PRAIRIE FIRE AS A SELECTIVE AGENT:
SECOND-GENERATION RESPONSES
AND PLANT COMMUNITY SHIFTS

by

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ABSTRACT

Prairie fire as a selective agent: Second-generation responses and plant community shifts

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Prescribed fire has been used extensively as a prairie restoration tool, but its specific impacts on prairie plant communities are not always interpreted within a spatially or evolutionarily explicit framework. Prairie management is also influenced by a variety of social factors, including neighboring landowners, Native American culture, and military training. Here, we used experimental paired prescribed fire and fire-exclusion plots to examine the effects of realistic large-scale prescribed fire on prairie communities in western Washington State. As a case study of fire's potential selective effects, we collected seeds from a common prairie plant (*Lomatium utriculatum*) to examine second-generation effects of burning (in the previous year) on seed vigor. We also explore some of the interactions between prairie restoration and the social issues surrounding it. In addition to these social issues, this research also addresses education and involvement of an underserved audience: prisoners. Inmates had active roles in the care, tracking, and measurement of the *Lomatium utriculatum* seed germination and seedling growth. This partnership was made possible through the Sustainability in Prisons Project, and provided a valuable opportunity for science education and inmate contributions to ecological restoration. *Lomatium utriculatum* is an essential nectar source for the federally endangered Taylor's checkerspot butterfly (*Euphydryas editha taylori*), and it may serve as a surrogate for the effects of fire on endangered species recovery. Plant communities varied between burn treatments, and richness was increased in burned treatments. *Lomatium utriculatum* seeds collected from burned plots showed increased germination following the exposure of parent plants to fire, exhibiting a second-generation effect of burning the parent plant. Overall, this study demonstrates that prescribed fire may play an important role in altering prairie composition and may be a potential selective force driving plant micro-evolution in ecologically important species.

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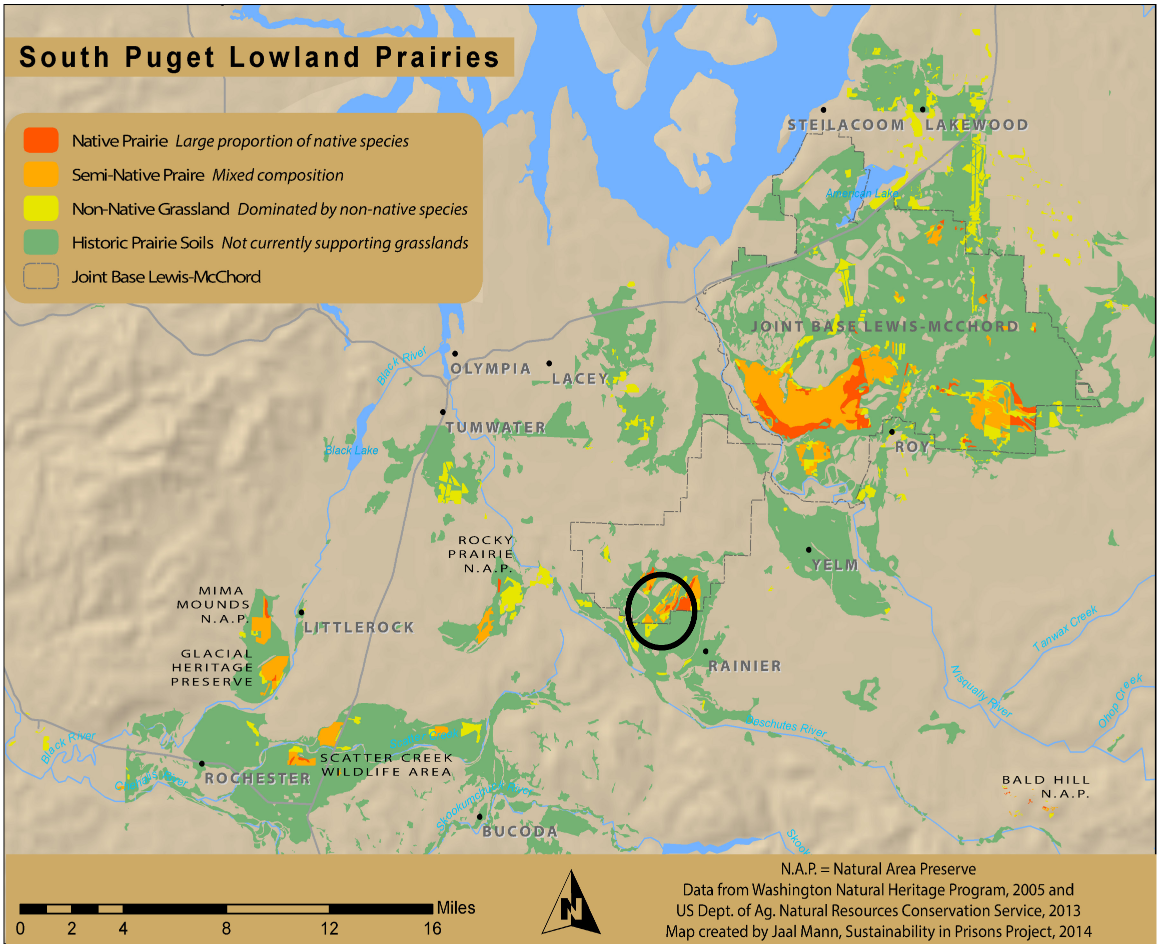
Chapter 1: Literature Review

Puget lowland prairies are greatly diminished from their past range, with native prairies occupying only 3% of historical grassland area (Crawford and Hall 1997). I will describe Puget lowland prairies, their associated restoration goals, common restoration practices, and the effectiveness of these practices. Next I will examine prescribed fire as a restoration tool and the ideal methods to implement it, with a focus on one of the largest remaining prairie remnants at Joint Base Lewis-McChord (JBLM). Plant community alterations and increased heterogeneity can be outcomes of some prescribed fires, and I include a discussion of the importance of heterogeneity for prairie habitats and the use of prescribed fire as a tool to increase native plant cover. Next I discuss fire as a selective agent and various plant adaptations to fire-dependent landscapes. I describe how fire can increase target species both directly through beneficial chemicals and heat, and indirectly through increased nutrients, thatch removal, and enhanced pollination. Finally, I discuss *Lomatium utriculatum*, a forb native to Puget lowland prairies, which serves as a case study in this thesis for the effects of fire on native target species.

PUGET LOWLAND PRAIRIES

Glacial prairies in North America were formed by warming and drying after glacial recession at the end of the last ice age (Pielou 1991). Gravelly deposition from melting glaciers created a soil that did not hold water well, and a warm climatic period around 10,000 years ago dried out the landscape and turned the newly formed forests into prairies free of woody plants (Pielou 1991). As the climate cooled slightly, trees began to encroach on the prairies, particularly in the maritime Pacific Northwest. Native

Americans in these areas, who prized the prairies for their edible crops and valuable hunting areas, began to implement prescribed burning to prevent tree encroachment and improve yields of staple food crops (White 1975). As white settlers arrived, burning was largely halted and most prairie landscapes were converted to agriculture and grazing. Today only small remnants of the original Pacific Northwest glacial prairies remain, and these small patches are managed intensively to keep them in as close to historical conditions as possible. Puget lowland prairies are anthropogenic ecosystems, and as such they require continual maintenance in order to preserve characteristics needed to support endemic and endangered species.



N.A.P. = Natural Area Preserve
Data from Washington Natural Heritage Program, 2005 and
US Dept. of Ag. Natural Resources Conservation Service, 2013
Map created by Jaal Mann, Sustainability in Prisons Project, 2014

Figure 1-1. This map shows the historic and present extent of Puget lowland prairies. Our study site location is circled.

Puget lowland prairies often share a common soil type, and they are highly suitable for various forms of land use. These prairies are largely located in the southern Puget lowland area, with the majority of remaining prairies on Joint Base Lewis-McChord (JBLM; Figure 1-1). JBLM's prairie soils are in the Spanaway series (Tveten and Fonda 1999), and are classified in Zulauf et al. (1979) as "somewhat excessively well drained"—often shallow soils with a coarse texture and very little or deep free water (Schoeneberger et al. 2002)—consisting of glacial outwash and volcanic ash. Mean annual precipitation is 89-114 cm, mean air temperature is 10.6˚C, slope is 0-6% (Zulauf and Washington Agricultural Experiment Station 1979), and urban development, gravel mining, and grazing are suggested by Zulauf et al. (1979) as the primary human uses for these soils.

Land use has been a major force in the destruction of native prairies, but ironically, military use of prairies on JBLM has led to the preservation of the largest remaining fragments. European settlers commonly used the flat, open landscapes as agricultural lands and later as sites for development. While some prairie species can coexist with grazing animals, tilling and fertilizing for agriculture or building over prairie removed large tracts of native species. On JBLM, home to the majority of remnant Puget lowland prairies, 40% of grassland areas remain "native prairie sites" (Crawford and Hall 1997). This large proportion of native prairie combined with frequent fires from military training exercises make JBLM a local hotspot for prairie restoration management and research. Federally endangered *Euphydryas editha taylori* W. H. Edwards (Taylor's checkerspot butterfly) are present in some areas along with other endangered or threatened prairie-obligate birds and mammals, including *Thomomys mazama* (Mazama pocket gopher), *Eremophila alpestris strigata* (streaked horned lark), and *Sciurus griseus* (western gray squirrel). While JBLM's prairies are some of the most intact, ongoing management and restoration are necessary to keep them open and with a large proportion of native cover.

PUGET LOWLAND PRAIRIE RESTORATION

Prairie restoration is a field fraught with moral dilemmas, and sometimes it can seem impossible to keep up with the challenges of invasive species and land use change. While in some cases restoration ecologists are able to facilitate functional assemblages resembling pre-European-settlement prairies, it is impossible to truly return prairies to their historical forms and completely eradicate the multitudes of established invasive species (Seastedt 1995, Agee 1996). In addition, recent research in restoration ecology argues that communities should not be restored to historic conditions but instead to communities that can withstand future climatic conditions (Millar et al. 2007, Thorpe 2012). Immense quantities of resources are expended to restore native prairies, but how do practitioners decide how much is enough in a field where complete success may be unattainable?

A variety of ecological and cultural goals must be considered when determining management plans. Dunwiddie and Bakker (2011) ranked several ecological and cultural prairie restoration goals, respectively, by most to least conservative and low to high ecological impact (Figure 1-2). This ranking serves to illustrate the broad and sometimes divergent interests of stakeholders in prairie management, as a way of finding areas of compromise that can satisfy as many parties as possible. Invasive species can be suppressed in many cases, but are rarely eradicated, and often warrant continued removal efforts (Dennehy et al. 2011). In this section, I will discuss some of the major challenges to Puget lowland prairie restoration, and how they are addressed. This will be followed by an examination of management techniques and their effectiveness at achieving various ecological goals.

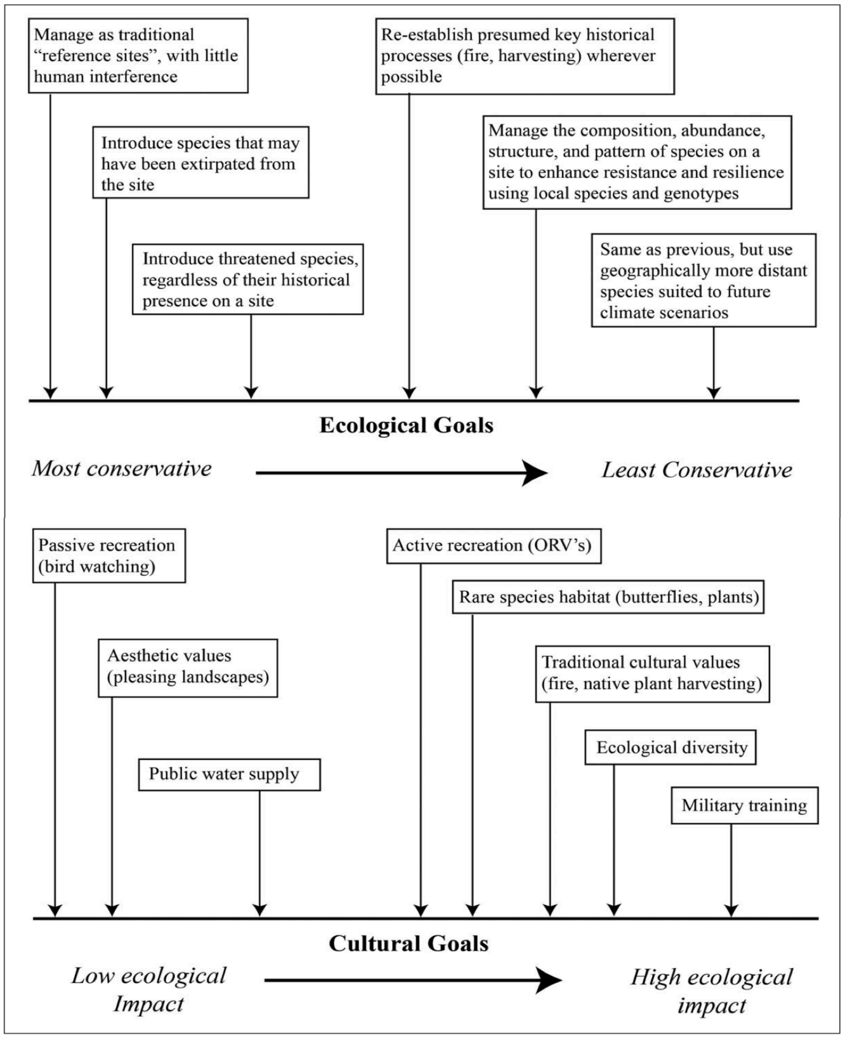


Figure 1-2. From Dunwiddie and Bakker (2011). Shows examples of ecological and cultural site management goals and their respective management intensity and ecological impacts.

