

## AN ABSTRACT OF THE THESIS OF

Lisa E. Lantz for the degree of Master of Science in Botany and Plant Pathology  
presented on April 25, 1997. Title: Population Characteristics of Exotic Plants in a  
Willamette Valley Native Prairie.

*Redacted for Privacy*

Abstract approved: \_\_\_\_\_

Mark V. Wilson

Invasions by exotic species are one of the most serious environmental issues the world faces. Noble (1989) proposed a model to determine the probability of successful terrestrial plant invasion. I evaluated three aspects of this model - seed production, seed predation, and seedling establishment - at a native prairie site in western Oregon's Willamette Valley. In addition, my study provided a first description of some of the demographic processes of four study species in the Willamette Valley.

High seed production is one of the first indicators that a species may be a successful invader. I measured seed production for all species at the site over two seasons, 1991-1993. Exotic species produced significantly more viable seeds per cm<sup>2</sup> cover than native species for both years of the study and more viable seeds per biomass the second year. Differences in seed production between the two groups may be attributable in part to life history. Annuals produced significantly more seeds than perennials. The majority of exotics were annuals, while the majority of natives were perennials.

The presence of a high flowering or fruiting effort suggests that, under native conditions, population processes, such as seed predation and competition, keep the species in check. I measured post-dispersal seed predation and the effects of competition during seedling establishment for four species known to have high seed production: *Bromus carinatus* (native grass), *Prunella vulgaris* var. *lanceolata* (native forb), *Cynosurus echinatus* (exotic grass), and *Daucus carota* (exotic forb). When seeds were sown directly into the soil, there were no differences in seed predation for native and exotic species. In contrast, when seeds were set out in dishes, significantly more native seeds were eaten than exotic seeds. In addition, significantly more grass seeds were eaten than dicot seeds. The dish results were consistent with the idea that exotic species may be successful in part because they are escaping from their native seed predators. However, the results were strongly influenced by the negligible seed predation on *D. carota*, which has spines and an aromatic flavor that may make it unpalatable.

To evaluate the role of competition in determining invasive success, seeds were sown in intact vegetation and in reduced competition plots, and their establishment was followed. During year 2, significantly more *B. carinatus* seedlings established in reduced competition plots than in intact vegetation; the trend was less clear year 1. More *P. vulgaris* seedlings also tended to establish in the reduced competition plots. Competition from existing vegetation may inhibit establishment of the native species, helping to keep their populations in check. Significantly more *C. echinatus* seedlings also established with reduced competition; native species may also play a role in inhibiting seedling establishment for this exotic species. There was no difference in establishment for *D. carota* between the two plot types, suggesting that *D. carota* seedlings can compete

effectively with the native vegetation at this site, which may help explain its invasive success.

Although the four study species were selected based on their high seed production, the two exotic species produced vastly more seeds. This high seed production for exotics overshadowed the effects of post-dispersal seed predation and competition during seedling establishment.

The population characteristics of the species studied at this Willamette Valley prairie site were generally consistent with Noble's (1989) model. For the four study species, high seed production was a strong indicator of invasive success, but studies on additional species are needed before generalities can be drawn for this system.

**Population Characteristics of Exotic Plants in a  
Willamette Valley Native Prairie**

by

**Lisa E. Lantz**

**A THESIS**

submitted to

**Oregon State University**

in partial fulfillment of  
the requirements for the  
degree of

**Master of Science**

**Presented April 25, 1997  
Commencement June 1998**

Master of Science thesis of Lisa E. Lantz presented on April 25, 1997

APPROVED:

*Redacted for Privacy*

---

Major Professor, representing Botany and Plant Pathology

*Redacted for Privacy*

---

Head of Department of Botany and Plant Pathology

*Redacted for Privacy*

---

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

*Redacted for Privacy*

---

Lisa E. Lantz, Author

## ACKNOWLEDGMENTS

I would like to express my gratitude to Dr. Mark Wilson for his long-term guidance and encouragement on this project. I would also like to thank my dear friend Dr. Deborah Clark for her insight, field assistance, and tireless ability to listen to my thesis woes. The loving support of my parents, John and Elaine Lantz, was instrumental in the completion of this work. I would also like to thank Benton County Parks and Dennis Williamson for permitting me to use their properties for my field work. Financial assistance from the Hardman Foundation for Conservation Research and the Mazamas made this project possible.

In addition, the advice and encouragement of Dr. Dan Schafer, Dr. Patricia Muir, Dr. Jeff Miller, Dr. Cheryl Ingersoll, Scott Springer, and Laurie McLellan were invaluable. Finally, I would like to thank Dr. Susan Singer of Carleton College for teaching me to believe in myself.

## TABLE OF CONTENTS

INTRODUCTION.....	1
HISTORY OF INVASIONS.....	2
EFFECTS OF INVASIONS.....	3
WHAT MAKES A COMMUNITY INVASIBLE?.....	4
WHAT MAKES A SUCCESSFUL INVADER?.....	6
PRAIRIES OF THE WILLAMETTE VALLEY.....	9
PURPOSE OF STUDY.....	12
COMPARATIVE POPULATION CHARACTERISTICS OF NATIVE AND EXOTIC SPECIES IN A WILLAMETTE VALLEY UPLAND PRAIRIE.....	14
INTRODUCTION.....	14
METHODS.....	17
Study area.....	17
Objective 1 - Seed production.....	18
Objective 2 - Seed predation.....	20
Objective 3 - Seedling establishment.....	25
Demography.....	26
RESULTS.....	28
Seed production.....	28
Seed predation.....	32
Seedling establishment.....	33
Demography.....	34

## TABLE OF CONTENTS (Continued)

DISCUSSION.....	36
Seed production.....	36
Seed predation.....	39
Seedling establishment.....	42
Demography.....	44
CONCLUSION.....	45
CONCLUSIONS.....	46
BIBLIOGRAPHY.....	49
APPENDICES.....	57



## LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
2.1	Experimental design for Willamette Valley prairie post-dispersal seed predation experiment, 1991-1993.....	23
2.2	Demographic data for four Willamette Valley prairie species, 1992-1993.....	36

## LIST OF TABLES

<u>Table</u>	<u>Page</u>
1.1 Characteristics of the ideal weed.....	8
1.2 Typical Willamette Valley upland prairie species.....	12
2.1 Species sampled in Willamette Valley seed production study, 1991-1992.....	29
2.2 Average number of viable seeds produced per 1 cm <sup>2</sup> cover and per biomass(g) for all native and exotic species sampled at a Willamette Valley prairie site, 1991-1992.....	30
2.3 Regression equations for predicting biomass from cover estimates for native and exotic Willamette Valley prairie species sampled in the seed production study, 1991-1992.....	30
2.4 Results of multi-factor analysis of variance for 1992 Willamette Valley prairie seed production per unit cover data.....	31
2.5 Mean number of seeds lost to post-dispersal seed predation in a Willamette Valley prairie, 1991-1992.....	32
2.6 Mean number of seeds lost to post-dispersal seed predation in a Willamette Valley prairie, 1992-1993.....	33
2.7 Mean number of seedlings of four Willamette Valley prairie species that established with competition and with reduced competition.....	34
2.8 Demographic data for four Willamette Valley prairie species in 1992-1993.....	35

## LIST OF APPENDICES

<u>Appendix</u>	<u>Page</u>
1      Pre-dispersal seed predation of selected native and exotic Willamette Valley prairie species.....	58
2      Seed production data for native and exotic plants in a Willamette Valley prairie, 1991.....	61
3      Seed production data for native and exotic plants in a Willamette Valley prairie, 1992.....	63
4      Number of seeds produced per 1 cm <sup>2</sup> cover for native species in a Willamette Valley prairie, 1991.....	65
5      Number of seeds produced per 1 cm <sup>2</sup> cover for exotic species in a Willamette Valley prairie, 1991.....	68
6      Number of seeds produced per 1 cm <sup>2</sup> cover for native species in a Willamette Valley prairie, 1992.....	71
7      Number of seeds produced per 1 cm <sup>2</sup> cover for exotic species in a Willamette Valley prairie, 1992.....	74
8      Number of seeds lost to post-dispersal seed predation for four species in a Willamette Valley prairie, adjusted for background counts.....	80
9      Seedling establishment data for four Willamette Valley prairie species, 1991-1992.....	81
10     Seedling establishment data for four Willamette Valley prairie species, 1992-1993.....	82

This thesis is dedicated in loving memory of Elaine Lantz.

# POPULATION CHARACTERISTICS OF EXOTIC PLANTS IN A WILLAMETTE VALLEY NATIVE PRAIRIE

## Chapter 1

### INTRODUCTION

Many of the natural resource and conservation problems the world presently faces can be directly linked to human-induced environmental changes. Coblenz (1990) suggests that invasions by exotic species, along with improper resource use and pollution, are the three major causes of natural resource problems today. The latter two categories have received most of the attention, but increasing focus is being placed on introduced species because of their observed impacts. Non-native, invasive species may destroy natural ecosystems by outcompeting natives for limiting resources or devastating native populations through predation or disease (Huenneke 1988). In some cases, they may even reduce biological diversity (Coblenz 1990; Lodge 1993). Documentation of the adverse effects of many invasions is readily available (Groves and Burdon 1986; Mooney and Drake 1986; Drake et al. 1989; Stone et al. 1992; Groves and di Castri 1992; OTA 1993), but the actual invasion process remains poorly understood. As the world becomes increasingly interconnected through modern transportation, the continued spread of many exotic species is likely. Therefore, learning more about the invasion process is an important task for ecology. By determining which characteristics are important in invasions, it may become possible to predict future invasions or to mitigate their effects.

## HISTORY OF INVASIONS

In geologic time, biological invasions are common events, as changes in species ranges occur constantly (Lodge 1993). Plate tectonics brought about major biotic interchanges (Vermeij 1991). However, humankind has greatly accelerated the rate of these interchanges. Human-facilitated species introductions have been recognized for centuries. Exotic species were carried to the New World with the first European explorers, and many species became firmly established. Non-native, invasive species have had most of their success in the regions of the New World that were most hospitable to European settlers. These areas include the eastern third of the United States and Canada, the southeast corner of Australia, all of New Zealand, and the humid grassland of southern South America, which encompasses portions of Argentina and Brazil and all of Uruguay (Crosby 1986). In these areas, many exotic plant species have been able to establish and spread aggressively. When Charles Darwin visited South America in 1833, he noted that the introduced cardoon (*Cynara cardunculus*) had rendered an estimated several hundred square miles of land useless (Darwin 1962). By the 1920's, only twenty-five percent of the plants growing wild in the South American pampa were native (Crosby 1986).

Initially, the negative impacts of species introductions were not considered; many introductions were actually encouraged (Huenneke 1988). In the first part of this century, the United States Department of Agriculture intentionally introduced plants for "useful" purposes, but these plants have gone on to make up ninety percent of the current agricultural pests in the U.S. (Mooney and Drake 1987). As the effects of invaders have become more apparent, the ecology of invasions has grown in interest to biologists.

## EFFECTS OF INVASIONS

Evidence suggests that the effects of invaders may depend on the complexity of the community they are invading (Lewin 1987; Lodge 1993). Diverse communities may be more resistant to invasion because an invader is more likely to meet with a competitor (Pimm 1989). Impacts are usually most severe when species are introduced to environments where predators or competitors are absent, or to simple communities, where the removal of a few plant species can lead to the collapse of the entire food chain (Pimm 1989).

Invasions by a single species can have dramatic, ecosystem-level effects. In some cases, non-native, invasive plants have altered biogeochemical cycling, geomorphological processes, hydrological cycles, and fire regimes (Mooney and Drake 1989). Clear examples of ecosystem-level effects have been demonstrated in Hawaii Volcanoes National Park. The nitrogen-fixing exotic plant *Myrica faya* has altered the nitrogen cycle in parts of the park. Invading areas where nitrogen is limiting, *Myrica* can fix more than four times as much nitrogen as all native nitrogen fixers combined (Vitousek and Walker 1989). By altering the nitrogen availability of the ecosystem, *Myrica* may provide the means for other exotic plants, which would ordinarily be unable to survive low nitrogen levels, to invade the area (Vitousek and Walker 1989). Invasion by non-native grasses has also had ecosystem-level effects in portions of the park where fire was previously rare or absent. Annual alien grasses have invaded previously unburned areas, providing fine fuel for fire (Hughes et al. 1991). After fire, annual grass cover increases rapidly, while the diversity and cover of native shrubs and trees drops sharply.

While definitive evidence is lacking, successful invaders may also replace native species in a community and lead to widespread extinctions (Pimm 1989). Simberloff (1981) examined the effects of 850 plant and animal introductions cited in ten papers. He found that less than ten percent of these introductions resulted in extinctions. However, Simberloff later stated that he may have overlooked some effects (Pimm 1989).

There are inadequate data to support the impression that species introductions necessarily have an adverse effect on the communities that they invade (Pimm 1989). Many introduced species fail to establish. Examples of failed invasions can be seen through biological control programs. Of the roughly 600 biocontrol agents that have been released, approximately two-thirds have been unsuccessful (Lewin 1987). Some successful invaders may simply add to the existing community (Pimm 1989; Lodge 1993). Crosby (1986: 169) called invasive weeds "the Red Cross of the plant world; they deal with ecological emergencies." Exotic plants often thrive in severely disturbed areas, where they may prevent soil erosion (Lugo 1990). However, the bulk of the literature on introduced species is concerned with cases that have had adverse consequences.

#### WHAT MAKES A COMMUNITY INVASIBLE?

Based on case-studies of invasions, some areas appear more susceptible to invasions by non-native species than others. In his classic work, *The Ecology of Invasions by Animals and Plants* (1958), Elton concluded that invaders were more likely to colonize disturbed sites. In the forty years since Elton's work, little progress has been made on



evaluating community invasibility. The same widely-accepted generality about invulnerable habitats still exists: habitat disturbance tends to promote invasion (Rejmanek 1989).

Disturbance can be defined as the destruction of plant biomass (Grime 1979). Some forms of disturbance, such as hurricanes, can be considered endogenous; communities have been exposed to endogenous disturbances over evolutionary time. Exogenous disturbances are human-induced and may include the alteration of the endogenous disturbance regime (Fox and Fox 1986). The list of exotic species that have invaded undisturbed or naturally disturbed habitats is brief (Rejmanek 1989). It is exogenous disturbance that often accompanies invasions by exotic species (D'Antonio and Mahall 1991).

Most evidence on community invasibility is unsatisfying, as it is based on observations of past invasions (Rejmanek 1989), but some experimentation does support the role of disturbance. In the wheatbelt of Western Australia, spading has been shown experimentally to enhance the establishment of some exotic species, while having little effect on native species (Hobbs 1989).

In areas with frequent endogenous disturbance, the removal of disturbance has also been implicated in invasion. For example, the vegetation patterns on serpentine grasslands in California are affected by the disturbance of burrowing gophers (*Thomomys bottea*) (Hobbs et al. 1988). The gopher creates mounds on the soil surface, which may bury the existing vegetation and mulch, allowing for the establishment of native forbs. In areas where gopher disturbance has been removed, non-native grasses have been able to dominate the landscape (Hobbs et al. 1988).

Other studies suggest that disturbance is not necessarily the key trait. In Britain, alien plant species are closely correlated with communities with low vegetative cover (Crawley 1986; Crawley 1987). While disturbance is one cause of low cover, several other factors, such as intense belowground competition for water, may produce limited vegetative cover (Crawley 1986). Increases in nutrient availability have also been shown to increase the invasive success of non-native plants, particularly in areas where nutrient availability is naturally low (Huenneke et al. 1990). In addition, species-poor communities may be more susceptible to invasion by a given species than species-rich communities (Lodge 1993). Unfortunately, these generalizations are inadequate when it comes to predicting accurately the invasibility of a given community. This inability to make successful predictions is linked to the fact that characteristics of the invading and native species are also critical.

