989. Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). Ecology **70**:1286-1293.

St. Clair, L. L., B. L. Webb, J. R. Johansen and G. T. Nebeker. 1984. Cryptogamic soil crusts: enhancement of seedling establishment in disturbed and undisturbed areas. Reclamation and Revegetation Research **3**:129-136.

Stamp, N. E. and J. R. Lucas. 1983. Ecological correlates of explosive seed dispersal. Oecologia **59**:272-278.

Stamp, N. E. and J. R. Lucas. 1990. Spatial patterns and dispersal distances of explosively dispersing plants in florida sandhill vegetation. Journal of Ecology **78**:589-600.

Stanton, M. L., J. K. Bereczky and H. D. Hasbrouck. 1987. Pollination thoroughness and maternal yield regulation in wild radish *Raphanus raphanistrum* Brassicaceae. Oecologia **74**:68-76.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annual Review of Ecology and Systematics **12**:253-279.

Swaine, M. D. and T. Beer. 1977. Explosive seed dispersal in *Hura crepitans* L. (Euphorbiaceae). New Phytologist **78**:695-708.

Taylor, S. E. and B. H. Walker. 1984. Autecology of an invading population of the cactus *Cereus peruvianus* (Queen of the Night) in the central Transvaal. South African Journal of Botany **3**:387-396.

Thompson, J. N. 1994. The Coevolutionary Process. Edited by University of Chicago Press, Chicago.

Tilton, V. R., L. W. Wilcox, R. G. Palmer and M. C. Albertson. 1984. Stigma, style, and obturator of soybean, Glycine max (L.) Merr (Leguminosae) and their function in the reproductive process. American Journal of Botany **71**:676-686.

Townsend, C. R. 1996. Ecological and evolutionary effects of an invader on its receiving community: the case of brown trout (*Salmo trutta*) in New Zealand. Ecology **in press**:

Usher, M. B., T. J. Crawford and J. L. Banwell. 1992. An American invasion of Great Britain: the case of the native and alien squirrel (*Sciurus*) species. Conservation Biology **6**:108-115.

Valentine, D. H. 1978. The pollination of introduced species with special reference to the British Isles and the genus *Impatiens*. pp. 117-121 *in* A. J. Richards eds. Pollination of flowers by insects (Linn. Soc. Symp. Ser. 6). Academic Press, London.

van Tongeren, O. and I. C. Prentice. 1986. A spatial simulation model for vegetation dynamics. Vegetatio **65**:163-173.

von Broembsen, S. L. 1989. Invasions of natural ecosystems by plant pathogens. pp. 77-83 *in* J. A. Drake, H. A. Mooney, F. d. Castri, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson eds. Biological Invasions: A Global Perspective. Wiley & Sons, New York.

Waser, N. M. 1978. Competition for hummingbird pollination and sequential flowering in Colorado wildflowers. Ecology **59**:934-944.

Watson, M. A. and B. B. Casper. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. Annual Review of Ecology and Systematics **15**:233-258.

Weinberger, H. F. 1978. Asymptotic behavior of a model of population genetics. pp. 47-98 *in* J. Chadam eds. Nonlinear Partial Differential Equations and Applications. Springer-Verlag, New York.

Weiner, J. and P. T. Conte. 1981. Dispersal and neighborhood effects in an annual plant competition model. Ecological Modelling **13**:131-147.

Werner, P. A. and H. Caswell. 1977. Population growth rates and age vs. stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). Ecology **48**:1103-1111.

White, P. S. and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. pp. 3-13 *in* S. T. A. Pickett and P. S. White eds. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, Florida.

Widén, B. and M. Widén. 1990. Pollen limitation and distance-dependent fecundity in females of the clonal gynodioecious herb *Glechoma hederaceae* (Lamiaceae). Oecologia **83**:191-196.

Williamson, M. 1994. Community response to transgenic plant release: predictions from British experience of invasive plants and feral crop plants. Molecular Ecology **3**:75-79.

Wolfram, S. 1983. Statistical mechanics of cellular automata. Reviews of Modern Physics **55**:601-643.

Wolfram, S. 1984. Computer software in science and mathematics. Scientific American **251**:188-203.

Wood, D. M. and M. C. Anderson. 1990. The effect of predispersal seed predators on colonization of *Aster ledophyllus* on Mount St. Helens, Washington. Am. Midl. Nat. **123**:193-201.

Young, H. J. and T. P. Young. 1992. Alternative outcomes of natural and experimental high pollen loads. Ecology **73**:639-647.

Youngman, B. J. 1951. Germination of old seeds. Kew Bulletin **23**:423-426.

Zar, J. H. 1984. Biostatistical analysis. 2nd ed. Edited by Prentice-Hall, Inc., Englewood Cliffs, NJ.