Restoration of Puget lowland prairie faces the continuing challenges of habitat destruction, social reluctance to preserve prairies, and invasive species. Determining achievable goals, functional assemblages, and necessary maintenance are essential to the preservation of native prairie communities (Agee 1996, Dunwiddie and Bakker 2011, Dennehy et al. 2011). Tools that are commonly used by land managers include herbicides, mowing, carbon additions, and prescribed fire (Dennehy et al. 2011, Hamman et al. 2011, Mitchell and Bakker 2011). Prescribed fire has numerous benefits for prairie communities but can sometimes be met with social resistance due to health concerns such as smoke inhalation (Bowman and Johnston 2005; see Chapter 4 for a complete discussion of this issue). While social issues can usually be overcome with careful planning and timing, in some cases they can conflict with ideal prescribed burn timing for ecological restoration, which is still largely unknown. Invasive species are the threat that most land managers are directly concerned with, and many tactics are employed with the goal of reducing their populations.

Invasive species can alter overall prairie community types, converting them to shrubland or forest in the absence of fire (Collins and Gibson 1990). Invasive species include non-native *Cytisus scoparius* L. Link (Scotch broom) and native *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir). *Cytisus scoparius* is a nitrogen-fixing shrub that may also inhibit growth of some nearby species through soil alterations (Haubensak and Parker 2004). In the absence of fire, *P. menziesii* eventually colonizes prairies and converts them to forest (Hamman et al. 2011). There are some researchers, however, who argue that once a non-native species is well-established, impact assessments should be done to see if it is still a threat or if it can be a non-disruptive or functionally desirable species (Shackelford et al. 2013). Nevertheless, where invasive species do constitute a major threat to the overall composition of the ecosystem, a variety of restoration methods have been employed.

Herbicides, mowing, and manual removal are some of the main prairie restoration tools used in Puget lowland prairies, and carbon addition has potential for more widespread use. Herbicides are commonly used on prairies in the Pacific Northwest to remove target invasive species. While they can be highly effective, these herbicides can be toxic and caution must be exercised in choosing an herbicide to make sure to avoid excessive toxicity to people, non-target species, and wildlife (Dennehy et al. 2011). Mowing, pulling, and cutting of invasive vegetation can be successful if used at the right time of year and repetitively (Dennehy et al. 2011). Manual removal methods can be labor-intensive and repeated control is usually necessary. Carbon can be added to the soil in the form of activated carbon or sugar, in order to adsorb excess available nitrogen or increase microbial activity to use up soil nitrogen, respectively (Mitchell and Bakker 2011). Excess soil nitrogen can increase productivity, but favors invasive species, driving some rare native species towards extinction (Suding et al. 2005, Clark et al. 2007). Mitchell and Bakker (2011) found that by adding sugar to the soil they were able to reduce the growth of several invasive forbs, potentially giving native species a boost. To reach the various goals of native species enhancement, invasive biomass removal, and the creation of beneficial disturbances, prescribed fires can also be used in prairie restoration.

USES OF PRESCRIBED FIRE FOR RESTORATION

Joint Base Lewis-McChord (JBLM) is a 36,684 ha military reservation (JBLM 2012) that is home to the majority of remaining native Puget lowland prairie. Along with other management practices, they began implementing regular prescribed fires on 3,000 ha of native prairie and oak woodlands in 1978, using 3-5 year burn intervals (Tveten and Fonda 1999). Military operations have also been essential to maintaining native cover, and the largest native prairie remnant on the base is located in the artillery impact area, which has burned nearly every year for 50 years because of artillery fire (Tveten and Fonda 1999).

The optimal season and frequency of prescribed burns have been objects of much study (Pollak and Kan 1998, Tveten and Fonda 1999), but methods to address the questions have been varied. Experimental methods employed for this purpose include intensive burning of small plots (Tveten and Fonda 1999) and placement of plots within larger prescribed burns (Pollak and Kan 1998). I argue that placement of paired plots within larger prescribed burns is more effective at evaluating real-world prescribed fire effects because of the heterogeneity inherent in low-intensity grassland fires. Larger burns may also increase flowering plant growth over a large enough area to attract more insect pollinators (Van Nuland et al. 2013), an effect that would likely not be seen in small-area burn treatments. Questions persist about how to use prescribed fire most efficiently, but in most cases it is still superior to alternative restoration methods.

Fire has major benefits over herbicides and manual weed removal in both effectiveness and cost. It has a long history of use to increase the prevalence of desirable species and decrease invasive species abundance (Aldous 1934), and it can remove larger woody vegetation to help maintain the open structure required by many native prairie species (Hamman et al. 2011). Fire has historically been a common occurrence on Puget lowland prairies and therefore the growth of many native species has been enhanced by it (one of the major reasons for Native American burning; Boyd 1999). Fire has a relatively low cost per acre that decreases with increasing treatment scale (Bidwell et al. 2002, Hesseln and Berry 2008). Prescribed fires also provide a myriad of indirect benefits including elimination of excess nitrogen (Seastedt 1995) and improving germination in some species (Boyd 1999). While prescribed fire is an affordable tool with a number of benefits, the various effects of fires that occur at different return intervals or over different seasons are not well understood.

The ideal season for burning can vary depending on specific restoration goals, and Native American burning practices may be an effective guide for some prescribed fires today. However, changes in past management, habitat fragmentation, and invasive species may have altered the effects of fire, and understanding the influences of fire on modern native/non-native mixed plant communities is vital to restoration (Hamman et al. 2011, Sprenger and Dunwiddie 2011). Pollak and Kan (1998), studying a prairie in California, mention that fall prescribed burns can kill seedlings of both native and non-native plants indiscriminately, but late-spring burning does much less damage to plants that have already dispersed their seeds—as most of the native plants have. In contrast, in Washington State, Tveten and Fonda (1999) found that fall fires were more effective than spring fires at promoting native communities. In tallgrass prairies of the Midwest, Howe (1995) found that summer burns increased annual and biennial species, while many other species were affected in different ways on an individual basis by fire season. Tveten and Fonda (1999) also found that both annual burns and burning with intervals greater than 5 years increased invasive species populations, such as *Hypochaeris radicata* (hairy cats-ear). Sprenger and Dunwiddie (2011) used dendrochronology on *P. menziesii* trees on Waldron Island, WA, to construct a fire history for the area, concluding that the majority of fires were started by Native Americans who burned preferentially in the fall (Sprenger and Dunwiddie 2011). Some of these results can be conflicting, and it is clear that more research is needed locally on Puget lowland prairies with modern native/non-native mixed plant assemblages to determine ideal burn regimes.

Fire can have important effects on prairie soils by altering nitrogen content and changing plant behavior. When fire eliminates excess soil nitrogen, it simultaneously increases evaporation and plant growth (Seastedt 1995). Faced with increased growth concurrent with decreased water and nitrogen availability, plants are forced to allocate more resources to further developing their root systems, an adaptation which is important for building up soil organic matter (Seastedt 1995). The invasive species that often dominate in nitrogen-enriched soils tend to have smaller root systems than native species, thereby depositing less organic matter in the soil than the native plant communities and altering the composition of prairie soils (Seastedt 1995). Over time this alteration of soil organic matter content could lead to a soil environment for which native plant species are poorly adapted.

FIRE AND PLANT COMMUNITIES

Fire may play a formational role in prairie plant communities (Collins and Gibson 1990), but its role can be altered by soil fertility (Knops 2006). Knops (2006) found that in infertile prairies with low productivity fire had a minimal effect on plant community composition. Fire in many grassland ecosystems, however, has been found to alter species richness, diversity, and community interactions (Collins and Gibson 1990).

Ewing and Engle (1988) argue that fire can cause persistent alterations to native tallgrass prairie communities, and that fire intensity is important for predicting community change. A large part of the observed community change was due to the decrease in bunchgrass cover in high-intensity burned areas (Ewing and Engle 1988).

Regardless, Puget lowland prairies may interact differently with fire intensity than tallgrass prairies. Additionally, Howe (1995) argued that fire intensity may not be highly relevant to herbaceous plant cover because most intensities of fire manage to kill the majority of herbaceous aboveground vegetation. Because of the different ways that communities in specific regions can respond to fire intensity, local studies may be needed for reliable information. Other research topics such as community stability, however, may be more easily generalized.

Prairie communities can be inherently unstable, with directional change over time (gradual but continuous community change) recorded for tallgrass prairie communities (Collins 2000). Over 10 years of data from the Konza Prairie Long-Term Ecological Research site in Kansas show that native tallgrass prairie communities are not stable and are progressing directionally instead. Prairies that were burned annually were progressing more rapidly than occasionally burned prairies, and their plant communities varied significantly. A 4-year fire frequency was hypothesized to be the most stable as it most closely mimicked historical burn regimes, but instead the 20-year fire return interval produced a more stable plant community. Consumer communities (birds, grasshoppers, and small mammals) were also more stable under the 20-year fire return interval because although the species composition was changing, the three-dimensional vegetation structure remained fairly constant (Collins 2000).

Invasive species can change how fire interacts with plant communities, complicating restoration efforts. McGranahan et al. (2012) found that a high-moisture invasive grass required much greater wind speed to burn—often beyond safe levels—and that this fire resistance could lead to large unburned areas that increase the risk of tree encroachment. Prescribed fires with the goal of reducing invasive species populations ideally should occur after native species have released their seeds to the soil—where there is less heat from the fire—and while invasive species still have theirs in the understory canopy where they are more susceptible to heat (Ditomaso et al. 2006). This technique means that invasive late-season annual forbs are much easier to control with fire than winter annuals (Ditomaso et al. 2006). Unless burn timing is targeted for a certain species, fire can increase populations of invasive perennial forbs, often requiring other management techniques for their removal (Ditomaso et al. 2006). Ditomaso et al. (2006) advocate integrated approaches to managing recalcitrant invasive species with fire, using other control methods in conjunction with burning in order to avoid having to create unnaturally short fire intervals—which could in turn promote other invasive species.

TECHNIQUES FOR EVALUATING PRESCRIBED BURNING OUTCOMES

Previous studies of fire's effects on herbaceous species at JBLM have used small plots (1 m^2) as their experimental units (Tveten and Fonda 1999). This could put them at a disadvantage because the small plots can be completely burned, and any larger patterns of more natural and heterogeneous burning are lost. Designing studies with large burn exclusion plot pairs within a matrix of heterogeneous burning is a preferable method to capture the variability of large-scale prairie fires (Risser 1990). In addition, larger plot sizes, like Modified-Whittaker plots (Figure 1-3) may be more suitable for identifying rare species, analyzing diversity patterns, and identifying trends over time in long-term plots (Stohlgren et al. 1995). Pollak and Kan (1998) put their plot pairs within a larger burned area using transects within their plots and ¼ m^2 frames to estimate cover classes of species guilds. This design places plots within large and heterogeneous burns, but their method of collecting cover data within the plots may not provide the higher resolution results that would be possible with a Modified-Whittaker sampling method and identification of all species within the plots.

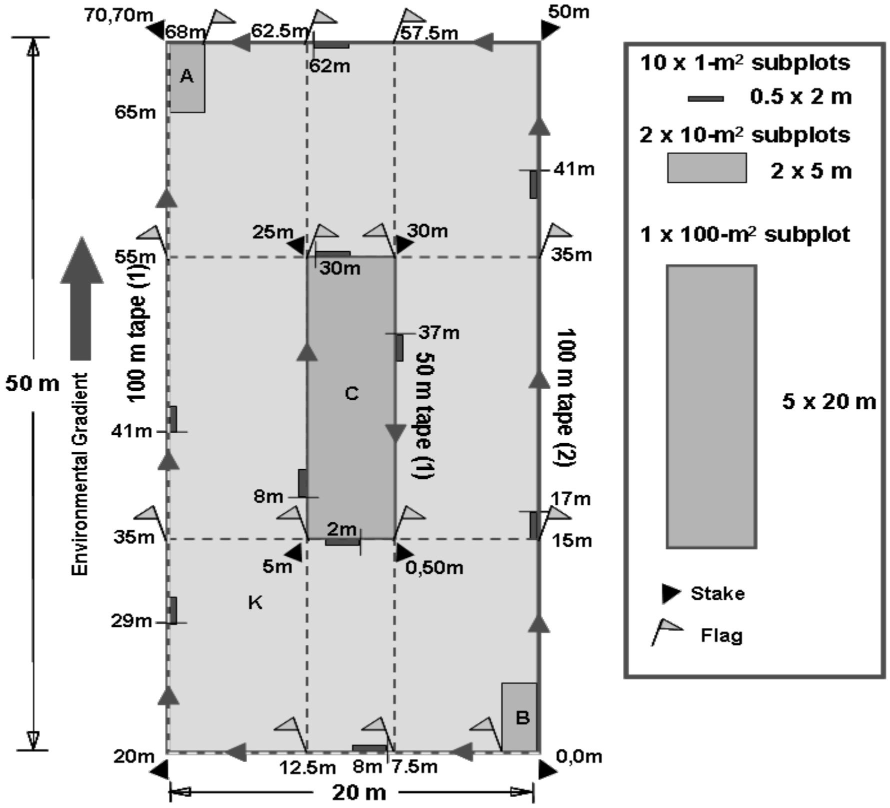


Figure 1-3. From National Institute of Invasive Species Science (n.d.). A typical Modified-Whittaker plot layout for measuring plant communities. Because of the three different sizes of subplots, Modified-Whittaker plots are well suited to quantify abundance and diversity of both rare and common species.