#### WHAT MAKES A SUCCESSFUL INVADER?

One reason for the lack of progress in determining community invasibility is that attention has shifted from environmental characteristics to characteristics of the invaders themselves (Orians 1986). A wide range of characteristics may influence the colonizing success of certain species. At the genetic level, polyploidy is a trait that tends to be associated with invasion (Gray 1986). Of the 18 plants listed as the world's worst weeds (Holm et al. 1977), all are polyploids (Gray 1986). This apparent connection between polyploidy and invasion may be the result of several factors (Gray 1986). First of all, the chance of an invader being polyploid is large simply based on the fact that 70% to 80% of

all flowering plants and ferns are polyploids. In addition, an association seems to exist between polyploidy and apomixis or vegetative spread, two other characteristics that are also considered advantageous to invaders. Finally, invaders may receive buffering from inbreeding depression through polyploidy, which may increase the success of a population founded by one or a few individuals.

Studies of invasion also indicate that varying levels of genetic variation may affect the success of an invader. Some empirical evidence suggests that genetically diverse individuals are better colonizers. In California, studies conducted with the introduced legume, *Trifolium hirtum*, tentatively found that populations of high and medium genetic diversity may have a colonizing edge over populations of low genetic diversity (Martins and Jain 1979).

Compilations of eco-physiological, as well as genetic characteristics, have been used to attempt to characterize successful invaders. Baker (1965) provided one of the first attempts at generalization, with his list of characteristics of the "ideal weed" (Table 1.1). While no plant is likely to possess all of these characteristics, many of them are often associated with successful invaders. For example, *Bromus tectorum*, a Mediterranean annual that has become a widespread invader in western North America, displays more than half of the traits on Baker's list (Mack 1981).

While many of Baker's characteristics are often found in successful invaders, possession of these characteristics does not necessarily make a successful invader (Noble 1989; Newsome and Noble 1986). In addition, aspects of modern society may be changing the characteristics of an ideal invader (Newsome and Noble 1986). For

Table 1.1. Characteristics of the "ideal" weed (from Baker 1965).

1.	Has no special environmental requirements for germination.
2.	Has discontinuous germination (self-controlled) and great longevity of seed.
3.	Shows rapid seedling growth.
4.	Spends only a short period of time in the vegetative condition before beginning to flower.
5.	Maintains a continuous seed production for as long as growing conditions permit.
6.	Is self-compatible, but not obligatorily self-pollinated or apomictic.
7.	When cross-pollinated, this can be achieved by a non-specialized flower visitor or by wind.
8.	Has very high seed output in favorable environmental circumstances.
9.	Can produce some seed in a very wide range of environmental circumstances. Has high tolerance of (and often plasticity in face of) climatic and edaphic variation.
10.	Has special adaptations for both long-distance and short-distance dispersal.
11.	If a perennial, has vigorous vegetative reproduction.
12.	If a perennial, has brittleness at the lower nodes or of the rhizomes or rootstocks.
13.	If a perennial, shows an ability to regenerate from severed portions of the rootstock.
14.	Has ability to compete by special means: rosette formation, choking growth, exocrine production (but no fouling of soil for itself), etc.

example, many invasive seeds are now dispersed by humans, so other dispersal mechanisms are less important. Therefore, Baker's list lacks predictive power for determining what species are likely to be successful invaders in a particular habitat (Noble 1989).

Noble (1989) proposed modeling combinations of population processes that work together to determine the probability of a successful terrestrial plant invasion. Noble's model emphasizes the importance of four factors: (1) high flowering or fruiting effort, (2) increase in the probability of survival from flower to seed pool, (3) increase in the number of seedlings that establish, and (4) increase in the number of plants that survive to reproductive maturity. The presence of a high flowering or fruiting effort suggests that

under native conditions, there are probably great losses between flowering and the maturation of a replacement adult. Native population checks may not be in effect in a new habitat. Therefore, when a species invades a new habitat, it may be escaping these population checks. One such escape would be from seed predators; this escape would increase the probability of survival from flower to the seed pool. Likewise, competition under native conditions might reduce the number of seedlings that establish and the number of plants that survive to reproductive maturity. In new habitats, site-specific factors, such as disturbance or species composition, may reduce competition for some exotic species. Noble's model appears consistent with the historical and observational information available on plant invasions. However, as is the case with most of the models in this area of ecology, it has not been directly tested.

### PRAIRIES OF THE WILLAMETTE VALLEY

The grasslands of western Oregon's Willamette Valley provide an appropriate setting for studying the characteristics of plant invasions. Historically, much of western Oregon's Willamette Valley consisted of prairie and open woodland maintained by annual fire (Sprague and Hansen 1946; Smith 1949; Habeck 1961; Johannessen et al. 1971; Boyd 1986). After European settlement, fire was suppressed and many areas were converted to agriculture. As a result of these changes, few of the native prairies remain, and many of the prairie remnants are being degraded by invasions of exotic plant species.

The Willamette Valley runs approximately 220 km from near Portland, in the north, to near Eugene, in the south. A structural depression, the valley consists largely of

wide alluvial flats occasionally separated by low hills. These flats are bordered by the sandstone and shale foothills of the Coast Range to the west and by the basaltic foothills of the Cascade Mountains to the east (Thilenius 1968).

While the Willamette Valley itself has never been glaciated, it has been inundated many times by meltwater floods from the Columbia River (Thilenius 1968; Orr et al. 1992). Before flood control dams were built in the 1960's, the Willamette River and its tributaries periodically flooded their banks (Savonen 1988). As a result, much of the level valley floor is covered with silts, sands, and clays, and many areas have poor drainage qualities (Savonen 1988).

The valley climate is characterized by mild, wet winters and hot, dry summers, with a precipitation deficit in the driest months of July and August (Moir and Mika 1972). Although the climate of the Willamette Valley is characteristic of the humid forest region (Moir and Mika 1972), early European settlers encountered an area dominated by prairies and oak savannas (Smith 1949; Habeck 1961; Johannessen et al. 1971). The original grasslands of the Willamette Valley can be divided into two types: wetland prairies and upland prairies. The wetland prairies are found in areas of the valley floor with poorly drained alluvial soils that often experience flooding during the winter months. Upland prairies are found on better drained soils and often intergrade with areas of oak savanna. Based on the accounts of early settlers, these grasslands were maintained by annual fires set by the Native Americans (Sprague and Hansen 1946; Smith 1949; Habeck 1961; Johannessen et al. 1971; Boyd 1986). After European settlement, these fires were

suppressed and much of the highly productive prairies were lost to agriculture and urbanization.

Many of the remaining grasslands are being lost through succession. Most Willamette Valley prairies are considered seral communities that have been maintained by fire or other exogenous disturbances (Franklin and Dyrness 1973). With fire suppression, trees (*Quercus garryana*, *Fraxinus latifolia*, *Pseudotsuga menziesii*, *Acer macrophyllum*, *Arbutus menziesii*) and shrubs (*Rhus diversiloba*, *Crataegus* spp., *Rosa* spp.) have established (Johannessen et al. 1971; Habeck 1962; Towle 1982). Therefore, unlike much of the United States, pioneer settlement in the Willamette Valley led to an increase in forest cover (Towle 1982). These changes have left less than one percent of the original grassland intact (Johannessen et al. 1971), causing The Nature Conservancy (1983) to list Willamette Valley prairies as one of the most endangered habitats in Oregon.

My study focused on Willamette Valley upland prairie species. There is little descriptive information on the floristic composition of these prairies prior to European settlement. Since agriculture, urbanization, and natural succession to forest have drastically altered the upland prairie community, any descriptions of the original vegetation must be conjecture (Franklin and Dyrness 1973). However, the species composition of upland prairies is thought to have contained several native grass and forb species. Euro-American settlers introduced many new plants to the Willamette Valley, and some of these species have become naturalized and widespread (Table 1.2). As early as 1919, about half of the grass species near Salem, in the mid-Willamette Valley, were introduced (Nelson 1919). Non-native species now dominate many areas.

Table 1.2. Typical Willamette Valley upland prairie species (Nelson 1919; Habeck 1961; Franklin and Dyrness 1973; personal observation).

	Native	Exotic
Grasses	<i>Agrostis hallii</i>	<i>Aira caryophyllea</i>
	<i>Bromus carinatus</i>	<i>Arrhenatherum elatius</i>
	<i>Danthonia californica</i>	<i>Avena fatua</i>
	<i>Elymus glaucus</i>	<i>Bromus mollis</i>
	<i>Festuca idahoensis</i>	<i>Bromus rigidus</i>
	<i>Koeleria cristata</i>	<i>Cynosurus echinatus</i>
	<i>Sitanion hystrix</i>	<i>Dactylis glomerata</i>
	<i>Stipa occidentalis</i> var. <i>minor</i>	<i>Elymus caput-medusae</i>
		<i>Gastridium ventricosum</i>
		<i>Holcus lanatus</i>
Forbs		<i>Lolium perenne</i>
	<i>Achillea millefolium</i>	<i>Daucus carota</i>
	<i>Brodiaea</i> spp.	<i>Galium parisiense</i>
	<i>Calochortus</i> spp.	<i>Hypericum perforatum</i>
	<i>Eriophyllum lanatum</i>	<i>Hypochaeris radicata</i>
	<i>Fragaria virginiana</i>	<i>Plantago lanceolata</i>
	<i>Madia</i> spp.	<i>Sherardia arvensis</i>
	<i>Potentilla gracilis</i>	<i>Torilis arvensis</i>
	<i>Prunella vulgaris</i> var. <i>lanceolata</i>	
	<i>Ranunculus occidentalis</i>	

## PURPOSE OF STUDY

Because exotic plants can have wide-reaching impacts on native ecosystems, learning more about the invasion process is an important task for ecology. Noble's (1989) model provides a framework for examining the invasion process that has not been tested in the field. With their assortment of native and exotics species, Willamette Valley upland prairies provide an appropriate setting for field-testing Noble's model. Therefore, the goal of my study was to use Noble's model as a framework for understanding the relative



importance of various population processes in exotic plant invasions of a Willamette Valley upland prairie. Three processes in particular were investigated (chapter 2). Seed production for all grassland species, both native and exotic, was quantified for two years. The effects of post-dispersal seed predation and the role of competition in seedling establishment were also explored for selected native and exotic species known to be high seed producers. Comparisons were made between native and exotic species to determine if the population processes stressed by Noble have power in explaining the patterns of exotic plant invasion in a Willamette Valley prairie. In addition, since very few demographic studies exist for Willamette Valley prairie plant species, the seed production, seed predation, and seedling establishment data were combined to look at the population trends for study species.

## Chapter 2

### COMPARATIVE POPULATION CHARACTERISTICS OF NATIVE AND EXOTIC SPECIES IN A WILLAMETTE VALLEY UPLAND PRAIRIE

#### INTRODUCTION

Introductions of non-native species have been implicated in many of the natural resource and conservation problems the world faces today (Coblentz 1990). Exotic organisms can outcompete natives for limited resources or devastate native populations through predation or disease (Huenneke 1988). They can also reduce biological diversity through habitat degradation (Coblentz 1990). Documentation of the adverse effects of many invasions is readily available (Groves and Burdon 1986; Mooney and Drake 1986; Drake et al. 1989; Stone et al. 1992; Groves and di Castri 1992; OTA 1993), but the actual invasion process remains poorly understood. As the world becomes increasingly interconnected through modern transportation, the continued spread of many exotic species is likely. Therefore, learning more about the invasion process is an important task for ecology. By determining which characteristics are important in invasions, it may become possible to predict future invasions or to mitigate their effects.

Much debate has taken place concerning characteristics of invaders and invulnerable communities (Hobbs 1989). While habitat traits clearly play a role in the success of the invader, only one widely-accepted generality about invulnerable habitats has emerged: the idea that habitat disturbance tends to promote invasion (Rejmanek 1989). A variety of attempts has also been made to generalize characteristics of invasive plant species. In

1965, Baker published a description of the "ideal weed." Newsome and Noble (1986) summarize Baker's ideal as a plastic perennial that will germinate under many conditions, will grow quickly, flower early, is self-compatible, produces many seeds that disperse widely, expands vegetatively, and is a good competitor. Many of these characteristics are often found in successful invaders. However, a single species is unlikely to have or need all these characteristics to be successful. The possession of one or more of these traits does not necessarily result in a successful invader. Baker's list lacks predictive power for determining what species are likely to be successful invaders in a particular habitat because it fails to assess the relationship between species characteristics and environmental factors (Noble 1989).

Noble (1989) proposed a model of population processes that work together to determine the probability of a successful terrestrial plant invasion. The model emphasizes the importance of four factors: (1) high flowering or fruiting effort, (2) increase in the probability of survival from flower to seed pool, (3) increase in the probability of seedling establishment, and (4) increase in the probability of survival to reproductive maturity.

The presence of a high flowering or fruiting effort suggests that under native conditions, there are probably great losses between flowering and the maturation of a replacement adult. Native population checks may not be in effect in a new habitat. Therefore, when a species invades a new habitat, it may be escaping these population checks. One such escape would be from seed predators; this escape would increase the probability of survival from flower to the seed pool. Likewise, competition under native conditions might reduce the probability of seedling establishment. As a result of

disturbance, species composition, or other site-dependent factors, exotic species in new habitats may no longer experience the competition that helped keep their populations in check in their native lands. This competitive change would increase the probability of survival from seed to the maturation of a replacement adult. The traits described in Noble's population processes model are consistent with the historical and observational information on successfully invading plants. However, the predictions of this model have not been tested by controlled field studies.

The grasslands of western Oregon's Willamette Valley provide an appropriate setting for studying the characteristics of plant invasions. Native grassland vegetation in the Willamette Valley consists of perennial bunchgrasses interspersed with annual and perennial forbs. Although the native species persist, many annual grasses and forbs native to Eurasia have become established. Historically, much of the Willamette Valley consisted of prairie and open woodland maintained by annual fire (Sprague and Hansen 1946; Smith 1949; Habeck 1961; Johannessen et al. 1971; Boyd 1986). After European settlement, fire was suppressed and many areas were converted to agriculture. As a result of these changes, few of the native prairies remain, and many of the prairie remnants are being degraded by invasions of exotic plant species.

The goal of my study was to determine if the population processes stressed by Noble (1989) have power in explaining the patterns of exotic plant invasion in Willamette Valley grasslands. The specific objectives were to:

- 1) Determine if exotic species produce significantly more viable seeds than native species;

- 2) Determine if two exotic species with high seed production lose significantly fewer seeds to post-dispersal seed predation than two native species with high seed production;
- 3) Examine the effects of competition on seedling establishment for two native and two exotic species with high seed production.

In addition, the data were used to provide a first description of some of the demographic processes of the four study species in the Willamette Valley.

## METHODS

### Study Area

The study site was a remnant Willamette Valley upland prairie on a northwest-facing 30 -50% slope (elevation ~ 305 m) located approximately 8 km northwest of Corvallis, Oregon. The Willamette Valley, which runs ~ 220 km from north to south, lies just east of Oregon's Coast Range. In this area, the climate is relatively free of extremes, with moderate, moist winters, and warm, dry summers. The average annual precipitation at the nearest weather station (Corvallis, elev. ~ 69 m) is 108 cm (NOAA 1985). During the two years of the study, the weather was warmer and drier than normal (NOAA 1991; NOAA 1992).

The soil at the site is a silty clay loam of the Dixonville series (well-drained, formed in colluvium from basic igneous rocks) (Knezevich 1975). On most of the site, *Festuca idahoensis* Elmer var. *roemerii* Pavlick is the dominant grass species, but some smaller

patches are dominated by non-native grasses, such as *Bromus sterilis*, *Elymus caput-medusae*, and *Cynosurus echinatus*. (Plant taxonomy follows Hitchcock and Cronquist (1973) unless otherwise noted). Native and non-native forbs are scattered throughout the area. Pocket gopher (*Thomomys bulbivorus*) activity was apparent throughout the site, and a few experimental plots were disturbed by gophers. White-tail deer (*Odocoileus virginianus*) were also common. However, no domestic livestock grazing had occurred at the site in the recent past.

#### Objective One - Seed production

In 1991, a study was undertaken to determine if there were differences in seed production between the native and exotic species at the study site. The vegetation was sampled in 24 randomly located 100 cm<sup>2</sup> quadrats. Estimations of cover were made for each plant species in the quadrat. All infructescences were bagged while the seeds were immature, using plastic, air- and water-permeable bags. Multiple visits were made to bag species with various phenologies. The bagged seeds were allowed to mature in the field and then collected. After collection, the seeds were dried at room temperature, then placed in a cardboard box in dry storage at a temperature of approximately 3° C for four to seven months. The seeds were counted, and the number of seeds produced per species per plot was then determined. This study was repeated in 1992.