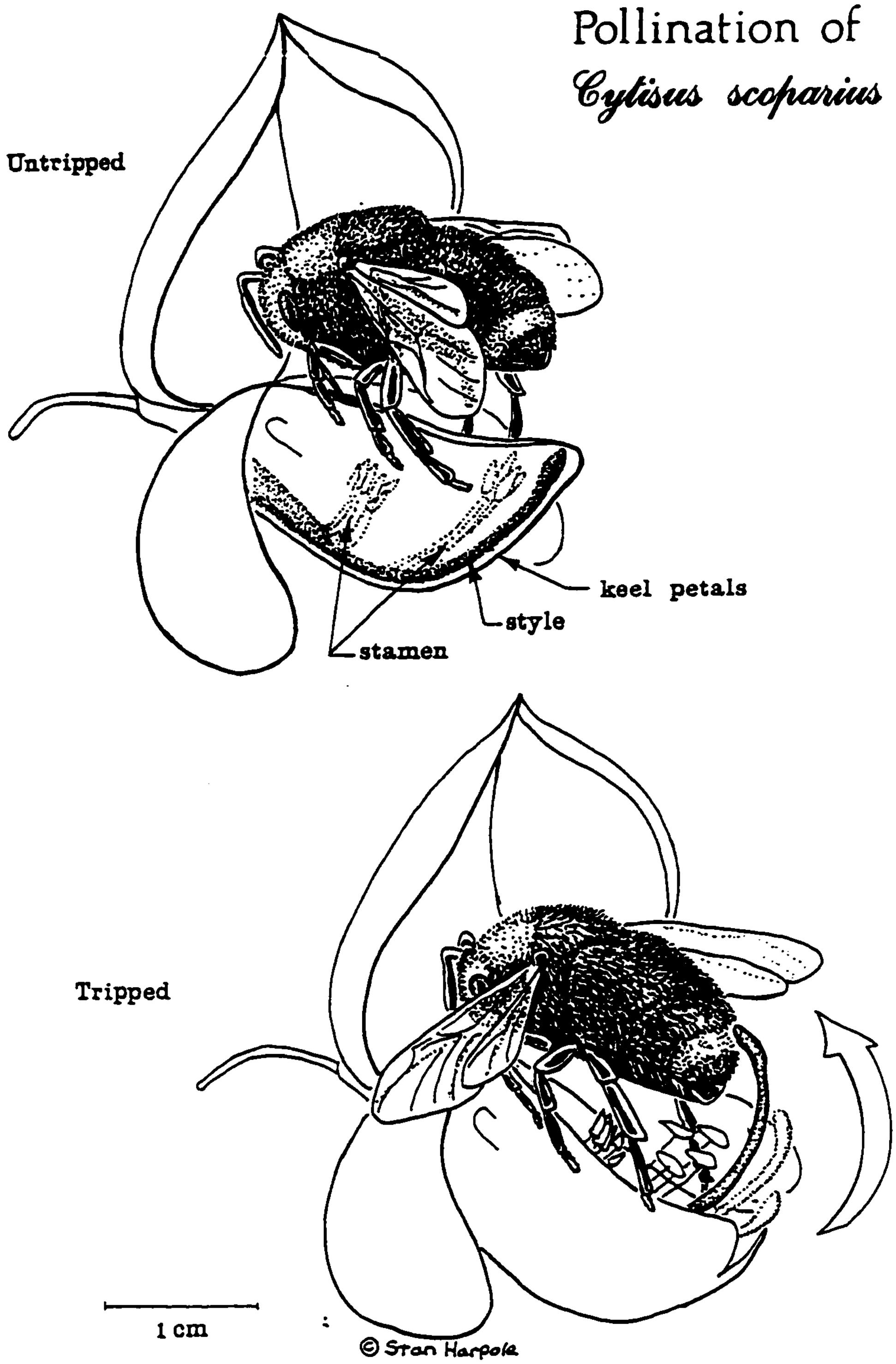
Zimmerman, J. K. and T. M. Aide. 1989. Patterns of fruit production in a neotropical orchid: pollinator vs. resource limitation. American Journal of Botany **76**:67-73.

Zimmerman, M. 1980. Reproduction in Polemonium: competition for pollinators. Ecology **61**:497-501.

Zimmerman, M. and G. H. Pyke. 1988. Reproduction in *Polemonium*: assessing the factors limiting seed set. American Naturalist **131**:723-738.

APPENDIX 1:

Pollination of *Cytisus scoparius*



APPENDIX 2: TRANSITION MATRICES FOR EACH POPULATION, STAGE OF INVASION, AND YEAR

Numbers of individuals in parentheses below each stage class.
Elasticities in parentheses below each transition.

JOHNSON PRAIRIE, LOW DENSITY PLOT, 1993-94.