FIRE AND HETEROGENEITY

Using grazing by cattle and a variety of burn treatments Fuhlendorf et al. (2006) attempted to determine the importance of prairie heterogeneity for conservation. In order to accomplish this they used paired patches, burning one in spring and the other in late summer or fall. They also allowed cattle to graze freely in order to assess their preference of fire treatment. To compare this patchy burn structure to more traditionally managed pastures they also included samples in pastures that were all burned at once. Point counts were used in all of the pastures in order to determine bird abundance by species, and plant cover was recorded by functional group in each patch (Fuhlendorf et al. 2006). Tallgrass and bare ground heterogeneity were increased up to 40 times in the patchy treatments compared to traditional management (Fuhlendorf et al. 2006). They also found that annual fires in traditional treatments removed nearly all of the litter, while in the patchy experimental sections only portions were removed (Fuhlendorf et al. 2006). This uneven litter buildup could lead to even more heterogeneity and diversity in the future. Once they had determined optimal management techniques to foster heterogeneity, Fuhlendorf et al. (2006) sought to examine how heterogeneity can help meet conservation objectives.

In order to determine the value of increased heterogeneity Fuhlendorf et al. (2006) recorded bird abundance in their different treatments and found that bird species varied more in the patchy treatment. The buildup of litter in sections of the patchy treatment had a strong effect on bird communities, with some species avoiding areas with low litter cover (Fuhlendorf et al. 2006). Grazing animals were more likely to choose burned areas to graze, and grazed areas were less likely to burn. This feedback loop would make unburned areas increasingly likely to burn due to lower grazing, and burned areas less likely to burn due to higher grazing, leading to less uniform disturbance overall (Fuhlendorf et al. 2006).

Collins (1989) observed the effect of fire on plant community heterogeneity within micro-disturbance areas and found that in areas with disturbances fire had no effect on heterogeneity; however, in undisturbed areas fire decreased heterogeneity.

Collins and Gibson (1990) also found that annual burning decreased heterogeneity. In general, however, with longer fire return intervals the patchiness of burns due to variable fuels, moisture levels, and wind can cause an increase in the heterogeneity of plant communities (Risser 1990). Heterogeneity is especially important for prairie-associated organisms—including pollinators—which depend on diverse plant assemblages for nectar and larval hosts and could survive during fires in small unburned patches. Heterogeneity can also extend the flowering season and attract more diverse pollinator species, and that diversity could be vital if certain pollinators decline (Wratten et al. 2012).

FIRE AND POLLINATION

Insect pollination is an essential ecosystem service and most vegetables, nuts, fruits, and edible oil crops depend on it (Gallai et al. 2009). In Puget lowland prairies, habitat fragmentation can lead to pollinator-limitation in some species (Fazzino et al. 2011), but this effect may be ameliorated by fire's enhancement of pollination (Van Nuland et al. 2013).

A majority of the world's crops depend on insect pollination, providing a service valued at around $\$US_{2005}$ 200 billion (Gallai et al. 2009). With recent declines of *Apis mellifera* (honey bee) populations, native pollinators may become more important for food pollination (Campbell et al. 2007). Monitoring pollinator decline is difficult due to large annual variation in population sizes, and large-scale sampling efforts are required (Lebuhn et al. 2013). While determining precise estimates of pollinator decline may be cost prohibitive on Puget lowland prairies, we can hypothesize that as the prairies become increasingly fragmented, pollination may be decreased (Fazzino et al. 2011). Fazzino et al. (2011) found that *Balsamorhiza deltoidea* Nutt. (Puget balsamroot) was pollinator-limited on three prairie sites at JBLM (two of which were used in this study), but a follow-up study by Husby (2012) did not find pollinator limitation for *B. deltoidea* or *Lupinus albicaulis* (in both sites at JBLM used in this study as well as in a native plant nursery setting). This indicates that while pollinator limitation may be a concern in some situations, in different sites or years it may be less of a problem. Fire can lead to better pollination, largely because many plants increase their density after fire, creating larger nectar resources for pollinating insects (Van Nuland et al. 2013). On pollinator-limited prairies, using prescribed fire to create higher-density flower clumps that are capable of attracting more pollinators could be a viable management technique. Ground nesting bee communities can be increased more directly by fire, since they depend on bare ground (Potts et al. 2005, Campbell et al. 2007)—which tends to increase post-fire. Changes in pollen availability due to fire may even affect seed size as plants can allocate their resources differently based on pollination (Sakai 1995, Sakai and Sakai 1995, 1996).

SEED MORPHOLOGY AND VIABILITY

Changes in seed morphology following fire can be important for a variety of reasons. Seed size can have an effect on germination success, and seed size can vary in response to individual seed genetics, parent plant genetics, and environmental conditions (Tavşanoğlu and Serter Çatav 2012). Tavşanoğlu and Serter Çatav (2012) examined a Mediterranean species and found that larger seeds germinated at higher rates when exposed to heat stratification but saw no pattern in those not exposed to heat. This means that in some species seed size interacts with fire to increase germination. Larger seeds can emerge from deeper under the soil surface, allowing them more protection from excessive heat during high intensity fires (Bond et al. 1999), and this could potentially select for plants that produce larger seeds in areas with frequent, high-intensity fires. This relationship is somewhat complicated, however, by Hanley et al.'s (2003) finding that small seeds of some species may withstand higher temperatures than larger seeds. Therefore, while smaller seeds can only emerge from closer to the surface—where heat is more intense during a fire—they can tolerate higher heat than the deeper and larger seeds, meaning that fire intensity could play a crucial role in determining optimal seed sizes for survival.

Seed mass can vary greatly within species and even within individual plants (Thompson 1984). Moles et al. (2005) examined seed mass data from nearly thirteen thousand plant species and determined that differences in growth form—between herbs/grasses, shrubs, and trees/vines—explained more than three times as much variation in seed mass as any other variable. This supports the idea that while seed size can vary due to other factors, the most important drivers of seed size are based on the plant's growth form (Moles et al. 2005). Thompson and Pellmyr (1989) studied *Lomatium salmoniflorum* (salmonflower biscuitroot) and found that the majority of variation in seed mass (46%) was among umbels within plants in contrast to only 19% among plants. Thompson (1984) grew *Lomatium grayi* (Gray's biscuitroot) seedlings under controlled conditions and found that the heaviest seed on each plant weighed 4.7 times as much as the lightest seed. From his results, Thompson (1984) was able to assert that weighing large numbers of seeds and averaging to obtain seed mass does not adequately display the variance among seeds of the same individual plant (where 59.5% of seed mass variation occurs). Intra-plant seed mass variation in *Lomatium* may be too high for fire to have a discernible effect on it.

Sakai and Sakai (1995) observed that when plants of the same species growing in the same environment experienced higher resource availability they sometimes produced seeds of heavier weights rather than increased numbers, terming this the "fertilization efficiency hypothesis" (Sakai and Sakai 1996). Sakai (1995) refined this hypothesis to note that as resource availability increases plants allocate more resources to producing larger numbers of flowers (and hence seeds), as long as pollination increases in a linear relationship with the number of flowers. If pollen availability is low, plants will produce a smaller number of larger seeds because there is not enough pollen for additional seeds. While pollen availability did appear to influence seed size in *Lilium auratum* (gold band lily), Sakai (1995) noted that competition between flowers for resources also plays a role in determining seed size. In a wind-dispersed species like *Lomatium utriculatum*, seed size could be important for dispersal—in particular the weight-to-area ratio, or wing-loading (Augspurger and Franson 1993)—where lighter seeds and/or those with larger wing-to-mass ratios can be transported farther.

FIRE AND SEED DISPERSAL

Seed dispersal can play a role in how well a plant is able to colonize newly burned areas, therefore the distance that a wind-dispersed seed can travel may be an adaptation to fire. *Lomatium utriculatum* diaspores have winged achenes (or samara) that allow wind to transport the seeds some distance from the parent plant. The diaspore wing-loading determines in part the dispersal characteristics of a seed, where increased wing-loading decreases how far the seeds can travel (Augspurger and Franson 1993). Wing-loading may decrease (increasing dispersal distance) in plants that are exposed to more fire, just as *Pinus contorta* (lodgepole pine) wing-loading has decreased as it migrates north

(Pielou 1991). This occurs because the trees with seeds that can travel farthest disperse more quickly and tend to also have seeds that can travel far, eventually leading to seed dispersal distances increasing towards the extremes of the plants' range (Pielou 1991).

Fire may also be able to aid in the dispersal of *L. utriculatum* seeds as large-scale fires can cause powerful updrafts. This could lead to widespread long-distance seed dispersal increases during years with fire (Murray 1987). In *Taraxacum officinale* (common dandelion), Tackenberg et al. (2003) found that updraft is far more important than horizontal wind-speed at determining dispersal distance. The potential increase in the dispersal distance of *L. utriculatum* seeds when fire is present could be an important driver of the distribution and evolution of this species.

FIRE AS A SELECTIVE AGENT

Fire may be a driver of evolution in some systems, playing a fundamental role in the formation of grassland plant communities (Vogl 1974) and even causing plants to evolve flammability in order to eliminate their neighbors (Bond and Midgley 1995). Hoffmann and Franco (2003) found that savanna plants tend to allocate more resources to growing large roots, which may be an adaptation to fire to be able to resprout quickly (Bond and Keeley 2005). Even where woody plants do resprout they can lose years of growth and their competitive advantage over herbaceous species, whose aboveground biomass often dies back during winter and quickly resprouts in spring (Anderson 2006). Due to this seasonal adaptation to resprout quickly, after a disturbance herbaceous species have an advantage over woody species that take years to re-grow their more durable tissue and may not be able to re-establish under the canopy of their fast-growing herbaceous competitors.

Fire can act indirectly as a selective agent through alteration of the local environment following burning. “Postfire environments” can have altered soil conditions, be more vulnerable to drought, and have reduced surface moisture availability—all of which can select for species that are tolerant of these conditions (Keeley and Fotheringham 2000). Andrusyszyn (2013) measured soil surface and sub-surface temperatures in winter on two prairies at JBLM and found that areas burned four years prior were significantly cooler than those burned within the subsequent three years. In contrast, burns did not seem to affect soil moisture, possibly due to topographical variation (Andrusyszyn 2013). Since many native species (including *L. utriculatum*) germinate in the cold temperatures of early spring, higher soil temperatures may be important for seedling survival. While some plants are fire-adapted simply due to their tolerance of postfire conditions, others directly rely on fire for their survival.

Serotiny, heat scarification, and chemicals in smoke can be essential for many plants that rely on the direct effects of fire. Trees with serotinous seeds retain the seeds until a fire spreads through the area, when the heat releases the seeds and they can establish on bare ground with less competition. Scarification weakens the seed coat, speeding germination in seeds with longer dormancy periods. In some fire-adapted species, their seeds will lay dormant in the soil until a fire passes over, cracking open the seed coat and allowing the plant to germinate in a landscape free of larger competing plants. Chemicals in smoke can enhance or inhibit germination, and they can be distilled into “smoke water” used for the propagation of prairie plants (Yi-Fang Chou et al. 2012). Smoke water, derived of compounds from plant-based smoke infused in water, can enhance the germination of some species of prairie plants and inhibit others (Jefferson et al. 2008, Yi-Fang Chou et al. 2012). One possible reason for this enhancement effect could be plant growth regulators (or karrikins; Chiwocha et al. 2009) from smoke being stored in the parent plant's tissue. *Lomatium utriculatum* does not exhibit serotiny or heat scarification and has not been tested for smoke water response (likely because it has not proven refractory to standard cultivation without the addition of smoke water), but may show as yet undefined adaptations to fire.

Both parent plant genetics and "environmentally induced parental effects" can alter germination and seedling vigor (Schmid and Dolt 1994, Lacey 1998). Lacey (1998) notes that stimulus to the parent plant leading to an effect on offspring (second-generation effect) can be brief and occur long before the affected seeds are produced. In the case of fire this means that the parent plant could be burned years before and still pass the effects of this burning to its offspring. Lacey (1998) defines parental effects in order to clarify the difference between these and genetic or direct environmental effects:

> A parental effect is any parental influence on offspring phenotype that cannot be attributed solely to offspring genotype, to the direct action of the nonparental components of the offspring's environment, or to their combination.