Seed viability was determined using germination and tetrazolium tests on a subsample of seeds. Unsterilized seeds were placed on filter paper in Petri plates and moistened with distilled water. The dishes were placed in a growth chamber, with 15 hour

days at 20° C and a night temperature of 15 ° C, after Grime et al. (1981). Dishes were inspected every five to seven days, and germinated seeds were counted and removed. A seed was considered to have germinated when the radicle or plumule first emerged. The tests were continued until all germination had ceased. Stratification or scarification was tried on some species that failed to germinate under standard conditions. Some seeds failed to germinate under any of the tested conditions. In these cases, tetrazolium tests were used to determine viability. The seed coats were pierced and then soaked in a 1 % 2,3,5-triphenyltetrazolium chloride solution for 24 hours. The embryos were then evaluated under a dissecting scope. Embryos that stained evenly red or pink were considered viable.

My goal was to compare the number seeds produced per aboveground biomass for native and exotic species. However, it was impossible to measure seed production and biomass in the same plot, since biomass measurements require destructive sampling. Therefore, cover estimates were taken as a surrogate for biomass estimates in the seed production plots. To be able to relate these cover estimates to biomass, destructive sampling was done in June of 1993. Cover estimates were taken for all species in 12 randomly located 100 cm<sup>2</sup> plots. After these estimates were taken, all aboveground biomass was removed, dried and weighed. Allometric equations of the form  $Y = aX^b$ , where X = cover and Y = biomass, were used to estimate biomass from the existing cover data taken in 1991 and 1992.

Seed production per cover and per biomass for native and exotic species were compared using a two-sample t-test on log-transformed data.

To assess the effect life history might have on differences in seed production between natives and exotics, a multi-factor ANOVA was performed on the 1992 data, using native versus exotic, dicot versus monocot, and annual versus perennial as factors. In order to meet the assumptions of the ANOVA, the data were transformed, using  $\log(Y + 1)$ , where  $Y$  = seed number per 1 cm<sup>2</sup> cover.

### Objective Two - Seed predation

1991. To determine if a species is escaping population checks when it invades a new habitat, it would be desirable to examine seed predation for exotic species occurring in Oregon and in their native habitats. However, since the exotic species in the Willamette Valley are of Eurasian origin, this approach was not easily workable. Instead, I chose two native and two non-native species for this study. The species were selected based on their high seed production, with the idea that native species with high seed production do not become widespread problems because their populations are controlled by native population checks. In addition, in order to be able to collect adequate numbers of seed for study, the species needed to be relatively common at the site. Two grasses and two dicots were selected for this study: *Cynosurus echinatus*, *Bromus carinatus*, *Daucus carota*, and *Prunella vulgaris* var. *lanceolata*.

*Cynosurus echinatus* is an annual grass of Eurasian origin that is well-established west of the Cascade Mountains in Oregon and Washington (Hitchcock and Cronquist 1973). *Bromus carinatus* is a perennial grass native from Alaska to Baja California and east to Alberta and New Mexico; this species is sometimes considered weedy, growing on



waste ground (Hitchcock and Cronquist 1973). *Daucus carota* (Umbelliferae) is a biennial species of European origin that is established in much of the Pacific Northwest (Hitchcock and Cronquist 1973). *D. carota* can produce up to 40,000 seeds per plant (Dale 1974). *Prunella vulgaris* var. *lanceolata* (Labiatae) is an American native that is common in disturbed and natural habitats in the Pacific Northwest (Hitchcock and Cronquist 1973). An annual to short-lived perennial, *P. vulgaris* reproduces mainly by seed (Winn and Werner 1987; Winn 1991). While it would have been desirable to select four species with the same life history, this was not possible because the native plants at the site were primarily perennials, and the exotic species were primarily annuals.

Pre-dispersal seed predation. Initially, I hoped to examine both pre-dispersal and post-dispersal seed predation. A pilot study was done to look at pre-dispersal predation rates. In this study, 20 randomly selected inflorescences of each species were treated with the insecticide Lindane to prevent pre-dispersal insect seed predation. An additional 20 random inflorescences of each species were sprayed with water alone, as a control. Before the seeds dispersed, each infructescence was covered with a plastic, water-permeable bag and allowed to mature. The seeds from each bag were counted, and the number of seeds lost to pre-dispersal seed predation for each species was calculated as the number of seeds from insecticide-treated inflorescences minus the number of seeds from the control inflorescences. Due to the tremendous observed variation in seed production by individual plants, it became apparent that the necessary sample size to carry out this study was prohibitively large. Therefore, the study was not pursued further. The data for the pilot study are included in Appendix 1.

Post-dispersal seed predation 1991. To compare the rates of post-dispersal seed predation for the native versus non-native species, I sowed field-collected seeds of the four study species in the soil. The design was blocked by location, with 20 blocks of one replicate each. Each block consisted of a 5 m x 5 m area. Within each block, two 20 x 35 cm plots were randomly located. One plot was left open and the other was caged to keep out vertebrate predators. The cages consisted of 1.27 cm mesh hardware cloth driven approximately 3 cm into the ground and anchored with u-nails. The base of the cage was treated with a sticky substance (Tanglefoot Co., Grand Rapids, Michigan) to deter crawling insects from entering the cage. In each plot, 25 seeds each of the four study species were randomly assigned to separate 5 cm x 5 cm subplots (Figure 2.1).

The seeds were sown at each species' usual dispersal time and left out for one year. The soil in each subplot was collected in 1992, before natural seed dispersal. The soil samples were then sieved using water and sieves matched to the size of the seed sowed in the particular subplot. After sieving, the residues were dried at 30 ° C for two to three days, and any remaining seeds were identified using a magnifying glass. For each subplot, the number of seeds recovered for each species was determined. The numbers of seeds of a given species retrieved from subplots where that species was not sown were averaged to obtain a background count of the number of seeds in the existing soil seed bank. The background count was then subtracted from the number of seeds recovered, in subplots where that species was sown, to adjust the number of seeds remaining after one year.

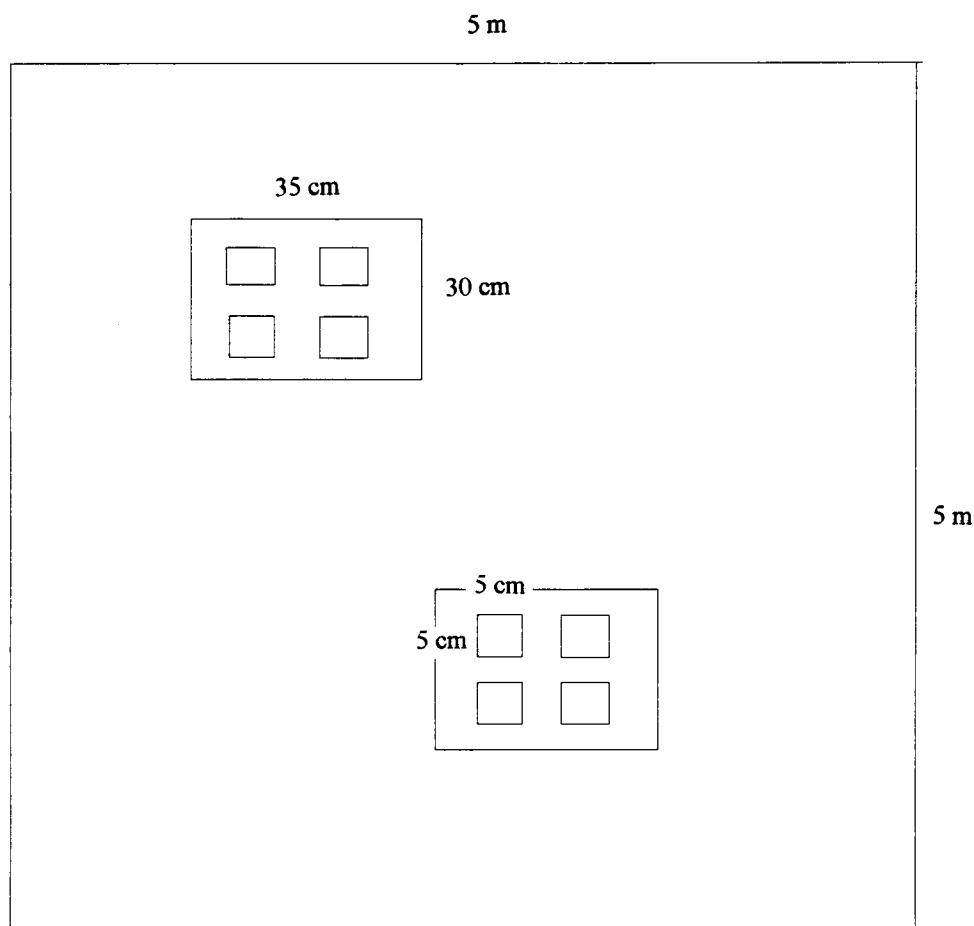


Figure 2.1. Experimental design for Willamette Valley prairie post-dispersal seed predation experiment, 1991-1993. Two 30 cm x 35 cm plots (one caged, one open), were placed within each 5 m x 5 m block to measure seed predation. Seeds of the four study species were sown in separate 5 cm x 5 cm subplots.

To determine the number of seeds lost to predation rate for each species, the following equation was used:

$$SP = (SS_o - SR_o) - (SS_i - SR_i),$$

where SP is the number of seeds lost to predation,  $SS_o$  is the number of seeds sown outside the cage,  $SR_o$  is the number of seeds remaining outside the cage,  $SS_i$  is the number of seeds sown inside the cage, and  $SR_i$  is the number of seeds remaining inside the cage. The number of seeds missing inside the cage ( $SS_i - SR_i$ ) was subtracted from the number of seeds missing outside the cage ( $SS_o - SR_o$ ) because seed loss from adverse environmental factors or germination operated equally inside and outside cages. By subtracting these losses, I was left with the number of seeds that were lost strictly to predation.

Post-dispersal seed predation 1992. Because of concerns about the effectiveness of the sieving methods, the experimental methods for measuring post-dispersal seed predation were altered in 1992. The same randomized block design was used. However, instead of sowing seeds into the soil, the seeds were set out in dishes. Each dish consisted of a 9 cm diameter metal Mason jar rim with a 0.01 mm mesh bottom to prevent rainwater from collecting. In the caged plots, the dishes were suspended approximately 5 cm above the ground on a wooden stake, and all overhanging vegetation was clipped back. The stakes were coated with Tanglefoot to prevent insects from climbing into the dish. The dishes were put out in early August 1992, just after the study species had dispersed. Every one to two months, the dishes were checked, and the number of missing seeds were counted and replaced. Counts were made until early June 1993, just before 1993 seed

dispersal for the study species. The total number of seeds lost over the entire year was then totaled. To determine the number of seeds lost to predation, the number of seeds lost from the caged plot was subtracted from the number lost from the open plot.

Multi-factor analysis of variances (ANOVA's) were used for each years' data to determine the statistical significance of the native versus exotic and grass versus dicot classifications.

### Objective Three - Seedling establishment

To examine the influence of competition on seedling establishment, I used the same four species as in the seed predation study: *Cynosurus echinatus*, *Bromus carinatus*, *Daucus carota*, and *Prunella vulgaris* var. *lanceolata*. The experiment consisted of 20, 5 m x 5 m areas. Within each area, a 20 cm x 35 cm plot was randomly located. Ten of the plots were randomly selected as reduced competition plots. To reduce shading, the bulk of the vegetation was removed in these plots with a string trimmer. In the remaining ten plots, the vegetation was left intact. In the mowed plots, five 7 cm x 7 cm holes were dug approximately 5 cm deep and filled with sterile potting soil. This technique was used to remove existing root biomass and most of the soil seed bank. Twenty field-collected seeds of the four study species were sown in these holes - one species per hole - with one hole left as a background sample. The background sample was used to determine the number of seedlings emerging from seeds in the soil seed bank. In the unmowed plots, the seeds were sown in four 7 cm x 7 cm subplots set up in the intact vegetation; a fifth subplot was used as a background.

Seeds were sown at roughly their natural dispersal times. *B. carinatus*, *C. echinatus*, and *P. vulgaris* were sown in early August 1991, while *D. carota* was sown in mid-September 1991. Starting in January, plots were monitored each month. Any seedlings of the study species that emerged were marked with a toothpick. In the reduced competition plots, any other species were removed. The plots were monitored until late June 1992, at which point the number of surviving seedlings were counted. Seedlings surviving to this date were considered to have established. This date was chosen because it required seedling survival for several months but did not include mortality due to summer drought. The study was repeated during the same time period in 1992-1993. However, in 1992-1993, all plots were enclosed with a hardware cloth cage, as in the predation experiment, to reduce predation as a confounding factor in the experiment.

To adjust for the seeds in the seed bank, the number of seedlings of a given species that established in the background subplot was subtracted from the number of seedlings of that species that established in the sowed subplot of the same plot. In cases where more seedlings established in the background subplot than in the sowed subplot, the number of established seedlings was recorded as zero. For each species, a Mann-Whitney *U* test was used to determine if more seedlings established in the plots with reduced competition versus in intact vegetation.

### Demography

The seed production, seed predation, and seedling establishment data were combined to look at the population trends for the four study species: *Bromus carinatus*,

*Cynosurus echinatus*, *Prunella vulgaris*, and *Daucus carota*. The calculations were done using the data from the second year of the study because they were more reliable. The mean seed production per 1 cm<sup>2</sup> cover was calculated for each species. Determining the percentage of seeds that had been lost to post-dispersal seed predation required calculating the number of seeds that had been displayed during the experiment. Since seeds had been replaced throughout the predation experiment, the number of seeds displayed was considered to be the number of seeds originally set out per plot (five) plus the number of seeds replaced during the study. As a result, the number of seeds displayed varied between plots. To calculate the percentage lost to predation, the number of seeds lost inside cages was divided by the number of seeds displayed inside the cages for each plot. This calculation was repeated for the uncaged subplot. The ratio inside the cage was then subtracted from the ratio outside the cage to determine the percentage lost to post-dispersal seed predation; the numbers were then averaged to obtain the mean percentage of seeds lost to post-dispersal seed predation. To determine the reduction in seedlings due to competition during seedling establishment, the mean number of seedlings that established with competition was subtracted from the mean number of seedlings that established with reduced competition; the difference was then divided by the number of seeds originally sown (20) to obtain the percentage of seeds lost to competition. These percentages of post-dispersal seed predation and competition loss were then applied to the seed production data to determine the seed losses due to each factor.

## RESULTS

### Seed production

In the two years of the study, 45 species were sampled - 21 native and 24 exotic (Table 2.1). Most of the species were observed both years. Of the native species, 13 were perennial, and eight were annual. The relative composition was reversed for exotic species, which included 15 annuals, seven perennials, and two biennials.

Seed production per cover differed significantly between natives and exotics for both years of the study (Table 2.2). In 1991, the median viable seed production per cover for exotic species was estimated to be 4.1 times as great as the median viable seed production per cover for native species (95% confidence interval: 1.8 to 9.0 times as great). The differences in 1992 were not as dramatic, but were still statistically significant; median viable seed production per cover for exotic species was estimated to be 1.9 times as great as the median viable seed production per cover for native species (95% CI: 1.2 to 3.2 times as great).

The results of the regression analysis (Table 2.3) were used to predict biomass from the cover data. Some cover values from the seed production plots fell outside of the range of the regression model for relating cover to biomass (exotic cover values from one plot and native cover values from six plots). Examination of the residuals indicated no systematic deviation from the regression model. In addition, theory suggests that the allometric model should hold for values larger and smaller than those used to calibrate the



model. Therefore, it seemed reasonable to use the model to predict biomass for all cover values recorded in the study.

Table 2.1. Species sampled in Willamette Valley prairie seed production study, 1991-1992. Taxonomy follows Hitchcock and Cronquist (1973), except where otherwise noted.

