AN ABSTRACT OF THE THESIS OF

Brie-Anne McKernan for the degree of Master of Science in Botany and Plant Pathology presented on April 19, 2004.
Title: The Influence of Prescribed Fire on the Rare Endemic Plant *Delphinium pavonaceum* (Peacock larkspur)

Abstract ap **Redacted for privacy**

Robert J. Meinke

In the wetland prairie of William L. Finley National Wildlife Refuge (FNWR) in western Oregon, we investigated the response of *Delphinium pavonaceum* Ewan (peacock larkspur, Ranunculaceae), an endangered perennial forb, to four unreplicated dormant season fire regimes of 0, 2, 4, or 10 fires that were applied over a 12-year period. Additionally, an unexpected removal of woody plants by refuge staff within some portions of our control area offered an unplanned opportunity for study. In 2002 we measured the density and vigor of reproductive plants, and performed seed germination trials. In 2003 we repeated previous field measurements, sampled immature plant density, and recorded observations of the insects visiting *D. pavonaceum* in burned and unburned habitats. We hypothesized that this rare endemic species and its insect visitors would respond positively to prescribed burning or the removal of woody species.

Low seedling density was found in the unburned and hand-removal areas, likely due to interference from litter and/or taller, shading plants. We also found low seedling density in sites burned the previous year, implying that fire consumes or damages

unprotected seeds in the litter layer or exposed on the soil surface. Seedling density was greater in a site burned three seasons previously, suggesting that fire ultimately leads to the enhancement of seedling density following the replenishment of the seed bank. The largest density of recruits was detected in a subunit recently returned to fire management in 1999, and also burned in 2002 following our first field season. However, the other, more-frequently burned sites did not exhibit an increased density of recruits, possibly due to a reduction of the seed bank following repeated burns, and increased intraspecific competition with mature plants. The elevated density of seedlings and recruits we observed in some burned areas may lead to population growth, as we observed a greater density of reproductive plants in the two most-frequently burned subunits during both years of study. Our results also suggest that fewer plants enter summer dormancy in burned areas, and that increases in flowering plant density may decline after 3 years.

Plants in the burned and hand-removal sites were shorter, likely resulting from water stress following the removal of shading plants and litter. Additionally, plants in unburned areas might have experienced greater stem elongation due to competition with tall and dense vegetation. Plants in the burned and hand-removal areas were generally similar to the unburned control site for flower and fruit production, fruit set, seed production and seed mass. However, plants in the burned and hand-removal areas produced more flowers per centimeter of height, indicating that they allocated more energy to reproduction than plants in the unburned area. We suggest that the decreased productivity we observed in some vigor traits is not problematic to *D. pavonaceum* conservation goals and may be ameliorated after 3 years.

Bombus californicus, B. appositus, and several large moths were the only insects we observed visiting *D. pavonaceum* during the two years of this study. We did not

detect a difference in bumblebee abundance between a frequently burned and unburned study plot during the peak flowering time of *D. pavonaceum*. However, our small sample size requires that this result be cautiously interpreted and further studied, as it is possible that our visitation data would change appreciably with a broader range of observations.

Our results indicate that the current FNWR fire management plan is not in conflict with *D. pavonaceum* conservation. The choice of fire-return interval seems to influence *D. pavonaceum* populations and plant vigor, but because the fire-schedule at FNWR was altered in 1997, our ability to recommend an appropriate fire-regime for this species is limited. Although not directly investigated, we suggest that annual fires, when applied for more than five consecutive years, might lead to population declines for this species because fire appears to consume the seed bank and reduce seedling density. If annual fires are returned to FNWR, the potential for this undesirable result should be investigated for at least 10 years by population monitoring.

The Influence of Prescribed Fire on the Rare Endemic Plant
Delphinium pavonaceum (Peacock larkspur)

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Brie-Anne McKernan, Author

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX TABLES

for my parents

Gregory and Laura McKernan

.

The Influence of Prescribed Fire on the Rare Endemic Plant

Delphinium pavonaceum (Peacock larkspur)

Chapter 1

Introduction

Modern conservation goals frequently demand that the managers of natural areas restore ecosystem function by engaging in direct habitat manipulations (Falk 1992, Morse 1996). For example, fire is increasingly used as a management tool in prairies to promote grassland species (Howe 1994) and manage rare and endangered plants (Hessl and Spackman 1995, Grigore and Tramer 1996). Since not all plant species respond favorably to prescribed burning, the effects of fire on sensitive plant species should be understood before fire is applied to manage their habitat (Jacobson *et al.* 1991, Kirkman *et al.* 1998, Pendergrass *et al.* 1999). However, limited resources and the immediate management need to reduce woody plant invasions in prairie systems may require that studies on rare species be conducted after controlled burns have been applied (Borchert 1991, Johnson *et al.* 1994). In this thesis I examine population and plant vigor of the endangered peacock larkspur (*Delphinium pavonaceum* Ewan, Ranunculaceae) in several local populations treated over the last 12 years with dissimilar fire-regimes.

INFLUENCE OF FIRE ON GRASSLANDS

Most North American grasslands have been exposed to periodic fires ignited both naturally and anthropogenically (Risser 1985). Fire disturbance plays an important role in shaping ecosystem processes and species composition (Collins 1992, Ojima *et al.*

1994). Fire typically promotes the abundance of forb species and reduces woody cover, but the effect of burning varies by species, even in fire-adapted ecosystems (Whelan 1995). For example, species that are killed by fire and regenerate only by seed may take longer to recover to pre-fire abundances, while resprouting species quickly recover (Norton and de Lange 2003). Also, fire may influence plant life-cycle stages in different ways. For instance, while vegetative growth and seed set of *Lupinus perennis* responds favorably to burning, seedling mortality can be high, limiting recruitment and population growth (Grigore and Tramer 1996).

Fire greatly influences the microclimate by consuming dead plant material. The removal of litter by fire reduces the organic content of soil (Ojima *et al.* 1994) and exposes bare ground (Wilson and Shay 1990). These alterations increase sunlight exposure of the soil and elevate soil temperatures, which ultimately increase evaporation and reduce soil moisture as the growing season progresses (Kucera and Ehrenreich 1962, Antos *et al.* 1983, Hulbert 1988, Ojima *et al.* 1994). These changes in microclimate tend to favor early season growth, lengthen the growing season, and often increase primary productivity (Kucera and Ehrenreich 1962, Hulbert 1988, but see Wilson and Shay 1990).

Burning also alters soil nutrient content. Increased available soil nitrogen in the form of nitrate and ammonium is often reported in grasslands immediately following fire (Hulbert 1988, Dudley and Lajtha 1993, Ojima *et al.* 1994). Warmer soil temperatures in the post fire environment also stimulate non-symbiotic nitrogen-fixing bacteria, leading to elevated levels of mineral nitrogen (Hulbert 1988, Ojima *et al.* 1994). Together with the altered microclimate, these changes in soil chemistry tend to increase plant productivity (Hulbert 1988, Ojima *et al.* 1994). In contrast to the immediate increases in

available soil nitrogen following fire, total soil nitrogen is lost via volatilization during a burn (Hulbert 1988) and leaching after a burn (Dudley and Lajtha 1993). Consequently, repeated burning commonly leads to lowered total soil nitrogen (Ojima *et al.* 1994), and can decrease plant productivity (Wilson and Shay 1990). Plants may be able to overcome nitrogen limitation, however, by increasing their nitrogen-use-efficiency, a compensatory mechanism that allows increased carbon fixation per unit nitrogen utilized (Ojima *et al.* 1994).

WILLAMETTE VALLEY PRAIRIES

Fire has greatly influenced the composition of the prairie vegetation in the Willamette Valley of western Oregon. Bordered by the Coast Range to the west and Cascade Mountains to the east, the Willamette Valley is the wettest interior valley of western Oregon (Franklin and Dyrness 1973). Total annual precipitation approximates 100 cm, most of which falls as rain during the mild, wet winter months (Franklin and Dyrness 1973). Summers are dry with warm to hot days and cool nights. Mean monthly temperature in January is 4.5°C, and mean temperature in July is 19°C (National Oceanic and Atmospheric Administration, Oregon State University Station, 1970-2002). The broad, flat topography of the Willamette Valley is intercepted by low elevation hills, extending roughly 200 km north to south from Portland to Eugene with a varying width of 30-50 km (Franklin and Dyrness 1973).

Wetland prairie and upland prairie are the two distinctive grasslands in the Willamette Valley. While upland prairies occur on well-draining soils at relatively higher elevations, the alluvial soils of wetland prairies are located on the valley floor and

are characteristic for seasonal winter flooding (Wilson 1998). Standing water can reach 15 cm above the soil surface in the rainy season (November to April), and is caused by a semi-impervious clay layer at a depth of one to three meters (Finley 1995). The topography of wetland prairies, although generally level, includes small to large-area mounds that are approximately 50 cm higher than the surrounding intermounds (Streatfeild and Frenkel 1997). The mounds have a deeper clay layer, and are thus inundated for shorter durations at shallower water levels than intermounds, leading to a noticeable difference in the vegetation (Wilson 1998). Despite the abundance of water in wetland prairies in the winter, the soil and vegetation become quite dry in the summer months and susceptible to fire (Finley 1995, Wilson 1998). The dramatic seasonal change in soil water content, along with fire disturbance, has resulted in a very distinct and diverse plant community in Willamette Valley wetland prairies.

At the time of Euro-American settlement in the 1840s, wetland prairies comprised approximately half of the total prairie area in the Willamette Valley (Hulse *et al.* 1999 cited in Taft and Craig 2003). However, early settlers recorded little information about the plant composition of wetland prairies (Wilson 1998). The area of upland prairies and wetland prairies have been drastically reduced by more than 99% since Euro-American settlement, and are critically endangered due to habitat loss and degradation (Noss *et al.* 1995). Today there is a significant need for science to provide knowledge on these unique and interesting ecosystems, and information that can guide restoration efforts.

HISTORY OF FIRE IN WILLAMETTE VALLEY PRAIRIES

Although most Willamette Valley grasslands can support forest vegetation (Franklin and Dyrness 1973), the Willamette Valley was dominated by open prairie and oak savanna when Euro-American pioneers began to settle the area in the early 1840s (Smith 1949, Habeck 1961, Johannessen *et al.* 1971). It is generally agreed that the valley grasslands and savannas were maintained by the widespread fires annually set by Kalapuya Indians as a tool for their subsistence practices (Sprague and Hansen 1946, Smith 1949, Johannessen *et al.* 1971, Boyd 1986, Williams 2000; but see Whitlock and Knox 2002). The Kalapuya primarily used fire to enhance the growth and facilitate the collection of plant crops (such as *Camassia* ssp., *Madia* ssp., insects, acorns, berries, and tobacco), hunt white-tailed deer (*Odocoileus virginianus leucurus*, now federally Endangered), and provide open areas for deer forage (Boyd 1986). Ultimately, these frequent fires favored tolerant grasses and early season forbs, while restricting the influence of trees and shrubs on the valley floor.

Specific historical information concerning native-set fires was only sporadically recorded by early settlers of the Willamette Valley, resulting in an unclear picture of the Kalapuya's burning activity (Boyd 1986). The few pioneer accounts on record indicate that native-set fires were ignited annually in the late summer and early fall (Boyd 1986). Burning by indigenous people appears to have been infrequent in July and early August, and were ignited no later than mid October (Boyd 1986). Little is known about the fire-return interval of different habitats or locations (Pendergrass 1996), but it has been suggested that wetland prairies may have been exposed to longer fire return intervals than open dry prairies (Kaye *et al.* 2001).

Increased pioneer settlement of the Willamette Valley resulted in the complete cessation of native-set fires by the mid 1840s (Sprague and Hansen 1946, Boyd 1986). Most of the valley floor was converted to a mosaic of agrarian, urban, and industrial use and today less than 0.1% of the native Willamette Valley prairies remain in small, fragmented remnants (Noss *et al.* 1995). The removal of a natural fire regime from the few remaining prairies has allowed tree and shrub encroachment, while agricultural activity has further degraded the habitat by enhancing the spread of exotic weeds (Sprague and Hansen 1946, Habeck 1961, Johannessen *et al.* 1971). Despite these offenses, remaining prairie fragments still offer refuge to many native plants and animals, including rare and endangered species (Wilson 1998), compounding the importance of restoring the little habitat left.

RESPONSE OF WILLAMETTE VALLEY WETLAND PRAIRIE TO FIRE

Fire has recently been returned to Willamette Valley wetland prairies to meet management goals of reducing woody species, and promoting or maintaining native herbaceous species. Prescribed fires are set in the fall when most native herbaceous species have completed reproduction and have senesced. The few studies of fire in Willamette Valley prairies have generated mixed reports of the capacity of fire to meet restoration goals, and have found that the response of native and non-native species is greatly influenced by the fire-return interval applied.