In an area where a parent plant was burned, effects on its seeds, if germinated ex situ, could certainly fall under this definition of a parental effect.

Donohue (2009) takes maternal effects beyond just germination and discusses how they can also affect "overall phenology, projected population performance and even the genetic basis of life stage transitions." Flowering phenology, a maternal effect, can vastly alter the life cycle of some species, where seeds of the same plant germinating in fall exhibit a winter annual life history while those germinating in spring follow a biennial life history (Donohue 2009). Donohue (2009) specifies what is considered a maternal effect, including effects based on direct genetic inheritance, endosperm, seed coat, maternal nutrients and other provisions, and release of seeds into a particular environment (i.e. in a particular season or following an event such as fire). It can be a challenge to determine whether observed parental effects are maternal or based on endosperm (two-thirds from the mother plant) or embryo (one-half from the mother plant; Donohue 2009). Building a stronger understanding of parental effects on germination and phenology is important to understand plant responses to both natural and artificial selection (Donohue 2009).

LOMATIUM UTRICULATUM IMPORTANCE

Lomatium utriculatum (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose is found west of the Cascade Mountains from British Columbia to California. It is a perennial forb on Puget lowland prairies and a primary nectar source for two endangered butterflies: *Euphydryas editha taylori* W. H. Edwards (Taylor's checkerspot butterfly) in the Puget lowland area (Shepard 2000), and *Callophrys mossii bayensis* R. M. Brown (San Bruno elfin butterfly) in California (Arnold 1983). Puget lowland prairies are home to several reintroduced populations of *E. e. taylori*, and *L. utriculatum* has been planted in reintroduction sites for *E. e. taylori* at JBLM (Figure 1-4).

Figure 1-4. Taylor's checkerspot butterfly (*Euphydryas editha taylori*) resting on *Lomatium utriculatum*. Photo courtesy of Rod Gilbert, Joint Base Lewis-McChord

Lomatium utriculatum serves here as a case study to examine changes in seed size, viability, and germination following prescribed fire. Its seeds have not been shown to be adapted to direct exposure to fire, but the parent plants are perennial and can survive regular burns, and tolerance or adaptations to the post-fire environment may be passed along to their offspring. In this way, *Lomatium utriculatum* is representative of other fire-adapted species with seeds that do not depend on direct exposure to fire. *Lomatium utriculatum* has a thickened taproot, compound umbels with many yellow flowers (Hitchcock and Cronquist 1973) and seeds that are wind-dispersed with varying samara size. Seed size may be influenced by pollinator availability, following the "fertilization efficiency hypothesis" of diminishing returns from increasing numbers of seeds (Sakai 1995, Sakai and Sakai 1996).

While *Lomatium* plants can support endangered species, there are also several federally endangered *Lomatium* species, including *Lomatium cookii* J.S. Kagan in Oregon (Cook's lomatium; USDA NRCS National Plant Data Team n.d., Pendergrass 2010) and *Lomatium bradshawii* (Rose) Math. & Const. in Oregon and Washington (Bradshaw's lomatium; Pendergrass et al. 1999, Kaye et al. 2001). Information about *L. utriculatum*'s response to fire may be applicable to these other species, and its relative abundance makes it a good surrogate for studying these more protected species.

CONCLUSION

While prairie restoration is an active topic of continued discussion, there is still much left to learn about the effects of various restoration practices. Prescribed fire is a commonly used restoration tactic, but further study is needed to identify ideal seasonality and return intervals in many ecological systems. Even if an ideal season and interval for burning is determined, deviations from this schedule frequently occur for logistical reasons, including local landowner opposition and weather. Depending on the seasonality, intensity, and return interval, prescribed fire may result in a more diverse and heterogeneous plant community.

Burning alters pollination and soil nitrogen, with results that are not well understood. If fire increases both nutrient availability and pollination (Van Nuland et al. 2013), then based on Sakai's (1995) "fertilization efficiency hypothesis" the increase in resource availability and pollen abundance may lead plants to create more numerous seeds rather than larger seeds. This is due to the higher abundance of pollen and thus decreased costs of pollen capture, leading plants to invest resources into more numerous smaller seeds since there is sufficient pollen to make this an effective strategy (Sakai

1995). Increased soil nutrient availability may also increase pollination if nectar plants are more abundant or have more numerous flowers.

Since some fire-adapted species have increased germination and/or sprouting capabilities after fires (Agee 1996), and *L. utriculatum* is native to prairies with frequent burn histories, *L. utriculatum* seeds may have higher germination and vigor if the parent plant was burned, through environmentally induced parent effects (Lacey 1998). This could be due to improved pollination, nutrient availability, or chemical compounds released by the fire. Knowing the specific mechanisms by which the germination and vigor of essential prairie species can be increased would allow for targeted management to more easily achieve conservation objectives.

Prescribed fire may be a highly effective tool to alter plant communities, reduce non-native plants, and increase fitness of key species—which are all important restoration goals. Its continued use and study as a restoration tool is essential to the survival of many endangered prairie species that are adapted to and depend on fire. Fire has maintained Puget lowland prairies for thousands of years, and today it remains a cost-effective restoration tool with a myriad of indirect benefits that we are only beginning to understand.

Chapter 2: Manuscript formatted for the journal Ecology

ABSTRACT

Prescribed fire has been used extensively as a prairie restoration tool, but its specific impacts on prairie plant communities are not always interpreted within a spatially or evolutionarily explicit framework. For example, plant community responses to fire can be related to both treatment scale and the selective impact of fire on plant phenotypes, but neither factor is accounted for in most plant community studies. Here, we used experimental paired prescribed fire and fire-exclusion plots to examine the effects of realistic large-scale prescribed fire on prairie communities in western Washington State. As a case study of fire's potential selective effects, we collected seeds from a common prairie plant (*Lomatium utriculatum*) to examine second-generation effects of burning (in the previous year) on seed vigor. *Lomatium utriculatum* seeds were germinated and grown in cooperation with the Sustainability in Prisons Project, where inmates had active roles in the care, tracking, and measurement of the plants, providing a valuable opportunity for science education and inmate contributions to ecological restoration. *Lomatium utriculatum* is an essential nectar source for the federally endangered Taylor's checkerspot butterfly (*Euphydryas editha taylori*) and may serve as a surrogate for the effects of fire on endangered species recovery. Prescribed fire altered plant communities, increased species richness, and enhanced germination of *L. utriculatum*. *Lomatium utriculatum* seeds collected from burned plots had increased germination following the exposure of parent plants to fire, exhibiting a second-generation effect of burning the parent plant. Overall, this study demonstrates that prescribed fire could play an important role in altering prairie composition and may be a potential selective force driving plant micro-evolution in ecologically important species.

INTRODUCTION

Many grassland ecosystems around the world are subjected to regular burning and the plants that inhabit these areas have become adapted to and thrive under the frequent disturbance of fire. As plants in these environments have been burned regularly for millennia, fire has played a fundamental role in shaping the communities that exist today (Vogl 1974). In response to fire, plants can evolve flammability to eliminate their neighbors (Bond and Midgley 1995), grow proportionately large roots in order to resprout quickly (Bond and Keeley 2005), and become more well-suited to "postfire environments" that often have reduced moisture availability and altered edaphic factors (Keeley and Fotheringham 2000). Some species thrive under regular burning, but are more responsive to the indirect effects of fire. These plants may be able to utilize resources in a postfire environment effectively, resprout quickly to outcompete neighbors, or produce offspring that are more viable when the parent plant is exposed to fire. One such species is *Lomatium utriculatum* (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose (spring gold).

Lomatium utriculatum is a native perennial forb common to Puget lowland prairies and an important nectar source for the federally endangered *Euphydryas editha taylori* W. H. Edwards (Taylor's checkerspot butterfly) as well as other important pollinators (Shepard 2000). It is used here as a case study to identify patterns in seed size and viability following fire, through the indirect second-generation fitness effects that burning a parent plant can have on offspring.

Prescribed fire was commonly used by Native Americans on Puget lowland prairies (Boyd 1999) to enhance native plant species and create open hunting ranges, and it is still widely used in prairie restoration today. It is a particularly effective tool at large scales, where it becomes far more affordable per acre than other treatment methods (herbicide or manual weed removal; Bidwell et al. 2002, Hesseln and Berry 2008). Along with maintaining the open structure that many native species require (Hamman et al. 2011), burning can increase the germination rates of some native species (Boyd 1999) and remove excess nitrogen that may otherwise give invasive species a competitive edge (Seastedt 1995).

Fire can alter plant competition and success in many ways. It can be a driver of plant evolution (Bond and Midgley 1995), affect soil characteristics (Bond and Keeley 2005), and even alter soil surface temperatures for years afterwards (Andrusyszyn 2013).

Fire can help disperse seeds with powerful updrafts (Murray 1987, Tackenberg et al. 2003) and enhance seed germination directly through heat and/or chemical cues (Keeley and Fotheringham 2000, Yi-Fang Chou et al. 2012). In some species, germination may be increased indirectly due to a higher abundance of pollinators (Van Nuland et al. 2013) and/or healthier parent plants following fire.

We hypothesized that *L. utriculatum* seeds from burned plots would be smaller than those from unburned plots, based on the "fertilization efficiency hypothesis" (Sakai 1995, Sakai and Sakai 1995, 1996) due to increased nutrient and pollination availability (Van Nuland et al. 2013). Where pollination availability increases along with nutrient availability, plants produce a larger number of smaller seeds, because pollination does not limit the potential viability of the seeds (see Sakai 1995). These seeds were also expected to have higher viability (because of increased parent plant fitness in postfire environments) and therefore higher seed density due to a higher proportion of fully developed seeds. Higher viability seeds from burned plots were expected to have more complete and rapid germination.

We expected that prescribed burns would also alter overall plant communities (Ewing and Engle 1988, Collins and Gibson 1990), enhancing the ability of prairies to meet wildlife habitat and other restoration goals (Hamman et al. 2011). We predicted that plant diversity and richness would increase after fire, since removing species that tend to dominate an area would allow for several new species to take hold, and that evenness would increase due to the potential removal of dominant non-native species. Heterogeneity may be increased after fire because of the patchy burn pattern that occurs in prairie fires with low fuel loads (Risser 1990, Fuhlendorf et al. 2006). We also expected to find a higher native/non-native ratio in burned plots, which is a major goal of prescribed fire used for restoration. We anticipated differences in species presence/absence between treatments, as some species may be present in unburned plots that would not survive in burned plots or vice versa. We also hypothesized that overall community composition would vary by burn treatment and by year: by burn treatment due to increased heterogeneity and possible decreases in less fire-adapted species, and by year because of different weather conditions between the two years.

METHODS

STUDY AREA

Puget lowland prairies are a rare and greatly diminished ecosystem, with "intact prairies" extant on only 3% of historical grassland areas (Crawford and Hall 1997). As an anthropogenic system, Puget lowland prairies require continual maintenance by humans, usually in the form of prescribed burning. Prescribed fire has been increasingly used as a restoration tool for Puget lowland prairies (Hamman et al. 2011), but monitoring and evaluation of restoration efforts in these ecosystems have been lacking. This study attempts to quantify some of the community and individual-species changes instigated by prescribed fire.

Our study took place in remnant Puget lowland prairies southeast of Olympia, Washington, on Joint Base Lewis-McChord (JBLM), home to some of the largest and most native remaining prairie habitats in Washington State. This 36,684 ha military reservation (JBLM 2012) has been subject to regular burns resulting from military activities and widespread prescribed fires on 3,000 ha of prairie and oak woodlands since 1978 (Tveten and Fonda 1999). These prairies have soils in the Spanaway series (Tveten and Fonda 1999) that are well-drained and made up of glacial outwash and volcanic ash (Zulauf and Washington Agricultural Experiment Station 1979). They receive mean precipitation of 89-114 cm, air temperatures of 10.6˚C, and have average slopes of 0-6% (Zulauf and Washington Agricultural Experiment Station 1979). The prairies of interest in this study are located at approximately 46.92˚N, 122.73˚W.

These prairie sites host a wide variety of native plants and pollinator insects, and are burned for ecological preservation. Invasive species are common, including some such as *Cytisus scoparius* (Scotch broom) that alter the habitat type from grassland to shrubland. Another species of concern on the prairies is *Pseudotsuga menziesii* (Douglas-fir); in the absence of regular fires it will gradually turn prairies in this region into forests.

EXPERIMENTAL DESIGN

In order to observe patterns in plant community structure between burned and unburned prairie sites at a relatively large and heterogeneous scale, 11 plot pairs (burned and unburned; Figure 2-1) were measured for two consecutive years. The plots in this study are located within a mosaic of burn histories at Johnson and Upper Weir prairies. A Modified-Whittaker (20 m x 50 m) nested subplot design (Stohlgren et al. 1995) was used in order to account for rare-but-present species and analyze species-area curves. Plot pairs were established randomly in 2010 using Arcmap 9.2 (ESRI 2009) and designed to have similar species composition and communities at the outset of the study. Large-scale prescribed burns were completed in 2011 and 2012, with the unburned plots being excluded from fire by the use of mowed fireguards in buffers around the plots. The corners of plots were permanently marked, and GPS coordinates were taken at each corner with a Trimble GeoXT and TerraSync software, using point-averaging for 200 readings per point. All plots were burned in 2011, but only three sets of plots were burned in 2012 (Figure 2-1). The three plots that were burned in both years were used to examine the second-generation effects that burning a parent plant can have on its offspring.