Native	Exotic
<i>Achillea millefolium</i> (p)	<i>Aira caryophylla</i> (a)
<i>Brodiaea congesta</i> (p)	<i>Avena</i> sp. (a)
<i>Bromus carinatus</i> (p)	<i>Bromus mollis</i> (a)
<i>Clarkia amoena</i> (a)	<i>Bromus sterilis</i> (a)
<i>Clarkia quadrivulnera</i> (a)	<i>Centaureum umbellatum</i> (a)
<i>Crataegus douglasii</i> (p)	<i>Cerastium viscosum</i> (a)
<i>Danthonia californica</i> (p)	<i>Chrysanthemum</i>
<i>Elymus glaucus</i> (p)	<i>leucanthemum</i> (p)
<i>Epilobium paniculatum</i> (a)	<i>Cynosurus echinatus</i> (a)
<i>Eriophyllum lanatum</i> (p)	<i>Dactylis glomerata</i> (p)
<i>Festuca idahoensis</i> Elmer var. <i>roemerii</i> Pavlick (p)	<i>Daucus carota</i> (b)
<i>Fragaria virginiana</i> (p)	<i>Elymus caput-medusae</i> (a)
<i>Geranium carolinianum</i> (a)	<i>Galium parisiense</i> (a)
<i>Linum angustifolium</i> (a)	<i>Gastroidium ventricosum</i> (a)
<i>Lotus denticulatus</i> (a)	<i>Hypericum perforatum</i> (p)
<i>Luzula campestris</i> (p)	<i>Hypochaeris radicata</i> (p)
<i>Madia gracilis</i> (a)	<i>Lathyrus sphaericus</i> (a)
<i>Madia sativa</i> (a)	<i>Lolium perenne</i> (p)
<i>Potentilla gracilis</i> (p)	<i>Myosotis discolor</i> (a)
<i>Prunella vulgaris</i> var. <i>lanceolata</i> (p)	<i>Plantago lanceolata</i> (p)
<i>Pteridium aquilinum</i> (p)	<i>Poa pratensis</i> (p)
	<i>Senecio jacobaea</i> (b)
	<i>Sherardia arvensis</i> (a)
	<i>Torilis arvensis</i> (a)
	<i>Vicia sativa</i> (a)

(a) = annual; (b) = biennial; (p) = perennial

Table 2.2. Average number of viable seeds produced per 1 cm<sup>2</sup> cover and per biomass (g) for all native and exotic species sampled at a Willamette Valley prairie site, 1991-1992. P is the probability that native and exotic species produce the same number of seeds. n = 24 samples.

	Seeds per 1 cm <sup>2</sup> cover		Seeds per biomass (g)	
	mean	SE	mean	SE
Exotic 1991	43.91	8.45	93.59	17.54
Native 1991	12.51	3.30	42.06	10.07
	P* = 0.0009		P* = 0.03	
Exotic 1992	77.04	19.73	207.85	50.93
Native 1992	38.45	6.77	151.80	26.33
	P* = 0.01		P* = 0.20	

\*Two-sample t-test on log-transformed data. P-values are upper-tailed.

Table 2.3. Regression equations for predicting biomass from cover estimates for native and exotic Willamette Valley prairie species sampled in the seed production study, 1991-1992.

Species	Equation	N	SE	R <sup>2</sup>
Exotic	$Y = 1.22 (X)^{0.632}$	12	0.30	0.69
Native	$Y = 0.42 (X)^{0.85}$	12	0.45	0.65

In 1991, the median viable seed production per biomass for exotics was estimated to be 2.4 times as great as the median viable seed production per biomass for the natives (95% CI: 1.1 to 5.3 times as great). In 1992, median viable seed production per biomass for exotics was estimated to be 1.4 times as great as the median viable seed production per biomass for the natives, but this difference was not statistically significant (95% confidence interval: 0.9 to 2.2 times as great).

Annual species produced significantly more viable seeds per 1 cm<sup>2</sup> cover than perennial species in 1992, even after accounting for differences in native versus exotic and dicot versus monocot (ANOVA,  $P < 0.0001$ ) (Table 2.4). All the native monocots were perennials. There was a significant interaction between native versus exotic and monocot versus dicot ( $P < 0.0001$ ).

Table 2.4 . Results of multi-factor analysis of variance for 1992 Willamette Valley prairie seed production per unit cover data. There is 1 df for each main effect and for each interaction term. The residual df for each analysis is 137.  $n = 24$  plots.

Source of variation	SS	F	P
native vs. exotic (A)	0.01	0.01	0.91
monocot vs. dicot (B)	51.97	41.67	<0.0001
annual vs. perennial (C)	49.28	39.51	<0.0001
A x B	29.70	23.81	<0.0001
A x C	0.29	0.24	0.63
B x C	0.03	0.03	0.88
residual	170.88	(MS 1.25)	

### Seed predation

When seeds were sown directly into the soil, native seeds tended to be eaten at a higher rate than exotic seeds (Table 2.5), but the difference was not statistically significant ( $P = 0.35$ ). Grasses also tended to be taken at a higher rate than dicots, but, again the trend was not statistically significant ( $P = 0.59$ ). The ANOVA showed no significant interactions.

Table 2.5. Mean number of seeds lost to post-dispersal seed predation in a Willamette Valley prairie, 1991-1992. Numbers lost are out of 25 seeds originally sown of each of the four study species. Effects corresponding to native vs. exotic and grass vs. dicot were calculated using a multi-factor ANOVA.  $n = 20$  blocks.

	grass	dicot	total
native	2.20	1.06	3.26
exotic	0.53	0.29	0.82
			$P = 0.35$
total	2.73	1.35	4.08
			$P = 0.59$

The second year, when seeds were placed out in dishes, significantly more native seeds were eaten than exotic seeds (Table 2.6). In the dish experiment, grass versus dicot ( $P = 0.0002$ ), and native versus exotic ( $P < 0.0001$ ) were both highly significant. There were no significant interactions.

Table 2.6. Mean number of seeds lost to post-dispersal seed predation in a Willamette Valley prairie, 1992-1993. Effects corresponding to native vs. exotic and grass vs. dicot were calculated using a multi-factor ANOVA.  $n = 20$  blocks.

	grass	dicot	total
native	6.10	2.70	8.80
exotic	2.00	-0.85	1.15
			$P < 0.0001$
total	8.10	1.85	9.95
			$P = 0.0002$

#### Seedling establishment

The four species showed two different patterns of seedling establishment in response to the experimental treatments (Table 2.7). For three species, more seedlings tended to establish in the plots with reduced competition. In 1991-1992, more *Cynosurus echinatus* (Mann-Whitney test,  $P = 0.10$ ), *Prunella vulgaris* ( $P = 0.10$ ), and *Bromus carinatus* ( $P = 0.28$ ) seedlings tended to establish in the reduced competition plots, although the trend was not statistically significant. In 1992-1993, when seed predation was reduced as a confounding factor, this establishment trend was more pronounced. *C. echinatus* ( $P = 0.003$ ) and *B. carinatus* ( $P = 0.02$ ) both produced significantly more seedlings in the reduced competition plots, while the trend remained less pronounced for *P. vulgaris* ( $P = 0.10$ ).

Table 2.7. Mean number of seedlings of four Willamette Valley prairie species that established with competition and with reduced competition. Number established is out of 20 seeds sown of each species per plot. P is the probability that seedling establishment is the same with competition and with reduced competition. n = 10 plots per treatment.

	<u>Number of seedlings established</u>				P*
	<u>reduced competition</u>		<u>competition</u>		
	mean	SE	mean	SE	
1991					
<i>Cynosurus echinatus</i>	9.06	2.44	4.70	1.73	0.10
<i>Bromus carinatus</i>	5.50	2.23	2.57	0.87	0.28
<i>Daucus carota</i>	7.30	1.69	6.78	1.77	0.45
<i>Prunella vulgaris</i>	3.22	1.05	1.22	0.70	0.10
1992					
<i>Cynosurus echinatus</i>	8.80	1.40	2.20	0.77	0.0003
<i>Bromus carinatus</i>	6.00	1.06	3.00	0.79	0.02
<i>Daucus carota</i>	5.70	1.67	5.70	1.02	0.34
<i>Prunella vulgaris</i>	1.44	0.44	0.90	0.53	0.09

\* Mann-Whitney U test on number of seedlings established for each species. P-values are upper-tailed.

*Daucus carota* responded differently than the other species to the experimental treatments. The seedling establishment for *D. carota* did not differ between treatments for either year of the study (1991: P = 0.45; 1992: P = 0.34) (Table 2.7).

### Demography

Although efforts were made to select four species that produced large numbers of seeds, the two exotic species produced many more viable seeds per cover than the two native species (Table 2.8). The fecundity of *Daucus carota* at the seed production stage was further enhanced by essentially no seed losses to either predation or competition. Forty percent of *Cynosurus echinatus* seeds were lost to the combined factors of

predation and competition; however, because of its high seed production, *C. echinatus* still produced more seedlings per unit cover than the other species, even after accounting for losses (Fig. 2.2).

Table 2.8. Demographic data for four Willamette Valley prairie species in 1992-1993. Seed production refers to the mean number of seeds produced per 1 cm<sup>2</sup> cover. The percentage of seeds lost to predation and competition refers to the mean number of seeds lost to each factor divided by the number of seeds sown. These percentages were applied to the seed production numbers to determine the re-scaled number of seeds lost out of the number produced.

Species	seed production	% of seeds lost to		re-scaled # of seeds lost to		total seeds after losses
		pre- dation	com- petition	pre- dation	com- petition	
<i>Bromus carinatus</i>	5.8	36	15	2.1	0.9	2.8
<i>Cynosurus echinatus</i>	140.8	7	33	9.9	46.5	84.4
<i>Prunella vulgaris</i>	4.2	9	3	0.4	0.1	3.7
<i>Daucus carota</i>	43.7	*	0	*	0	43.7

\*No estimate of loss to predation because uneven seed dispersal led to more seeds in predation plots than in control plots.

Both native species produced fewer than six viable seeds per 1 cm<sup>2</sup> cover. The low seed production of *Bromus carinatus* was exacerbated by predation and competition during seedling establishment, which caused a loss of over half of the individuals. While *Prunella vulgaris* suffered relatively few losses, its seed production was the lowest of all four species (4.2 seeds per 1 cm<sup>2</sup> cover).

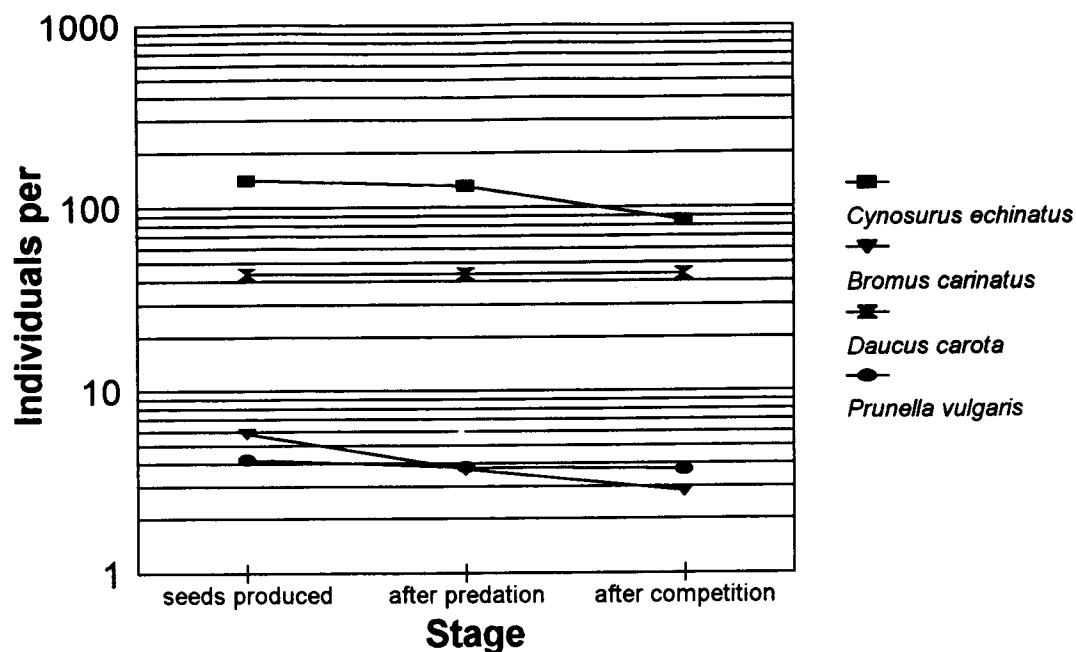


Figure 2.2. Demographic data for four Willamette Valley prairie species, 1992-1993. "Seeds produced" refers to the mean number of seeds produced per 1 cm<sup>2</sup> cover. "After predation" refers to the mean number of individuals remaining after post-dispersal seed predation losses. "After competition" refers to the mean number of individuals remaining after predation and competition losses.

## DISCUSSION

### Seed production

Based on Noble's (1989) model, one of the first indicators that a species may be a successful invader is the presence of a high flowering or fruiting effort. At the community level, my study indicates that exotic species do produce more seeds than the native species at this Willamette Valley grassland site.



While the overall seed production was greater for exotics than for natives in this study, there was much variation in seed production within each group. *Centaureum umbellatum*, an exotic forb, averaged 2,327 viable seeds per 1 cm<sup>2</sup> cover (SE = 1,937) in 1992, roughly four times greater than the seed production for any other exotic species (Appendices 6 and 7). Other species were apparent exceptions to the general trend of higher seed production for exotic species. In 1992, *Festuca idahoensis*, the dominant native grass at the site, had the third highest viable seed production of any species, native or exotic (mean = 537 viable seeds per 1 cm<sup>2</sup> cover, SE = 289) (Appendices 6 and 7). Certain exotic species were also exceptions. *Plantago lanceolata*, a common exotic herb, averaged only 4.7 viable seeds per 1 cm<sup>2</sup> cover (SE = 1.3) (Appendix 7). Therefore, while high seed production may be a warning sign that a species could be invasive, it is certainly not conclusive. *P. lanceolata* is a widespread invader of disturbed areas, but it would not be considered invasive based on its seed production alone.

Annual variations in seed production for individual species also make it difficult to predict invasive success. While *Festuca idahoensis* was a high seed producer in 1992, its viable seed production was an order of magnitude lower in 1991 (mean = 51 viable seeds per 1 cm<sup>2</sup> cover, SE = 17) (Appendix 6). There was also a tremendous variation in seed production between individual plants (personal observation). Although this variation is difficult for the researcher, it may be adaptive for the species, allowing at least some plants to survive annual fluctuations in the environment (Ewing and Menke 1983).

Differences in seed production between natives and exotics may be attributable in part to differences in life histories between the two groups. The majority of the native

Differences in seed production between natives and exotics may be attributable in part to differences in life histories between the two groups. The majority of the native species at this site were perennials, while the majority of exotics were annuals.

Characteristically, annuals have a greater reproductive effort, since they must concentrate all seed production into one terminal burst (Harper 1977; Silvertown 1987). As would be expected, the annual species produced more seeds per unit cover than the perennials.

This result is consistent with data from other grasslands in the western U.S. Jackson and Roy (1986) found that the biomass allocated to reproduction was higher for annuals (60%) than for perennials (40%) in a California annual grassland.

While differences between native and exotic seeds produced per unit cover was statistically significant both years, the number of seeds produced per biomass was only significant in 1991. This difference may be due to several factors. Statistical comparisons between native and exotic seeds per biomass did not take into consideration the error term associated with the regression used for biomass estimation, due to inadequacies of the statistical methods available. In addition, because the destructive sampling required for biomass estimation was incompatible with collecting seed production data, biomass sampling was done in 1993, rather than 1991 and 1992 when seed production and cover estimations were taken. Factors that can vary between years, such as competition and environmental elements, can affect allometric relationships (Johnson et al. 1988; Weiner and Thomas 1992 ). However, while allometric relationships may change between years, the main purpose of the biomass estimation was to provide a scale for comparing seed production of natives and exotics. Therefore, shifts in allometry between years would

only alter comparative results if the ratio of biomass to cover systematically differs for native and exotic species, which is unlikely.