	Seeds	Seedlings (18)	Juveniles (40)	Small adults (33)	Medium adults (17)	Large adults (22)	X-large adults (38)
Seeds	0.45 (0.056)	–	19.0 (0.006)	161.2 (0.016)	461.4 (0.048)	611.5 (0.026)	1094.2 (0.079)
Seedlings	0.014 (0.174)	0.11 (0.011)	–	–	–	–	–
Juveniles	–	0.50 (0.149)	0.15 (0.013)	–	–	–	–
Small adults	–	0.056 (0.025)	0.35 (0.046)	–	–	–	–
Medium adults	–	–	0.32 (0.069)	0.61 (0.042)	0.29 (0.021)	–	–
Large adults	–	–	0.075 (0.020)	0.15 (0.013)	0.24 (0.021)	0.36 (0.013)	–
X-large adults	–	–	0.025 (0.008)	0.030 (0.003)	0.35 (0.040)	0.59 (0.028)	0.84 (0.067)

JOHNSON PRAIRIE, MEDIUM DENSITY PLOT, 1993-94.

	Seeds	Seedlings (44)	Juveniles (50)	Small adults (4)	Medium adults (5)	Large adults (12)	X-large adults (37)
Seeds	0.45 (0.050)	–	7.2 (0.002)	21.0 (0.002)	57.6 (0.006)	313.2 (0.027)	877.2 (0.086)
Seedlings	0.0081 (0.122)	0.36 (0.037)	–	–	–	–	–
Juveniles	–	0.52 (0.122)	0.32 (0.032)	–	–	–	–
Small adults	–	–	0.28 (0.038)	0.24 [0.25] (0.007)	–	–	–
Medium adults	–	–	0.26 (0.059)	0.75 (0.037)	0.13 [0] (0.010)	0.071 [0.08] (0.005)	0.015 [0.03] (0.001)
Large adults	–	–	0.04 (0.013)	–	0.69 [0.8] (0.072)	0.50 (0.046)	0.054 (0.006)
X-large adults	–	–	0.02 (0.010)	–	0.17 [0.2] (0.027)	0.42 (0.059)	0.92 (0.157)

JOHNSON PRAIRIE, HIGH DENSITY PLOT, 1993-94.

	Seeds	Seedlings (107)	Juveniles (10)	Small adults (12)	Medium adults (29)	Large adults (26)	X-large adults (26)
Seeds	0.45 (0.0002)	–	–	36.5 ($6.3x10^{-8}$)	117.8 ($4.5x10^{-8}$)	483.4 ($9.6x10^{-8}$)	1057.9 (0.0002)
Seedlings	0.0011 (0.0002)	0.065 (0.00001)	–	–	–	–	–
Juveniles	–	0.009 (0.0002)	0.40 (0.0001)	–	–	–	–
Small adults	–	–	0.10 (0.0002)	0.58 (0.0003)	0.034 ($3.5x10^{-6}$)	0.038 (0)	–
Medium adults	–	–	–	0.083 (0.0002)	0.52 (0.0002)	0.15 (0.00004)	–
Large adults	–	–	–	–	0.21 (0.0002)	0.58 (0.0003)	–
X-large adults	–	–	–	–	–	0.15 (0.0002)	0.97 [1] (0.997)

DISCOVERY PARK, LOW DENSITY PLOT, 1993-94.

	Seeds	Seedlings (26)	Juveniles (29)	Small adults (41)	Medium adults (34)	Large adults (15)	X-large adults (11)
Seeds	0.74 (0.134)	–	3.4 (0.0003)	47.1 (0.002)	108.7 (0.003)	1120 (0.022)	3339 (0.059)
Seedlings	0.001 (0.086)	0.31 (0.029)	–	–	–	–	–
Juveniles	–	0.35 (0.070)	0.31 (0.024)	0.024 (0.0009)	–	–	–
Small adults	–	0.038 (0.016)	0.29 (0.049)	0.39 (0.031)	–	–	–
Medium adults	–	–	0.069 (0.021)	0.44 (0.063)	0.32 (0.032)	–	0.091 (0.006)
Large adults	–	–	–	–	0.44 (0.080)	0.53 (0.070)	0.091 (0.011)
X-large adults	–	–	–	–	0.029 (0.007)	0.40 (0.069)	0.73 (0.114)

DISCOVERY PARK, MEDIUM DENSITY PLOT, 1993-94.