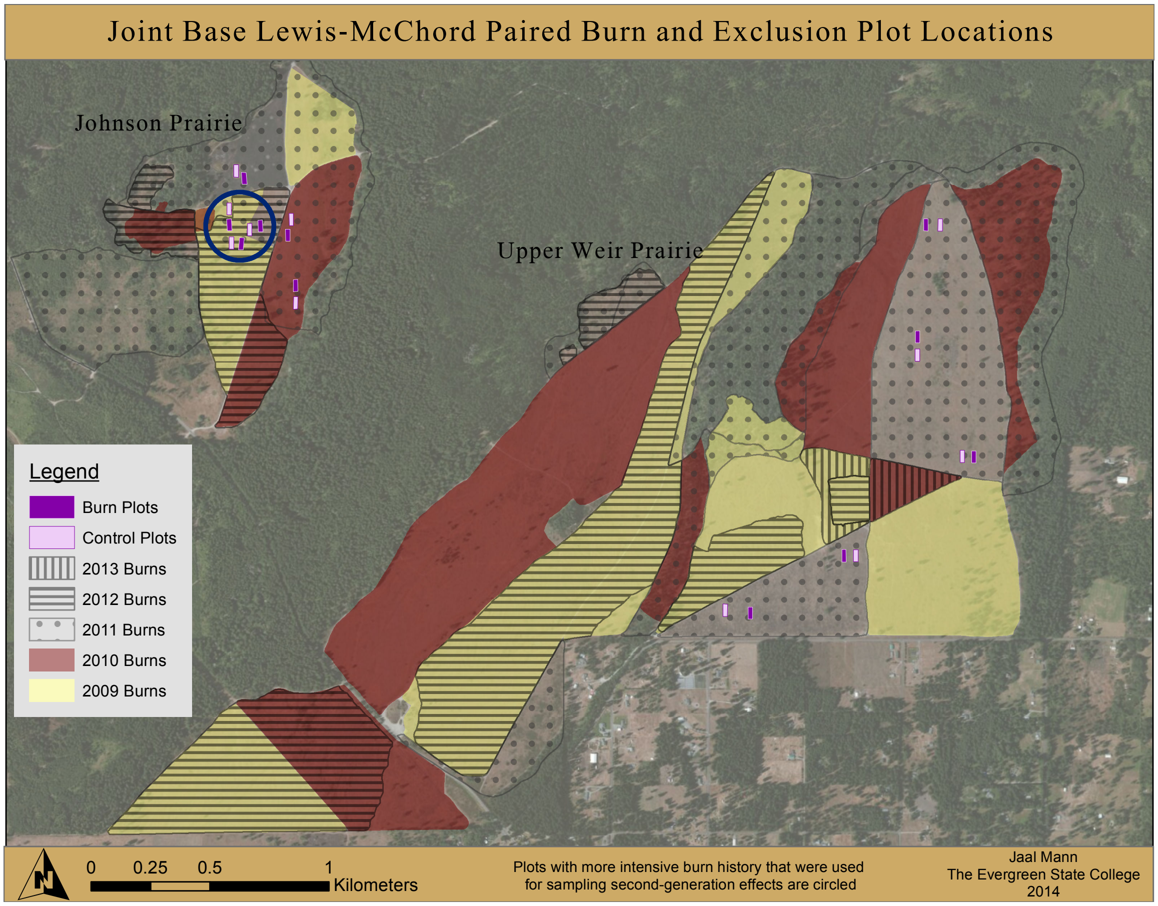


Figure 2-1. Map showing the paired plot locations on Johnson and Upper Weir prairies. The three plots used for the *Lomatium utriculatum* sampling are circled. These were the only plots that had been burned in both 2011 and 2012, and therefore were hypothesized to show more pronounced effects of burning. Only a small patch of prairie was burned in 2013, and none of the plots were within it.

PLANT COMMUNITY RESPONSE TO PRESCRIBED FIRE

Within each Modified-Whittaker plot, 1 m^2 subplots were measured using a 0.5 m x 2 m sampling frame, recording species presence and estimating percent cover. Due to time constraints in 2012, only four 1 m^2 subplots were measured for each of the 22 plots and the 10 m^2 subplots were not measured; in 2013 all ten 1 m^2 subplots (the typical number for Modified-Whittaker plots) were measured for each plot along with the two 10 m^2 subplots. In both years species presence/absence was determined for the 10 m x 20 m subplots and the entire 20 m x 50 m plots at all 22 locations.

SECOND-GENERATION EFFECTS OF PRESCRIBED FIRE

Lomatium utriculatum seeds were collected in three burned and three unburned plots to analyze how a fire-adapted species may display second-generation effects of burn treatments. These collections focused on the three pairs of plots with the most recent burn history (burned in 2011 and 2012). Plants were identified for collection by walking in a random direction (determined by the second hand of a watch) and stopping at the first *L. utriculatum* encountered. All of the seeds possible were collected when multiple stalks were coming from the same plant. The seeds were then dried at room temperature for a month and stored dry for another 2.5 months. After the dry storage period, the seeds were weighed and measured to calculate mass per seed and approximate seed density (mass/length). Seed mass and length were calculated for a subset of five seeds from each plant. Up to 20 seeds from each plant were then placed into cold and moist dark stratification for 64 days at 3˚C in a germination chamber (Hoffman Manufacturing, Inc.) followed by one month of 15˚/7˚C 12-hour germination cycles with light during the 15˚C "day" cycle. Time-to-germination—functionally defined as completion of germination, as in McNair et al. (2012)—was recorded for each seed and after germination each seed was planted into an individual cone-tainer (Bergeron and Leach 1975). Germination began at approximately 45 days, therefore the majority of the seeds had already been sown by the time germination temperature cycles began and germination rates did not seem to be affected by the changes in temperature and lighting.

Germination testing took place at a Center for Natural Lands Management nursery through the native prairie plant production program run by the Sustainability in Prisons Project (www.sustainabilityinprisons.org). Several inmates had the opportunity to be involved in germination counting, monitoring of the seedlings, and prairie plant education programs (LeRoy et al. 2012). Seedling leaf area was measured after approximately three months of growth by photographing a randomly selected subset of 68 plants and calculating leaf area using ImageJ 1.48v (Wayne Rasband, National Institutes of Health).

STATISTICAL ANALYSIS

Lomatium utriculatum seed mass and density were compared by burn treatment to observe any changes to the parent plant's seed characteristics due to past fires. Statistical analyses were carried out using JMP 10.0 (SAS Institute 2012) with a t-test for seed mass, and resampling t-tests using the resampling stats 4.0 add-in (Resampling Stats, Inc.) for Microsoft Excel 2010, with 10,000 iterations for intra-plant seed mass ratios, seed density, and seed number, which were not normally distributed. Survival analysis, or time-to-event analysis, was run in JMP to analyze time-to-germination with a log-rank test to compare curves between treatments. This analysis was used because the germination data were "right-censored" since ungerminated seeds, which could theoretically have germinated at some later date, remained at the end of the experiment (McNair et al. 2012). To compare seedling leaf area between treatments, a resampling t-test with 10,000 iterations was used in the resampling stats add-in.

We hypothesized that prescribed burns would increase species diversity and richness. Species richness was determined by burn treatment in PC-ORD 6.0 (McCune and Mefford, 2005) and analyzed using the resampling stats add-in with 10,000 iterations. This analysis was carried out with combined data from both the 2012 and 2013 1,000 m^2 species presence/absence (P/A) plots. Richness, evenness, and Shannon's and Simpson's diversity indices were calculated for both 2012 and 2013 separately for the 1 m^2 plots using PC-ORD. These diversity metrics were analyzed using resampling due to non-normality for Simpson's diversity index and evenness in both years, and for Shannon's diversity index in 2013. T-tests were used in JMP for richness in 2012 and 2013, and Shannon's diversity index in 2012. Species-area curves were compared for each year to examine the differences in species accumulation between treatments (Clay and Holah 1999, McCune and Grace 2002). Native/non-native ratios between burn treatments were analyzed for 2012 and 2013 combined using the resampling stats add-in with 10,000 iterations due to non-normality.

To examine community variation due to burn treatment, we collected species cover data in 1 m^2 plots and P/A data in 1,000 m^2 plots. Data from these plots were analyzed separately for each year (2012 and 2013). For our 1,000 m^2 species P/A plots, Multiresponse Permutation Procedures (MRPP) and Nonmetric Multidimensional Scaling (NMS) ordinations were run in PC-ORD. For analysis of our 1 m^2 species cover plots, NMS ordinations were run in PC-ORD. All NMS ordinations used 3 dimensions, 1,000 runs, and 500 maximum iterations. Overall community change (plant cover by species) was compared for each plot by burn treatment, with separate analyses for each year. These analyses used MRPPs in PC-ORD to identify any changes in the structure of plant cover in the community due to burn history. Data from the two collection years (2012 and 2013) were compared separately by burn treatment using MRPPs in PC-ORD to examine succession following a burn and ensure that year of data collection was not a confounding factor due to variable weather between the years. Indicator Species Analysis (Dufrene and Legendre 1997) was run in PC-ORD to identify species that were more often present in certain burn treatments.

RESULTS

SECOND-GENERATION EFFECTS OF PRESCRIBED FIRE

Lomatium utriculatum time-to-germination varied significantly between burn treatments, with seeds from burned parent plants germinating at higher rates (Figure 2-2; P<0.0001).

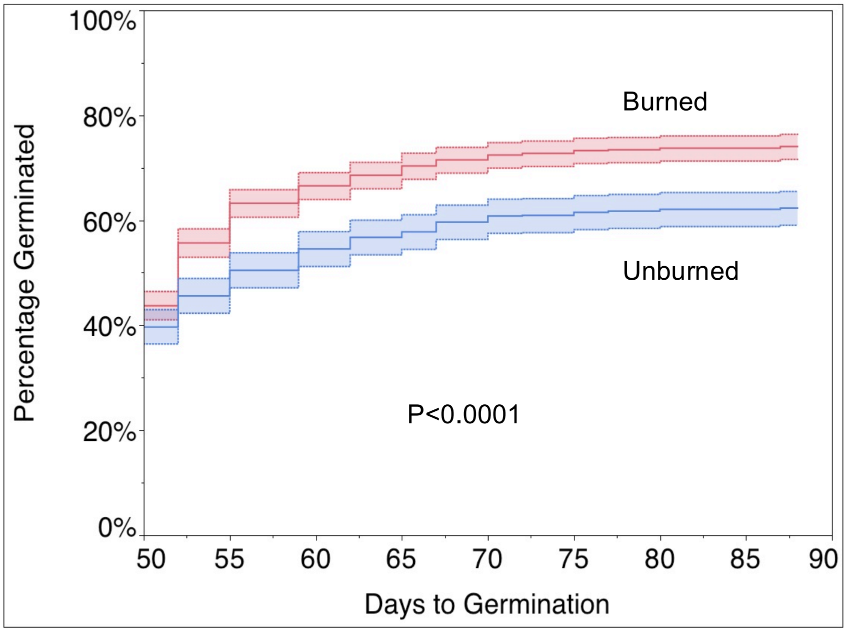


Figure 2-2: Time-to-event analysis of seed germination data by days since seed imbibing. Germination rates varied between burn treatments, with seeds from burned parent plants germinating earlier and more successfully (log-rank P<0.0001).

Germination of seeds from burned parent plants also occurred earlier and to an overall higher percentage of the total seeds by the end of the experimental period.

Intra-plant seed mass ratios, seed density (g/mm), and seed number showed no significant effect of burn treatment (intra-plant seed mass ratio P=0.5487; density P=0.3701; seed number P=0.4309). Mass per seed also did not vary significantly by burn treatment (DF=119, T=0.8820, P=0.3795). Seeds varied greatly in mass within plants, with the largest seed nearly 16 times the mass of the smallest for one individual.

Seedling leaf area did not vary between treatments (P=0.2275), between plots (P=0.8429), or by germination date (P=0.4333). While some seedlings did not survive, those that did and were large enough to measure photographically varied in size nearly five hundredfold (2.6 mm^2 to 1,261.2 mm^2).

PLANT COMMUNITY RESPONSE TO PRESCRIBED FIRE

1000 m^2 Presence/Absence Scale

Richness was significantly higher (increased nearly 19%) in burned treatments for the 1000 m^2 P/A plots (Figure 2-3; P=0.0004).

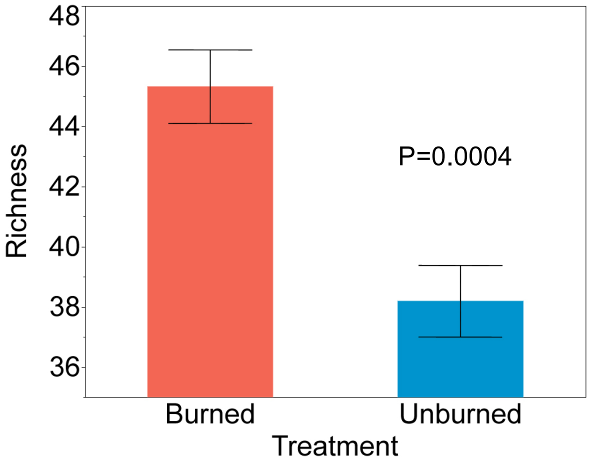


Figure 2-3. Species richness was nearly 19% higher in burned plots (P=0.0004), indicating that species had been lost from unburned plots after only 1-2 years of burn exclusion. Data are from the 2012 and 2013 1000 m^2 presence/absence plots combined and bars represent means ± standard errors.