Variations in weather may also help explain the differences in results for seed production per biomass. The weather in the spring of 1991 was cool and moist, while it was warm and dry in 1992, with no precipitation in May (NOAA 1992). Studies on other grassland systems in the western U.S. have indicated that weather condition can impact reproduction, growth, density, biomass production, and species composition (Evans et al. 1975; Ewing and Menke 1983; Jackson and Roy 1986; Evans and Young 1989; Coffin and Laurenroth 1992). While 1992 was a better seed production year for both natives and exotics by either measure, differences in weather conditions between 1991 and 1992 may have affected the relationship between natives and exotics.

### Seed predation

Noble's (1989) model suggests that the higher seed production observed in exotic species is somehow kept in check under native conditions. The four species in the seed predation study were all high seed producers. The natives were expected to experience higher rates of seed predation based on the idea that exotics were escaping from their native predators. Predation losses were indeed higher for the two native species in 1992, matching model predictions. Since only four species were studied the results have limited interpretations. However, these results are consistent with seed predation studies in England, where small mammals in dry grasslands took native seeds at significantly higher rate (49% versus 35%) than exotic seeds (Hulme 1990 cited in Crawley 1992).

In 1991-1992, effectively only the vertebrate predation losses were measured, and there were no statistically significant results. In 1992-1993, experimental methods excluded both vertebrate and invertebrate sources, and there were significant differences in seed predation for natives and exotics. Because of differing methods, comparisons between the two years' data are difficult. Variations in results between the two years could be attributed to several factors. Seeds set out in dishes are more obvious to predators than those sown in intact vegetation. In addition, seeds sown in intact vegetation were subject to burial and lateral movement. Seed burial is a major determinant of predation rate because buried seeds are lost at a lower rate (Crawley 1992). Lateral movement out of the study plots would have prevented seed retrieval. At this study site, Clark (1996) found that up to a quarter of the seeds sown in the study plots were lost due to lateral movement. However, another possible explanation of the differences between the two years would be the impact of invertebrate predation. Invertebrate seed predators may be more selective than vertebrates, which would explain the differing results. Although information is not available for Willamette Valley seed predators, this hypothesis is consistent with what is known about seed predators in other systems. Rodents tend to be generalist feeders (Hansson 1985 cited in Hulme 1994), so they are less likely to differentiate between species. Invertebrate predators, such as harvester ants, show distinct preferences for certain seeds in other grassland systems (Mittelbach and Gross 1984; Hobbs 1985; Thompson 1985; Risch and Carroll 1986; Beattie 1989; Crist and MacMahon 1992). Some ants are able to distinguish between congeneric and even conspecific seeds (Thompson 1985), so they would seem more likely

to select between familiar native seeds and unfamiliar exotic seeds in this study.

Information on *Daucus carota* also supports this hypothesis. *D. carota* seeds in a Michigan old field were rarely consumed by ants; seeds were only taken from plots with access to rodents (Mittelbach and Gross 1984). *D. carota* seeds have spines and an aromatic flavor that may protect them from some predators (Dale 1974; personal observation). Therefore, selective predators may avoid *D. carota* seeds.

The seed predation losses for grasses were also higher than for forbs. Once again, the trend was apparent both years, but was statistically significant only in year 2. This trend has been observed in other systems, as well. Fire ants, *Solenopsis geminata* (native to Mexico and Central America), selectively remove grass seeds, influencing weed community succession in the direction of a dicot-dominated community (Risch and Carroll 1986). The seed morphology of the grass species used in this study may help explain their higher predation rate. Some work indicates ants have difficulty carrying seeds smooth in outline; seeds with conspicuous awns or hairs are easier to carry (Pulliam and Riley Brand 1975). Both *C. echinatus* and *B. carinatus* have awns, which may make them preferable over the forb species in this study.

Both comparisons (native vs. exotic and grass vs. forb) were heavily influenced by the seed predation losses for *D. carota*. In both years of the study, the seed predation losses for *D. carota* were negligible. Studies from a Michigan old field also indicate that fewer *D. carota* seeds were taken than other species' seeds (Mittelbach and Gross 1984). Since the other study species lacked *D. carota*'s spines and aromatic flavor, they may have been more susceptible to predation. Therefore, it would have been more desirable to

role of seed predation in this system, additional studies on a greater number of species are necessary.

### Seedling establishment

Reductions in seedling establishment due to competition would alter the number of seeds that survive to produce replacement adults. As a result of disturbance, species composition, or other site-dependent factors, exotic species in new habitats may no longer experience the competition that helped keep their populations in check in their native lands. Based on this hypothesis, reducing competition should increase the number of native seedlings that established in this study because the native species are still growing in the presence of their competitors.

More *Bromus carinatus* seedlings established in the reduced competition plots in the second year of the study, although the trend was less clear the first year. This pattern is consistent with the idea that this native is still growing in the presence of key competitors. While the trend was not statistically significant, more seedlings of the other native species, *Prunella vulgaris*, also tended to establish in the reduced competition plots. This trend is supported by other work that indicates litter and herbaceous cover inhibit seedling emergence of *P. vulgaris* in woodland and old field sites (Winn 1985). In contrast, there was no significant difference in establishment between the two plots for the exotic forb, *Daucus carota*; Willamette Valley species do not appear to be key competitors in terms of seedling establishment for *D. carota*. Other data support this finding; *D. carota* seeds are

known to establish in a broad range of ground cover types, both vegetated and unvegetated (Gross and Werner 1982).

The situation was different for *Cynosurus echinatus*, the exotic grass. Significantly more *C. echinatus* seedlings established in the reduced competition plots, suggesting that native species do play a role in inhibiting seedling establishment of this species. Whether competition from Willamette Valley species is less limiting than competition from species in *C. echinatus*' native habitat is unknown. Examples exist where exotic species clearly do better with reduced competition from existing vegetation in a new habitat (Hobbs and Atkins 1988; Hobbs 1989). The importance of competition may depend on whether resources are limiting.

Data trends were stronger in the second year of this study, when predation was reduced as a confounding factor. One explanation of the difference between years is that seeds may be more obvious when sown on potting soil. If this were true, the predation rate would be higher in the reduced competition plots, thus reducing the number of seeds available to establish. This preferential predation might have masked the effect of competition. However, there were no obvious differences in establishment in the reduced competition plots between the two years; the data were simply more variable in year one (Appendices 9 and 10). It is difficult to know if predation was the cause of this variation.

To evaluate more fully the role of competition, additional studies are needed. First, it is important to establish that competition inhibits seedling establishment in a species' native habitat. My study addresses this effect for *B. carinatus* and *P. vulgaris*, but not for *C. echinatus* and *D. carota*; the latter two species need to be studied in their native

habitats. Secondly, it is necessary to compare competition in native versus new habitats to see if competition is reduced in a new habitat. If competition is important in the native habitat and reduced in a new habitat, then it would be possible to say that reduced competition may contribute to the species invasive success. My study is only a first step in examining this hypothesis.

### Demography

For the four species in this study, the vastly higher seed production of the exotic species overshadowed the effects of post-dispersal seed predation and competition during seedling establishment. Even after a loss of 40 percent of its seeds to predation and competition, *Cynosurus echinatus* still effectively produced twenty times as many seeds as the native species. *Daucus carota*'s high seed production was further complemented by the fact that it was essentially unaffected by predation and competition.

Enormous seed production is associated with many successful invasive species. *Lythrum salicaria*, an emergent aquatic plant that has invaded thousands of acres of wetland in North America, can produce as many as 2.7 million seeds per plant (Thompson et al. 1987). However, high seed production is not a consistent predictor of invasive success. For example, all the *Myriophyllum aquaticum* plants introduced to other parts of the world from South America are female, so the species produces no seed in these areas. In spite of its lack of seed production, *M. aquaticum* has successfully invaded many lakes and slow moving streams in the U.S. The species' success is facilitated by its ability to spread by fragmentation (Orchard 1981).



many lakes and slow moving streams in the U.S. The species' success is facilitated by its ability to spread by fragmentation (Orchard 1981).

## CONCLUSION

The population characteristics of the species studied at this Willamette Valley prairie site are consistent with Noble's (1989) model. As a group, the exotic species produced more viable seed than the native species. This higher seed production suggests that, in their native habitats, there are factors that help keep the exotic species in check. The lower post-dispersal seed predation rate of the exotic species is also consistent with Noble's model. The four study species were all selected for their high seed production, but because of fewer post-dispersal seed predation losses in 1992, more of the two exotic species' potential offspring could survive from flowering to the seed pool. While the results from the seedling establishment study are less clear, competition tended to reduce the number of seedlings that established for the two native species.

Overall, high seed production appeared to be the strongest indicator of invasive success for the four study species. For *Daucus carota* and *Cynosurus echinatus*, invasive success from high seed production was complemented by partial escape from predation. *D. carota* was further aided by its ability to establish in the presence of competing vegetation. While high seed production was a strong indicator of invasive success for these four species, studies on additional species are needed before generalities can be drawn for this system.

## Chapter 3

## CONCLUSIONS

The statistician G.E.P. Box stated, "All models are wrong, but some are useful." As is the case with all models, Noble's functional group model of invasions is an oversimplification of reality. But does this oversimplification have uses? In chapter 2, the model was useful as a framework for examining data from species that have already been introduced. These data suggest that the population processes stressed in the model do have power in explaining the patterns of exotic plant invasion in the Willamette Valley.

Additional advantages may result from using this functional group approach. Some of the key processes identified in the model may also indicate vulnerabilities that could be used in controlling undesirable exotics. For example, one of Noble's assertions is that the presence of a high flowering or fruiting effort suggests that under native conditions, there are probably great losses between flowering and the maturation of a replacement adult. If those losses, namely seed predation, are lacking or reduced in a new environment, then the introduction of an appropriate seed predator into that environment may help control the introduced species. This concept is the basis for classical biological control of weeds. Other processes in the model may provide useful insight into control options, as well. In chapter 2, native species inhibited seedling establishment for the exotic grass, *Cynosurus echinatus*. This finding suggests that establishing desirable, competitive vegetation may be an effective tactic for suppressing *C. echinatus*.

Many non-native species are introduced to new areas and either fail to establish, have little effect, or have beneficial effects. In the U.S., many treasured ornamentals are introduced species that have never spread beyond intentional plantings to cause problems. However, because of the myriad of negative impacts associated with some introductions, there is a true need to be able to predict invasive success and possible impacts.

In science, there has been a hope for a beautiful simplicity - the discovery of a few basic laws that would explain observed phenomena (Peters 1991). The study of biological invasions has been no exception. Much of the literature on invasions has focused on large-scale issues in hope of unearthing that beautiful simplicity. Unfortunately, this simplicity has not been forthcoming. Many attempts have been made to generalize about both species and environmental characteristics that tend to promote invasions. Often, these attempts have consisted of reviews of past invasions that have had devastating effects. The resulting checklists of traits have been unsatisfactory because they are not predictive. Baker's list of characteristics of the "ideal weed" cannot be used to predict definitively whether a particular species would be successful if introduced to a Willamette Valley native prairie. Instead, invasions appear to be context-specific events that require knowledge of local population dynamics and local conditions (Brown 1989; D'Antonio 1993; Burke and Grime 1996; Kareiva et al. 1996). The virtually infinite number of possible interactions between species and environment make accurate, large-scale prediction of invasions extremely impractical (Brown 1989). It is unlikely that models, such as Noble's, will unearth a beautiful simplicity, but this fact does not make such models useless.

Invasions can be viewed on a variety of scales. From a practical standpoint, much of the information needed is on a relatively small scale. How would a new species interact with the existing species assemblage at a given site? What types of impacts might it cause if it established? Addressing these types of issues does not require broad-scale theories; it requires long-term, experimental studies of specific species and habitats. This type of work is not as glamorous as the quest for the elusive beautiful simplicity. Instead, it falls under the category of what Kuhn (1970) referred to as "normal science" - research based on past scientific achievements. It is at the normal science level where science is applied to the problems of society. However, in spite of its practicality, normal science is underappreciated in ecology (Peters 1991).

Noble's model has the potential to be useful at this practical level. A functional group approach, such as Noble's, can be used to structure and interpret basic species and habitat studies on invasions. Increasing our fundamental knowledge of invaders and invulnerable habitats is likely to improve our predictive ability. The use of such models, in concert with long-term, experimental studies of invaders and invulnerable habitats, will increase our understanding of the processes involved and may suggest potential control methods. As more detailed information becomes available about particular invaders and invulnerable habitats, predictions may be possible in specific cases (e.g. Tucker and Richardson 1995). The ecology of invasions will never be a predictive science in the manner of physics, but increased knowledge in this area will certainly increase the potential for successful environmental problem-solving.

## BIBLIOGRAPHY

- Baker, H.G. 1965. Characteristics and modes of origin of weeds. *In* Baker, H.G. and C.L. Stebbins, eds. *The genetics of colonizing species*, pp. 147-169. Academic Press, New York.
- Beattie, A.J. 1989. The effects of ants on grasslands. *In* Huenneke, L.F. and H.A. Mooney, eds. *Grassland structure and function: California annual grassland*, pp. 104-116. Kluwer Academic Publishers, Dordrecht.
- Boyd, R. 1986. Strategies of Indian burning in the Willamette Valley. *Canadian Journal of Anthropology* 5:65-86.
- Brown, J.H. 1989. Patterns, modes and extents of invasions by vertebrates. *In* Drake, J.A., H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, eds. *Biological invasions: a global perspective*, pp. 85-109. John Wiley, Chichester, England.
- Burke, M.J.W. and J.P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77:776-790.
- Clark, D.A. 1996. Post-dispersal seed fates in a western Oregon native prairie. Ph.D. thesis. Oregon State University, Corvallis.
- Coblentz, B.E. 1990. Exotic organisms: a dilemma for conservation biology. *Conservation Biology* 4:261-265.
- Coffin, D.P. and W.K. Laurenroth. 1992. Spatial variability in seed production of the perennial bunchgrass *Bouteloua gracilis* (Gramineae). *American Journal of Botany* 79:347-353.
- Cohen, J. 1988. *Statistical power analysis for the behavioral sciences*, second edition. Lawrence Erlbaum Associates, Publishers, Hillsdale, NJ.
- Crawley, M.J. 1986. The population biology of invaders. *Philosophical Transactions of the Royal Society of London* B314:711-731.
- Crawley, M.J. 1987. What makes a community invisable? *In* Gray, A.J., M.J. Crawley, P.J. Edwards, eds. *Colonization, succession, and stability*, pp. 429-453. Blackwell, Oxford.

- Crawley, M.J. 1992. Seed predators and plant population dynamics. *In* Fenner, M., ed. *Seeds: the ecology of regeneration in plant communities*, pp.157-191. CAB International, Wallingford, UK.
- Crist, T.O. and J.A. MacMahon. 1992. Harvester ant foraging and shrub-steppe seeds: interactions of seed resources and seed use. *Ecology* 73:1768-1779.
- Crosby, A.W. 1986. *Ecological imperialism: the biological expansion of Europe 900-1900*. Cambridge University Press, Cambridge.
- Dale, H.M. 1974. The biology of Canadian weeds. 5. *Daucus carota*. *Canadian Journal of Plant Science* 54:673-685.
- D'Antonio, C.M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology* 74:83-95.
- D'Antonio, C.M. and B.E. Mahall. 1991. Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany* 78:885-894.
- Darwin, C. 1962. *The voyage of the Beagle*. Anchor Books, New York.
- Drake, J.A., H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, eds. 1989. *Biological invasions: a global perspective*. John Wiley, Chichester, England.
- Elton, C.S. 1958. *The ecology of invasions by animals and plants*. Methuen, London.
- Evans, R.A. and J.A. Young. 1989. Characterization and analysis of abiotic factors and their influences on vegetation. *In* Huenneke, L.F. and H.A. Mooney, eds. *Grassland structure and function: California annual grassland*, pp.13-28. Kluwer Academic Publishers, Dordrecht.
- Evans, R.A., B.L. Kay, and J.A. Young. 1975. Microenvironment of a dynamic annual community in relation to range improvement. *Hilgardia* 43:79-102.
- Ewing, A.L. and J.W. Menke. 1983. Reproductive potential of *Bromus mollis* and *Avena barbata* under drought conditions. *Madrono* 30:159-167.
- Flemion, F. And J. Olson. 1950. *Lygus* bugs in relation to seed production and occurrence of embryoless seeds in various umbelliferous species. *Contributions from Boyce Thompson Institute* 16:39-46.