	Seeds	Seedlings (18)	Juveniles (24)	Small adults (57)	Medium adults (45)	Large adults (20)	X-large adults (11)
Seeds	0.74 (0.010)	–	3.2 (4.4×10^{-8})	27.7 (4.4×10^{-7})	97.0 (1.2×10^{-6})	396 (0.0002)	1284 (0.002)
Seedlings	0.00001 (0.002)	0.11 (0.0003)	–	–	–	–	–
Juveniles	–	0.056 (0.002)	0.12 (0.0003)	–	–	–	–
Small adults	–	–	0.29 (0.002)	0.63 (0.005)	0.022 (0.0002)	–	–
Medium adults	–	–	–	0.30 (0.002)	0.53 (0.003)	–	–
Large adults	–	–	–	–	0.31 (0.002)	0.55 (0.110)	0.091 (0.068)
X-large adults	–	–	–	–	0.022 (0.0002)	0.30 (0.070)	0.82 (0.718)

DISCOVERY PARK, HIGH DENSITY PLOT, 1993-94.

	Seeds	Seedlings (14)	Juveniles (16)	Small adults (20)	Medium adults (33)	Large adults (20)	X-large adults (31)
Seeds	0.74 (0.004)	–	–	19.2 (2.6×10^{-7})	201.6 (1.6×10^{-6})	548.8 (2.6×10^{-5})	2173 (0.001)
Seedlings	1.9×10^{-5} (0.001)	0.21 (0.0003)	–	–	–	–	–
Juveniles	–	0.14 (0.001)	0.38 (0.0007)	–	–	–	–
Small adults	–	–	0.19 (0.001)	0.55 (0.001)	–	–	–
Medium adults	–	–	–	0.10 (0.001)	0.48 (0.003)	0.05 (0.002)	–
Large adults	–	–	–	–	0.27 (0.003)	0.60 (0.042)	0.032 (0.022)
X-large adults	–	–	–	–	–	0.25 (0.024)	0.94 (0.892)

JOHNSON PRAIRIE, LOW DENSITY PLOT, 1994-95.

	Seeds	Seedlings (96)	Juveniles (34)	Small adults (20)	Medium adults (40)	Large adults (21)	X-large adults (54)
Seeds	0.45 (0.046)	-	12.6 (0.003)	162.0 (0.008)	1043 (0.048)	1655 (0.034)	3956 (0.058)
Seedlings	0.031 (0.151)	0.47 (0.049)	-	-	-	-	-
Juveniles	-	0.17 (0.151)	0.18 (0.016)	-	-	-	-
Small adults	-	-	0.41 (0.069)	0.20 (0.008)	0.025 (0.0009)	-	-
Medium adults	-	-	0.18 (0.064)	0.65 (0.055)	0.32 (0.025)	0.048 (0.002)	0.037 (0.001)
Large adults	-	-	0.029 (0.015)	0.05 (0.006)	0.52 (0.060)	0.33 (0.017)	0.037 (0.001)
X-large adults	-	-	-	-	0.075 (0.014)	0.57 (0.047)	0.89 (0.052)

JOHNSON PRAIRIE, MEDIUM DENSITY PLOT, 1994-95.

	Seeds	Seedlings (148)	Juveniles (65)	Small adults (15)	Medium adults (18)	Large adults (15)	X-large adults (41)
Seeds	0.45 (0.045)	-	0.74 (0.001)	10.8 (0.003)	21.0 (0.014)	57.0 (0.008)	559.2 (0.052)
Seedlings	0.028 (0.078)	0.61 (0.076)	-	-	-	-	-
Juveniles	-	0.16 (0.078)	0.62 (0.078)	-	-	-	-
Small adults	-	-	0.22 (0.038)	0.40 (0.018)	-	-	-
Medium adults	-	-	0.14 (0.040)	0.47 (0.034)	0.78 (0.13)	-	0.007 (0.0002)
Large adults	-	-	-	-	0.17 (0.060)	0.40 (0.030)	0.049 (0.0024)
X-large adults	-	-	-	-	-	0.20 (0.054)	0.93 (0.16)

JOHNSON PRAIRIE, HIGH DENSITY PLOT, 1994-95.

	Seeds	Seedlings (31)	Juveniles (5)	Small adults (10)	Medium adults (20)	Large adults (21)	X-large adults (30)
Seeds	0.45 (0.001)	–	–	9.1 ($2.3x10^{-6}$)	52.8 ($4.0x10^{-6}$)	159.6 ($5.1x10^{-5}$)	605.7 (0.001)
Seedlings	0.0086 (0.001)	0.19 (0.0003)	–	–	–	–	–
Juveniles	–	0.032 (0.001)	0.20 (0.0004)	–	–	–	–
Small adults	–	–	0.13 [0] (0.001)	0.20 (0.0004)	–	–	–
Medium adults	–	–	–	0.067 [0] (0.001)	0.30 (0.002)	0.095 (0.002)	–
Large adults	–	–	–	–	0.25 (0.004)	0.43 (0.027)	0.067 (0.028)
X-large adults	–	–	–	–	–	0.19 (0.029)	0.90 (0.90)

13TH DIVISION PRAIRIE, LOW DENSITY PLOT, 1994-95.