Several indicator species were identified for each treatment in both years, mostly indicating for burned treatments. In 2012, four significant indicator species were identified, all indicative of burned plots. Of these, only one was native (*Zigadenus venenosus* var. *venenosus*). In 2013, eight burned indicator species and two unburned indicator species were present. All five non-native indicators were for burned treatments, while three natives indicated for burned and two for unburned treatments (Table 2-1).

Indicator Species Analysis

Year	Species	Family	Treatment	P-value	Native?
2012	*Zigadenus venenosus* var. *venenosus*	*Liliaceae*	Burned	0.0072	Yes
	Medicago sp.	*Leguminosae*	Burned	0.0384	No
	Parentucellia viscosa	*Scrophulariaceae*	Burned	0.0316	No
	Vicia sativa var. *angustifolia*	*Leguminosae*	Burned	0.0216	No
2013	*Apocynum androsaemifolium*	*Apocynaceae*	Unburned	0.0414	Yes
	Lupinus albicaulis	*Leguminosae*	Unburned	0.013	Yes
	Camassia quamash	*Liliaceae*	Burned	0.0002	Yes
	Delphinium menziesii	*Ranunculaceae*	Burned	0.0282	Yes
	Lotus micranthus	*Leguminosae*	Burned	0.0068	Yes
	Aira sp.	*Poaceae*	Burned	0.0002	No
	Medicago sp.	*Leguminosae*	Burned	0.0398	No
	Parentucellia viscosa	*Scrophulariaceae*	Burned	0.0288	No
	Rumex acetosella	*Polygonaceae*	Burned	0.0026	No
	Teesdalia nudicaulis	*Brassicaceae*	Burned	0.0290	No

Table 2-1. Indicator Species Analysis (Dufrene and Legendre 1997) determined that several species of plants were indicative of the various burned and unburned treatments. These included a number of native and non-native species.

Multiple Spatial Scales

In order to examine our hypothesis that burned plots would be more diverse at all scales than unburned plots, we created species-area curves for both treatments (Figure 2-4).

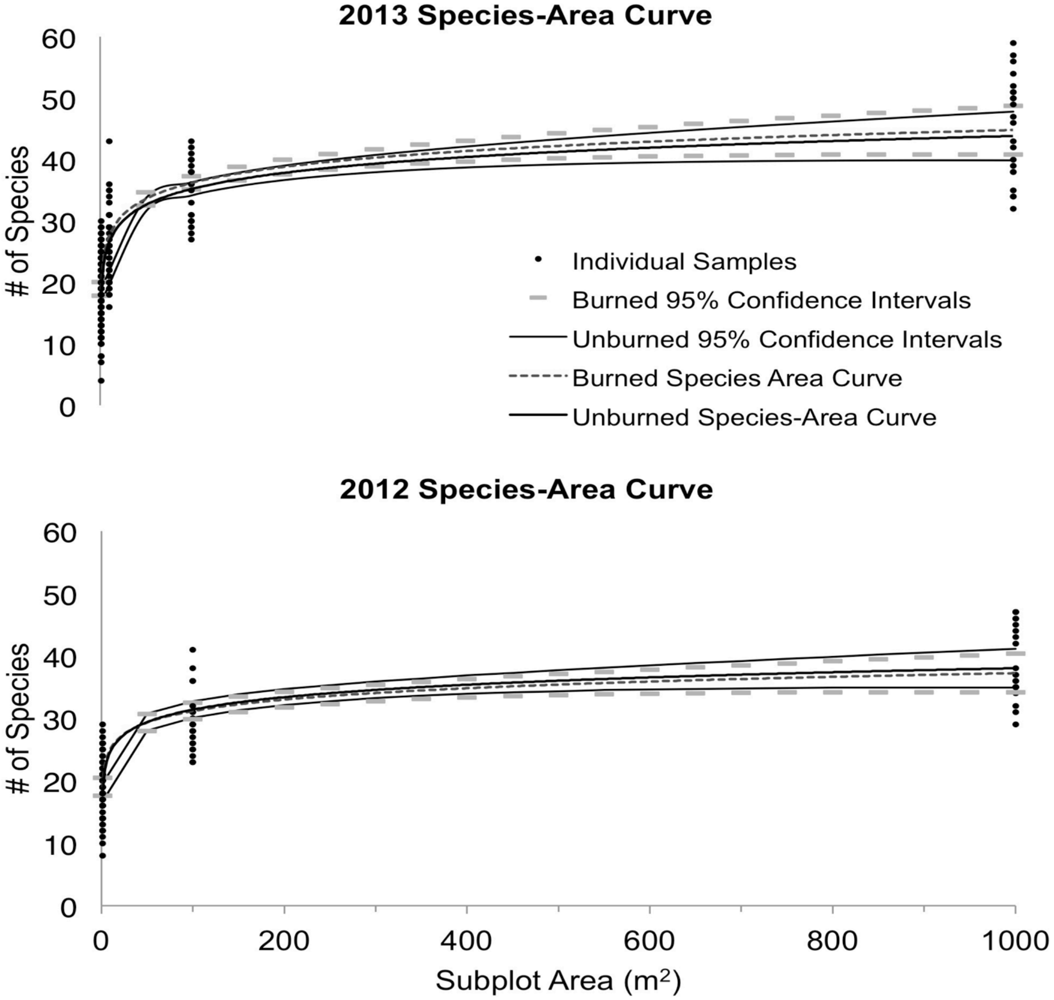


Figure 2-4. Species-area curves for 2012 and 2013, with 95% confidence intervals illustrating the lack of significant differences between burned and unburned plots in species accumulation.

The confidence intervals for these curves overlapped heavily, indicating that a pattern in species diversity at various scales was too subtle to determine using this method (although richness did vary significantly at the 1000 m^2 plot size). Species-area curves for both years appear to approach asymptotes, demonstrating that our largest plot size (1000 m^2) is representative of the overall number of species in the community.

1 m^2 Species Cover Scale

Native/non-native ratio was analyzed for both 2012 and 2013 combined as a way to determine if prescribed fire is increasing the proportion of native cover. No significant difference was found in native/non-native ratio between the treatments (P=0.1172). In both 2012 and 2013, our hypothesis that burned and unburned communities would vary based on cover was affirmed (Figure 2-5; 2012: A=0.0088, P=0.0188; 2013: A=0.0090, P=0.0002). For the 2012 plots, burn treatments explained 22.589% of the variation between burned and unburned communities; in 2013, burning explained 19.244% of the variation in plant community structure.

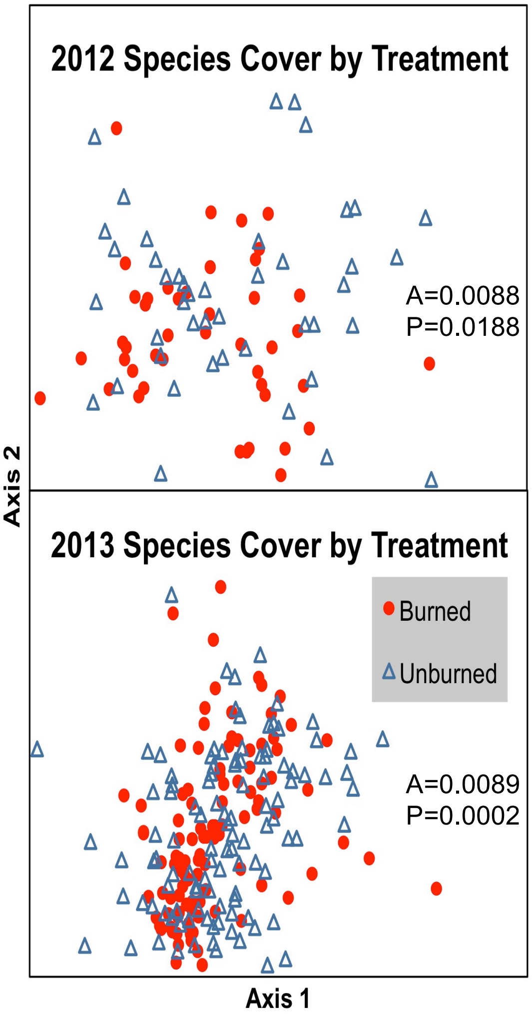


Figure 2-5. NMS ordinations for species cover from our 1 m^2 plots show weak but significant differences between burn treatments in both years (2012: F=2.1672, P=0.0002; 2013: F=3.383, P=0.0002). The 2013 data appear to be more clustered in both treatments, possibly due to varying climatic conditions between years.

Diversity metrics were compared by burn treatment separately for 2012 and 2013, with no significant trends (2012: richness t=–1.0353, DF=94.5, P=0.3035; evenness P=0.2687; Simpson's diversity index P=0.1143; Shannon's diversity index t=–1.1996, DF=80.9, P=0.2338; 2013: richness t=–0.9164, DF=217.8, P=0.3603; evenness P=0.9724; Simpson's diversity index P=0.4818; Shannon's diversity index P=0.3808).

We compared communities between 2012 and 2013 in order to determine how much weather altered species cover. Species cover changed significantly between years for both communities (Figure 2-6; Burned: A=0.0269, P<0.0001; Unburned: A=0.0218, P<0.0001), and sampling year explained a higher percentage of the variation for the burned plots (28.3% for burned, 21.5% for unburned).

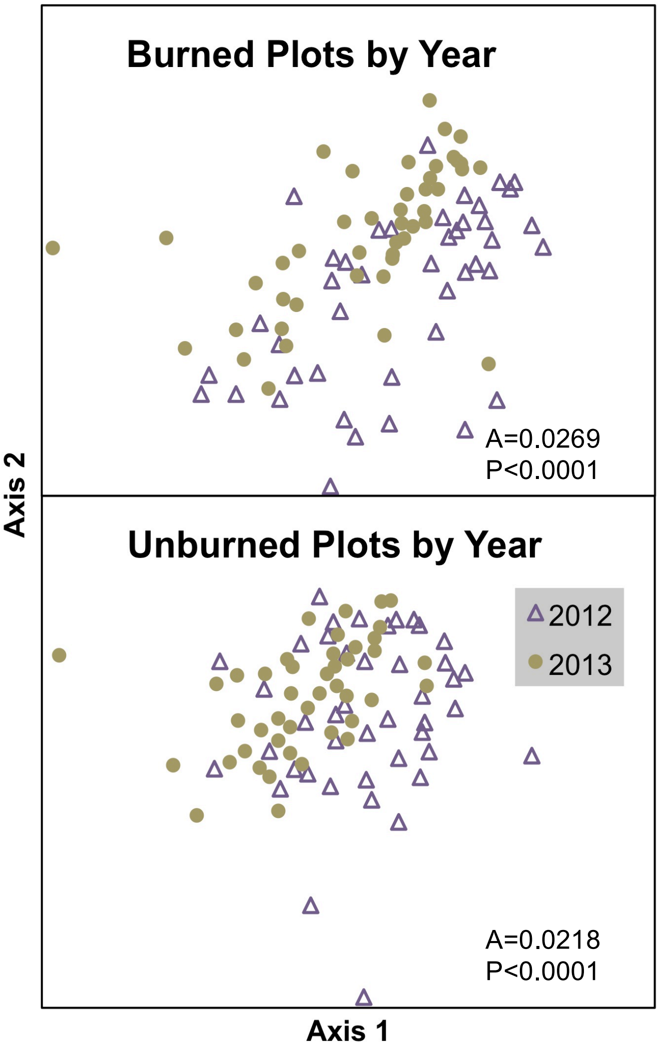


Figure 2-6. Comparison by year for each burn treatment, to examine the effects of temporal succession within plots in terms of plant community change. Year significantly affected plant communities in both treatments (Burned: A=0.0269, P<0.0001; Unburned: A=0.0218, P<0.0001). Year explained 28.3% of the community variation in burned plots, and 21.5% in unburned.

DISCUSSION

SECOND-GENERATION EFFECTS OF PRESCRIBED FIRE

Germination was increased in seeds from burned plots, which could be explained by increased pollination, chemicals from smoke absorbed through the parent, or more vigorous parent plants due to increased soil nitrogen following fire. Parent plants may also be more fit in burned areas because healthier parent plants are more likely to survive fires. Seed mass did not vary significantly between treatments, likely because of the huge intra-plant variation in seed mass observed for many *Lomatium* species, both in this study and elsewhere (Thompson 1984, Thompson and Pellmyr 1989). We were not able to obtain accurate counts for the number of seeds on each plant because many plants had already dispersed some of their seeds. For this reason, we were unable to test the "fertilization efficiency hypothesis" that smaller numbers of heavier seeds are produced with increased resource availability (Sakai and Sakai 1996).