Reducing the cover of woody species is an important objective of fire management because shrubs reduce prairie physiognomy and suppress native herbs (Wilson 1999). For example, rose shrubs, including native *Rosa nutkana*, exotic *R.*

eglanteria, hybrids of these two species, and possibly other *Rosa* sp., are especially problematic woody plants in Willamette Valley wetland prairies (Wilson 2002). On the largest remaining fragment of wetland prairie in the Willamette Valley, *Rosa* sp. account for over 20% of the vegetative cover (Wilson 1999). There are inconsistent reports of the ability of fire to control rose shrubs. Studies investigating the short-term effects of fire have found rose density to be unaffected or increase (Pendergrass *et al.* 1998), rose cover to be unchanged (Streatfeild and Frenkel 1997) or reduced (Wilson 1999), and rose mortality to increase with fire (Clark and Wilson 2001). These conflicting results may be explained by the different techniques used to measure rose abundance, variation in the characteristics of fire at different sites, and the ability of rose shrubs to resprout following fire (Clark and Wilson 2001, Wilson 2002). Regardless, the stature of surviving shrubs decreases following fire, probably resulting in less shading and suppression of surrounding herbaceous vegetation (Streatfeild and Frenkel 1997, Pendergrass *et al.* 1998, Clark and Wilson 2001, Wilson 2002). Ultimately, reducing rose abundance will require killing individual plants, potentially by repeated fire application or other means (Clark and Wilson 2001). However, a six-year study has found that rose cover continued to increase even with annual and triennial burning, although at a slower rate than in unburned habitats, indicating that burning alone may not be enough to reduce problematic woody pests in this sensitive ecosystem (Wilson 2002).

Fire is also employed in prairie ecosystems to maintain and promote native grasses and forbs. Short-term studies have found the abundance of some native species to increase or remain unchanged after fire, but the abundance of other species to decrease (Pendergrass 1996, Streatfeild and Frenkel 1997, Clark and Wilson 1998, Wilson 1999,

Clark and Wilson 2001, Wilson 2002). When examined as a group, native herbs (Wilson 1999) and forbs (Clark and Wilson 2001) tended to increase in cover after fire, while the cover of native graminoids was maintained (Clark and Wilson 2001). A long-term study found that native herb cover slightly increased after seven years of annual burning, but declined with triennial fire, although at a slower rate than in unburned habitats (Wilson 2002).

Prescribed fire appears to be a somewhat successful tool in reducing the cover of exotic species (Streatfeild and Frenkel 1997, Clark and Wilson 2001, Wilson 2002). Streatfeild and Frenkel (1997) found a negative correlation between fire and the abundance of 77% of the 94 exotic species they measured. Clark and Wilson (2001) found that fire reduced the cover of exotic forbs as a group, but increased the flowering of the exotic grass *Anthoxanthum ordatum*. A six-year study found only triennial burning to be effective at reducing exotic herb cover (Wilson 2002). Troublingly, annual burning increased exotic herb cover at greater rates than unburned controls, likely because frequent burns released exotic herbs from shrub suppression (Wilson 2002).

Fire management in Willamette Valley wetland prairie is complicated by the relative elevation of microsites within the prairie (Wilson 1999, 2002). As previously discussed, slightly raised mounds of various size occur throughout wetland prairies. Although the abundance of native herbs increased during seven years of prescribed annual or triennial fire on the wetter intermounds, these species decreased on the slightly raised, drier mounds (Wilson 2002). Non-native species are more abundant on the drier mounds, and are increasing at a distressing rate in this microsite with annual burning, but decreasing with triennial burns (Streatfeild and Frenkel 1997, Wilson 1999, 2002). In the

wetter intermounds, non-native cover also increases with annual fire and decreases with triennial fire, although at lower rates than on drier mounds (Wilson 2002). Annual fires on drier mounds effectively minimize woody plants, but triennial fires are more effective in wet sites (Wilson 2002).

Although fire shows promise as a restoration tool, it does not meet all desired management goals because the fire response varies by species and microsite. Thus, it is unlikely that fire, in the absence of other forms of management, will return remnants of Willamette Valley wetland prairie to pre-settlement conditions (Wilson 1999, 2002). Complementary management techniques, such as herbicide application, seeding or transplanting native plants, and mechanical removal of woody species, will also be necessary to restore and conserve this endangered ecosystem (Wilson 1999, 2002). However, the willingness of those charged with land management to establish a scientifically based conservation strategy and the limitations of resources such as money will ultimately decide which tools will be used.

RARE PLANT CONSERVATION

Although nearly 40% of the estimated 17,000 native vascular plants in the United States are catalogued as at-risk of extinction on one or more conservation listing (Morse 1996), the importance of conserving plants as a natural resource is generally under appreciated by the public and policy-makers (Roberson 2002). Plants were neglected in early conservation laws, and it was not until the passage of the Endangered Species Act of 1973 (ESA) that plants threatened or endangered with extinction were afforded any legal protection (16 U.S.C. §§1531-44). Legal protection under the ESA, however, is not

as strong for imperiled plants as it is for animals, as plants are only protected from destruction on land subject to Federal regulation. This weakness of the ESA, as well as the disproportionate allocation of Federal tax-dollars and jobs to animal conservation, results in plants being effectively treated as "second-class conservation citizens" (Campbell 1991, Roberson 2002). By the year 2004, 742 plant taxa were protected by the Endangered Species Act, while 143 species were designated as candidates or proposed for listing status (USFWS 2004). Most listed species have declined to less than 1,000 individuals in fewer than five populations by the time they were protected under the ESA (Wilcove *et al.* 1993). Thus, the ESA confers legal protection to only the rarest taxa on the brink of extinction. Following the passage of the ESA, 45 states also enacted endangered species laws to protect imperiled species on State owned and leased lands (Roberson 2002). However, only 29 of these states, including Oregon, gave protection to endangered plants (ORS 564.100-564.135). While the ESA lists 18 Oregon plant species as threatened or endangered (USFWS 2004), Oregon state law protects 61 species (ONHP 2001). This difference reflects the relatively easier listing process at the state level, and the ability to list species that are rare in Oregon but less imperiled in other regions.

In today's altered landscape, the creation of refugia is often not enough to allow for the recovery of imperiled plants. Rare plant habitat is often degraded by exotic invasions, hydrological alterations, multiple land-use activities, and the removal of historical disturbance regimes, sometimes leading to the continued decline of diversity even in protected areas (Morse 1996). Additionally, populations of imperiled plants are typically small, and may be subject to the deleterious effects of genetic drift, inbreeding

depression, reduced pollinator attraction, and demographic and environmental stochastisity. Accordingly, modern conservation efforts demand that land managers intervene with and restore the functioning of natural systems, or engage in population restoration activities (Falk 1992, Morse 1996). For example, in prairies, savannas, and chaparral, successional management may be required to change or maintain the seral stage of the plant community by introducing disturbances such as prescribed fire (Falk 1992). As of the early 1990s, four percent of Federally listed plants with recovery plans were endangered by fire suppression (Schemske *et al.* 1994). Thus, directly manipulating the habitat of endangered plants by ending fire suppression and applying prescribed burns is playing an increased role in plant conservation (Falk 1992).

RESPONSE OF RARE AND ENDANGERED PLANTS TO FIRE

Careful planning is necessary when fire is prescribed as a management tool, particularly in the habitat of endangered, threatened, or rare plants (Hessl and Spackman 1995). Scientific studies must provide information to guide conservation strategy, and need to consider the potential consequences of management on the plant of interest (Schemske *et al.* 1994, Pendergrass *et al.* 1999). Little work has focused on the influence of fire management on sensitive species in Willamette Valley wetland prairies, yet some insight might be gained from studies of rare and endangered plants in other regions (**Table 1**).

Increased growth (Barker and Williamson 1988, Menges 1988, Hartnett and Richardson 1989, Menges and Kimmich 1996, Grigore and Tramer 1996) and/or

Table 1. Influence of fire on 20 endangered, threatened, or rare species. R = rare but not of special status, S = state listed, T = federal threatened status, E = federal endangered status. "+" = statistically significant increase, "-" = statistically significant decrease, "0" = no detected change. Empty cell indicates uncollected data.

Species (status)	Veg. Biomass	Flowers	Fruits	Fruit Set	Seed Set	Seeds / Plant	Germin- ation	Recruit- ment	Pop'n growth	Source
Acacia cochlocarpa ssp. *cochlocarpa* (E)							+			Yates and Broadhurst 2002
A. aprica (E)							+			Yates and Broadhurst 2002
Agalinis acuta (E)									+	Jordan *et al.* 1997
Agave palmeri (R)				0	0					Slauson 2002
Blandflordia nobilis (R)		+								Johnson *et al.* 1994
Bonamia grandiflora (T)	+		+	+	0	+		+	+	Hartnett and Richardson 1989
Corema conradii (R)								+		Dunwiddie 1990

Table 1, continued.

Species (status)	Veg. Biomass	Flowers	Fruits	Fruit Set	Seed Set	Seeds / Plant	Germin-ation	Recruit-ment	Pop'n growth	Source
Corybas carsei (E)		+							+	Norton and de Lange 2003
Cypripedium acaule (S)	-	0								Primack *et al.* 1994
Hedeoma diffusum (R)								+		Phillips *et al.* 1992
Helianthemum dumosum (R)		+						+	+	Dunwiddie 1990
Iliamna corei (E)							+	+		Jacobs 1993
Lomatium bradshawii (E)	+	+	+					+	+	Pendergrass *et al.* 1999
Lupinus perennis (S)	+		+			+	-	0, -		Grigore and Tramer 1996
Pediocactus paradinei (S)		0								Warren *et al.* 1992

Table 1, continued.

Species (status)	Veg. Biomass	Flowers	Fruits	Fruit Set	Seed Set	Seeds / Plant	Germin-ation	Recruit-ment	Pop'n growth	Source
Platanthera leucophaea (T)		+								Currier 1984
Sarracenia psittacina (S)	+									Barker and Williamson 1988
Schwalbea americana (E)				0				0, +		Kirkman *et al.* 1998
Silene regia (R)								+	+	Menges and Dolan 1998
		-								Menges 1995
S. spaldingii (T)		+						+	+	Lesica 1999
	0, -	0	0	0, -	0				+	Menke 2003
Thermopsis macrophylla var. *agnina* (R)			+			+	+	+		Borchert 1989

reproduction (Borhcert 1989, Hartnett and Richardson 1989, Menges 1995, Grigore and Tramer 1996, Menges and Kimmich 1996, Lesica 1999) following fire has been reported in several rare and endangered plants. Fire stimulates the flowering of vegetative plants in many monocot species (Currier 1984, Johnson *et al.* 1994, Norton and de Lange 2003), and some dicot species (Kirkman *et al* 1998). Increased seed production is sometimes reported following burns, but fire may also consume seeds stored in the soil (Borchert 1989, Hartnett and Richardson 1989, Grigore and Tramer 1996).

Fire sometimes increases plant survivorship (Menges 1988, Menges and Kimmich 1996), but in some species adults are killed by fires (Hartnett and Richardson 19889, Dunwiddie 1990, Warren *et al* 1992, Primack *et al.* 1994). Often, fire-induced plant mortality is balanced by benefits in other life-stages, such as the promotion of seedling establishment (Dunwiddie 1990, Whelan 1995). Timing prescribed burns to occur when sensitive species are dormant can help to mitigate undesired outcomes (Phillips *et al.* 1992).

The burning of plant litter, along with the fire-induced mortality of competitors, encourages plant regeneration via sexual reproduction by creating sites for seedling establishment (Wilson and Shay 1990, Whelan 1995). Greater seedling establishment following fire is commonly reported in rare and endangered forbs (Borchert 1989, Hartnett and Richardson 1989, Phillips *et al.* 1992, Whelan 1995, Kirkman *et al.* 1998, Menges and Dolan 1998, Lesica 1999), and is required to trigger germination in some species (Borchert 1989, Jacobs 1993, Keeley and Fotheringham 1997). Although few studies have investigated the long-term survival of seedlings after fire, it is generally assumed that post-fire pulses in seedlings leads to increased population growth (Whelan

1995, Lesica 1999). However, if seedling densities become too high, greater intraspecific competition and herbivory may reduce recruitment rates, and result in negligible population growth (Whelan 1995).

A small number of recent studies have begun to evaluate the role of fire as a conservation tool in Willamette Valley wetland prairies. Fire increased growth and reproduction in the Federally Endangered forb *Lomatium bradshawii*, although not in all years and at all sites (Pendergrass *et al.* 1999), and potentially reduced the risk of population extirpation (Kaye *et al.* 2002). However, re-emergence, growth, flowering intensity, and seed production was unchanged in the Federally Threatened forb *Sidalcea nelsoniana* one year after fire (Bartels and Wilson 2001). Although population densities are greater in burned habitats of the State Endangered forb *Delphinium pavonaceum*, the influence of fire on plant growth and reproductive output is unclear (Finley and Ingersoll 1995, Page 1996).

More research is needed to investigate the influence of fire on the seedling establishment of sensitive wetland prairie species. Seedlings of *Aster curtus*, *Horkelia congesta*, *Lomatium bradshawii*, and *Sidalcea cusickii* var. *purpurea* did not establish at greater rates in plots that were burned two seasons earlier (Clark *et al.* 2001). However, a study that investigated the establishment of naturally dispersed *L. bradshawii* seeds after fire reports more seedlings in burned plots (Pendergrass 1999). It is unknown, and worth investigating, if the establishment of these other Willamette Valley species would be improved if sown before or directly after fire.