	Seeds	Seedlings (86)	Juveniles (64)	Small adults (29)	Medium adults (33)	Large adults (21)	X-large adults (13)
Seeds	0.40 (0.040)	–	5.5 (0.014)	36.4 (0.014)	134.4 (0.038)	403.3 (0.051)	472.5 (0.020)
Seedlings	0.052 (0.14)	0.16 (0.014)	–	–	–	–	–
Juveniles	–	0.79 (0.13)	0.75 (0.096)	–	–	–	–
Small adults	–	0.017 (0.010)	0.20 (0.091)	0.30 (0.021)	–	–	–
Medium adults	–	–	0.028 (0.023)	0.69 (0.086)	0.54 (0.048)	–	–
Large adults	–	–	–	–	0.46 (0.071)	0.71 (0.049)	0.070 (0.002)
X-large adults	–	–	–	–	–	0.29 (0.022)	0.92 (0.024)

13TH DIVISION PRAIRIE, MEDIUM DENSITY PLOT, 1994-95.

	Seeds	Seedlings (65)	Juveniles (38)	Small adults (33)	Medium adults (61)	Large adults (24)	X-large adults (8)
Seeds	0.40 (0.040)	-	2.6 (0.001)	29.5 (0.004)	195.0 (0.020)	639.2 (0.022)	1675 (0.040)
Seedlings	0.008 (0.088)	0.34 (0.030)	-	-	-	-	-
Juveniles	-	0.46 (0.088)	0.50 (0.052)	-	-	-	-
Small adults	-	-	0.29 (0.087)	0.48 (0.049)	-	-	-
Medium adults	-	-	-	0.42 (0.083)	0.77 (0.11)	-	-
Large adults	-	-	-	-	0.21 (0.063)	0.73 (0.074)	-
X-large adults	-	-	-	-	-	0.25 (0.040)	0.98 (0.11)

WEIR PRAIRIE, LOW DENSITY PLOT, 1994-95.

	Seeds	Seedlings (56)	Juveniles (107)	Small adults (47)	Medium adults (22)	Large adults (11)	X-large adults (10)
Seeds	0.42 (0.042)	-	0.21 (0.0006)	3.1 (0.002)	82.2 (0.052)	147.2 (0.022)	401.3 (0.031)
Seedlings	0.069 (0.11)	0.52 (0.057)	-	-	-	-	-
Juveniles	-	0.38 (0.11)	0.61 (0.073)	-	-	-	-
Small adults	-	-	0.23 (0.069)	0.60 (0.046)	-	-	-
Medium adults	-	-	0.056 (0.038)	0.38 (0.067)	0.73 (0.10)	0.15 [0.18] (0.005)	-
Large adults	-	-	-	-	0.23 (0.058)	0.54 (0.033)	-
X-large adults	-	-	-	-	-	0.27 (0.031)	0.97 [1.0] (0.056)

WEIR PRAIRIE, MEDIUM DENSITY PLOT, 1994-95.

	Seeds	Seedlings (65)	Juveniles (40)	Small adults (37)	Medium adults (39)	Large adults (17)	X-large adults (18)
Seeds	0.42 (0.039)	–	11.2 (0.004)	36.3 (0.005)	146.5 (0.025)	329.3 (0.018)	1029.6 (0.016)
Seedlings	0.017 (0.067)	0.52 (0.055)	–	–	–	–	–
Juveniles	–	0.077 (0.067)	0.65 (0.087)	–	–	–	–
Small adults	–	–	0.12 (0.037)	0.78 (0.082)	0.014 [**0.026**] (0.002)	–	–
Medium adults	–	–	0.05 (0.026)	0.19 (0.034)	0.87 (0.20)	0.06 (0.0044)	–
Large adults	–	–	–	–	0.10 (0.038)	0.82 (0.097)	0.044 [**0.056**]
X-large adults	–	–	–	–	–	0.06 (0.017)	0.94 (0.078)

DISCOVERY PARK, LOW DENSITY PLOT, 1994-95.

	Seeds	Seedlings (14)	Juveniles (25)	Small adults (30)	Medium adults (32)	Large adults (24)	X-large adults (15)
Seeds	0.74 (0.13)	–	3.3 (0.0003)	19.8 (0.002)	76.8 (0.002)	57.8 (0.0008)	2510 (0.057)
Seedlings	0.0013 (0.062)	0.048 [0] (0.003)	–	–	–	–	–
Juveniles	–	0.36 (0.062)	0.20 (0.014)	–	–	–	–
Small adults	–	–	0.52 (0.062)	0.60 (0.078)	0.031 (0.001)	–	–
Medium adults	–	–	–	0.13 (0.061)	0.56 (0.065)	–	–
Large adults	–	–	–	–	0.28 (0.058)	0.54 (0.057)	–
X-large adults	–	–	–	–	–	0.38 (0.057)	0.87 (0.23)

DISCOVERY PARK, MEDIUM DENSITY PLOT, 1994-95.