While fire is known to directly increase germination in some species through heat scarification and chemical compounds in smoke—sometimes distilled to "smoke water" for use in plant propagation from seed (Yi-Fang Chou et al. 2012)—and indirectly through "postfire environments" with altered growing conditions (Keeley and Fotheringham 2000), the second-generation indirect effects seen here are novel because they did not rely on fire's direct effects on seeds. The effects of fire were seen here on seeds that were germinated under controlled lab conditions and had never been directly exposed to fire, fire surrogates, or the post-fire environment.

Many chemicals produced during the burning of vegetation may be able to stimulate germination, including nitrogen oxides, cyanohydrins, and karrikins (Nelson et al. 2012). It is possible that the second-generation germination increases seen in this study were the result of one or more of these germination-stimulating compounds being taken up by the parent plant and imparted into the seeds before they were released, as these compounds may have been more prevalent in the soil of burned plots. Another potential explanation is that *L. utriculatum* can sense postfire conditions and alter its development in response, as some fire-adapted plants can (Nelson et al. 2012). Finally, the influences of compounds in smoke may be expressed in a plant's genetic makeup (Nelson et al. 2012), potentially with effects that could carry over to its seeds. DNA was found to be changed by exposure to chemicals from smoke (Jain et al. 2008), and smoke-response genes can increase stress during germination in order to better prepare seedlings for environmental stressors (Soós et al. 2009).

PLANT COMMUNITY RESPONSE TO PRESCRIBED FIRE

Overall plant cover and richness varied between burn treatments, which is consistent with most previous studies that found fire to have a formational role in prairie plant communities (Collins and Gibson 1990). We expected to find increased native to non-native ratios in the burned plots, but this may depend to some extent on the season in which the plot was burned, which could obscure patterns (Howe 1995, Pollak and Kan 1998, Tveten and Fonda 1999). In this study, no significant differences in native/non-native cover between treatments were found, but there was a slight trend towards increased native cover in burned plots. This is consistent with research demonstrating that fire can control some non-native species, but unless it is carefully targeted at a certain species, prescribed fire can either be ineffective for invasive species control or lead to an increase in some non-native species (Ditomaso et al. 2006).

Depending on the restoration goals and local climate, the ideal season for prescribed burning may vary. In some cases burning in late spring may be better suited than fall for eliminating invasive species, as native plants tend to disperse their seeds earlier in the year (Pollak and Kan 1998), while Tveten and Fonda (1999) found fall fires more effective for promoting native species. Howe (1995) found variable effects of season on many individual species along with an increase in annual and biennial species following summer burning.

Prairies, which are dominated by herbaceous species, develop at different rates each year due to variation in weather and other variables. While we did find patterns in community change between years, hotter and drier weather in 2013 (compared to 2012) combined with sampling later in the season may have driven some of these changes. This created a challenge when comparing data between years and also led to the senescence of some species, making them difficult or impossible to identify. While our timeframe for this study was too short to be able to analyze long-term instability in plant communities, as found by Collins (2000) in tallgrass prairie, future sampling in these plots could identify any instability found in the communities at our study site.

This study supports recent findings that prescribed fire in Puget lowland prairies can change plant community composition, but also demonstrates that further research is necessary to determine optimal techniques for improving the ratio of native plants in restoration sites. At least on the time scales involved in this research (two seasons of burning), fire did not lead to a significantly increased proportion of native species. With more time the trend towards native cover may strengthen, but for shorter-term restoration projects other methods such as herbicide and manual removal may need to be employed in order to see rapid and consistent results.

Chapter 3: Extended discussion and future research

In this chapter, I will expand on conclusions and analysis, make recommendations for future research and actions, and explain how my results fit into the larger picture of prairie research and management. There were some results and conclusions that were left out of the manuscript because they were either non-significant or less relevant, and others that can benefit from further in-depth explanation. Throughout the research and writing of this thesis, I have encountered many areas where more research is needed, and have developed ideas for how to implement modified land management practices using current knowledge. Finally, I will share some of these thoughts on future research and management techniques as a way for this study to become a building block in our understanding of how prairie plant communities function.

EXPANSION OF CONCLUSIONS

Despite this study's many fascinating findings, there were several hypotheses that did not have their expected outcomes. Plant cover at the 1 m^2 plot scale was found to be different overall between treatments, but diversity metrics did not differ at this scale. At the 1000 m^2 plot scale diversity and evenness still did not vary, but richness was increased in burned treatments. This signifies that plant communities are changed by fire and that unburned plots had fewer species present after only one to two years of burn exclusion. Indicator Species Analysis (Dufrene and Legendre 1997) demonstrates that some species tended to be present in larger numbers in burned areas, but 60% (6/10) of these were non-native. The cover of only two species was increased in unburned areas and both were native.

Prairie plant community studies often use small-scale fires, but this study attempted to accurately represent the variable intensity of prairie fires by using large-scale burns that were more similar to natural fires. Within a burned plot there are many different fire intensities evident due to variations in topography and fuel load. It was hypothesized that this varying fire intensity may create novel microhabitats and lead to an increase in plant diversity, but this pattern was not seen. This may be because these plots have only experienced different burn treatments for two years and it would take more time for plant communities to shift.

A primary goal of prescribed fire is increasing the native/non-native ratio of the plant community. While native cover did appear to increase slightly, these differences were not statistically significant (P=0.1172). This could indicate that native cover is being increased, but only slightly, and larger-scale surveying would be needed to determine if there is an actual statistically significant trend. Community analysis determined that plant communities did vary due to prescribed fire although the differences were subtle. Our weak trend towards increased native cover in burned plots could imply that current prescribed fire practices are effective at increasing the proportion of native cover.

When collecting and analyzing *L. utriculatum* seeds, my methods limited some of the analyses I could perform. I collected data on the number of seeds per plant, but these were not truly representative of all of the seeds on the plant in many cases. When I arrived to collect seeds some of the plants that were riper had already lost many seeds in the wind, and the seeds I collected were only a subset of the original seed number. While seed number was significantly different between plots, this may not be indicative of a real pattern because one of the plants was a large outlier (several times the second-largest's number of seeds) and caused this result. Future studies could include a mesh bag to collect any seeds that fall off before sampling or count the numbers of unripe seeds on the plants prior to collection in order to have a more accurate count of the total number of seeds on the plant.

Insect damage can influence seed size but high variability in *L. utriculatum* seed size may obscure any effects. Ellison and Thompson (1987) found that weevils feeding on *Lomatium grayi* seeds could have either a positive or negative effect on surviving seed size depending on the weevil species. While the intact seeds from the weevil-damaged groups had lower germination than control groups, those that germinated grew to an equal size at 45 days compared to the controls (Ellison and Thompson 1987). They also found that 45-day plant mass was correlated with seed mass except in greenhouse conditions with no competition and large pots. Seed size and mass for *L. utriculatum* in this study were highly variable among plants (but fairly consistent within plants) and no trend due to burning was identified. Seed size in *L. utriculatum* may be driven by other factors such as plant genetics, obscuring any influence that changes in pollination or other effects of fire could have on seed size or mass. Further research into *L. utriculatum* seed size could seek to identify the primary causes of variation, by controlling for genetic lineage and/or pollination.

FURTHER RESEARCH

While I found increases in germination due to the second-generation effects of fire, the direct cause of this increase is difficult to identify. Increased germination could occur because of direct effects of chemicals from burning that could be sequestered in the parent plant or simply due to increased parent plant vigor after burning for a variety of reasons including altered competition, pollinator availability, and/or soil nutrient composition.

Maternal effects from a seed's parent plant can be passed through hereditary pathways and also through the mother plant's environment (Luzuriaga et al. 2006). Schmid and Dolt (1994) used *Solidago altissima* L. as a case study of environmental vs. genetic effects on seedling vigor and found both maternal and paternal genetic effects along with effects based on the parent plant's environmental conditions (i.e. second-generation effects). They grew *S. altissima* in garden and greenhouse experiments and found that seedlings from plants growing in different soil media had varying germination and seedling size (Schmid and Dolt 1994). In this study I found similar effects based on parental environment, but using a field-based approach and the environmental variable of exposure to fire instead of varied growth media.

It is possible that parent plant age can affect seed germinability, with older plants producing fewer viable seeds (Fenner 1991). If burning killed some older *L. utriculatum* plants and increased the abundance of young plants, subsequent seeds could have higher germination due to the younger average parent plant age. Unfortunately, it would be impossible to test for parent plant age in this experimental system because *L. utriculatum* has no age indicators.

Increased temperature can promote germination in many species of plants, and at Joint Base Lewis-McChord's Johnson and Upper Weir prairies Andrusyszyn (2013) found that soil surface temperature was higher in more recently burned areas. While my *L. utriculatum* seeds in this research were germinated ex situ so germination temperature did not alter results, warmer temperatures in burned plots may still correlate with more vigorous parent plants or increased in situ germination.

The order of umbel that a seed is borne on—which was not analyzed in this study—can also influence germination rates (Fenner 1991). Working with *Apium graveolens* L. (celery), in the same family as *L. utriculatum* (Umbelliferae), Thomas et al. (1979) found that primary umbels produced heavier seeds but that viable seeds from quaternary umbels germinated more readily, while the heaviest seeds produced the largest seedlings. Future research with *Lomatium* could separate each plant's seeds by umbel during collection and analysis to determine if these effects occur.

While the second-generation germination increases seen here on *L. utriculatum* did not rely on direct exposure to fire, testing its seeds for response to smoke water would help build a more complete understanding of the species' germination. Thomas and Staden (1995) found that smoke water increased the germination of some varieties of *A. graveolens*, and if similar effects were identified for *L. utriculatum* it would further complicate our understanding of how this species responds to fire.

Tetrazolium chloride testing (Cottrell 1947, Smith 1951, Witty 2012) is a method that verifies what percentage of seeds were viable and had the potential to germinate. This technique has been successfully used on Umbelliferae species (Rita et al. 2012). Tetrazolium chloride testing prior to germination tests would allow a better understanding of why some seeds do not germinate and what percentage of viable seeds do successfully germinate. The test kills the seed being examined, so tests would have to be carried out on a separate subsample of seeds from the same parent plant as those being germinated.

Increased pollination could lead to a larger abundance of viable seeds, and higher pollination can occur in burned sites (Van Nuland et al. 2013). While this higher pollination rate may simply be due to the fact that more vigorous plants after burning produce more flowers (Van Nuland et al. 2013), it could still be an important environmental effect that cannot be controlled for by germinating seeds ex situ. Research observing pollinator abundance on sites where seeds are collected or excluding pollinators and pollinating by hand would help to determine how pollination might alter the second-generation effects of fire.

The plants that were produced in this study could be planted back onto the prairie that their seeds were collected from into reciprocal burn treatments and monitored to determine if observed differences between treatments are due to their environment or their genetics. If the plants originally from the burned plots continue to produce more viable seed even when planted in unburned areas then it would imply that increased seed viability in burned areas is due to genetic adaptations and not environmental conditions.

While some research has discussed the optimal season for burning to increase native cover (Pollak and Kan 1998, Tveten and Fonda 1999), there is a lack of studies designed to directly answer this question. Further research experimentally comparing burns during different seasons at the same location could help land managers plan their burns in accordance with maximizing ecological benefit. One of the reasons that such studies do not exist currently is the difficulty of burning during most of the year. If the weather is not optimal it can either be too wet (natural restriction) or too hazardous (human restriction) to burn.

While it appeared that the proportion of native cover might be increased slightly by prescribed fire, future research to solidify this trend would be helpful to encourage prescribed fire as a technique to increase native plant dominance. Such research would be especially relevant to conservation groups whose main goals with prescribed fire often include increasing the proportion of native species.

PRAIRIE RESPONSE TO A CHANGING CLIMATE

In the 21st century, the Pacific Northwest is expected to have fairly constant annual precipitation but with wetter winters and drier summers (Mote and Salathé 2009). As climate change progresses, droughts will become more common, reducing prairie productivity and favoring a plant community shift towards species that grow quickly, early in the year (Thorpe 2011). Native prairie species tend to grow quickly and early in spring, dispersing their seeds before many non-native species (Pollak and Kan 1998), which may be a benefit to native species as climate change progresses. Species with longer dispersal distances will be more able to migrate and keep up with the changes in climate (Thorpe 2011). Species' ranges are broadly shifting northward as the climate warms and prairie ecosystems are no exception. Two responses that a prairie land manager can take to facilitate this northward shift are increasing landscape connectivity and/or assisted migration (Thorpe 2012).

The three categories of possible action in response to a changing climate are resistance, resilience, and response (Millar et al. 2007). *Resistance* means attempting to maintain the current state of the ecosystem, at least temporarily. This likely will not be a permanent solution, so *resilience* may often be a more powerful tool that can allow ecosystems to more easily return to a previous state after a disturbance. In the case of climate change, however, the disturbance may be ongoing, leaving *response* as the preferred adaptation method. Response from a management perspective means taking actions that can accommodate long-term climate change, including assisted migration and planting species outside their core historical ranges (Millar et al. 2007) in areas that may become preferred under the projected climate changes.

HOW THIS RESEARCH FITS INTO PRAIRIE MANAGEMENT

LAND MANAGEMENT

An understanding of the second-generation effects of fire is important to prairie restoration to plan and meet goals. Land managers seeking to improve habitat for butterflies and other pollinators can use knowledge of the second-generation effects of fire to select seeds from plants that were burned previously, even in cases where the seeds are not exposed directly to fire. Planning with second-generation effects in mind may also help more effectively predict outcomes of prescribed fires.