Fox, M.D. and B.J. Fox. 1986. The susceptibility of natural communities to invasion. *In* Groves, R.H. and J.J. Burdon, eds. Ecology of biological invasions: an Australian perspective, pp. 57-66. Australian Academy of Science, Canberra.

Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service Gen. Tech. Report PNW-8, Portland, OR.

Gray, A.J. 1986. Do invading species have definable genetic characteristics? Philosophical Transactions of the Royal Society of London B314:655-674.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley, Chichester, England.

Grime, J.P., G. Mason, A.V. Curtis, J. Rodman, S.R. Band, M.A.G. Mowforth, A.M. Neal, and S. Shaw. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology* 69:1017-1059.

Gross, K.L. and P.A. Werner. 1982. Colonizing abilities of "biennial" plant species in relation to ground cover: implications for their distributions in a successional sere. *Ecology* 63:921-931.

Groves, R.H. and J.J. Burdon, eds. 1986. Ecology of biological invasions. Cambridge University Press, Cambridge.

Groves, R.H. and di Castri, F., eds. 1992. Biogeography of Mediterranean invasions. Cambridge University Press, Cambridge.

Habeck, J.R. 1961. The original vegetation of the mid-Willamette Valley, Oregon. *Northwest Science* 35:65-77.

Habeck, J.R. 1962. Forest succession in Monmouth Township, Polk County, Oregon since 1850. *Proceedings of the Montana Academy of Sciences* 21:7-17.

Hansson, L. 1985. The food of bank voles, woodmice and yellow-necked mice. *Symposia of the Zoological Society of London* 55:141-168.

Harper, J.L. 1977. Population biology of plants. Academic Press, London.

Hitchcock, C.L. and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Hobbs, R.J. 1985. Harvester ant foraging and plant species distribution in annual grassland. *Oecologia* 67:519-523.

Hobbs, R.J. 1989. The nature and effects of disturbance relative to invasions. *In* Drake, J.A., H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, eds. *Biological invasions: a global perspective*, pp. 389-405. John Wiley, Chichester, England.

Hobbs, R.J. and L. Atkins. 1988. Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Australian Journal of Ecology* 13:171-179.

Hobbs, R.J., S.L. Gulmon, V.J. Hobbs, and H.A. Mooney. 1988. Effects of fertiliser addition and subsequent gopher disturbance on a serpentine annual grassland community. *Oecologia* 75:291-295.

Holm, L.G., D.L. Plunkett, J.V. Pancho, and J.P. Herberger. 1977. *The world's worst weeds: distribution and biology*. University Press of Hawaii, Honolulu.

Huenneke, L. 1988. SCOPE program on biological invasions: a status report. *Conservation Biology* 2:8-10.

Huenneke, L.F., S.P. Hamburg, R. Koide, H.A. Mooney, and P.M. Vitousek. 1990. Effects of soils resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71:478-491.

Hughes, F., P.M. Vitousek, and T. Tunison. 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. *Ecology* 72:743-747.

Hulme, P.E. 1990. Small mammal herbivory and plant recruitment in grassland. Ph.D. thesis, University of London.

Hulme, P.E. 1994. Post-dispersal seed predation in grassland: its magnitude and sources of variation. *Journal of Ecology* 82:645-652.

Jackson, L.E. and J. Roy. 1986. Growth patterns of Mediterranean annual and perennial grasses under simulated rainfall regimes of southern France and California. *Acta Oecologia* 7:191-212.

Johannessen, C.L., W.A. Davenport, A. Millet, and S. McWilliams. 1971. The vegetation of the Willamette Valley. *Ann. Assoc. Amer. Geogr.* 61:286-302.

Johnson, P.S., C.L. Johnson, and N.E. West. 1988. Estimation of phytomass for ungrazed crested wheatgrass plants using allometric equations. *Journal of Range Management* 41:421-425.



- Kareiva, P., I.M. Parker, and M. Pascual. 1996. Can we use experiments and models in predicting the invasiveness of genetically engineered organisms? *Ecology* 77:1670-1675.
- Knezevich, C.A. 1975. Soil survey of Benton County Area, Oregon. USDA Soil Conservation Service, Washington, D.C.
- Kuhn, T.S. 1970. The structure of scientific revolutions, second edition. The University of Chicago Press, Chicago.
- Lewin, R. 1987. Ecological invasions offer opportunities. *Science* 238:752-753.
- Lodge, D.M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8:133-137.
- Lugo, A.E. 1990. Removal of exotic organisms. *Conservation Biology* 4:345.
- Mack, R.N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* 7:145-165.
- Martins, P.S. and S.K. Jain. 1979. Role of genetic variation in the colonizing ability of rose clover (*Trifolium hirtum* All.). *The American Naturalist* 114:591-595.
- Mittelbach, G.G. and K.L. Gross. 1984. Experimental studies of seed predation in old-fields. *Oecologia* 65:7-13.
- Moir, W. and P. Mika. 1972. Prairie vegetation of the Willamette valley, Benton County, Oregon. Unpublished report on file at USDA Forest Service Forestry Sciences Lab, Corvallis, Oregon.
- Mooney, H.A. and J.A. Drake, eds. 1986. Ecology of biological invasions of North America. Springer-Verlag, New York.
- Mooney, H.A. and J.A. Drake. 1987. The ecology of biological invasions. *Environment* 29:10-15, 34-37.
- Mooney, H.A. and J.A. Drake. 1989. Biological invasions: a SCOPE program overview. In Drake, J.A., H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, eds. Biological invasions: a global perspective, pp. 491-506. John Wiley, Chichester, England.
- Nature Conservancy, The. 1983. Survey of Willamette Valley 1981-1983 (A report to the Mason Trust). The Oregon Natural Heritage Data Base. Portland, Oregon.

Nelson, J.C. 1919. The grasses of Salem, Oregon and vicinity. *Torreyana* 19:216-227.

Newsome, A.E. and I.R. Noble. 1986. Ecological and physiological characters of invading species. *In* Groves, R.H. and J.J. Burdon, eds. *Ecology of biological invasions*, pp. 1-20. Cambridge University Press, Cambridge.

NOAA. 1985. *Climates of the states*, vol. 2. Gale Research Company, Detroit.

NOAA. 1991. *Climatological data annual summary - Oregon.*, vol. 97. NOAA, Environmental Data and Information Service, National Climatic Center, Asheville, NC.

NOAA. 1992. *Climatological data annual summary - Oregon.*, vol. 98. NOAA, Environmental Data and Information Service, National Climatic Center, Asheville, NC.

Noble, I.R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. *In* Drake, J.A., H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, eds. *Biological invasions: a global perspective*, pp. 301-313. John Wiley, Chichester, England.

Office of Technology Assessment, U.S. Congress. 1993. *Harmful non-indigenous species in the United States*. OTA-F-565. U.S. Government Printing Office, Washington, D.C.

Orchard, A.E. 1981. A revision of the South American *Myriophyllum* (Haloragaceae), and its repercussions on some Australian and North American species. *Brunonia* 4:27-65.

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

Orr, E.L., W.N. Orr, and E.M. Baldwin. 1992. *Geology of Oregon*, fourth edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Peters, R.H. 1991. *A critique for ecology*. Cambridge University Press, Cambridge.

Pimm, S.L. 1989. Theories predicting success and impact of introduced species. *In* Drake, J.A., H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, eds. *Biological invasions: a global perspective*, pp. 351-367. John Wiley, Chichester, England.

Pulliam, H.R. and M. Riley Brand. 1975. The production and utilization of seeds in plains grassland of southeastern Arizona. *Ecology* 56:1158-1166.

Rejmanek, M. 1989. Invasibility of plant communities. *In* Drake, J.A., H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson, eds. *Biological invasions: a global perspective*, pp. 369-388. John Wiley, Chichester, England.

Risch, S.J. and C. R. Carroll. 1986. Effects of seed predation by a tropical ant on competition among weeds. *Ecology* 67:1319-1327.

Savonen, C. 1988. Historical wetlands of the West Eugene Study Area. Unpublished report on file at the Oregon Field Office of The Nature Conservancy.

Silvertown, J. W. 1987. *Introduction to plant population ecology*, second edition. Longman Scientific and Technical, Essex, England.

Simberloff, D. 1981. Community effects of introduced species. *In* Nitecki, M.H., ed. *Biotic crises in ecological and evolutionary time*, pp. 53-81. Academic Press, New York.

Smith, J.E. 1949. Natural vegetation of the Willamette Valley, Oregon. *Science* 109:41-42.

Sprague, F.L. and H.P. Hansen. 1946. Forest succession in the McDonald Forest, Willamette Valley, Oregon. *Northwest Science* 20:89-98.

Stone, C.P., C.W. Smith, and J.T. Tunison. 1992. *Alien plant invasions in native ecosystems of Hawaii: management and research*. University of Hawaii, Honolulu.

Thilenius, J.F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. *Ecology* 49:1124-1133.

Thompson, D.Q., R.L. Stuckey, and E.B. Thompson. 1987. Spread, impact and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. U.S. Department of the Interior Fish and Wildlife Service, Washington, D.C.

Thompson, J.N. 1985. Postdispersal seed predation in *Lomatium* spp. (Umbelliferae): variation among individuals and species. *Ecology* 66:1608-1616.

Towle, J.C. 1982. Changing geography of Willamette Valley woodlands. *Oregon Historical Quarterly* 83:66-87.

Tucker, K.C. and D.M. Richardson. 1995. An expert system for screening potentially invasive alien plants in South African fynbos. *Journal of Environmental Management* 44:309-338.

Vermeij, G.J. 1991. When biotas meet: understanding biotic interchange. *Science* 253:1099-1104.

Vitousek, P.M. and L.R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* 59:247-265.

Weiner, J. and S.C. Thomas. 1992. Competition and allometry in three species of annual plants. *Ecology* 73:648-656.

Winn, A.A. 1985. Effects of seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. *Journal of Ecology* 73:831-840.

Winn, A.A. 1991. Proximate and ultimate sources of within-individual variation in seed mass in *Prunella vulgaris* (Lamiaceae). *American Journal of Botany* 78:838-844.

Winn, A.A. and P.A. Werner. 1987. Regulation of seed yield within and among populations of *Prunella vulgaris*. *Ecology* 68:1224-1233.

## APPENDICES

## Appendix 1

PRE-DISPERSAL SEED PREDATION OF SELECTED  
NATIVE AND EXOTIC WILLAMETTE VALLEY PRAIRIE SPECIESINTRODUCTION

Predators can reduce seed numbers by feeding on seeds either before or after they disperse from the parent plant. Most pre-dispersal seed predators are small, sedentary, specialist feeders belonging to the insect orders Diptera, Lepidoptera, Coleoptera, and Hymenoptera. Post-dispersal predators tend to be larger, more mobile generalist feeders, such as rodents and some birds (Crawley 1992), although harvester ants are important in many grassland systems (Hobbs 1985; Hulme 1994).

Pre-dispersal seed predation can have considerable impacts on some species. *Lygus* bugs are known to produce embryoless seeds in *Daucus carota*, reducing overall germination by 3 to 37 percent (Flemion and Olson 1950). In this study, I attempted to compare the pre-dispersal seed predation rates of two native and two exotic species found in western Oregon native prairies.

METHODS

The study was conducted in 1992 using the same four species as the post-dispersal seed predation study described in chapter 2: *Bromus carinatus* (native grass), *Cynosurus echinatus* (exotic grass), *Prunella vulgaris* var. *lanceolata* (native forb), and *Daucus carota* (exotic forb). Just prior to anthesis, fifteen random inflorescences of each species

were treated with the insecticide Lindane to prevent pre-dispersal seed predation. An additional 15 random inflorescences of each species were sprayed with water alone, as a control. Before the seeds dispersed, each infructescence was covered with a plastic, water-permeable bag and allowed to mature. After maturation, the bags were collected and the seeds from each bag were counted.

Because of the initial observed variability in the data, power analysis was used to determine if a two-sample t-test on the difference in means between treated and untreated inflorescences of each species would yield statistically meaningful results. I wanted to be able to detect 50% or greater differences (effect size) between treated and control inflorescences. For the analysis, the type I error rate was set at 0.05, and a one-tailed significance criterion was used, since the number of seeds in the treated inflorescences was expected to be greater than those in the untreated inflorescences.

## RESULTS AND DISCUSSION

There was a tremendous observed variation in seed production by individual plants (Appendix table 1.1). For the two native species, more seeds were produced in the control inflorescences than in the treatment inflorescences ( $P = 0.04$  for *Bromus carinatus*;  $P = 0.47$  for *Prunella vulgaris*). For these species, power equaled zero because, by definition, a one-tailed test has no power to detect differences in the direction opposite of the one predicted (Cohen 1988). While more seeds were produced in the treated inflorescences of the exotic species ( $P = 0.18$  for *Cynosurus echinatus*;  $P = 0.39$  for *Daucus carota*), power was still low (0.48 for *C. echinatus*; 0.36 for *D. carota*).

Therefore, the probability of being able to detect a statistically significant pre-dispersal seed predation effect was low or non-existent for all of the species in this study.

The variability in inflorescence sizes for these species is the likely cause for the lack of any treatment effect. For example, the number of seeds in *D. carota* inflorescences varied by a factor of seven within the same treatment. To more effectively look at the effects of pre-dispersal seed predation in this system, future studies need to consider inflorescence size. Improved designs include (a) reducing the range of inflorescence sizes examined, (b) calculating seed yield as a proportion of potential seed yield, and (c) using inflorescence size as a co-variable in the analysis of variance.

Appendix table 1.1. Numbers of seeds produced, with and without the insecticide Lindane to reduce pre-dispersal seed predators, by four Willamette Valley prairie species in 1992. P is the probability that treated and control inflorescences produce the same number of seeds. Power indicates the probability of detecting a 50% or greater difference in mean seed production between treated and untreated inflorescences using a two-sample t-test, with an upper-tailed, type I error rate of 0.05.

Species	with insecticide			without insecticide			P	power
	n	mean	sd	n	mean	sd		
<i>Bromus carinatus</i>	14	28.9	19.9	14	40.2	19.3	0.04 <sup>1</sup>	0.00 <sup>2</sup>
<i>Cynosurus echinatus</i>	15	24.9	16.1	15	18.3	16.9	0.18	0.48
<i>Prunella vulgaris</i>	15	65.4	43.9	15	66.6	41.6	0.47	0.00 <sup>2</sup>
<i>Daucus carota</i>	14	274.4	267.7	14	245.9	253.2	0.39	0.36

<sup>1</sup>While this P-value is significant, it represents a difference in the direction opposite of the one predicted.

<sup>2</sup>Power equals zero because, by definition, a one-tailed test has no power to detect differences in the direction opposite of the one predicted.



