

The Short-Term
Effect of Fire on

Lupinus perennis (L.)

Michelle Trudeau Grigore

Metropolitan Park District
of the Toledo Area
5100 West Central Avenue
Toledo, Ohio 43615 USA

Elliot J. Frammer

Department of Biology
The University of Toledo
Toledo, Ohio 43606 USA

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ABSTRACT: Although wild blue lupine (*Lupinus perennis* [L.]) appears to respond favorably to burning, no detailed studies of the effect of fire on this species have been published. We evaluated the effect of fire on the germination, growth, flowering, and seed set of Lupine by comparing burned and unburned populations. Fire killed most lupine seeds and seedlings located on the surface of the burned sites. At one of three study sites, survival of lupine seedlings emerging after the fire was significantly higher in burned plots than in unburned plots. Adult lupines in burned plots produced more biomass, allocated more of this biomass to leaves and stems, and had significantly higher nitrogen content than plants in unburned plots. Burned portions of three lupine populations exhibited higher percent cover and number of leaves than unburned portions of the same populations. Significantly higher percentages of flowering stems set seed, and the number of pods per square meter increased in burned plots. These results suggest that burning lupine sites increases leaf production and seed set but also increases seed and seedling mortality. Timing burns to occur before seedlings emerge, and staggering burns a minimum of 2 years apart would reduce fire damage to lupine seedlings.

INTRODUCTION

Wild blue lupine (*Lupinus perennis* [L.]) is the sole larval food source of three species of butterfly listed as endangered in the state of Ohio: the frosted elfin (*Incisalia it-us* [Godart]), Persius dusky wing (*Erynnis persius* [Scudder]), and the Karner blue butterfly (*Lycaeides melissa samuelis* [Nabokov]); the latter also is listed as a federal endangered species (U.S. Fish and Wildlife Service 1992). The decline of these species in Ohio has been attributed to loss of nectaring plants and lupines (Shuey et al. 1987, Magdich 1989). Understanding the management needs of lupine is important for devising an effective plan to conserve lupine and these rare butterflies.

In northwestern Ohio, lupine is found in the oak savanna community that is scattered throughout the dry portions of a sandy soil belt known as the Oak Openings region. This community type was shaped by fire prior to settlement (Mayfield 1976) and consisted of grasses, prairie forbs, and small clumps of widely spaced oak trees, which gave the region its name. With settlement came the suppression of fire as well as drainage, pastures, and farms. Areas of the Oak Openings not put into production were colonized by woody species, which shaded out the lupine and other prairie plants (Campbell 1931, Mayfield 1976). As a result of these

successional processes, lupine has declined in abundance and is now listed as potentially threatened in the state of Ohio (Ohio Division of Natural Areas and Preserves 1992).

Several preserves in the Oak Openings are being managed with prescribed burning to decrease woody plant dominance and increase the abundance of prairie plants such as lupine. Following fire treatments, lupine has responded vigorously by increasing vegetative growth, flowering, and seed set (Mary Huffman, The Nature Conservancy, Lake Wales, Florida, and Jennifer Windus, Ohio Division of Natural Areas and Preserves, Columbus, pers. com.). These observations encouraged us to conduct a systematic study of the effect of fire on lupine. Specifically, our objectives were to (1) determine if lupine germination and seed mortality are affected by pre-scribed burning; (2) analyze the effect of fire on mature lupine plants' growth, nutrient content, flowering, and seed set using biomass and transect studies; and (3) study the effect of fire on lupine seedling mortality.

LIFE HISTORY AND FIRE EFFECTS

Information on the life history of lupine is scattered through the literature; we summarize it here for the convenience of land managers.

Lupinus perennis is a member of the Fabaceae (Gleason and Cronquist 1991) and a native of the eastern United States from Minnesota to Maine and south to the Gulf Coast (Haack 1993). Lupine grows well in full sun or partial shade, but shows limited survival under totally shaded conditions (Bess 1989, cited in Haack 1993). Lupines frequently are found in poor soils, benefiting from nitrogen fixation by *Rhizobium* bacteria that form nodules in their roots (Allen and Allen 1981). The rhizome of wild blue lupine has "eyes" that send up new shoots to form clumps (Foster 1984); these perennating buds are located 0–10 cm below the soil surface (Harshberger 1970). The shoots that emerge are ramets (Harper 1977) that produce clonal individuals through asexual reproduction. Zaremba et al. (1991) noted that 2-year-old lupine plants can have up to 5 vegetative shoots, and 3-year-old plants may support up to 17 stems under ideal conditions.

Lupine leaves develop from the taproot in April in northwest Ohio. Flowers bloom in mid-May and seed pods form by mid-June. A plant will produce all cream or all mottled seeds, with two to six seeds per pod, depending upon the growing conditions. The hairy seed pods dry and dehisce by twisting in early July, sending seeds distances of up to 5 m from the plant (authors, pers. obs.).