	Seeds	Seedlings (3)	Juveniles (4)	Small adults (44)	Medium adults (41)	Large adults (24)	X-large adults (16)
Seeds	0.74 (0.012)	–	0 –	19.2 (1.9×10^{-6})	147.8 (5.9×10^{-6})	267.6 (5.0×10^{-6})	2271 (0.003)
Seedlings	0.00007 (0.003)	0.21 [0] (0.001)	–	–	–	–	–
Juveniles	–	0.21 [0] (0.003)	0.16 [0] (0.0007)	–	–	–	–
Small adults	–	–	0.16 [0] (0.003)	0.25 (0.0012)	–	–	–
Medium adults	–	–	–	0.20 (0.003)	0.44 (0.003)	–	–
Large adults	–	–	–	–	0.24 (0.003)	0.42 (0.003)	–
X-large adults	–	–	–	–	–	0.25 (0.003)	0.94 (0.96)

DISCOVERY PARK, HIGH DENSITY PLOT, 1994-95.

	Seeds	Seedlings (4)	Juveniles (8)	Small adults (14)	Medium adults (19)	Large adults (22)	X-large adults (34)
Seeds	0.74 (0.006)	–	–	16.8 (3.0×10^{-6})	121.6 (3.0×10^{-6})	353.6 (1.0×10^{-6})	2189 (0.001)
Seedlings	0.00029 (0.001)	0.16 [0] (0.0002)	–	–	–	–	–
Juveniles	–	0.16 [0] (0.001)	0.08 [0] (0.0001)	–	–	–	–
Small adults	–	–	0.12 (0.001)	0.43 (0.001)	–	–	–
Medium adults	–	–	–	0.07 (0.001)	0.37 (0.0008)	–	–
Large adults	–	–	–	–	0.053 (0.001)	0.45 (0.001)	–
X-large adults	–	–	–	–	–	0.18 (0.001)	0.88 (0.98)

MAGNUSON PARK, LOW DENSITY PLOT, 1994-95.

	Seeds	Seedlings (43)	Juveniles (76)	Small adults (20)	Medium adults (22)	Large adults (17)	X-large adults (13)
Seeds	0.72 (0.12)	–	0.4 (0.00003)	41.8 (0.0012)	112.3 (0.0032)	563.0 (0.007)	3728 (0.064)
Seedlings	0.00058 (0.075)	0.12 (0.008)	–	–	–	–	–
Juveniles	–	0.66 (0.075)	0.428 (0.042)	–	–	–	–
Small adults	–	–	0.33 (0.062)	0.30 (0.021)	–	–	–
Medium adults	–	–	0.055 (0.014)	0.55 (0.051)	0.50 (0.047)	–	–
Large adults	–	–	–	0.05 (0.010)	0.32 (0.061)	0.29 (0.023)	–
X-large adults	–	–	–	–	–	0.35 (0.064)	0.95 [1] (0.25)

MAGNUSON PARK, MED DENSITY PLOT, 1994-95.

	Seeds	Seedlings (70)	Juveniles (76)	Small adults (57)	Medium adults (30)	Large adults (9)	X-large adults (10)
Seeds	0.72 (0.095)	–	1.6 (0.0002)	87.1 (0.003)	620.2 (0.013)	2977 (0.024)	8177 (0.039)
Seedlings	0.0016 (0.080)	0.46 (0.042)	–	–	–	–	–
Juveniles	–	0.30 (0.080)	0.62 (0.069)	–	–	–	–
Small adults	–	–	0.25 (0.057)	0.65 (0.056)	0.03 (0.002)	–	–
Medium adults	–	–	0.04 (0.022)	0.26 (0.056)	0.67 (0.078)	–	–
Large adults	–	–	–	–	0.23 (0.064)	0.74 (0.079)	–
X-large adults	–	–	–	–	–	0.22 (0.039)	0.96 (0.102)

MONTLAKE FILL, LOW DENSITY PLOT, 1994-95.

	Seeds	Seedlings (29)	Juveniles (63)	Small adults (26)	Medium adults (25)	Large adults (14)	X-large adults (7)
Seeds	0.73 (0.11)	-	2.4 (0.0002)	51.6 (0.004)	277.8 (0.018)	716.3 (0.009)	1993 (0.018)
Seedlings	0.0069 (0.049)	0.52 (0.047)	-	-	-	-	-
Juveniles	-	0.14 (0.049)	0.70 (0.10)	0.038 (0.005)	-	-	-
Small adults	-	-	0.25 (0.049)	0.77 (0.13)	-	-	-
Medium adults	-	-	0.016 (0.005)	0.15 (0.04)	0.84 (0.19)	0.07 (0.003)	-
Large adults	-	-	-	-	0.08 (0.030)	0.64 (0.046)	-
X-large adults	-	-	-	-	-	0.14 (0.018)	0.86 (0.08)

MONTLAKE FILL, MED DENSITY PLOT, 1994-95.