Studies investigating the response of rare and endangered plants to fire may have complex or misleading results (Hessl and Spackman 1995). One factor creating difficulty

is that the stimulating effect of fire on reproduction, recruitment, and population growth may occur several growing seasons after a fire, causing short-term studies to not detect a fire response (Hartnett and Richardson 1989, Johnson *et al* 1994, Norton and de Lange 2003). Additionally, demographic studies need to investigate multiple plant life-stages (Schemske *et al.* 1994), as negative fire effects in one life-stage may be balanced by a positive result in another (Dunwiddie 1990, Grigore and Tramer 1996).

CONSERVATION OF INSECT POLLINATORS

To conserve populations of rare and endangered plants with insect-pollinated flowers, managers must be sure that pollinator availability does not confound restoration efforts. However, there is growing consensus in the pollination ecology community that pollinator diversity and abundance is decreasing worldwide, causing some to label the event a "Pollination Crisis" (Buchmann and Nabhan 1996, Allen-Wardell 1998). It is largely unknown how reductions in pollinators might impact efforts to conserve rare and endangered plants (Buchmann and Nabhan 1996; Allen-Wardell 1998, Spira 2001).

Habitat loss and fragmentation are the most important causes of pollinator declines, as small habitats cannot support large and diverse populations of plants and pollinators (Spira 2001). Pesticides and herbicides, commonly used in agriculture and rangeland management, also threaten the pollination mutualism by impacting non-target species (Spira 2001). Exotic insects, such as the introduced European honeybee, may out-compete native pollinators for food resources, and are also poor pollinators of many native plants (Kearns *et al.* 1998, Spira 2001).

Alarmingly, prescribed fire has been associated with reduced abundance of some insect species in North American tall-grass prairies (Anderson *et al.* 1989), particularly in those endemic to or otherwise dependent on prairie habitats (Swengel 1996, Panzer 2002). Thus, the use of fire as a plant conservation tool might have undesired negative effects on important pollinators, reducing the success of plant conservation efforts. Habitat managers must include measures to reduce the impact of prescribed fire on pollinators, such as timing burns to occur after the active season of pollinators, and leaving some areas unburned (Kearns *et al.* 1998; Spira 2001, Panzer 2002).

PURPOSE OF STUDY

Delphinium pavonaceum is endemic to the historically burned wetland prairies of the Willamette Valley, and is recognized as one of the area's most imperiled species. Although formerly more abundant around the mid to southern Willamette Valley, its range has been primarily reduced to a single wildlife refuge and a few roadsides in Benton and Polk Counties (Oregon Natural Heritage Program 2002). Presently, 18 of 38 documented historical populations are confirmed to be extant, most of which contain fewer than 100 reproducing individuals (Oregon Natural Heritage Program 2002; B. McKernan, personal observation, **Figure 1**). Flowering plants have not been observed in the remaining 20 sites for at least 20 years, and many of these populations may be extinct. Declines in both population number and appropriate habitat prompted the State of Oregon to list *D. pavonaceum* as Endangered in 1995 (OAR 603-073-001 to 603-073-110). Until 1996, this species had Federal Candidate Threatened status under the ESA, but was

downgraded to a Species of Concern owing to insufficient information on the condition of remaining populations and prominent threats (Federal Register 61:7457-7463).

The overwhelming majority of *D. pavonaceum* plants in existence occur on the wetland prairie at William L. Finley National Wildlife Refuge (FNWR). The managers of this refuge are mandated to promote the long-term survival of this species, as well as other rare and endangered taxa. Because of the historic and cultural importance of fire in Willamette Valley prairies (Sprague and Hansen 1946, Smith 1949, Johannessen *et al.* 1971, Boyd 1986) and its perceived ability to reduce tree and shrub cover and promote some native grassland species, fire has been reintroduced as a conservation tool in the FNWR wetland prairie. However, few studies have investigated the effect of fire in wetland prairies (Clark and Wilson 2001), or the role fire might play in conserving sensitive species such as *D. pavonaceum*. Additionally, little is known about the pollination biology of this endangered species, or how its pollinators might be influenced by fire management.

RESEARCH OBJECTIVES

To provide recommendations for land managers implementing prescribed fire at William L. Finley National Wildlife Refuge and gather general information about the reproductive and pollination biology of *D. pavonaceum*, we investigated the following research objectives: (1) to examine the density, vigor, and fecundity of *D. pavonaceum* plants in habitats exposed to contrasting fire regimes, (2) to investigate the influence of an unplanned removal of woody plants in *D. pavonaceum* populations and plants one growing season after treatment, (3) to record observations of the insect

pollinators of *D. pavonaceum* and a preliminary assessment of their abundances in burned and unburned habitats, and (4) to complete a survey of *D. pavonaceum* populations on the Willamette Floodplain Research Natural Area at FNWR (see Appendices). Because Willamette Valley wetland prairies historically received frequent fires, we hypothesized that this species and its pollinators would respond positively to prescribed burning or the removal of woody species.

Figure 1. Number of flowering *D. pavonaceum* plants observed in historical populations. Presently, 18 of 38 documented historical populations are confirmed to be extant, most of which contain fewer than 100 reproducing individuals (Oregon Natural Heritage Program 2002; B. McKernan, personal observation). Flowering plants have not been observed in the remaining 20 sites for at least 20 years, and many of these populations may be extinct. It is unknown if non-flowering, immature plants or a seed bank persists in some of these sites.

Chapter 2

Methods and Materials

STUDY SPECIES

Delphinium pavonaceum Ewan (peacock larkspur, Ranunculaceae, **Figure 2**) is a

long-lived, herbaceous perennial. The plant resprouts from small tuberous roots after

fire, and mature individuals are easily distinguished, as the plant does not spread

vegetatively and reproduces only by seed. Under natural field conditions, seedlings

emerge in the winter and reach reproductive maturity after at least three, but perhaps as

many as five, growing seasons (Goodrich 1983). However, when sown in weed-free

garden beds, some plants may flower in their second year of growth (L. Boyer, personal

communication). Non-reproductive plants, and some mature plants, enter seasonal

dormancy with the onset of summer droughts. This phenomenon has also been observed

in other *Delphinium* species and is thought to be correlated with insufficient soil moisture

(Epling and Lewis 1952; Goodrich 1983).

The showy flowers of *D. pavonaceum* are distinctive from most other Willamette

Valley larkspurs by their large creamy white outer sepals and small purplish-blue inner

petals. The perfect, protandrous flowers open in early May, and following fertilization

produce a fruit bearing three follicles. *Delphinium pavonaceum* has a demonstrated

ability to both outcross and self-fertilize (Goodrich 1983). However, plants rarely auto-

pollinate, and insect pollinators are necessary for fruit production (Goodrich 1983, Page

1996). *Bombus californicus* and *B. appositus* are known pollinators (Goodrich 1983), but

nocturnal and daytime visits by large moths might also facilitate pollination (B.

Figure 2. *Delphinium pavonaceum* Ewan (photo courtesy of Steven Gisler).

McKernan, personal observation). Seeds are passively dispersed from fruits beginning in mid June. Under laboratory conditions seed germination can be as high as 96% (Turner 1992), though it is likely much lower in the field (Goodrich 1983).

Inflorescences and foliage of *D. pavonaceum* are browsed primarily by elk (*Cervis canadensis*), but also by brush rabbits (*Sylvilagus bachmani*) and an unidentified caterpillar (B. McKernan, personal observation). Black-tailed deer (*Odocoileus columbianus*) and camas pocket gophers (*Thomomys bulbivorous*) share habitat with *D. pavonaceum* and may possibly forage on the plants as well.

STUDY SITE

The study was conducted within the prescribed fire unit on the Willamette Flood Plain Research Natural Area (RNA) at William L. Finley National Wildlife Refuge (44° 25′ N 123° 18′ W), approximately 16 km south of Corvallis, Oregon (**Figure 3**). This 210-ha fragment, surrounded by intensively farmed agricultural fields, contains the largest remnant of wetland prairie remaining in the Willamette Valley, in addition to rose scrub and ash woodland. While native species compose approximately 65% of the flora in the RNA (Streatfeild and Frenkel 1997), the average relative cover of native herbaceous species during 1991-1997 was approximately 40% (Wilson 2002). Characteristic native species include grasses (*Deschampsia cespitosa*), rushes (*Eleocharis acicularis*), forbs (*Camassia quamash, Plagiobothrys figuratus, Sidalcea campestris, Geranium oreganum*), and intermittently distributed woody species (*Fraxinus latifolia, Spiraea douglasii, Crataegus douglasii*) (Streatfeild and Frenkel 1997, Wilson 2002). Exotic herbaceous species and invading shrubs and trees have developed a strong

Figure 3. Arial photograph of the study site (outlined in bold, approximately 1.5 km wide) at the Willamette Floodplain Research Natural Area in William L. Finley National Wildlife Refuge. Sampling was conducted in subunits 1 (North Prairie), 3 (Control Prairie with sites of hand-removal of woody species), 4 (Central Prairie), and 6 (South Prairie). Image courtesy of the U.S. Geological Survey via TerraServer (http://www.terraserver.com).

presence in the RNA, and were estimated to have an average relative cover of 33.5% and 27% respectively during 1991-1997 (Wilson 2002). Prominent exotics include the grasses *Holcus lanatus* and *Agrostis tenuis*, the forbs *Hypericum perforatum* and *Galium parisiense*, and shrubs such as *Rosa* sp. (Streatfeild and Frenkel 1997, Wilson 1999 and 2002).

Soils in the RNA are somewhat poorly draining, silty clay loams in the Amity Series (Soil Conservation Service 1975). Slightly raised mounds of small to large-area are located throughout the RNA (Streatfeild and Frenkel 1997). These mounds have a deeper clay layer, and are thus inundated for shorter durations at shallower water levels than intermounds, leading to a noticeable difference in the vegetation among these microsites (Wilson 1998). *Delphinium pavonaceum* is restricted to the slightly raised mounds (Meinke 1980, Goodrich 1983), and these sites also have a greater cover and richness of exotic plants such as *Rosa* spp. and *Hypericum perforatum* (Streatfeild and Frenkel 1997, Wilson 1999, 2002). Intermounds contain vegetation characteristic of wetter habitats, including natives *Deschampsia cespitosa, Camassia quamash,* and *Plagiobothrys figuratus* (Streatfeild and Frenkel 1997).

Heavy grazing by swine, sheep, and cattle ended on the RNA in 1966 (Frenkel and Streatfeild 1993, Streatfeild and Frenkel 1997), and it has been suggested that partial draining and light-intensity agriculture occurred there in the early 1900s (Streatfeild and Frenkel 1994, Streatfeild and Frenkel 1997). Following the cessation of native-set fires in the 1840s, fire is presumed to have remained absent from the RNA until its use in small-scale studies in 1972 (Frenkel and Streatfeild 1983).

TREATMENTS

Because of the historical significance of fire in Willamette Valley prairies

(Sprague and Hansen 1946, Smith 1949, Johannessen *et al.* 1971, Boyd 1986) and the

perceived ability of fire to control woody and exotic species, fire was reintroduced as a

conservation tool in the wetland prairie RNA (Streatfeild and Frenkel 1997). Several

small, prescribed fires were set in some areas of the RNA during 1972 to 1987, and an

accidentally ignited fire burned the entire RNA in 1979 (Frenkel and Streatfeild 1994,

Streatfeild and Frenkel 1997).

It was not until 1991 that permanent fire lines were established to partition the

prescribed fire unit into six subunits (**Figure 3**). This design was intended for

management purposes only, and because of the logistical difficulties and large expense of

conducting prescribed fires, burn treatments were not replicated. Several problems arise

in conducting an unreplicated study. In particular, such studies cannot control for

variation inherent among experiment units or for random stochastic influences (Hulbert

1984). The subunits we studied are located within a localized geographic area, are of a

specific habitat type, and have probably all experienced similar land-use and management

histories prior to 1990. However, habitat conditions moderately vary within the RNA,

and thus cannot be ruled out as an alternative explanation for a supposed treatment effect

(Wilson 1999). Nevertheless, studies with unreplicated treatments still can provide

useful information to benefit conservation science.

Substantial patches of *D. pavonaceum* are located in subunits 1 (North Prairie), 3

(Control Prairie), 4 (Central Prairie) and 6 (South Prairie). *Delphinium pavonaceum* is

also found in a seventh subunit, but because a complex series of experimental burns were

set there in the 1980s we excluded it from our study. From 1990 to 1997, annual and triennial prescribed burns were applied to North and South Prairie respectively, while Control and Central Prairie served as unburned controls (Streatfeild and Frenkel 1997, **Table 2, Appendix A**). In 1997, North and South Prairie were moved to a 2 to 3 year burn rotation. Fire was returned to the northern portion of Central Prairie in 1999 and 2002. An unexpected opportunity for study arose when trees and shrubs were removed with hand tools by refuge staff from some areas within Control Prairie in the winter of 2002 in preparation for a burn scheduled for 2004. We conducted all sampling for this study in the spring and early summer of 2002 and 2003.