Appendix 2. Seed production data for native and exotic plants in a Willamette Valley prairie, 1991. Seed production is reported as the number of seeds produced per 1 cm<sup>2</sup> cover, as well as the number of seeds produced per biomass. Biomass values are in grams.

plot #	# native seeds	% native cover	native biomass	# native seeds/cover	# native seeds/biomass	# exotic seeds	% exotic cover	exotic biomass	# exotic seeds/cover	# exotic seeds/biomass
1	460	9.75	2.91	47.18	158.15	1060	40.00	12.63	26.50	83.91
2	226	3.50	1.22	64.57	185.06	915	32.25	11.02	28.37	83.01
3	195	30.00	7.54	6.50	25.88	51	6.00	3.80	8.50	13.42
4	521	44.50	10.52	11.71	49.51	922	6.50	4.00	141.85	230.56
5	269	9.75	2.78	29.08	96.70	560	29.50	10.42	18.98	53.75
6	19	3.50	1.22	5.43	15.56	425	30.00	10.53	14.17	40.36
7	153	49.50	11.52	3.09	13.28	1052	13.00	6.20	80.92	169.63
8	96	5.50	1.79	17.45	53.60	315	20.50	8.27	15.37	38.07
9	221	7.50	2.33	29.47	94.89	1057	22.00	8.65	48.05	122.16
10	153	22.00	5.79	6.95	26.40	3353	26.50	9.73	126.53	344.46
11	120	51.00	11.81	2.35	10.16	4	6.00	3.80	0.67	1.05
12	13	24.25	6.29	0.54	2.07	72	6.50	4.00	11.08	18.00
13	48	10.00	2.97	4.80	16.15	674	12.00	5.90	56.17	114.33
14	116	12.75	3.65	9.10	31.78	165	20.00	8.15	8.25	20.26
15	6	26.75	6.84	0.22	0.88	175	3.50	2.70	50.00	64.75
16	45	28.75	7.27	1.57	6.19	827	7.75	4.47	106.71	185.01

## Appendix 2, Continued

plot #	# native seeds	% native cover	native biomass	# native seeds/cover	# native seeds/biomass	# exotic seeds	% exotic cover	exotic biomass	# exotic seeds/cover	# exotic seeds/biomass
17	365	28.75	7.27	12.70	50.21	622	20.00	8.15	31.10	76.36
18	31	17.25	4.72	1.80	6.57	87	24.00	9.14	3.63	9.52
19	302	11.25	3.28	26.84	91.98	1154	16.00	7.07	72.13	163.16
20	167	28.25	7.16	5.91	23.32	241	5.75	3.70	41.91	65.13
21	90	41.75	9.97	2.16	9.03	904	9.00	4.91	100.44	183.97
22	140	27.25	6.95	5.14	20.15	1362	24.75	9.32	55.03	146.10
23	128	35.00	8.59	3.66	14.91	41	9.50	5.08	4.32	8.06
24	25	12.50	3.59	2.00	6.96	158	48.00	14.18	3.29	11.14

Appendix 3. Seed production data for native and exotic plants in a Willamette Valley prairie, 1992. Seed production is reported as the number of seeds produced per 1 cm<sup>2</sup> cover, as well as the number of seeds produced per biomass. Biomass values are in grams.

plot #	# native seeds	% native cover	native biomass	# native seeds/cover	# native seeds/biomass	# exotic seeds	% exotic cover	exotic biomass	# exotic seeds/cover	# exotic seeds/biomass
1	2937	76.80	16.71	38.24	175.79	2231	19.90	8.12	112.11	274.76
2	156	25.60	6.59	6.09	23.68	601	36.00	11.82	16.69	50.86
3	3967	30.00	7.54	132.23	526.43	925	12.20	5.96	75.82	155.27
4	873	47.80	11.18	18.26	78.08	613	9.00	4.91	68.11	124.75
5	2302	31.00	7.75	74.26	297.11	3581	21.50	8.53	166.56	419.94
6	832	35.30	8.65	23.57	96.19	1500	18.00	7.62	83.33	196.85
7	566	32.40	8.04	17.47	70.37	11259	23.35	8.98	482.18	1253.13
8	1349	41.50	9.92	32.51	135.99	1464	49.90	14.53	29.34	100.75
9	953	53.30	12.26	17.88	77.72	1463	29.40	10.40	49.76	140.73
10	681	19.50	5.23	34.92	130.16	2759	41.05	12.84	67.21	214.86
11	1377	39.40	9.49	34.95	145.06	1838	36.50	11.92	50.36	154.18
12	518	33.50	8.27	15.46	62.61	1350	26.75	9.79	50.47	137.87
13	2723	22.00	5.79	123.77	469.91	1686	51.70	14.86	32.61	113.46
14	819	26.55	6.79	30.85	120.53	993	24.55	9.27	40.45	107.07
15	1072	44.00	10.42	24.36	102.84	1761	29.25	10.36	60.21	169.95
16	529	27.00	6.89	19.59	76.75	842	30.30	10.60	27.79	79.47

### Appendix 3, Continued

plot #	# native seeds	% native cover	native biomass	# native seeds/cover	# native seeds/biomass	# exotic seeds	% exotic cover	exotic biomass	# exotic seeds/cover	# exotic seeds/biomass
17	306	14.50	4.07	21.10	75.17	2529	60.00	16.33	42.15	154.88
18	341	10.00	2.97	34.10	114.75	905	60.10	16.35	15.06	55.37
19	2805	55.50	12.69	50.54	221.06	5574	28.80	10.26	193.54	543.27
20	219	30.00	7.54	7.30	29.06	1540	53.35	15.16	28.87	101.59
21	197	87.50	18.66	2.25	10.56	302	11.05	5.60	27.33	53.97
22	720	13.70	3.88	52.55	185.58	1637	44.30	13.48	36.95	121.48
23	1582	21.40	5.66	73.93	279.48	1631	27.80	10.03	58.67	162.55
24	770	21.00	5.57	36.37	138.22	1199	36.00	11.82	33.31	101.46

Appendix 4. Number of seeds produced per 1 cm<sup>2</sup> cover for native species in a Willamette Valley prairie, 1991.  
 "a" indicates species absent from plot.

Species	plot number								
	1	2	3	4	5	6	7	8	9
<i>Achillea millefolium</i>	a	a	0.0	0.0	a	a	0.0	a	a
<i>Bromus carinatus</i>	a	a	9.8	0.9	13.6	a	5.2	a	a
<i>Clarkia amoena</i>	a	a	a	a	a	a	a	a	a
<i>Clarkia quadrivulnera</i>	a	a	a	a	a	a	a	22.0	a
<i>Crataegus douglasii</i>	a	a	0.0	a	a	a	a	a	a
<i>Danthonia californica</i>	a	a	a	6.0	a	a	a	0.0	a
<i>Elymus glaucus</i>	a	a	a	30.3	a	a	3.4	a	30.0
<i>Epilobium paniculatum</i>	a	138.0	a	a	a	a	a	a	0.0
<i>Eriophyllum lanatum</i>	a	a	a	a	0.0	0.0	a	0.0	0.0
<i>Festuca idahoensis</i>	186.0	34.0	a	18.0	234.0	0.0	a	122.0	52.0
<i>Fragaria virginiana</i>	0.0	a	0.0	0.0	a	a	a	0.0	a
<i>Geranium carolinianum</i>	3.2	a	a	32.0	14.4	a	7.6	7.3	14.4
<i>Linum angustifolium</i>	282.0	a	a	61.7	a	20.0	62.0	a	54.0
<i>Luzula campestris</i>	a	a	a	19.7	a	a	a	a	a
<i>Madia grasilis</i>	106.4	0.0	a	0.0	52.8	18.0	a	4.0	270.0
<i>Madia sativa</i>	a	a	a	a	a	a	a	a	a
<i>Potentilla gracilis</i>	a	a	0.0	a	a	a	a	a	a
<i>Prunella vulgaris</i>	71.2	70.0	a	0.0	a	a	a	a	a
<i>Pteridium aquilinum</i>	a	a	a	a	a	a	0.0	a	

# Appendix 4, Continued

Species	plot number								
	10	11	12	13	14	15	16	17	18
<i>Achillea millefolium</i>	a	a	a	a	a	a	a	a	a
<i>Bromus carinatus</i>	0.0	1.2	a	0.0	0.0	4.8	1.9	0.0	a
<i>Clarkia amoena</i>	a	a	a	0.0	a	a	a	a	a
<i>Clarkia quadrivulnera</i>	184.0	a	a	a	87.2	a	a	a	a
<i>Crataegus douglasii</i>	a	a	a	a	a	a	a	a	a
<i>Danthonia californica</i>	a	a	a	a	a	a	a	a	a
<i>Elymus glaucus</i>	27.2	0.0	0.0	a	0.0	0.0	a	0.0	a
<i>Epilobium paniculatum</i>	a	0.0	a	a	a	a	0.0	a	a
<i>Eriophyllum lanatum</i>	0.0	a	a	0.0	a	a	0.0	0.0	0.0
<i>Festuca idahoensis</i>	0.3	52.8	0.0	9.3	a	0.0	6.4	79.2	0.5
<i>Fragaria virginiana</i>	0.0	0.0	0.0	a	0.0	a	0.0	a	0.0
<i>Geranium carolinianum</i>	8.7	14.0	6.5	a	5.6	a	a	14.0	14.0
<i>Linum angustifolium</i>	a	a	a	a	a	a	a	48.0	a
<i>Luzula campestris</i>	a	0.0	a	a	a	a	a	a	a
<i>Madia grasilis</i>	a	a	a	40.0	a	a	0.0	a	38.0
<i>Madia sativa</i>	a	a	a	0.0	a	a	a	12.6	a
<i>Potentilla gracilis</i>	a	a	0.0	a	a	a	a	a	a
<i>Prunella vulgaris</i>	a	a	a	a	a	a	a	a	a
<i>Pteridium aquilinum</i>	a	a	a	a	a	a	a	a	a

Appendix 4, Continued

Species	plot number						mean	SE
	19	20	21	22	23	24		
<i>Achillea millefolium</i>	0.0	a	a	a	a	a	0.0	0.0
<i>Bromus carinatus</i>	0.0	15.2	4.0	7.2	2.5	0.0	3.9	1.2
<i>Clarkia amoena</i>	a	a	a	a	a	a	0.0	-
<i>Clarkia quadrivulnera</i>	36.8	48.0	a	a	a	a	75.6	29.2
<i>Crataegus douglasii</i>	a	a	a	a	a	a	0.0	-
<i>Danthonia californica</i>	a	a	0.0	a	a	a	2.0	2.0
<i>Elymus glaucus</i>	a	0.1	1.3	0.0	a	a	7.7	3.8
<i>Epilobium paniculatum</i>	0.0	a	a	a	a	a	27.6	27.6
<i>Eriophyllum lanatum</i>	0.0	0.0	0.0	0.0	a	0.0	0.0	0.0
<i>Festuca idahoensis</i>	250.0	116.0	19.7	a	a	42.0	64.3	18.5
<i>Fragaria virginiana</i>	0.0	0.0	0.0	a	a	0.0	0.0	0.0
<i>Geranium carolinianum</i>	52.0	14.0	8.0	10.5	a	0.0	13.3	3.0
<i>Linum angustifolium</i>	a	a	a	a	a	a	87.9	39.3
<i>Luzula campestris</i>	a	a	a	a	5.3	a	8.3	5.9
<i>Madia grasilis</i>	54.0	a	a	5.6	a	a	49.1	22.1
<i>Madia sativa</i>	a	a	a	a	a	a	0.0	-
<i>Potentilla gracilis</i>	a	a	a	a	a	a	0.0	0.0
<i>Prunella vulgaris</i>	a	a	0.0	a	a	a	30.8	16.4
<i>Pteridium aquilinum</i>	a	a	a	a	a	a	0.0	-

Appendix 5. Number of seeds produced per 1 cm<sup>2</sup> cover for exotic species in a Willamette Valley prairie, 1991.  
 "a" indicates species absent from plot.

Species	plot number								
	1	2	3	4	5	6	7	8	9
<i>Aira caryophyllea</i>	a	a	a	a	a	a	a	a	a
<i>Bromus mollis</i>	66.0	6.0	a	2.0	a	20.0	a	34.0	2.0
<i>Centaureum umbellatum</i>	a	a	a	a	a	a	a	a	414.0
<i>Chrysanthemum leucanthemum</i>	a	a	a	a	a	a	a	a	a
<i>Cynosurus echinatus</i>	113.3	108.0	14.0	697.6	186.0	140.0	129.0	100.0	24.0
<i>Daucus carota</i>	105.8	0.0	0.0	0.0	71.7	6.8	0.0	0.0	0.0
<i>Elymus caput-medusae</i>	55.0	19.3	a	a	402.0	0.0	a	13.4	9.3
<i>Galium parisiense</i>	a	243.2	a	14.0	a	a	a	0.0	a
<i>Hypericum perforatum</i>	0.0	a	a	0.0	0.0	a	a	a	a
<i>Hypochaeris radicata</i>	0.0	a	a	a	a	a	a	a	a
<i>Lathyrus sphaericus</i>	40.0	0.0	a	a	a	a	a	a	a
<i>Myosotis discolor</i>	20.0	a	a	a	a	a	a	a	a
<i>Plantago lanceolata</i>	2.5	2.0	a	0.0	2.0	3.6	1.6	2.3	0.3
<i>Poa pratensis</i>	14.0	a	a	a	a	a	157.2	276.0	a
<i>Senecio jacobaea</i>	a	a	a	a	a	a	a	a	a
<i>Sherardia arvensis</i>	a	a	a	84.0	a	a	a	a	a
<i>Torilis arvensis</i>	0.0	a	82.0	a	a	a	0.0	40.0	150.0



Appendix 5, Continued

Species	plot number								
	10	11	12	13	14	15	16	17	18
<i>Aira caryophyllea</i>	a	a	a	a	a	a	4.0	334.0	a
<i>Bromus mollis</i>	2.0	0.0	22.0	280.0	42.0	10.0	58.0	96.0	60.0
<i>Centaureum umbellatum</i>	a	a	561.0	a	a	a	a	a	a
<i>Chrysanthemum leucanthemum</i>	a	a	a	a	a	a	a	a	a
<i>Cynosurus echinatus</i>	75.2	8.0	16.0	16.0	30.0	a	136.0	306.0	74.0
<i>Daucus carota</i>	0.0	0.0	a	0.0	0.0	0.0	0.0	4.0	0.0
<i>Elymus caput-medusae</i>	9.3	18.0	a	280.0	128.0	a	6.0	58.0	a
<i>Galium parisiense</i>	856.0	a	a	726.0	a	340.0	55.2	234.0	a
<i>Hypericum perforatum</i>	a	0.0	a	a	a	a	0.0	a	a
<i>Hypochaeris radicata</i>	a	a	a	a	a	0.0	a	a	a
<i>Lathyrus sphaericus</i>	a	0.0	0.0	0.0	a	a	a	a	a
<i>Myosotis discolor</i>	a	a	a	a	a	a	38.0	a	a
<i>Plantago lanceolata</i>	0.8	0.0	10.6	2.7	7.4	a	8.8	4.0	1.3
<i>Poa pratensis</i>	a	a	a	14.0	12.0	a	a	a	0.0
<i>Senecio jacobaea</i>	a	0.0	a	a	a	a	a	a	a
<i>Sherardia arvensis</i>	a	a	a	a	a	a	1252.0	80.0	a
<i>Torilis arvensis</i>	150.0	30.0	a	0.0	a	a	0.0	a	0.0

Appendix 5, Continued

Species	plot number						mean	SE
	19	20	21	22	23	24		
<i>Aira caryophyllea</i>	a	a	a	a	a	a	169.0	165.0
<i>Bromus mollis</i>	584.0	184.0	46.0	164.0	a	2.0	84.0	31.0
<i>Centaureum umbellatum</i>	a	a	588.8	a	a	0.0	391.0	135.9
<i>Chrysanthemum leucanthemum</i>	a	a	a	a	a	0.0	0.0	-
<i>Cynosurus echinatus</i>	96.0	0.0	68.0	179.2	38.0	100.0	115.4	30.4
<i>Daucus carota</i>	78.5	a	0.0	1.2	0.0	0.0	12.2	6.5
<i>Elymus caput-medusae</i>	38.0	56.0	28.0	4.0	a	9.7	70.3	28.2
<i>Galium parisiense</i>	488.0	10.0	a	a	a	a	296.6	97.2
<i>Hypericum perforatum</i>	a	a	a	a	a	a	0.0	0.0
<i>Hypochaeris radicata</i>	a	a	a	a	0.0	a	0.0	0.0
<i>Lathyrus sphaericus</i>	66.0	a	a	0.0	a	0.0	13.3	9.0
<i>Myosotis discolor</i>	a	a	a	a	a	a	29.0	9.0
<i>Plantago lanceolata</i>	a	18.5	a	1.2	7.3	1.8	3.9	1.0
<i>Poa pratensis</i>	a	a	92.0	a	a	a	80.7	39.1
<i>Senecio jacobaea</i>	a	a	a	184.6	a	a	92.3	92.3
<i>Sherardia arvensis</i>	a	0.0	a	a	a	a	354.0	300.0
<i>Torilis arvensis</i>	a	63.2	a	56.5	a	46.0	39.0	13.1

Appendix 6. Number of seeds produced per 1 cm<sup>2</sup> cover for native species in a Willamette Valley prairie, 1992.  
 "a" indicates species absent from plot.