	Seeds	Seedlings (24)	Juveniles (22)	Small adults (32)	Medium adults (25)	Large adults (14)	X-large adults (26)
Seeds	0.73 (0.061)	-	6.4 (9.6×10^{-6})	95.7 (0.0001)	274.0 (0.0002)	447.2 (0.0003)	4074 (0.02)
Seedlings	0.00002 (0.022)	0.54 (0.026)	-	-	-	-	-
Juveniles	-	0.17 (0.022)	0.64 (0.038)	-	-	-	-
Small adults	-	-	0.27 (0.022)	0.66 (0.042)	-	-	-
Medium adults	-	-	-	0.19 (0.022)	0.64 (0.039)	-	-
Large adults	-	-	-	-	0.32 (0.022)	0.64 (0.039)	-
X-large adults	-	-	-	-	-	0.31 (0.02)	0.96 (0.60)

APPENDIX 3a. Species lists for native plants in the six sites where demographic plots were established for *Cytisus scoparius*. This list only includes species that were found within the boundaries of the plots themselves. Data collected by W.S. Harpole and D. Dionne in August/September of 1995.

Species	Johnson Prairie	13th Division Prairie	Weir Prairie	Discovery Park	Magnuson Park	Montlake Fill
Lichen spp.	X		X			
Moss spp.	X	X	X	X	X	X
Acer glabrum				X		
Apocynum androsaemifolium			X			
Achillea millefolium	X			X		X
Anaphalis margaritaceae	X					
Aster curtis	X					
Aster hesperius		X				
Aster occidentalis	X					
Eriophyllum lanatum	X		X			
Solidago canadensis	X					
Solidago nemoralis			X			
Cerastium sp.				X		
Lupinus latifolius					X	
Lupinus sp.			X			
Juncus effusus						X
Prunella vulgaris	X					
Camassia quamash			X			
Epilobium minutum						X
Pseudotsuga menziesii	X	X	X			
Danthonia californica		X				
Festuca idahoensis	X		X			
Panicum occidentale			X			
Poa compressa		X				
Pteridium aquilinum	X					
Fragaria vesca	X		X			
Potentilla gracilis	X					

APPENDIX 3b. Species lists for exotic plants in the six sites where demographic plots were established for *Cytisus scoparius*. This list only includes species that were found within the boundaries of the plots themselves. Data collected by W.S. Harpole and D. Dionne in August/September of 1995.

Species	Johnson Prairie	13th Division Prairie	Weir Prairie	Discovery Park	Magnuson Park	Montlake Fill
Daucus carota					X	X
Hedera helix					X	X
Chrysanthemum leucanthemum	X	X	X		X	X
Cichorium intybus						X
Cirsium arvense		X				X
Hypochaeris radicata	X	X	X	X	X	X
Tragopogon dubius		X				
Tragopogon porriflius						X
Dianthus armeria	X					
Silene noctiflora	X					
"Fuzzy Pink"					X	
Medicago sativa						X
Robinia pseudo-acacia				X		
Trifolium dubium				X	X	X
Trifolium pratense	X				X	X
Trifolium sp.				X		
Vicia sp.				X	X	X
Centaurium umbellatum						X
Hypericum perforatum	X	X	X	X		
Mentha spicata		X				
Plantago lanceolata	X	X	X	X	X	X

(continued)

APPENDIX 3b. Exotic species list, continued.

Species	Johnson Prairie	13th Division Prairie	Weir Prairie	Discovery Park	Magnuson Park	Montlake Fill
Agropyron repens	X			X	X	X
Agrostis alba					X	X
Agrostis tenuis	X	X	X	X	X	X
Bromus rigidus				X	X	
Bromus tectorum		X		X	X	X
Dactylis glomerata				X		X
Festuca arundinaceae				X	X	X
Grass sp.1					X	
Grass sp.2		X				
Grass sp.fl.				X		
Holcus lanatus	X		X	X	X	X
Holcus mollis				X		
Phalaris arundinaceae					X	
Phleum pratense		X				
Rumex acetosella	X	X		X		X
Rumex crispus				X	X	X
Ranunculus repens						X
Crataegus monogyna						X
Rubus discolor				X	X	
Galium parisiense		X				
Populus sp.				X		

APPENDIX 4: DEMOGRAPHIC TRANSITIONS (IN MATRIX FORM) USED FOR SPATIAL SIMULATION MODEL.

Numbers of individuals per stage in parentheses under stage class, elasticities in parenthesis under value of the transition.