MEASUREMENTS

Flowering Plant Density. To investigate the influence of fire and hand-removal on the abundance of *D. pavonaceum*, we measured the density of flowering and immature plants during the peak flowering time of this species (mid May to early June). Mature, vegetative plants were not sampled because they were dormant by our sampling dates. Clusters of *D. pavonaceum* at FNWR are relatively close together (10-50 m apart) and probably experience extensive pollen-flow. Arguably, they are all part of one large and patchy FNWR population. We refer to these discrete plant groups as "patches" hereafter.

In 2002 and 2003 we measured the same patches of *D. pavonaceum* for flowering plant density (**Table 2**). In all management areas (except North Prairie), we sampled all patches for this measurement because of low patch occurrence in these areas. Flowering plant number was directly counted in patches of < 5,000 individuals. In large, dense patches we estimated flowering plant number by randomly placing 1.0 m × 0.5 m

Table 2. Frequency and time since fire in prescribed burn units on the Willamette Flood Plain Research Natural Area at W. L. Finley National Wildlife Refuge. The number of *D. pavonaceum* patches sampled for density measurements and the initial number of flowering plants randomly selected for vigor measurements at the beginning of the 2002 and 2003 field season are also presented. During the field season, the number of tagged plants was reduced by herbivory, dormancy, and flag removal (possibly by elk).

Management Unit	2002				2003			
	# Fires between 1990-2001	# Years post fire	# Patches sampled for density	Initial # plants tagged	# Fires between 1990-2002	# Years post fire	# Patches sampled for density	Initial # plants tagged
Control Prairie	0	23	3	22	0	24	3	75
hand-removal	0	23	2	20	0	24	2	55
Central Prairie	1	3	3	39	2	1	3	50
South Prairie	4	2	4	108	4	3	4	75
North Prairie	9	2	4	125	10	1	4	75

quadrats using a coordinate system. Fifteen quadrats per patch were placed in 2002, but we increased the number to 25 quadrats in 2003 in order to enhance the precision of our measurements. Patch area was estimated by measuring the distance to the patch center and aspect of 3 to 6 flags placed around the patch perimeter, creating 3 to 6 triangles of known dimensions from which the area could be calculated. We excluded plants on the patch edge that were greater than 5.0 m from the nearest neighbor from counts and area calculations. This method resulted in a very small number of plants being excluded. We chose to use the change in flowering plant density between years as a measure population growth, rather than changes in patch area or plant number. This approach was employed because the size of microsites suitable for *D. pavonaceum* is quite variable in the wetland prairie.

Immature Plant Density. We define seedlings as new germinants bearing two seedling leaves, and recruits as immature plants greater than 1-year in age (**Figure 4**, Goodrich 1983). Seedlings and juvenile plants were sampled from April 27 2003 to May 14 2003 before they entered summer dormancy. No sampling was conducted in 2002. To sample for immature plants, we used a coordinate system to randomly place ten 0.5 m × 0.5 m plots in a single randomly chosen patch in each management subunit.

Goodrich (1983) reports that seedlings produce two seedling leaves in their first year of growth. Recruits typically produce a single leaf bearing 3-leaflets of similar size to the seedling leaves in the second year of growth, and one to three divided leaves by the third year of growth (Goodrich 1983). However, after haphazardly extracting immature plants we found that recruits may produce one to several leaves bearing 3-leaflets,

Figure 4. A seedling (on left) and recruits of *D. pavonaceum*. We define seedlings as new germinants bearing two seedling leaves. Recruits have completed at least one year of growth, and may produce one to several leaves bearing 3-leaflets, one to several divided leaves, or both leaf types in the same growing season.

and some recruits produce both 3-leaflet and divided leaves in the same growing season. Thus, it is impossible to distinguish among individual recruits without extraction. To overcome this difficulty, we exhumed 138 plants and found that recruits typically produce 1.7 divided or 3-leaflet leaves per plant (SE = 0.1). Accordingly, we divided the total number of divided and 3-leaflet leaves we counted per plot by 1.7 to estimate the number of individual recruits. This calculated number was used in all data analyses. To determine the proportion of immature plants in our plots, we divided the sum of seedlings and recruits by the total number of *D. pavonaceum* plants per plot.

Plant Traits. We measured the response of plant height, leaf production, flower and fruit production, fruit set, seed production and mass, and seed germination to fire or hand-removal on randomly selected plants throughout the different treatment areas. Reproductive plants were randomly selected by systematically tagging every hundredth mature plant counted during patch density surveys (in North Prairie, plants were sampled from every known patch, although only 4 patches were sampled for density). If the plant was in bud at the time of selection but did not produce flowers later in the season (a condition that appeared to have been caused by resource limitation or herbivory), it was removed from our data set. Elk destroyed many of the pink and yellow pin flags used to mark selected plants in both years of study, further reducing our sample size.

Plant height was measured to the nearest half centimeter. Leaf number was counted only in 2003. We estimated flower and fruit production by counting the number of flowers and fruits on each marked plant at the beginning, middle, and end of the

reproductive season. We calculated fruit set as the proportion of flowers that bore fruits (# fruits / # flowers).

To estimate the number and mass of seeds produced by *D. pavonaceum* fruits, we randomly selected one inflorescence per plant and divided it evenly into three vertical positions (top, middle, and bottom). From one randomly selected position, we haphazardly chose a single flower and tagged it with colored string. If the selected flower produced a fruit, it was bagged with a Del-Net™ polyethylene mesh exclusion bag to prevent seed loss and collected when the follicles dehisced. Bagging did not appear to affect seed production; however this assumption was not formally tested. Collected fruits were allowed to dry, after which seeds were counted and weighed.

We tested the germination rates of seed collected in July 2002 from the management areas. After collection, the seed was stored in a 5°C cold room until April 2003. Five fruits per inflorescence position (top, middle, or bottom) were randomly drawn from different individuals in each management area (see above for methods). Thirty seeds were then haphazardly drawn from each fruit and evenly distributed on petri-dishes lined with autoclaved blue seed germination blotter paper (Packaging Converters™) that was moistened with sterile de-ionized water. There was a total of 15 petri-dishes for each of four management areas. The petri-dishes were incubated in an dark 7°C cold room on April 2 2003, and removed from the room every two weeks to be checked for germination and moistened (see Turner, 1992). Once seed germination commenced, the number of germinated seeds in each petri-dish was counted about every two weeks (day 86, 100, 115, 132, and 150). Germination was defined as when the radicle emerged from the seed coat.

The seed used in germination trials were from fruits collected in 2002, before our knowledge of the future hand-removal treatment. We combined these seeds with the control group after a three-way repeated-measures ANOVA revealed no evidence that the seeds from the future hand-removal site were different from the control in their germination rates ($F_{1,9} = 1.137$, $P = 0.314$).

Floral Visitors. To investigate how fire management might influence pollinators of *D. pavonaceum*, we observed its floral visitors in burned and unburned areas. In 2002 we recorded the emergence date and visitation of two species of bumblebees (*Bombus californicus*, *B. appositus*) to *D. pavonaceum*, but did not quantify their floral visits. In 2003, we randomly located a single 4.0 m × 4.0 m plot in both the burned North Prairie and unburned Control Prairie to characterize and observe the behavior of insect visitors to *D. pavonaceum*. The number of *D. pavonaceum* plants in flower was recorded for each plot. A total of seven 20-minute observations were made in both plots on the mid-morning and afternoon of May 25 and June 4, and on the evening of May 26 (**Appendix B**). Observations were conducted simultaneously in the burned and unburned prairie, with one observer in each area during the same interval. These observations were limited to the peak flowering time of the plant, as time constraints prevented a more expansive study. When a floral visitor entered the study plot, we recorded its species and the number of *D. pavonaceum* plants it visited. A plant was counted as visited if the insect manipulated and/or landed on at least one of its flowers in a direct and obvious manner. It is unlikely that an individual insect was counted more than once during a single observation time as only twice did we record more than one visit by an insect of the same

species during an observation interval. Voucher specimens of each floral visitor were collected and deposited in the Arthropod Collection at Oregon State University, Corvallis, Oregon.

ANALYSES

Statistical Software. One-way and two-way ANOVAs, *t*-tests, Mann-Whitney tests, and Fisher's Exact Tests were performed with the S-Plus 2000 professional package. Repeated-measures ANOVAs were performed with SPSS v8.0. Transformations of the data were performed as necessary, and are discussed below. The significance level was set *a priori* at $\alpha = 0.05$. Unless otherwise noted, raw means and two-sided *P*-values are presented throughout the results.

Outlier Strategy. We used scatter plots, residual verses fit plots, residual QQ plots, and Cook's Distance plots to check our data sets for potential outliers (Ramsey and Schafer 1996). When outliers were detected, we performed the analysis with and without the outlier, but in only one case did outlier removal change the results. In the density of flowering plants data, an outlier was detected in North Prairie. With this outlier included, there is no statistical evidence that any one management area contained a significantly greater density of flowering plants in 2002 or 2003 ($P = 0.249$ from a repeated-measures ANOVA). We present the results of this analysis without the outlier in Chapter 3.

Flowering Plant Density. The number of flowering plants per m^2 in 2002 and 2003 was analyzed by two methods. First, a two-way repeated-measures ANOVA was used to

compare flowering plant density in the management areas in 2002 and 2003. The within-subjects factor was year of measurement, and the between subjects factor was management subunit. As Mauchly's Test of Sphericity could not be used on this small and unbalanced data set, we assumed any deviation from sphericity would not invalidate the results. Second, a one-way ANOVA was used to compare the change in flowering plant density from 2002 to 2003 among the management units. The proportional change in density was calculated as $[(Density_{2003} - Density_{2002}) / Density_{2002}]$. In each analysis, a natural log-transformation of the data was necessary to meet the assumptions of equal variance and normal distribution of the data. When main-effects were significant at the $P \leq 0.05$ level, the Tukey-Kramer adjustment for unequal sample sizes was used in post-hoc tests.

Immature Plant Density. The total number of seedlings and recruits per plot was analyzed with a one-way ANOVA after a natural log transformation of the data to meet test assumptions. To account for discrepancies in flower plant density among management areas, a second one-way ANOVA compared the ratio of immature plants to mature plants. A third ANOVA compared the proportion of all plants in our plots that were seedlings or recruits. No transformations were needed for the second and third ANOVA, as the raw data met test assumptions. For all of the above tests, Tukey's HSD multiplier for equal sample sizes were used in post-hoc tests when main-effects were significant at the $P \leq 0.05$ level.

Plant Traits. Plant vigor and fitness traits of height, leaf production, flower and fruit production, fruit set, seed production per fruit, and seed mass per fruit were analyzed with separate one-way ANOVAs for each subsequent year of study. We chose this analysis method because the two years of study were climatically different (Chapter 4). When main-effects were significant at the $P \leq 0.05$ level, the Tukey-Kramer adjustment for unequal sample sizes was used in post-hoc tests. Natural log transformations of the data were required for height, flower production, and fruit production data to meet test assumptions, and a rank transformation was necessary for the fruit set data. No transformations were needed for leaf production, seed production per fruit or seed mass per fruit, as the data were normally distributed and the variances were approximately equal. For seed production and mass per fruit, we checked for interactions between the categorical explanatory variables of fruit position and management subunit, but the interaction was not significant in 2002 (seed production: $F_{8,187} = 0.878$, $P = 0.536$; seed mass: $F_{8,188} = 0.595$, $P = 0.781$) or 2003 (seed production: $F_{8,157} = 0.773$, $P = 0.627$; seed mass $F_{8,153} = 0.520$, $P = 0.840$).

To investigate the relationship between plant height and flower production among management units, we performed a multiple linear regression with the linear equation:

$$\ln(\text{Flowers Produced}) = \text{Plant Height} + \text{YEAR} + \text{SUBUNIT}$$

Explanatory variables in capital letters represent categorical variables. A natural log transformation of the number of flowers produced matched statistical assumptions of normality and equal variance.

Seed Germination. The percent of germinated seeds at day 86, 100, 115, 132, and 150 was analyzed using a three-way repeated-measures ANOVA. The between-subjects factors were treatment (management subunits) and the position on the inflorescence from which the fruit was drawn (top, middle, or bottom). Because the within-subjects factor (date) failed Mauchly's Test of Sphericity ($W = 0.253$, Huynh-Feldt Epsilon = 0.861, $P \leq 0.005$), the Huynh-Feldt correction was used to reduce the degrees of freedom in all tests of within-subjects effects. An arcsine square-root transformation was performed to meet the assumptions of the test. If tests of within and between-subjects main-effects were significant, Tukey's HSD multiplier was used in post-hoc tests.

Insect Visitors. Overall insect abundances of the two observed *Bombus* sp. and the average number of plants visited per insect were analyzed with a non-parametric Mann-Whitney test and a two-sample *t*-test, respectively. A natural log-transformation was performed on the later to meet test assumptions. The proportion of insect abundances in burned and unburned study plots was compared with Fisher's Exact Test.