Soil nutrients can alter both plant production and community composition on prairies, and they can be affected by burning. Excess soil nitrogen can increase productivity but favor invasive species (Suding et al. 2005, Clark et al. 2007). Since prescribed fire alone is often not enough to increase native/non-native ratios, excess soil nitrogen reduction—sometimes together with herbicide and manual removal—can be a powerful tool to improve the proportion of native species on prairies. This can be accomplished by adding activated carbon or sugar to the soil to adsorb nitrogen or increase microbial activity to consume excess nitrogen, respectively (Mitchell and Bakker 2011).

If further research into second-generation effects finds them in other target enhancement species, burn timing could be altered to promote these species. If the target species in an area exhibit second-generation increases in germination and/or growth after fire then an ideal burn interval would be to burn before each generation begins to set seeds. If a target plant takes six years to begin producing seeds then burning every five years may be most effective to generate strong second-generation effects. With burn intervals based on phenological timing, each larger generation occurring following a fire year would have time to develop and be burned before it entered seed production.

RESTORATION ECOLOGY RESEARCH

Understanding the second-generation effects of fire on native prairie plants is an important new area of research because second-generation effects can change how fire affects prairie communities in unexpected ways. An important piece of prairie ecosystem research is knowing how historic processes such as fire continue to influence plant communities today. While fire's beneficial direct effects on plants and seeds are fairly well understood, the second-generation indirect effects of fire explored in this study open up a new area of research into prairie plants' adaptations to fire.

Germinability can be increased by environmental factors such as high temperatures and nitrogen levels (Fenner 1991), both of which could be outcomes of prescribed fire. Therefore, fire may be selecting for phenotypes which germinate more readily following burning of the parent plant and driving rapid contemporary evolution (Carroll et al. 2007). More research is needed into second-generation effects on other species of prairie plants to see if this effect is widespread or an isolated occurrence.

The fractal geometry of trees can vary based on genetics, with important implications for organisms that use these habitats (Bailey et al. 2004). Species such as *L. utriculatum* that can have highly varied umbel geometry could also inherit these traits from their parent plants. Valuable research could be done to confirm if genetic variation drives changes in umbel geometry and if these changes could be affected by fire. The outcomes of this research would be important for studying arthropods, microbes, and mycorrhizal fungi, which are all affected by plant genotypic diversity (Bailey et al. 2009).

If there is a broad pattern of burned plants producing more viable seeds (as *L. utriculatum* did) it might explain part of fire's major role in prairie plant evolution, by promoting the continuation of genes from fire-adapted plants. This novel mechanism of natural selection could help explain how adaptations to fire and other disturbances have evolved throughout many ecosystems.

Most available research on grassland habitat is in the tallgrass prairie of the Midwest. In many cases, these habitats are similar and these studies can be applied to research on Puget lowland prairies. Midwest prairie ecosystems are much more expansive and widely studied and so applying many of these studies to Puget lowland prairies is an effective way to understand topics that have not been studied regionally, such as the effects of heterogeneity on birds (Fuhlendorf et al. 2006). Studies in the Midwest often do use prescribed fire but it can be for different reasons, including livestock grazing. Grazing is often one of the main variables considered in research on prairie disturbance. While the plant species on Midwest prairies are different, they usually fall under similar functional groups to Pacific Northwest prairie plants.

CONCLUSION

While prescribed fire has been used as a prairie restoration tool for years, there is a lack of solid research specific to the Puget lowland area supporting some of its ecological benefits. This study identified second-generation effects of fire on plants and reinforced fire's alteration of prairie plant communities, the former with the potential to alter how fire's community interactions are analyzed and the latter supporting prescribed fire's use as a land management tool. We also identified a possible trend towards an increased proportion of native plant cover with prescribed fire, which is often a goal of land management plans.

While further research is essential to determine the specific mechanisms of second-generation effects of fire on plants, their existence opens up a new realm of study beyond the direct effects that have been the focus of plant-fire interactions research in the past. If the seeds of a parent plant are affected by fire indirectly it could have important implications for plant evolution as another mechanism by which plants could evolve to adapt to regular disturbance by fire. Future studies examining a wider range of species under more varied conditions will help to uncover the specific mechanisms and extent of fire's second-generation effects on prairie plants and bring a stronger understanding of how our landscapes can be altered by this powerful management tool.

Chapter 4: Interdisciplinary connections

In this chapter I will discuss the human history of prairie habitats and why we should continue to protect them. Next, I will examine some of the conflicts that local landowners and developers have with prairie restoration in the areas of smoke pollution and wildfire risk, followed by whether our conservation efforts can be (or need to be) sustained indefinitely. Finally, I will discuss how prairie research can be intimately connected to a variety of fields surrounding restoration ecology including social justice and environmental education.

AN ANTHROPOGENIC ECOSYSTEM

Puget lowland prairies are an anthropogenic ecosystem, formed after glaciation around 8,000-12,000 years ago (Pielou 1991) and maintained by human activities since then in order to maximize hunting and gathering opportunities (Boyd 1999). When considering prairie restoration, people have to put aside the notion of "leaving nature be" and realize that the natural process on prairies is one of human intervention. Native American cultures shaped the prairies for thousands of years, and the species that are abundant today may even be an outcome of the cultivation techniques that they used to promote certain desirable food species:

> "Rather than being major Indian food sources because they dominated the prairies, bracken [*Pteridium aquilinum* (L.) Kuhn] and camas [*Camassia quamash* (Pursh) Greene] more likely dominated the prairies *because* they were major Indian food sources [emphasis added]" (White 1975).

The formational role that Native Americans played in Puget lowland prairie history should not be discounted, and the cultural significance of these prairie ecosystems is one of their many values.

Puget lowland prairies were maintained by Native American burning for thousands of years, but these burn practices may no longer produce the same desired outcomes as they have historically. Since European settlement, development, invasive species, and even climate change have altered how fire interacts with prairies. Some invasive species can even be benefited by fire, necessitating other control methods for removal. Finally, nearby landowners can reduce the opportunities for prescribed fire, limiting when burns can be completed.

SMOKE POLLUTION AND WILDFIRE RISK

Particulate smoke pollution is linked to asthma and other health problems, but smoke can be kept under safe thresholds (Bowman and Johnston 2005). Many cost/benefit analyses of prescribed fire smoke pollution focus mainly on burning to reduce fuel loads and prevent catastrophic wildfire (Yoder 2004, Black et al. 2008) but some argue that the risks of not burning are smaller in prairie restoration. For this reason land managers seeking to use prescribed fire for prairie restoration have a more difficult task of bringing the public on board.

A major barrier to prescribed fire is landowner concern about smoke pollution. If conditions are less than optimal, smoke can spread widely throughout areas and become a cause for concern among nearby residents. Limiting burning to days with the right weather conditions to achieve a strong updraft and disperse the smoke more widely can largely alleviate this issue.

Prairies are level sites that are often ideally suited for easy building, and much pristine prairie habitat has been lost to development. This encroachment of the built environment also poses another problem by increasing the potential cost presented by fires escaping control. Nearby landowners are often worried about fire damage and can oppose prescribed fire. Notifying landowners prior to burns, leaving large buffers, and burning only under optimal conditions can help reduce these concerns.

In the Puget lowland region, burn bans due to wildfire and/or pollution risk play a large role in determining when prescribed fires are permitted. In many years there is a narrow window where burns are both possible and allowed, reducing the potential for experimental changes in burn timing. These legal restrictions on prescribed fire have made research into ideal burn timing challenging since timing can vary greatly between years—and in some years burns may not be possible in all areas. Restoration of prairie landscapes is not without risk, and this problem is magnified by the ongoing maintenance that prairie ecosystems require.

COSTS OF MAINTAINING NATIVE PRAIRIE

Resource expenditure in prairie restoration can be high, with herbicides, hours of labor, and fossil fuels all being used in the name of restoring prairie habitat. These each have associated costs and care must be taken to minimize the collateral damage of restoration. At the most basic level, maintaining our prairies is a necessity if we are to conserve the numerous endangered plant and animal species that depend on them. The recent federal endangered species listing of *Euphydryas editha taylori* (Taylor's checkerspot butterfly) has brought increased urgency to prairie restoration and provided a boost to programs that have already been in place to conserve this butterfly for years, previously as a candidate for federal endangered species listing.

Many restoration measures are costly and much of the funding comes through the Army Compatible Use Buffer (ACUB) program at Joint Base Lewis-McChord (JBLM).

Conservation of federally endangered species also provides money needed for restoration projects, as there is funding available to remediate the organisms' critical habitats. JBLM was approved for the ACUB program in 2005, primarily for protection of *Polites mardon* (Mardon skipper butterfly), *Euphydryas editha taylori* (Taylor's checkerspot butterfly), *Eremophila alpestris* (streaked horned lark), and *Thomomys mazama* (Mazama pocket gopher; "JBLM ACUB Program fact sheet" n.d.). The Center for Natural Lands Management (CNLM) is JBLM's ACUB "Cooperative Agreement Partner" ("Joint Base Lewis-McChord Army Compatible Use Buffer program fact sheet" n.d.), and the Sustainability in Prisons Project's prairie restoration activities largely take place through partnership with CNLM.

WORK WITH THE SUSTAINABILITY IN PRISONS PROJECT

The Sustainability in Prisons Project (SPP) works in several areas of restoration ecology as part of its mission to "bring science and nature into prisons" (LeRoy et al. 2012). Along with raising endangered frogs, butterflies, and caring for endangered turtles, SPP has three conservation nursery sites that grow native prairie plants. These plants are used largely to establish butterfly reintroduction sites through intensive planting with native species that are beneficial to *Euphydryas editha taylori* (Taylor's checkerspot butterfly) and to plant in seed-production beds to produce larger quantities of seed for direct-seeding restoration of prairie sites.

Inmates were involved in this research in the counting and sowing of germinants, monitoring plant growth, and measuring plant vigor. They benefited from involvement with this project by getting an opportunity to contribute to scientific knowledge and increasing their interest in the science of plant restoration, and this study benefited by being able to more rapidly attain large numbers of measurements. I benefited from working with inmates by gaining assistance with data collection and monitoring and being able to clarify my results and their implications by discussing them with an audience that does not have a background in restoration.

A large part of what SPP does is science education. This ranges from a science and sustainability lecture series—monthly at two prisons—to regular workshops conducted at the conservation nursery sites. Workshops at the nursery sites are helpful not only to make sure that everyone knows how to complete the tasks at hand but also that they understand how their work fits into the big picture of restoration ecology.

Inmates involved in this research were excited to have the opportunity to contribute to the scientific process, and they worked hard to ensure the quality of the data they collected. Working in a nursery facility can be monotonous, and it helps to have a sense of contributing to a larger goal. Showing inmates how they can contribute to scientific research can be an empowering part of work in a nursery and help them understand the larger purpose of what they do.

Meaningful work while imprisoned can help develop a sense of self-worth, an improved work ethic, and has the potential to decrease the likelihood of infractions (LeRoy et al. 2012). Many inmates involved in SPP's projects have become interested in studying science when they are released or getting jobs in fields where they could work with living things. Working with living plants and animals can be restorative and can reduce aggression in prisons and possibly even bring down rates of recidivism (Rice and Remy 1998, Richards and Kafami 1999, LeRoy et al. 2012).

Watching plants grow can be therapeutic and it can help impart a sense of regularity. Gardening programs in a San Francisco Sheriff's Department jail were found to increase inmate "desire for help" with drug-use related issues (Rice and Remy 1998). Richards and Kafami (1999) found that horticultural therapy programs in prison decrease vulnerability to addiction (defined as "psychological symptoms, tension, and distress"), but do not increase resistance to addiction (defined as "behavioral controls and positive self esteem").

Growing native prairie plants requires good communications skills, attention to detail, and the work ethic to sow, weed, and water tens of thousands of plants. Seeds are scarce for some species and every seed has to count. Many of the inmates in SPP's conservation nurseries have become highly skilled at quickly and accurately dispensing seeds into containers, even competing against themselves to beat their previous records. The prairie restoration crew from Cedar Creek Corrections Center has learned many applicable job skills and provided immense benefits to SPP, its many partners, and the prairie ecosystem by making restoration that would otherwise be impossible a reality.

CONCLUSION

Despite the risks and challenges associated with prescribed fire, it is still a valuable restoration tool. Puget lowland prairies must be preserved in order to maintain biodiversity and their cultural heritage, although we must also accept that the prairies may never return to the way they were before European settlement. Funding is likely to continue for as long as prairie ecosystems are imperiled, through concerned non-profits and federal and state endangered species programs. In areas where prescribed fire alone cannot remediate a site, caution must be taken before investing large amounts of labor and/or herbicide into a project since they can quickly expend valuable resources and potentially cause further harm to the environment. One of the major goals for prairie restoration in the future should be determining what the target state for a modern "native prairie" will be, because while they will never return to historical conditions, Puget lowland prairies can be maintained in a state that preserves the functional assemblages of prairie communities and the birds, animals, and insects that depend on them.

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