Species	plot number								
	1	2	3	4	5	6	7	8	9
<i>Achillea millefolium</i>	a	a	0.0	a	a	a	a	a	a
<i>Brodiaea coronaria</i>	a	a	a	a	a	a	0.0	9.0	a
<i>Bromus carinatus</i>	a	a	0.5	a	8.5	8.2	5.1	a	a
<i>Clarkia quadrivulnera</i>	3.3	a	72.8	a	a	17.0	20.0	a	a
<i>Danthonia californica</i>	1.0	a	a	a	a	26.0	a	5.0	a
<i>Elymus glaucus</i>	a	a	a	a	a	20.0	a	a	a
<i>Epilobium paniculatum</i>	0.0	0.0	71.0	150.0	79.6	16.0	82.5	0.0	78.0
<i>Eriophyllum lanatum</i>	a	0.0	a	a	a	0.0	0.0	0.0	0.0
<i>Festuca idahoensis</i>	32.4	75.0	581.8	22.0	417.0	714.0	218.0	7653.0	51.6
<i>Fragaria virginiana</i>	a	0.0	a	a	a	a	0.0	a	a
<i>Geranium carolinianum</i>	4.8	14.2	5.7	4.9	0.0	32.2	12.8	3.8	5.1
<i>Linum angustifolium</i>	162.0	35.0	105.5	0.0	a	33.3	150.0	a	506.7
<i>Lotus denticulatus</i>	a	a	0.0	a	0.0	a	18.0	3.5	a
<i>Luzula campestris</i>	a	a	a	a	a	a	a	a	0.0
<i>Madia grasilis</i>	161.0	a	107.7	a	190.0	a	62.3	a	61.0
<i>Madia sativa</i>	a	a	0.0	a	a	0.0	a	a	a
<i>Prunella vulgaris</i>	a	a	a	a	a	a	a	12.7	13.3

Appendix 6, Continued

Species	plot number								
	10	11	12	13	14	15	16	17	18
<i>Achillea millefolium</i>	a	a	a	a	a	a	0.0	a	a
<i>Brodiaea coronaria</i>	a	a	a	a	a	a	a	a	a
<i>Bromus carinatus</i>	5.9	20.3	0.0	a	a	0.0	a	a	a
<i>Clarkia quadrivulnera</i>	0.0	a	a	a	a	a	5.0	23.8	50.5
<i>Danthonia californica</i>	a	a	a	a	3.2	a	a	a	a
<i>Elymus glaucus</i>	a	a	a	a	a	a	a	a	0.0
<i>Epilobium paniculatum</i>	a	69.5	11.5	0.0	26.0	44.0	a	0.0	17.0
<i>Eriophyllum lanatum</i>	0.0	0.0	0.0	a	0.0	0.2	0.0	0.0	0.0
<i>Festuca idahoensis</i>	1058.0	643.0	30.9	277.6	7043.0	86.4	9.0	404.0	111.5
<i>Fragaria virginiana</i>	a	a	0.0	a	a	a	a	a	a
<i>Geranium carolinianum</i>	11.5	4.9	6.2	8.8	12.4	3.3	3.2	4.5	0.0
<i>Linum angustifolium</i>	28.0	82.3	0.0	206.0	157.0	152.0	162.0	a	a
<i>Lotus denticulatus</i>	a	a	a	0.0	a	a	a	a	a
<i>Luzula campestris</i>	a	a	a	a	a	a	a	a	a
<i>Madia grasilis</i>	a	20.0	a	52.2	a	41.3	a	a	a
<i>Madia sativa</i>	a	a	a	a	a	a	a	a	a
<i>Prunella vulgaris</i>	a	8.9	a	a	a	a	38.1	a	a

Appendix 6, Continued

Species	plot number						mean	SE
	19	20	21	22	23	24		
<i>Achillea millefolium</i>	a	a	a	a	a	a	0.0	0.0
<i>Brodiaea coronaria</i>	a	a	a	a	a	a	5.8	2.0
<i>Bromus carinatus</i>	a	9.0	a	0.0	a	a	4.5	4.5
<i>Clarkia quadrivulnera</i>	0.0	a	a	a	a	0.0	19.3	7.8
<i>Danthonia californica</i>	a	a	a	a	a	a	8.8	5.8
<i>Elymus glaucus</i>	a	86.0	a	a	a	a	35.3	26.0
<i>Epilobium paniculatum</i>	2.0	0.0	0.0	0.0	0.0	47.0	31.6	8.7
<i>Eriophyllum lanatum</i>	0.0	a	a	a	a	0.0	0.0	0.0
<i>Festuca idahoensis</i>	66.4	5.0	2.3	121.6	104.3	132.7	536.7	288.8
<i>Fragaria virginiana</i>	a	0.0	a	a	a	a	0.0	0.0
<i>Geranium carolinianum</i>	12.1	a	a	10.5	7.3	15.3	8.4	1.5
<i>Linum angustifolium</i>	a	a	a	36.7	45.0	a	116.4	31.0
<i>Lotus denticulatus</i>	a	2.5	a	a	a	a	4.2	2.9
<i>Luzula campestris</i>	a	a	a	a	a	a	0.0	0.0
<i>Madia grasilis</i>	26.0	a	a	38.0	113.0	a	79.5	17.0
<i>Madia sativa</i>	a	a	a	a	a	a	0.0	0.0
<i>Prunella vulgaris</i>	a	11.0	a	a	28.5	13.0	18.0	4.2

Appendix 7. Number of seeds produced per 1 cm<sup>2</sup> cover for exotic species in a Willamette Valley prairie, 1992.  
 "a" indicates species absent from plot.

Species	plot number								
	1	2	3	4	5	6	7	8	9
<i>Aira caryophyllea</i>	65.0	a	a	a	320.0	215.0	a	a	a
<i>Avena sp.</i>	a	a	a	a	a	a	a	a	a
<i>Bromus mollis</i>	340.0	20.0	205.0	a	a	52.5	176.7	a	103.3
<i>Bromus sterilis</i>	a	a	a	a	a	a	a	a	a
<i>Centaureum umbellatum</i>	a	a	a	a	a	a	9991.0	a	0.0
<i>Cerastium viscosum</i>	a	a	a	a	13.3	320.0	a	a	0.0
<i>Chrysanthemum leucanthemum</i>	a	16.7	a	a	a	a	a	a	a
<i>Cynosurus echinatus</i>	364.0	105.0	88.5	14.0	162.0	128.0	99.5	56.0	124.5
<i>Daucus carota</i>	129.6	21.9	81.3	a	a	0.0	52.0	30.6	36.7
<i>Dactylis glomerata</i>	a	a	a	a	a	22.0	a	a	a
<i>Elymus caput-medusae</i>	95.5	140.0	42.3	242.5	a	66.0	8.0	29.7	44.7
<i>Galium parisiense</i>	313.0	a	a	a	252.2	158.0	178.7	a	540.0
<i>Gastridium ventricosum</i>	a	a	a	a	a	a	a	a	a
<i>Hypochaeris radicata</i>	a	a	a	a	a	a	a	25.0	a
<i>Lathyrus sphaericus</i>	40.0	26.0	a	10.0	a	75.0	4.0	0.0	a
<i>Lolium perenne</i>	a	a	a	a	a	a	a	a	a
<i>Myosotis discolor</i>	a	700.0	230.0	a	a	900.0	500.0	a	0.0

# Appendix 7, Continued

Species	plot number								
	1	2	3	4	5	6	7	8	9
<i>Plantago lanceolata</i>	0.0	a	1.0	a	a	2.0	2.2	1.7	0.0
<i>Poa pratensis</i>	a	a	a	18.0	a	23.3	a	a	75.5
<i>Sherardia arvensis</i>	a	a	a	a	a	a	a	0.0	48.8
<i>Torilis arvensis</i>	41.7	22.0	76.0	a	a	57.0	a	a	a
<i>Vicia sativa</i>	a	a	a	a	a	a	a	a	a

# Appendix 7, Continued

Species	plot number								
	10	11	12	13	14	15	16	17	18
<i>Aira caryophyllea</i>	a	a	a	a	a	a	a	a	a
<i>Avena sp.</i>	a	6.0	16.0	a	a	18.0	a	a	a
<i>Bromus mollis</i>	78.0	a	95.0	48.0	166.0	31.5	212.0	46.5	106.0
<i>Bromus sterilis</i>	165.0	a	a	a	a	a	a	a	2.7
<i>Centaureum umbellatum</i>	132.5	a	a	0.0	a	a	a	a	a
<i>Cerastium viscosum</i>	a	a	a	45.0	a	220.0	a	a	a
<i>Chrysanthemum leucanthemum</i>	271.0	a	a	a	a	a	a	a	a
<i>Cynosurus echinatus</i>	0.0	231.0	196.8	81.5	238.0	312.0	403.3	26.0	127.0
<i>Daucus carota</i>	a	74.0	29.7	0.0	45.1	a	0.0	47.1	50.5
<i>Dactylis glomerata</i>	a	a	a	a	a	a	a	a	a
<i>Elymus caput-medusae</i>	127.5	32.7	50.5	35.6	128.0	15.3	15.3	15.0	26.0
<i>Galium parisiense</i>	2180.0	a	800.0	93.3	a	91.2	a	108.4	40.0
<i>Gastridium ventricosum</i>	a	a	a	a	a	a	a	a	320.0
<i>Hypochaeris radicata</i>	a	a	a	a	a	a	a	a	a
<i>Lathyrus sphaericus</i>	22.0	15.0	a	14.0	31.0	18.0	59.0	a	22.0
<i>Lolium perenne</i>	30.0	a	24.3	a	a	a	a	5.0	19.0
<i>Myosotis discolor</i>	80.0	a	a	778.0	a	1060.0	a	a	140.0



Appendix 7, Continued

Species	plot number								
	10	11	12	13	14	15	16	17	18
<i>Plantago lanceolata</i>	2.9	5.3	3.0	1.2	6.1	4.0	0.4	0.4	20.3
<i>Poa pratensis</i>	a	66.7	a	a	0.0	a	a	a	a
<i>Sherardia arvensis</i>	a	50.0	a	a	a	a	a	a	a
<i>Torilis arvensis</i>	48.0	a	19.0	a	a	48.3	a	42.2	10.5
<i>Vicia sativa</i>	a	a	9.3	a	a	a	a	a	0.0

# Appendix 7, Continued

Species	plot number						mean	SE
	19	20	21	22	23	24		
<i>Aira caryophyllea</i>	85.0	a	a	a	a	128.0	162.6	47.0
<i>Avena sp.</i>	a	a	a	a	a	a	13.3	3.7
<i>Bromus mollis</i>	99.7	45.5	22.0	200.0	260.0	64.0	118.7	19.8
<i>Bromus sterilis</i>	a	0.0	a	a	a	a	56.0	54.5
<i>Centaureum umbellatum</i>	1512.3	a	a	a	a	a	2327.2	1937.1
<i>Cerastium viscosum</i>	140.0	a	a	a	a	a	123.0	52.2
<i>Chrysanthemum leucanthemum</i>	a	a	a	a	a	a	144.0	127.0
<i>Cynosurus echinatus</i>	62.0	110.0	44.0	156.0	114.8	132.0	140.8	21.4
<i>Daucus carota</i>	18.6	a	0.0	a	140.0	26.8	43.7	9.7
<i>Dactylis glomerata</i>	a	a	a	a	a	a	22.0	na
<i>Elymus caput-medusae</i>	194.0	a	45.0	27.0	68.0	42.0	69.1	13.1
<i>Galium parisiense</i>	43.0	241.4	52.0	41.2	38.0	91.5	309.5	126.9
<i>Gastrium ventricosum</i>	a	a	a	a	a	a	320.0	na
<i>Hypochaeris radicata</i>	a	a	a	a	a	a	25.0	na
<i>Lathyrus sphaericus</i>	0.0	a	19.5	19.6	31.0	a	23.9	4.8
<i>Lolium perenne</i>	a	a	a	a	a	a	19.5	5.3
<i>Myosotis discolor</i>	1300.0	0.0	1100.0	a	a	a	535.7	135.3

# Appendix 7, Continued

Species	plot number						mean	SE
	19	20	21	22	23	24		
<i>Plantago lanceolata</i>	0.0	0.3	19.0	1.8	9.7	5.1	4.7	1.3
<i>Poa pratensis</i>	25.0	a	a	a	a	a	38.2	14.4
<i>Sherardia arvensis</i>	a	a	a	a	a	0.0	16.7	16.7
<i>Torilis arvensis</i>	21.0	33.7	a	75.8	20.0	a	40.4	5.5
<i>Vicia sativa</i>	a	3.5	2.0	8.5	a	2.0	4.3	1.6

Appendix 8. Number of seeds lost to post-dispersal seed predation for four species in a Willamette Valley prairie, adjusted for background counts. Species include: *Bromus carinatus* (native grass), *Cynosurus echinatus* (exotic grass), *Prunella vulgaris* var. *lanceolata* (native dicot), and *Daucus carota* (exotic dicot). Negative numbers indicate that more seeds were lost in plots protected from predators than in plots open to predators.

1991-1992					1992-1993				
block #	grasses		dicots		block #	grasses		dicots	
	native	exotic	native	exotic		native	exotic	native	exotic
1	0	5		2	1	6	7	12	-1
2	12	-1		4	3	9	-8	1	-7
3	0	6	-6		4	7	1	3	-3
4	2	0	-1	8	5	8	10	9	6
5	0	0	4	-12	6	6	-2	1	1
6	-1		3	5	7	5	5	7	-1
7	-3	0	-1	-3	8	11	2	4	-5
9			-2		10	5	2	3	3
10	1	-2	1	-9	11	-2	-4	1	-2
11	0	1	15	12	12	-2	-3	0	-6
12	1	0		2	13	5	-4	1	-8
14	8	0	1		14	3	0	-7	-5
15	13	0	-1	-9	15	9	0	3	4
16		0	0	-1	17	2	2	2	-1
17	0	0	2	2	18	14	14	2	-5
18	1	1	3	-12	19	6	6	4	1
19		0	-3	0	20	9	4	6	2
21	-1	-1	-1	7	21	9	-1	3	3
22			1	15	22	4	3	-5	3
23		0	3	-6	23	8	6	4	4
total	33	9	18	5	total	122	40	54	-17
mean	2.2	0.5	1.1	0.3	mean	6.1	2	2.7	-0.9

Appendix 9. Seedling establishment data for four Willamette Valley prairie species, 1991-1992. Figures indicate number of seedlings that established out of 20 seeds originally sown. Blanks indicate plots that were lost due to gophers or other disturbance.

	reduced competition				competition			
	<i>Bromus carinatus</i>	<i>Prunella vulgaris</i>	<i>Cynosurus echinatus</i>	<i>Daucus carota</i>	<i>Bromus carinatus</i>	<i>Prunella vulgaris</i>	<i>Cynosurus echinatus</i>	<i>Daucus carota</i>
	0	0	7	3		2	4	0
	0	0	13	0	0		3	11
	1	5	11	12		0	17	
	9	0	18	3	4	0	8	1
	17	5	3	6	6	3	3	9
		5	0	8	3	0	10	15
	7	7	16	19		0	0	0
				6	1	0	1	9
	10	0	0	7	4	6	0	9
	0	7	18	9	0	0	1	7
mean	5.5	3.2	9.6	7.3	2.6	1.2	4.7	6.8
SE	2.2	1.1	2.4	1.7	0.9	0.7	1.7	1.8

Appendix 10. Seedling establishment data for four Willamette Valley prairie species, 1992-1993. Figures indicate number of seedlings that established out of 20 seeds originally sown. Blanks indicate plots that were lost due to gophers or other disturbance.

	reduced competition				competition			
	<i>Bromus carinatus</i>	<i>Prunella vulgaris</i>	<i>Cynosurus echinatus</i>	<i>Daucus carota</i>	<i>Bromus carinatus</i>	<i>Prunella vulgaris</i>	<i>Cynosurus echinatus</i>	<i>Daucus carota</i>
	9	4	9	15	8	0	1	4
	2	1	6	2	4	2	0	4
	7	3	4	2	3	2	3	10
	8	1	7	5	0	0	2	8
	13	2	20	0	3	0	0	8
	3		8	7	6	0	6	9
	5	1	10	6	1	0	0	2
	6	0	11	0	3	0	4	0
	3	1	7	6	1	0	0	7
	4	0	6	14	1	5	6	5
mean	6.0	1.4	8.8	5.7	3.0	0.9	2.2	5.7
SE	1.1	0.4	1.4	1.7	0.8	0.5	0.8	1.0