Chapter 3

Results

FLOWERING PLANT DENSITY

Overall, the average density of flowering plants was 2.58 per m^2 in 2002 and 7.16 per m^2 in 2003, a significant increase between years ($P \leq 0.005$ from a repeated-measured ANOVA, **Tables 3, 5**). The two most frequently burned habitats in the RNA (North and South Prairie), had over twice as many flowering plants per m^2 than Central Prairie in 2002 ($P = 0.032$ from a repeated-measures ANOVA). North and South Prairie also supported more plants per m^2 than the unburned habitats, but were not significantly denser. Although differences among subunits were not detected in 2003, North Prairie continued to have the greatest overall density, while South and Central Prairie had slightly more plants per m^2 than the unburned sites. Hand removal of woody plants did not increase flowering plant density compared to the control, at least in the first flowering season following treatment.

There is only weak statistical evidence that any management unit experienced an increase in flowering plant density from 2002 to 2003 that was greater than the other subunits ($F_{4,11} = 1.755$ from a one-way ANOVA, $P = 0.208$). Nevertheless, it is interesting to note that the largest increase in flowering plant density occurred in Central Prairie, which was burned in the fall of 2002 after being left unburned for 3 years. Additionally, North and South Prairie had increases that were approximately half as large as Central Prairie and the unburned sites.

IMMATURE PLANT DENSITY

Overall, the average seedling density was 8.36 per m^2 and the average recruit density was 32.01 per m^2 in the flowering patches we sampled in 2003 (**Table 4**). South Prairie, most recently burned in the fall of 2000 and intermittently during the 1990s, contained an exceptionally large density of seedling ($F_{4,45} = 2.698$ from a one-way ANOVA, $P = 0.042$). The two subunits burned in the fall of 2002 (North and Central Prairie) and the hand-removal area were not different from Control Prairie for seedling density.

Central Prairie, burned in the fall of 1999 and 2002, contained more than twice as many recruits per m^2 than the other study areas ($F_{4,45} = 4.175$ from a one-way ANOVA, $P = 0.006$). The other burned subunits (North and South Prairie) tended to supported more recruits per m^2 than the unburned sites, but were not significantly different. The hand-removal area was also similar to Control Prairie for recruit density.

Overall, there was an average of 11.56 immature *D. pavonaceum* plants per reproductive plant in the areas we sampled. Central Prairie supported approximately three times as many immature plants per mature plant as the other subunits ($F_{4,45} = 9.034$ from a one-way ANOVA, $P < 0.005$), while the hand-removal site was similar to Control Prairie for this measurement.

PLANT TRAITS

Height and Leaves. In 2002 there was evidence that *D. pavonaceum* plants were shorter in North and South Prairie, which were both burned two years prior to the 2002 measurements ($F_{4,308} = 8.144$ from a one-way ANOVA, $P \leq 0.005$, **Figure 5**). This trend

Table 3: Average number of flowering *D. pavonaceum* plants per m^2 in each treatment area in 2002 and 2003, and the average percent increase in flowering plant density between years ($\pm$ 1 SE). n = number of patches sampled in each treatment area. Within each year, subunits assigned the same letter were statistically indistinguishable. Subunits were not different for average % increase in reproductive plants between years (P = 0.208) or for density in 2003.

Management Subunit	n	Average # Flowering Plants per m^2		Average % Increase
		2002	2003	
Control Prairie	3	1.42 $\pm$ 0.48ab	5.46 $\pm$ 1.48	363.92 $\pm$ 128.27
hand-removal	2	1.20 $\pm$ 0.01ab	5.34 $\pm$ 1.24	344.58 $\pm$ 100.04
Central Prairie	3	1.15 $\pm$ 0.45a	6.43 $\pm$ 2.43	568.34 $\pm$ 239.17
South Prairie	4	3.59 $\pm$ 0.50b	7.55 $\pm$ 2.67	139.12 $\pm$ 94.17
North Prairie	3	4.77 $\pm$ 0.71b	10.27 $\pm$ 0.38	171.53 $\pm$ 52.18
Overall	15	2.58 $\pm$ 0.44	7.16 $\pm$ 0.94	295.53 $\pm$ 64.65

Table 4: Average number of seedlings and recruits per m^2 and average number of immature plants per mature plant in 2003 ($\pm$ 1 SE). Subunits assigned the same letter were statistically indistinguishable.

Management Unit	Average # Seedlings per m^2	Average # Recruits per m^2	Average # Immature Plants per Mature Plant
Control Prairie	2.80 $\pm$ 2.25a	17.45 $\pm$ 4.48a	8.63 $\pm$ 1.45a
hand-removal	4.20 $\pm$ 3.45a	15.42 $\pm$ 3.48a	7.87 $\pm$ 2.15a
Central Prairie	3.70 $\pm$ 2.25a	70.96 $\pm$ 18.34b	25.92 $\pm$ 4.64b
South Prairie	28.80 $\pm$ 11.50b	26.32 $\pm$ 10.93a	7.78 $\pm$ 2.03a
North Prairie	2.30 $\pm$ 0.63a	29.91 $\pm$ 7.41ab	7.58 $\pm$ 1.82a
Overall	8.36 $\pm$ 2.80	32.01 $\pm$ 5.32	11.56 $\pm$ 1.54

Table 5. Tests of within-subjects effects (a) and between-subjects effects (b) from a two-way repeated-measures ANOVA examining the natural log-transformed flowering plant density of *D. pavonaceum* patches in 2002 and 2003. Treatment refers to the management subunits plants were sampled from.

(a)

Source	Type III Sum of Squares	df	Mean Square	F	P - value
Year	10.356	1	10.356	47.763	< 0.005
Year × Treatment	1.598	4	0.400	1.843	0.197
Error	2.168	10	0.217		

(b)

Source	Type III Sum of Squares	df	Mean Square	F	P - value
Intercept	21.502	1	21.502	125.597	< 0.005
Treatment	2.821	4	0.705	4.120	0.032
Error	1.712	10	0.171		

continued in 2003, where plants in all burned subunits were shorter than plants in Control Prairie ($F_{4,327}$ = 49.234 from a one-way ANOVA, $P \leq 0.005$). This effect was especially large in the two subunits burned the year prior to the 2003 measurements (North and Central Prairie). Additionally, plants in the hand-removal area were also significantly shorter than plants in Control Prairie in the first season following treatment.

Leaf number per plant was not measured in 2002. In 2003, plants in Central Prairie produced slightly fewer leaves than plants in any other area ($F_{4,327}$ = 5.860 from a one-way ANOVA, P = 0.001). Plants in Central Prairie, along with those in North Prairie, were burned in 2002 and among the shortest in 2003, but plants in North Prairie did not experience as pronounced a reduction in leaf number.

Flowers and Fruits. In 2002, plants in the frequently burned North Prairie produced the fewest flowers ($F_{4,298}$ = 9.628 from a one-way ANOVA, $P \leq 0.005$, **Figure 6**). This value was significantly less than South Prairie. Differences among subunits for flower production were not detected in 2003 ($F_{4,293}$ = 1.793 from a one-way ANOVA, P = 0.130).

The subunits were not statistically different for fruit production in 2002 ($F_{4,275}$ = 0.860 from a one-way ANOVA, P = 0.488). In 2003, plants in South Prairie, burned three years previously, matured the greatest number of fruits, and significantly more than the hand-removal site ($F_{4,284}$ = 2.882 from a one-way ANOVA, P = 0.023). The other manipulated subunits tended to produce somewhat less fruits than the control, but were not significantly different.

(a)

(b)

Figure 5. Average height of *D. pavonaceum* plants in 2002 and 2003 (a) and average number of leaves produced in 2003 (b). Error bars are ± 1 SE. Within each year, subunits assigned the same letter were statistically indistinguishable.

Figure 6. Average number of flowers (a) and average number of fruits (b) produced per *D. pavonaceum* plant in 2002 and 2003. Error bars are $\pm$ 1 SE. Within each year, subunits assigned the same letter were statistically indistinguishable. Flower production did not differ among subunits in 2003 ($P = 0.130$), and fruit production did not differ among subunits in 2002 ($P = 0.448$).

Figure 7. Average percent of flowers matured to seed bearing fruit by *D. pavonaceum* plants in 2002 and 2003. Error bars are ± 1 SE. Differences among subunits only approached statistical significance in 2002 (*P* = 0.053). In 2003, subunits assigned the same letter were statistically indistinguishable.

There was only suggestive evidence that the management subunits differed in the proportion of flowers that they matured to seed-bearing fruit in 2002 ($F_{4,268}$ = 2.366 from a one-way ANOVA, P = 0.053, **Figure 7**). While not statistically significant, plants in Control and North Prairie matured a slightly larger proportion of fruits than the other subunits. However in 2003, plants from South Prairie, last burned in fall 2000, matured approximately 20% more fruits per flower than any other subunit ($F_{4,278}$ = 8.479 from a one-way ANOVA, P < 0.005).

Resource Allocation. A multiple linear regression of height on flower production revealed that although plants in burned and hand-removal areas were shorter than those in Control Prairie, they allocated more resources to flower production than the unburned site (**Figure 8, Table 6, 7**). This effect was most pronounced in plants of South Prairie, which produced 21% more flowers per cm of height than plants in Control Prairie ($P \le$ 0.005). Plants in the hand-removal site, North Prairie, and Central Prairie produced 8%, 10%, and 12% more flowers per centimeter of height than Control Prairie, respectively.

Seed Production and Mass. In general, seed production and seed mass per fruit decreased with increasing height of the fruit on the floral inflorescence in both 2002 ($P \le$ 0.005, 0.012 respectively, **Table 8**) and 2003 ($P \le 0.005$, 0.013 respectively). In 2002, plants in North Prairie produced fewer seeds per fruit than the unburned, future hand-removal site ($F_{4,195}$ = 3.910 from a two-way ANOVA, P = 0.004). By 2003 the differences only approached significance, with plants in burned and hand-removal sites producing fewer seeds per fruit than the control ($F_{4,165}$ = 2.258 from a two-way ANOVA, P = 0.065).

Figure 8. Predicted values for natural log-transformed flower production from a multiple linear regression where height, year, and management areas were explanatory variables ($F_{6,593}$ = 76.31, R^2 = 43.57%, P < 0.005). Data from 2002 data are presented. The median number of flowers produced was –8.41% less in 2003 ($P \leq 0.005$).

Table 6. Results of a multiple linear regression of height on natural log-transformed flower production. Year, Hand-Removal, Central Prairie, South Prairie, and North Prairie are categorical indicator variables. ($F_{6,593} = 76.31$, $R^2 = 43.57\%$, $P < 0.005$)

Explanatory Variable	Coefficient	SE	t-value	P-value
Intercept	1.0676	0.0673	15.8614	0.0000
Height	0.0273	0.0015	17.7437	0.0000
Year	-0.0879	0.0164	-5.3609	0.0000
Hand-Removal	0.0806	0.0296	2.7234	0.0067
Central Prairie	0.1161	0.0294	3.9509	0.0001
South Prairie	0.1926	0.0263	7.3217	0.0000
North Prairie	0.0941	0.0267	3.5210	0.0005

Table 7. Analysis of variance table for a multiple linear regression of height on natural log-transformed flower production. Year, Hand-Removal, Central Prairie, South Prairie, and North Prairie are categorical indicator variables. ($F_{6,593} = 76.31$, $R^2 = 43.57\%$, $P < 0.005$)

Explanatory Variable	df	MS	F	P-value
Height	1	45.915	333.913	0.0000
Year	1	8.756	63.678	0.0000
Hand-Removal	1	0.085	0.619	0.4317
Central Prairie	1	0.011	0.083	0.7733
South Prairie	1	6.486	47.169	0.0000
North Prairie	1	1.705	12.398	0.0004
Residuals	*593*	*0.137*		

Table 8. Average seed production per fruit (a) and average seed mass per fruit (b, ± 1 SE). Within each year, fruit positions assigned the same letter were statistically indistinguishable.

(a)

Fruit Position on Inflorescence	Average # Seeds per Fruit		
	Overall	2002	2003
top	30.15	29.48 ± 2.05a	30.81 ± 3.06a
middle	39.17	42.21 ± 2.32b	36.13 ± 2.00ab
bottom	54.36	59.18 ± 2.02c	49.54 ± 1.98b

(b)

Fruit Position on Inflorescence	Average Seed Mass per Fruit (mg)		
	Overall	2002	2003
top	0.55	0.57 ± 0.02a	0.53 ± 0.03a
middle	0.57	0.60 ± 0.02ab	0.54 ± 0.02ab
bottom	0.62	0.65 ± 0.02b	0.60 ± 0.02b

(a)

(b)

Figure 9. Average number of seeds per fruit (a) and average seed mass per fruit (b) of *D. pavonaceum* plants in 2002 and 2003. Error bars are $\pm$ 1 SE. Within each year, subunits assigned the same letter were statistically indistinguishable. Subunits approached statistical significance for average seeds per fruit in 2003 ($P = 0.065$) and average seed mass per fruit in 2002 ($P = 0.055$).