Johnson Prairie (early), 1993-94

	Seeds	Seedlings (18)	Juveniles (40)	Adults (110)
Seeds	0.45 (0.061)	-	19.0 (0.006)	619.9 (0.19)
Seedlings	0.014 (0.20)	0.11 (0.012)	-	-
Juveniles	-	0.50 (0.16)	0.15 (0.014)	-
Adults	-	0.056 (0.038)	0.77 (0.15)	0.89 (0.17)

Discovery Park (early), 1993-94

	Seeds	Seedlings (18)	Juveniles (40)	Adults (101)
Seeds	0.74 (0.20)	-	3.4 (0.0005)	585.7 (0.11)
Seedlings	0.0010 (0.11)	0.31 (0.041)	-	-
Juveniles	-	0.35 (0.090)	0.31 (0.033)	-
Adults	-	0.038 (0.023)	0.36 (0.090)	0.84 (0.30)

Johnson Prariie (early), 1994-95

	Seeds	Seedlings (96)	Juveniles (34)	Adults (135)
Seeds	0.45 (0.048)	-	12.6 (0.002)	2172.9 (0.18)
Seedlings	0.031 (0.19)	0.47 (0.051)	-	-
Juveniles	-	0.17 (0.19)	0.18 (0.017)	-
Adults	-	-	0.62 (0.18)	0.95 (0.14)

13th Division Prairie (early), 1994-95

	Seeds	Seedlings (86)	Juveniles (64)	Adults (96)
Seeds	0.40 (0.046)	-	5.5 (0.014)	209.4 (0.16)
Seedlings	0.052 (0.17)	0.16 (0.016)	-	-
Juveniles	-	0.79 (0.16)	.75 (0.11)	-
Adults	-	0.017 (0.015)	0.23 (0.14)	0.99 (0.18)

Weir Prairie (early), 1994-95

	Seeds	Seedlings (56)	Juveniles (107)	Adults (90)
Seeds	0.42 (0.052)	-	0.21 (0.0007)	84.3 (0.14)
Seedlings	0.069 (0.14)	0.52 (0.070)	-	-
Juveniles	-	0.38 (0.14)	0.61 (0.089)	-
Adults	-	-	0.29 (0.14)	0.98 (0.23)

Discovery Park (early), 1994-95

	Seeds	Seedlings (14)	Juveniles (25)	Adults (101)
Seeds	0.74 (0.21)	-	3.3 (0.0004)	416.7 (0.11)
Seedlings	0.0013 (0.11)	0.048 [0] (0.005)	-	-
Juveniles	-	0.36 (0.11)	0.20 (0.024)	-
Adults	-	-	0.52 (0.11)	0.84 (0.33)

Magnuson Park (early), 1994-95

	Seeds	Seedlings (43)	Juveniles (76)	Adults (78)
Seeds	0.72 (0.18)	-	0.4 (0.00005)	41.8 (0.11)
Seedlings	0.00058 (0.11)	0.12 (0.013)	-	-
Juveniles	-	0.66 (0.11)	0.43 (0.066)	-
Adults	-	-	0.38 (0.11)	0.83 (0.28)

Montlake Fill (early), 1994-95

	Seeds	Seedlings (29)	Juveniles (63)	Adults (72)
Seeds	0.73 (0.15)	-	2.4 (0.0002)	448.1 (0.069)
Seedlings	0.0069 (0.069)	0.52 (0.063)	-	-
Juveniles	-	0.14 (0.069)	0.70 (0.13)	-
Adults	-	-	0.27 (0.069)	0.92 (0.39)

VITA

Ingrid Marie Parker June 1996

Education:

B.A. 1989 Biology. University of Chicago, Chicago, IL.

Ph.D. 1996 Botany. University of Washington, Seattle, WA.
Dissertation title: "Ecological factors affecting rates of spread in *Cytisus scoparius*, an invasive exotic shrub."

Positions Held:

Mathematical Biology Fellow. Modelling rates of spread in *Cytisus scoparius*. NSF Training Grant in Mathematical Biology, University of Washington. 1994-96.

Research Assistant. Using experiments to predict risk of invasiveness in genetically engineered crops. Department of Zoology, University of Washington. 1993.

Teaching Assistant. Biology Program, Department of Zoology, Honors College. University of Washington. 1992-94.

Instructor of Marine Biology and Environmental Ecology. Catalina Island Marine Institute, residential program in environmental education. 1990.

Naturalist. Ryerson Conservation Area, Deerfield, Illinois. 1989.

Teaching Assistant. Department of Ecology and Evolution, University of Chicago. 1989.

Ecological Field Consultant. Land Trust of Santa Cruz County. 1987.

Resource Ecology Intern: Database on invasive exotic species in California State Parks. California Department of Parks and Recreation, Central Coast Region. 1987.

Hobbies:

Championship figure skating, going to the Bunny Planet, nitrogen narcosis, big hair, singing Nirvana covers, catching The Big One, tank-wrestling, looking for bottles.