In 2002, plants in burned subunits tended to produce seeds of slightly greater mass than Control Prairie, but this increase was barley statistically significant ($F_{4,196}$ = 2.484 from a two-way ANOVA, $P = 0.055$, **Figure 9**). However, in 2003 the two subunits that were burned the previous year (North and Central Prairie) clearly produced seeds that were lighter than those produced in other areas ($F_{4,161}$ = 8.750 from a two-way ANOVA, $P \leq 0.005$). Plants in South Prairie, burned three years prior, and the hand-removal site maintained seed mass trends in 2003 quite similar to those seen in 2002, and continued to produce slightly heavier seeds than Control Prairie.

Seed Germination. Under laboratory conditions, seed germination began at 86 days, approximately 3 months, after their placement in cold stratification. After 150 days (approximately 5 months), 91.11% of the seeds had germinated, despite a ubiquitous fungus contamination. Non-germinated seeds were determined to be not viable or fungus-killed rather than dormant.

Seed germination increased with the number of days in cold stratification ($P <$ 0.005 from a repeated measured ANOVA, **Table 9**). Additionally, the position of the fruit on the inflorescence from which the seeds were drawn influenced seed germination rates ($P = 0.014$ from a repeated measured ANOVA). There was significant evidence that the burn treatments influenced seed germination rates ($P < 0.005$ from a repeated measures ANOVA) and interacted with time in cold stratification ($P = 0.001$ from a repeated measured ANOVA, **Figure 10**). After 100 and 115 days of cold stratification, a greater proportion of seeds collected from South Prairie had germinated than seeds from North or Central Prairie. No treatment areas were significantly different in their proportion of

Figure 10. Average percent of germinated seeds from four management areas after 86, 100, 115, 132, and 150 days of 7°C cold stratification. Seeds used in germination trials were collected in 2002.

Table 9. Tests of within-subjects effects (a) and between-subjects effects (b) from a three-way repeated measures ANOVA examining the germination of seeds collected in 2002. Date, treatment, and position refer to the number of days seeds were in cold stratification, the management subunit they were collected from, and the position on the inflorescence the fruit matured, respectively. Because the within-subjects main effect (Date) failed Mauchly's Test of Sphericity ($W = 0.253$, P–value ≤ 0.005), the Huynh-Feldt correction was used to adjust the degrees of freedom.

(a)

Source	Type III Sum of Squares	df	Mean Square	F	P - value
Date	73.740	3.443	21.419	724.267	< 0.005
Date × Treatment	0.970	10.328	0.094	3.176	0.001
Date × Position	0.251	6.886	0.036	1.231	0.289
Date × Treatment × Position	0.525	20.657	0.025	0.860	0.641
Error	4.887	165.252	0.030		

(b)

Source	Type III Sum of Squares	df	Mean Square	F	P - value
Intercept	30.800	1	30.800	1609.224	≤ 0.005
Treatment	0.423	3	0.141	7.371	≤ 0.005
Position	0.179	2	0.089	4.672	0.014
Treatment × Position	0.125	6	0.021	1.086	0.384
Error	0.919	48	0.019		

germinated seed after 86, 132, or 150 days.

INSECT VISITORS

Bombus californicus and B. appositus were the only bees we observed visiting D. pavonaceum during the two years of study (**Figure 11**). On the evenings of May 29-30 2003, and on the afternoon on June 4 2003, we incidentally observed large moths actively nectaring on larkspur flowers. Unfortunately, we were not able to capture any moths for identification and do not know if they carry pollen between plants.

Our observations at FNWR suggest local asynchrony in the emergence of the founding queens for the two bumblebee species. Bombus californicus (May 11 2002 and May 8 2003) was observed actively visiting D. pavonaceum before B. appositus (May 27 2002 and May 17 2003) during both years of study. There was no indication in our data that the activity levels of these species contrasted throughout the day or with changing weather conditions.

We observed a moderate number of visits by the two Bombus sp. within our seven 20-minute observation intervals in burned and unburned plots. Bombus californicus was observed slightly more frequently than B. appositus, but there is no evidence that B. californicus was more abundant, at least during the peak flowering time of D. pavonaceum ($Z = 0.648$, $P = 0.517$ from a Mann-Whitney test, **Table 10**). Bombus appositus visited 2.35 times more plants per plot entry than B. californicus, but this difference only approached statistical significance ($t = -1.931$, $P = 0.075$ from a two-sample t-test).

The density of flowering *D. pavonaceum* plants was 6.19 plants per m^2 in the unburned plot, and 17.0 plants per m^2 burned study plots. We observed slightly more visits by individuals of both bee species in the burned study plot, but the proportion of bee abundance was not statistically different among areas ($P = 1.000$ from a Fisher's Exact Test). This result corresponds with the similar levels of pollinator-mediated fruit production, fruit-set, and seed production we observed in plants from the burned and unburned study area.

(a)

(b)

Figure 11. *Bombus appositus* (a) and *B. californicus* (b) visiting flowers of *D. pavonaceum* at W. L. Finley National Wildlife Refuge.

Table 10: Number of *Bombus* individuals observed visiting *D. pavonaceum* plants, total number of plants visited by the bumblebees, and the average number of plants visited per individual bee (± 1 SE) during seven 20-minute observation periods in burned and unburned study plots at FNWR.

	Overall		Burned Prairie		Unburned Prairie	
	B. californicus	*B. appositus*	*B. californicus*	*B. appositus*	*B. californicus*	*B. appositus*
Total # bees	9	6	5	4	4	2
Total # plants visited	44	70	26	48	18	22
Ave. # plants visited per bee	4.89 ± 0.53	11.67 ± 1.71	5.20 ± 1.34	12.00 ± 3.30	4.50 ± 0.25	11.00 ± 0.71

Chapter 4

Discussion

INFLUENCE OF FIRE

Large increases in seedling abundance in the growing season immediately following a burn has been reported in many perennial plant species (Whelan 1995), including rare species such as *Silene regia* in midwestern prairies (Menges and Dolan 1998), *Silene spaldingii* in the Palouse grasslands of the intermountain west (Lesica 1999), and *Bomania gradiflora* in Florida sand scrub. However, *D. pavonaceum* had low seedling density in sites burned the previous year (**Table 4**), suggesting that fire may consume or damage unprotected seeds in the litter layer or seeds exposed on the soil surface. Goodrich (1983) found very low rates of germination in *D. pavonaceum* seeds baked at 80°C or quickly passed through a flame, and no germination in seeds baked at 180°C. In Willamette Valley wetland prairies, the maximum soil surface temperature during prescribed burns typically exceeds 100°C, and can reach as high as 371°C (Pendergrass *et al.* 1998), likely rendering seeds of *D. pavonaceum* unviable. Some seed does appear to escape damage during burns, as low levels of germination were observed following fire. Temperatures 1 cm below the soil surface do not surpass 40°C-60°C (Pendergrass *et al.* 1998), and seeds buried at this depth might not be harmed by fire.

Although few seedlings were observed in the prairies burned the previous fall, a large number of seedlings was found in South Prairie, which was burned every two to three years beginning in 1990, and left unburned since 2000. This suggests that although fire may kill seeds, seedling density is ultimately enhanced in the years following a fire

once the seed bank has been replenished. Fire likely lead to increased seedling density in South Prairie by reducing litter interference of seed germination and seedling survival (Bergelson 1990). Fire may have also promoted seedling density by reducing the cover of competing vegetation, releasing nutrients such as nitrogen, and beneficially altering the microclimate.

Like the prairies burned the year prior, low seedling density was also found in Control Prairie and the hand-removal site, both of which had not been burned for over 20 years (**Table 4**). We suggest that litter accumulation interfered with seed germination and/or seedling survival in these unburned areas (Bergelson 1990, Lesica 1999). In Willamette Valley wetland prairies litter accumulation is slow and does not reach great depths (Pendergrass *et al.* 1998), allowing some limited seedling establishment. We have also observed pocket-gopher and elk activities that may create of open sites for seedling establishment throughout our study area. These non-fire disturbances may promote some regeneration in unburned *D. pavonaceum* populations, but could doubtfully serve as a long-term replacement more widespread disturbances such as fire.

We found the greatest density of *D. pavonaceum* recruits in Central Prairie, a subunit that was burned in 1999 for the first time in 20 years, and three years later in 2002 (**Table 4**). These recruits likely originated from the seed rain of plants that reproduced in the first few years after the 1999 fire. The more-frequently burned North Prairie also supported elevated numbers of recruits, but not to levels as great as those in Central Prairie. This was possibly due to a reduction of the seed bank following repeated burns, and increased intraspecific competition with mature plants, which were of greater density in North Prairie. Interestingly, South Prairie, which had the greatest density of

seedlings, was similar to Control Prairie for recruit density. This result is puzzling, as the two to four year fire-return intervals experienced by South Prairie could have allowed for elevated seedling establishment and recruitment. This might suggest self-thinning of the population to more moderate densities following flushes in seed germination after fire (Whelan 1995).

Increased density of seedlings and recruits following fire is often suggested to result in population growth. However, enhanced seedling density may also result in greater intraspecific competition, disease, and herbivory, leading to elevated rates of seedling mortality in the post-fire environment, and no net increase in the number of individuals in a population (Whelan 1995, Lesica 1999). Nevertheless, the elevated density of seedlings and recruits we observed in the burned areas likely does lead to population growth for *D. pavonaceum*, as we observed a greater density of reproductive plants we observed in the two most-frequently burned subunits (North and South Prairie) during both years of study (**Table 3**). Flowering plant density in the unburned Control Prairie and the hand-removal site was consistently lower than North and South Prairie in both years of study, although the differences were not as pronounced for South Prairie in 2003.

Although we did not find increased density of reproductive plants in Central Prairie, which was burned in 1999 and 2002, the life-history of *D. pavonaceum* and the prescribed fire schedule explains this seemingly spurious result. Our observations occurred three and four years after the 1999 fire in Central Prairie, but it may take at least five years for plants of this species to reach reproductive maturity (Goodrich 1983). We

predict that the density of reproductive plants will increase in Central Prairie in the near future as recruits mature.

By the second year of our study, the trend of elevated flowering plant density in repeatedly burned sites was no longer significant in South Prairie, which by 2002 had not been burned for three seasons. It is possible that a greater proportion of plants in South Prairie were dormant in 2003, perhaps because the positive benefits of fire on the habitat diminished after three years of no burning. Alternatively, it is possible that this subunit was burned too infrequently to maintain a habitat capable of supporting elevated levels of survival in immature and reproductive plants, leading to reduced flowering plant density.

The ability of some perennial plant species such as *D. pavonaceum* to invoke occasional summer dormancy complicates measurements of population growth (Lesica 1999). Although significant differences were not detected, we found smaller increases in flowering plant density between our two years of study in North and South Prairie, which were burned several times in the 1990s and in 2000 (**Table 3**). We suggest that there were fewer dormant plants in these recently burned subunits in 2002, leading to the relatively small change we observed between years. The greatest increase in flowering plant density occurred in Central Prairie, which was first burned in the fall of 1999 and again three years later in 2002. We suggest that fire promoted plants to break dormancy, and lead to the large increase in flowering plants we observed in Central Prairie. Fire may have also expedited the maturation of some juvenile plants by reducing competition and altering soil nutrient levels and the microclimate.

We hypothesized that the vigor and fecundity of *D. pavonaceum* would respond positively to prescribed burning and the removal of woody species. However, we found that plants were shorter in burned areas, and generally showed no improvement in flower production, fruit production, fruit set, seed production, or seed mass compared to Control Prairie (**Figures 5-7, 9**). These results are inconsistent with our hypothesis, and suggest that burning does not lead to increases in plant vigor and fecundity.

Plants may have been shorter in burned and hand-removal areas because of water stress. Fire removes soil-shading plants and litter, leading to greater incident light on the soil surface, elevated of soil temperatures, and increased water evaporation (Kucera and Ehrenreich 1962, Antos *et al.* 1983, Hulbert 1988, Ojima *et al.* 1994). Additionally, plants in Control Prairie might have experienced greater stem elongation to compete for light with denser vegetation, whereas the vegetation in burned and hand-removal sites was less dense and of shorter stature (Dudley and Schmitt 1996). Our results indicate that plant height tends to increase with time after fire, reaching pre-burn levels after at least three years.

Plant in burned and hand-removal areas did not produce more flowers than plants in unburned areas. However, we found that *D. pavonaceum* plants in habitats treated with fire or the hand-removal of woody species produced more flowers per centimeter of height. This suggests that these plants allocated more resources to reproduction than plants in the unburned Control Prairie. However, other researchers have found reduced reproductive effort in an annually burned habitat of *D. pavonaceum* compared to an unburned prairie (Page 1996). It is possible that plants investigated by the 1996 study

experienced greater water stress from the annual burning, leading to reduced reproductive effort. In midwestern tall-grass prairies, the perennial forb *Ratibida columnifera* also displayed greater reproductive efficiency in long-unburned habitat (Hartnett 1991).

CLIMATIC DIFFERENCE AMONG YEARS

We observed an average of three times as many flowering plants per m^2 in our second year of study (**Table 3**). Because *D. pavonaceum* plants are long-lived and may require up to 5 years to reach reproductive maturity (Goodrich 1983), it is unlikely that this increase resulted from recruitment. Rather, it is likely from the maturation of juveniles and the re-emergence of dormant plants. Similar to other *Delphinium* spp. (Epling and Lewis 1952), seasonal dormancy under droughty conditions has been reported for *D. pavonaceum* (Goodrich 1983). We suspect that inadequate rainfall likely triggered a majority of mature plants to enter summer dormancy in 2002, but after the return of normal rainfall conditions the following winter, these plants re-emerged and flowered in 2003. Prior to our first field season in 2002, the wet months of October to May received less than half the rainfall (48.89 cm) of our second field season in 2003 (108.84 cm), which was a typical rain year (NOAA, Oregon State University Station). The ability of *D. pavonaceum* to invoke dormancy under droughty conditions signifies that a single year of study would severely misrepresent the flowering plant density of this species.

Although conditions were drier in 2002, plants were less productive for reproductive traits in 2003. The reduced reproductive biomass observed in 2003 may

have resulted because a decreased amount of photosynthetic resources were put in reserve during the previous dry year to be used for growth the following year. Additionally, the greater flowering plant densities of 2003 might have increased intraspecific competition, resulting in reduced growth.

INSECT VISITORS

Bombus californicus, *B. appositus*, and several large moths were the only insects we observed visiting *D. pavonaceum* during the two years of this study. Goodrich (1983) also reports *B. californicus* and *B. appositus* to be the sole visitors of *D. pavonaceum* and the presence of *Delphinium* pollen on their bodies, likely indicating that these species transfer pollen among plants. Additionally, the size and early-season activity of these insects suggests that they are nest-founding queen bumblebees (Goodrich 1983). Other species of *Delphinium* are also pollinated by these *Bombus* species. In western Oregon, *Bombus californicus* also visits *D. menziesii*, *D. leucophaeum*, and *D. nuttalii* (Goodrich 1983). *Bombus californicus* and *B. appositus* service *D. nuttallianum* in other western states (Schulke and Waser 2001). Additional species reported to visit *D. pavonaceum* include Halictid bees, *Apis* spp., and possibly *Synhalonia* spp., but the ability of these insects to transfer pollen between plants in unknown (R.J. Meinke, personal communication). Future research is needed to confirm the identity of the moth visitors and evaluate the effectiveness of both bees and moths in pollinating *D. pavonaceum*.

We did not detect a difference in bumblebee abundance between a frequently burned and unburned study plot during the peak flowering time of *D. pavonaceum*, a result consistent with our null hypothesis. However, prescribed fire has been associated

with short-term reductions in the abundance of some insect species in midwestern prairies (Anderson *et al.* 1989), particularly in insects endemic to or otherwise dependent on prairie habitats (Swengel 1996, Panzer 2002). Although we did not find any reduction in bumblebee abundance in the burned site, our small sample size requires that this result be cautiously interpreted and further studied, as it is possible that our visitation data would change appreciably with a broader range of observations. Additionally, our samples occurred in plots with quite different flowering plant densities, which might have resulted in different rates of pollinator attraction and lead to misleading conclusions (Groom 1998). A more appropriate technique to determine insect abundances might have been to tally the number of individuals of the two bumblebee species observed while walking along random transects in a burned and unburned area (as in Swengel 1996). This technique, however, would not give any insight to the behavior of the species, which was also a goal of the present study.

Nevertheless, it is unlikely that fire, when timed appropriately, directly harms these species. Most *Bombus* colonies are inactive by the fall, and over-wintering, colony-founding queens should be burrowed deep enough (2" - 12") to prevent harm from fire (W.P. Stephens, personal communication). It is unknown how fire indirectly influences these species. For example, it is possible that fire favorably affects bumblebees by improving the quality and quantity of forage (Potts *et al.* 2003), and provides opens sites for colony establishment.

We evaluated insect abundance at the peak flowering time of *D. pavonaceum*, when both *B. californicus* and *B. appositus* were highly active. Because *B. californicus* appears to emerge earlier than *B. appositus*, it is unlikely that the abundance of these

species is comparable throughout the flowering period of *D. pavonaceum*. Further

observations, spaced throughout the flowering season, are necessary to investigate any

asynchrony in peak activity levels for the two *Bombus* species. Although the difference

was not statistically significant, *B. appositus* appears to visit more individual *D.*

pavonaceum plants per plot entry than *B. californicus*. Casual observations also imply

that *B. appositus* manipulates fewer flowers per plant than *B. californicus*. Together, this

could result in greater interplant pollen transfer by *B. appositus*, and more geitonogamous

pollination by *B. californicus*. In primarily outcrossing species, geitonogamous

pollination is believed to be an undesired consequence of large floral displays designed to

attract animal pollinators, and may result in inbred offspring of reduced vigor (Eckert

2000). In *D. pavonaceum*, Goodrich (1983) found that only 6% of the seed from a

geitonogamous pollination germinated, compared to 24.5% germination in open-

pollinated seed. Thus, the varied behavior of the two bee species may result in offspring

of different genetic and competitive character, and offers an interesting area of future

study.

Chapter 5

Conclusions and Management Implications

In the Willamette Valley, where much of the landscape has been converted to agrarian or urban uses, nature reserves such as W. L. Finley National Wildlife Refuge are essential for the conservation of rare and endangered plants and other native species. This refuge contains the largest remaining fragment of Willamette Valley wetland prairie and is habitat for several sensitive plant species, placing upon land managers a great ecological responsibility. Prescribed fire is currently used to reduce the abundance of woody species in the wetland prairie, but how does fire influence *D. pavonaceum* and other rare plants? Since not all plant species respond favorably to burning, the effects of fire on sensitive plant species should preferably be understood before it is used to manage rare plant habitat (Borchert 1991, Jacobson *et al*. 1991, Johnson *et al*. 1994, Kirkman *et al*. 1998, Pendergrass *et al*. 1999). However, limited economic resources, personnel, and the immediate need to halt woody plant invasions in wetland prairie may necessitate that prescribed fire be applied before studies on rare taxa can be completed.

Because our study is retrospective, and the prescribed fire plan was designed for management purposes only, there are several limitations of our study. First, we examined the influence of fire on *D. pavonaceum* following twelve years of prescribed fire in its wetland prairie habitat, and thus lack pre-burn information for comparison. Second, our interpretation of the results is complicated by the 1997 adjustment of the fire-return interval in North and South Prairie (**Appendix A**). Finally, because the fire treatments were unreplicated in our study area, it would be inappropriate to conclude that differences

among management subunits resulted from fire alone. Other non-fire factors remain potential causes. Recent studies in the RNA accounted for variation in hydrology, animal disturbances, and geographic position among three subunits, and found a moderate amount of variation among them (Wilson 1999). However, the study also found that fire frequency likely explained a reduced shrub volume and greater relative abundance of native herbaceous species in burned areas (Wilson 1999). Although we cannot unquestionably link fire with the differences we observed in this study, the extensive observations of other researchers add increased plausibility to our assumption that fire strongly influences *D. pavonaceum* in the RNA.

Despite its limitations, our study detected several important influences of fire on *D. pavonaceum*. The main influence of fire on this species may be to limit seedling establishment in the first post-fire season, but fire may greatly promote seedling establishment in subsequent unburned years, likely leading to increases in flowering plant density. Additionally, fire seems to reduce the proportion of dormant plants, and may encourage fire-stimulated dormancy breaking. Our results on the influence of fire on several vegetative and reproductive traits are mixed. We found decreased height and seed mass in plants of recently burned habitats, but measurements of flower and fruit production, fruit set, seed production, and seed mass were generally similar to the unburned Control Prairie. Although total reproductive output does not appear to be augmented, plants in burned habitats increased resource allocation to flower production, and produced more flowers per centimeter of height.

Hand-removal of woody species has sometimes been suggested as an alternative to prescribed fire because it removes the risk of wildfire and the problem of smoke-management near residential areas. The hand-removal of woody plants did not appear to negatively impact *D. pavonaceum*, but neither did it improve the density of immature or reproductive plants or promote plant vigor, at least one-season following treatment. It is possible that improvements might be detected by the second year following treatment, but we doubt that hand-removal would be equivalent to prescribed fire in promoting seedling density, recruitment, and mature plant density.

A great difficulty in interpreting the results of this study was caused by the 1996 decision to alter the fire-regimes applied to the wetland prairie at FNWR. North Prairie, previously given annual fire treatments, was shifted to a biennial fire schedule, while South Prairie, previously prescribed triennial fires, now experiences burns of inconsistent fire-return intervals. This management change ended an important experiment, and unfortunately now complicates the ability of observational studies to draw conclusions about the fire-regimes currently in place. For *D. pavonaceum* in particular, it appears important to investigate the long-term effect of annual burning on flowering plant density, as fire may consume seeds and lead to low seedling establishment in the first post-fire growing season. If this observation is found to be consistent in other years and sites, we predict that annual burning could eventually lead to population declines. Two previous studies examined *D. pavonaceum* four and five years after the implementation of the annual burning regime in North Prairie, and both found elevated plant density in North Prairie compared to unburned sites (Finley and Ingersoll 1994, Page 1996). This suggests that mature plants can tolerate annual fires. However, it is unlikely that

investigations conducted only four to five years after the initiation of annual fire can assess population change in a long-lived plant that is capable of dormancy and may take as long as 5 years to reach reproductive maturity. Also, since no sampling of *D. pavonaceum* was conducted prior to the application of fire in 1990, it remains possible that the greater plant density existed in North Prairie prior to burning. If annual fires are returned to FNWR, we emphasize the importance of population monitoring to evaluate the potential for undesirable outcomes on population growth. Preferably, this could be accomplished by establishing permanent plots in North Prairie and an unburned control to be evaluated at least every other year for 10 years. We do not intend for this recommendation to deter a future decision to re-implement annual fire in *D. pavonaceum* habitat. Rather, we suggest that if the decision to annually burn is made, measurements be taken that allow adaptive management. This is particularly important for *D. pavonaceum*, because >99% of all plants of this species known to exist occur on the RNA.

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APPENDICES

Appendix A. Dates of prescribed burns in *D. pavonaceum* study areas on the Willamette Flood Plain Research Natural Area at William L. Finley National Wildlife Refuge between 1990-2003 (J. Beall and R. Blacker, personal communication). No-burn and hand removal treatments were located in Control Prairie, where the last recent burns occurred in 1972 and 1979. Measurements for the present study were conducted in the spring and early summer of 2002 and 2003.

Prescribed Fire Subunit		
North Prairie	Central Prairie	South Prairie
Sep ??, 1990	---	---
Sep 14, 1991	---	Sep 12, 1991
Oct 13, 1992	---	---
Oct 19, 1993	---	---
Oct 5, 1994	---	Oct 5, 1994
Oct 5, 1995	---	---
Sep 26, 1996	---	---
---	---	---
Sep 11, 1998	---	Sep 16, 1998
---	Oct 14, 1999	---
Sep 27, 2000	---	Sep 28, 2000
---	---	---
Oct 22, 2002	Oct 22, 2002	---

Appendix B. Weather conditions at the beginning of the 20-minute floral visitor observation intervals.

Date	Time (hrs)	Temperature (°F)	Wind Speed (mph)	Weather
May 25, 2003	1020	60.8	6.9	overcast
	1215	62.6	6.9	overcast
	1415	62.6	10.0	overcast
May 26, 2003	1925	64.4	9.0	mostly cloudy
	2045	60.8	5.8	mostly cloudy
June 4, 2003	1020	73.4	7.0	clear
	1115	78.8	5.0	clear

Appendix C. Average vigor and fecundity of *D. pavonaceum* plants sampled in 2002 ($\pm$ 1 SE). $n =$ number of plants sampled in each treatment area. Within each response, subunits assigned the same letter were statistically indistinguishable. Leaf production was not measured in 2002.

	Overall	Control Prairie	Hand Removal	Central Prairie	South Prairie	North Prairie
Height (cm)	38.41 ± 0.55	42.97 ± 1.70ab	44.42 ± 3.07ab	43.80 ± 1.74a	37.16 ± 0.80bc	36.10 ± 0.81c
n	*313*	*22*	*20*	*38*	*108*	*125*
Flowers (#)	7.19 ± 0.28	7.33 ± 0.88ab	8.60 ± 1.36ab	7.16 ± 0.66ab	8.89 ± 0.59a	5.44 ± 0.29b
n	*303*	*21*	*20*	*38*	*105*	*119*
Fruits (#)	4.85 ± 0.21	5.14 ± 0.64	6.21 ± 1.06	5.11 ± 0.65	5.11 ± 0.41	4.26 ± 0.29
n	*280*	*22*	*19*	*37*	*91*	*111*
Fruit Set	0.72 ± 0.02	0.77 ± 0.07	0.71 ± 0.06	0.71 ± 0.03	0.67 ± 0.03	0.76 ± 0.03
n	*273*	*21*	*19*	*36*	*91*	*106*
Seeds per Fruit (#)	44.31 ± 1.50	50.50 ± 4.93ab	53.07 ± 6.68a	50.54 ± 3.76ab	44.73 ± 2.76ab	39.41 ± 2.18b
n	*202*	*18*	*15*	*22*	*64*	*83*
Seed Mass per Fruit (mg)	6.10 ± 0.11	5.56 ± 0.28	5.94 ± 0.44	5.79 ± 0.28	6.55 ± 0.20	5.99 ± 0.17
n	*202*	*18*	*15*	*22*	*64*	*83*

Appendix D. Average vigor and fecundity of *D. pavonaceum* plants sampled in 2003 ($\pm$ 1 SE). $n =$ number of plants sampled in each treatment area. Within each response, subunits assigned the same letter were statistically indistinguishable.

	Overall	Control Prairie	Hand Removal	Central Prairie	South Prairie	North Prairie
Height (cm)	37.36 $\pm$ 0.64	47.46 $\pm$ 1.58a	39.90 $\pm$ 1.45b	28.93 $\pm$ 0.86c	38.86 $\pm$ 0.85bd	29.46 $\pm$ 0.75c
n	330	75	55	50	75	75
Leaves (#)	3.42 $\pm$ 0.05	3.52 $\pm$ 0.10a	3.53 $\pm$ 0.13a	2.90 $\pm$ 0.11b	3.61 $\pm$ 0.10a	3.40 $\pm$ 0.09a
n	330	75	55	50	75	75
Flowers (#)	5.03 $\pm$ 0.20	5.46 $\pm$ 0.52	4.98 $\pm$ 0.28	4.31 $\pm$ 0.32	5.62 $\pm$ 0.45	4.62 $\pm$ 0.31
n	298	71	51	49	58	69
Fruits (#)	3.61 $\pm$ 0.16	3.92 $\pm$ 0.44ab	3.06 $\pm$ 0.25a	3.07 $\pm$ 0.27ab	4.57 $\pm$ 0.36b	3.25 $\pm$ 0.25ab
n	289	71	51	44	56	67
Fruit Set	0.74 $\pm$ 0.02	0.68 $\pm$ 0.04a	0.67 $\pm$ 0.04a	0.74 $\pm$ 0.04b	0.91 $\pm$ 0.02a	0.72 $\pm$ 0.03a
n	283	71	50	44	51	67
Seeds per Fruit (#)	40.91 $\pm$ 1.45	45.16 $\pm$ 2.88	42.44 $\pm$ 3.97	40.89 $\pm$ 4.24	39.84 $\pm$ 3.00	35.95 $\pm$ 2.65
n	172	45	25	27	37	38
Seed Mass per Fruit (mg)	5.78 $\pm$ 0.14	5.89 $\pm$ 0.27a	6.30 $\pm$ 0.22ab	4.80 $\pm$ 0.17c	6.85 $\pm$ 0.42ab	4.98 $\pm$ 0.23c
n	172	45	25	27	37	38

Appendix E. Average percent germinated seeds after 86, 100, 115, 132, or 150 days in cold stratification ($\pm$ 1 SE). No treatment areas were different from one another in their percent germination after 86, 132, or 150 days in cold stratification. For day 100 and 115, management subunits assigned the same letter were statistically indistinguishable.

Management Subunit	Days in Cold Stratification				
	86	100	115	132	150
Control Prairie	0.22 $\pm$ 0.22	13.78 $\pm$ 3.39ab	51.11 $\pm$ 5.00ab	83.78 $\pm$ 3.62	91.11 $\pm$ 3.11
Central Prairie	0 $\pm$ 0	6.00 $\pm$ 2.74a	40.22 $\pm$ 7.51a	77.56 $\pm$ 6.44	91.78 $\pm$ 1.69
South Prairie	3.56 $\pm$ 2.90	27.56 $\pm$ 6.29b	71.33 $\pm$ 4.86b	87.87 $\pm$ 2.60	94.67 $\pm$ 1.25
North Prairie	0 $\pm$ 0	5.11 $\pm$ 1.71a	38.22 $\pm$ 5.10a	76.67 $\pm$ 4.87	88.44 $\pm$ 3.30
Overall	0.22 $\pm$ 0.22	13.78 $\pm$ 3.39	51.11 $\pm$ 5.00	83.78 $\pm$ 3.62	91.11 $\pm$ 3.11

Appendix F. Location, number of flowering plants, and area of *D. pavonaceum* plant units on the Willamette Flood Plain Research Natural Area at Finley National Wildlife Refuge (1994-2002). "---" indicates uncollected data.

Plant Unit	Location	Management Subunit	# Flowering Plants			Area (m²)		
			1994 [a]	1995 [b]	2002 [c]	1994 [a]	1995 [b]	2002 [c]
1	N 44° 25.464′ W 123° 18.267′	North Prairie	600	785	499	---	55	212
2	N 44° 25.359′ W 123° 18.174′	North Prairie	400	---	1354	---	---	1651
3	N 44° 25.255′ W 123° 18.150′	North Prairie	>2000	859	14758	---	286	4868
4	N 44° 25.252′ W 123° 18.233′	North Prairie	1000	1367	15534	---	---	7014
5	N 44° 25.202′ W 123° 18.300′	North Prairie	>1000	428	18974	---	---	4179
6	N 44° 25.110′ W 123° 18.161′	North Prairie	900	---	9971	---	---	6770
7	N 44° 25.120′ W 123° 18.305′	North Prairie	1200	---	7091	---	---	8431
8	N 44° 25.043′ W 123° 18.028′	North & Central	>100	---	10139	---	---	14099
9	---	Central Prairie	400	---	---	---	---	---
10	N 44° 24.744′ W 123° 17.636′	South & 5	200	---	5185	---	---	7198
11	N 44° 25.450′ W 123° 17.560′	Control Prairie	800	---	3574	---	---	40399
12	N 44° 25.470′ W 123° 17.716′	Fire-break	3	12	121	---	---	45
13	N 44° 24.270′ W 123° 17.652′	South Prairie	12	350	12292	---	---	4881
14	N 44° 25.435′ W 123° 18.444′	North Prairie	30	---	1286	---	---	1480
15	N 44° 25.361′ W 123° 18.250′	North Prairie	250	680	1656	---	168	1404
16	N 44° 24.595′ W 123° 17.545′	Subunit 7	---	322	429	---	---	199
17	N 44° 24.530′ W 123° 17.575′	Subunit 7	---	149	858	---	---	268
18	N 44° 24.308′ W 123° 17.612′	South Prairie	---	---	5822	---	---	2368
19	N 44° 25.457′ W 123° 18.373′	Subunit 7	---	83	324	---	---	455
20	N 44° 25.064′ W 123° 17.584′	Control Prairie	---	538	266	---	2365	581

[a] Source: Finley and Ingersoll (1994). [b] Source: Page (1996). [c] The # of flowering plants was directly counted by hand except in clusters 3-6, 8, and 18 where randomly placed quadrats were used in estimations (please refer to Chapter 2 and Appendix G).

Appendix G. Location, number of flowering plants, area, and density of *D. pavonaceum* patches on the Willamette Flood Plain Research Natural Area at Finley National Wildlife Refuge. "---" indicates uncollected data.

Patch	Location	Management Subunit	# Flowering Plants ($\pm$ 1 SE) 2002[a]	# Flowering Plants ($\pm$ 1 SE) 2003[b]	Area (m^2) 2002[c]	Area (m^2) 2003[c]
1	N 44° 25.464′ W 123° 18.267′	North Prairie	499	---	212	---
2	N 44° 25.359′ W 123° 18.174′	North Prairie	1354	5413	1651	1584
3a	N 44° 25.255′ W 123° 18.150′	North Prairie	14326 $\pm$ 2469	---	3582	---
3b	N 44° 25.216′ W 123° 18.114′	North Prairie	423	---	195	---
3c	---	North Prairie	9	---	1	---
4a	N 44° 25.252′ W 123° 18.233′	North Prairie	13348 $\pm$ 3965	---	2713	---
4b	N 44° 25.221′ W 123° 18.232′	North Prairie	594	---	324	---
4c	N 44° 25.195′ W 123° 18.202′	North Prairie	468	---	182	---
4d	N 44° 25.173′ W 123° 18.224′	North Prairie	66	---	---	---
4e	N 44° 25.190′ W 123° 18.230′	North Prairie	1058	3412	245	356
5	N 44° 25.202′ W 123° 18.300′	North Prairie	18974 $\pm$ 2212	---	4179	---
6a	N 44° 25.149′ W 123° 18.210′	North Prairie	553	---	485	---
6b	N 44° 25.110′ W 123° 18.161′	North Prairie	9335 $\pm$ 2160	23634 $\pm$ 3215	1515	2172
6c	N 44° 25.079′ W 123° 18.165′	North Prairie	83	---	11	---
7a	N 44° 25.120′ W 123° 18.305′	North Prairie	6038	---	5128	---
7b	N 44° 25.066′ W 123° 18.278′	North Prairie	183	---	75	---
7c	N 44° 25.048′ W 123° 18.253′	North Prairie	870	---	1214	---

[a] Where indicated with SE, the number of flowering plants was estimated with 15 randomly placed 1 m x 0.5 m quadrats.
[b] Where indicated with SE, the number of flowering plants was estimated with 25 randomly placed 1 m x 0.5 m quadrats.
[c] Please refer to Chapter 2 for procedure.

Appendix G, continued.

Patch	Location		Management Subunit	# Flowering Plants ($\pm$ 1 SE)		Area (m^2)	
				2002[a]	2003[b]	2002[c]	2003[c]
8a	N 44° 25.098′	W 123° 18.099′	North Prairie	6101 $\pm$ 1182	---	1525	---
8b	N 44° 25.082′	W 123° 18.102′	Central Prairie	279	---	236	---
8c	N 44° 25.072′	W 123° 18.082′	Central Prairie	922	---	421	---
8d	N 44° 25.075′	W 123° 18.111′	Central Prairie	300	---	763	---
8e	N 44° 25.043′	W 123° 18.028′	Central Prairie	643	7302	643	1366
8f	N 44° 24.995′	W 123° 18.003′	Central Prairie	1271	11837	613	1068
8g	N 44° 25.028′	W 123° 17.950′	Central Prairie	623	3290	713	1146
9	---		Central Prairie	---	---	---	---
10a	N 44° 24.797′	W 123° 17.646′	Subunit 5	197	---	1311	---
10b	N 44° 24.744′	W 123° 17.636′	South Prairie	4988	5082	1112	1258
10c	N 44° 24.700′	W 123° 17.643′	South Prairie	---	306	---	103
10d	N 44° 24.671′	W 123° 17.651′	South Prairie	---	85	---	3
10e	N 44° 24.648′	W 123° 17.641′	South Prairie	---	1645	---	445
11a	N 44° 25.457′	W 123° 17.623′	Control Prairie	183	615	85	131
11b	N 44° 25.426′	W 123° 17.599′	Control Prairie	241	1650	149	198
11c	N 44° 25.450′	W 123° 17.560′	Control Prairie	386	1983	752	593
11d	N 44° 25.456′	W 123° 17.487′	Control Prairie	153	---	48	---
11e	N 44° 25.456′	W 123° 17.487′	Control Prairie	43	---	30	---
11f*	N 44° 25.426′	W 123° 17.560′	Control Prairie	498	4282	411	649
11g	N 44° 25.385′	W 123° 17.528′	Control Prairie	755	---	1608	--
11h*	N 44° 25.330′	W 123° 17.505′	Control Prairie	1315	6656	1106	1623
12	N 44° 25.470′	W 123° 17.716′	Fire-Break	121	---	45	--
13	N 44° 24.270′	W 123° 17.652′	South Prairie	12292	43389 $\pm$ 5152	4881	5215

* These areas experienced hand-removal of woody plants in the Winter of 2002.

Appendix G, continued.

Patch	Location	Management Subunit	# Flowering Plants (± 1 SE)		Area (m^2)	
			2002[a]	2003[b]	2002[c]	2003[c]
14a	N 44° 25.435′ W 123° 18.444′	North Prairie	1127	---	283	---
14b	N 44° 25.439′ W 123° 18.428′	North Prairie	105	---	36	---
14c	N 44° 25.458′ W 123° 18.427′	North Prairie	18	---	8	---
14d	N 44° 25.465′ W 123° 18.433′	North Prairie	29	---	6	---
15a	N 44° 25.390′ W 123° 18.286′	North Prairie	157	884	41	85
15b	N 44° 25.405′ W 123° 18.283′	North Prairie	224	---	99	---
15c	N 44° 25.378′ W 123° 18.277′	North Prairie	217	---	158	---
15d	N 44° 25.361′ W 123° 18.250′	North Prairie	1018	---	409	---
15e	N 44° 25.400′ W 123° 18.240′	North Prairie	33	---	14	---
16	N 44° 24.595′ W 123° 17.545′	Subunit 7	429	---	199	---
17	N 44° 24.530′ W 123° 17.575′	Subunit 7	858	---	277	---
18a	N 44° 24.308′ W 123° 17.612′	South Prairie	5630 ± 1013	29735 ± 3013	1759	2009
18b	---	South Prairie	192	521	51	170
19a	N 44° 25.469′ W 123° 18.368′	Subunit 7	124	---	62	---
19b	N 44° 25.457′ W 123° 18.373′	Subunit 7	200	---	99	---
20	N 44° 25.064′ W 123° 17.584′	Control Prairie	266	---	581	---