Seeds of the genus *Lupinus* exhibit dormancy characteristics that may be altered by fire or scarification. The seeds can lie dormant for many years because they are impermeable, and they will germinate under increasing relative humidity (Quinlivan 1971) or when the seed coat is cracked by pressure or temperature fluctuations (Bewley and Black 1982). Seeds of wild blue lupine do not require cold treatment for germination (Nichols 1934, Zaremba et al. 1991); however, Boyonoski (1992) found that stratified lupine seed exhibits 100% germination versus 65% for unstratified seed. Zaremba (The Nature Conservancy, Albany, New York, pers. com.) found that germination in lupine is asynchronous, possibly owing to variation in the hardness of the seed coat, and that germination occurs throughout the year under favorable conditions.

The literature on the effects of fire on prairie plants covers species other than lupine. Prairie grasses tend to flower and fruit more heavily and exhibit increased growth after a fire. Most studies (Curtis and Partch 1950, Robocker et al. 1953, Hulbert 1969, Peet et al. 1974) point to a reduction in litter and increased light availability as the reasons for this increased vigor, although higher spring temperatures due to blackening of the soil and the release of minerals from ash have also been suggested. Schivarin et al. (1987) concluded that fire does not affect mycorrhizal fungi and nutrient storage in fire-treated little bluestem (*Schizachyrium scoparium* Michx). Reichert and Reeder (1971) noted that the soil temperature 1.0 cm below the surface remained unchanged by a prairie fire. These latter two studies are significant in light of the potential effect of heat on the *Rhizobium* bacterium involved in root nodule formation and nitrogen fixation in lupine.

METHODS

Study Sites

The Oak Openings geologic region extends through portions of Henry, Lucas, and Fulton counties in northwestern Ohio and continues into southeastern Michigan (Figure 1). Several public agencies have preserved portions of this region in western Lucas County, including The Nature Conservancy, the Ohio Department of Natural Resources—Division of Natural Areas and Preserves, and the Metropolitan Park District of the Toledo Area. Preserves owned by these agencies are being managed with prescribed burning to restore degraded oak savanna communities to presettlement conditions; these areas provided the burned sites used in this study. Several private landowners granted permission to study lupine populations in the Oak Openings that are not subjected to fire.

A total of six study sites were chosen for 1991 biomass studies; three were subjected to prescribed burns and three had not been burned for at least 10 years. Lupine was scattered throughout each site in openings ranging in size from 0.2 to 0.5 ha.

Populations had to be dense enough to support a 25-m transect with a maximum of 1-m spacing between lupine clumps to enable consistent sampling over all six populations. Soils at all six sites are classified as Ottokee and Tedrow series, formed in sandy material on postglacial beach ridges and dunes (Stone et al. 1980). The three burned sites were utilized in 1992 to continue the transect studies on burned and unburned portions of the same lupine population.

Germination Studies

Only cream-colored *L. perennis* seeds were used for germination experiments to eliminate possible permeability differences based on pigment variation in the seed coat (Werker et al. 1979, Egley et al. 1983). To test the effect of fire on hardened lupine seed, and to remove any seed that had not developed a hard seed coat, the method outlined by the International Seed Testing Association for germinating seeds of the genus *Lupinus* (Anonymous 1966) was employed on 500 cream-colored seeds. Fifty of the seeds (10%) germinated during the test, which meant they had permeable seed coats; the other 450 seeds were impermeable to water. These "hard" seeds were used for testing the effect of fire on germination; seeds were not cold stratified prior to heat treatments.

To simulate the various fuel types that lupine seeds would be subjected to under natural conditions, two mesh envelopes, each containing 50 seeds, were randomly placed at the base of little bluestem (*Schizachyrium scoparium*), two in a leaf litter mix of sweet-fern (*Comptonia peregrina* L.) and dewberry (*Rubus flagellaris* Wind.), and two in light oak leaf litter at 1 cm below the surface to simulate lupine seed that had become stratified in the soil. Two envelopes of 50 cream-colored lupine seeds each were placed on the ground in an unburned prairie to serve as a control. The burned site was subjected to a prescribed burn on March 20, 1991. The range and duration of temperature that the seeds were subjected to during the fire were recorded by an adjacent thermocouple. The seeds were then returned to the laboratory and placed between moist filter paper and kept at 21 °C.

Seeds were kept under conditions of natural light and photoperiod and examined daily. Seeds that developed a hypocotyl were removed from the petri dish, and the number of days since sowing was recorded. The germination observations continued for 90 days, until all seeds had either germinated or appeared dead. The envelopes were treated as the experimental unit, and the proportion of seeds germinating after treatment was recorded. Analysis of variance was used to determine if heat treatments decreased mean days to germination in *Lupinus*

perennis, as had been demonstrated in Australian lupines (Quinlivan 1968, 1970).

Lupine Growth, Flowering, and Seed Set—1991 Biomass Studies

Twenty lupine plants, selected at 1-m intervals on alternate sides of a transect, were lagged in the three burned and three unburned 1991 study sites, for a total of 120 plants. Because lupine grows in clumps with several ramets possible per genet, the 1-m interval was chosen to minimize the

likelihood of sampling the same individual twice. However, upon excavating "individuals" for biomass measurements, we found that individual lupine plants could not reliably be distinguished by examining aboveground parts, even at 1-m intervals. Thus, no conclusions could be made on the performance of individual plants without destructive sampling. (See Results for more details on this phenomenon.) Not knowing this until the end of the 1991 growing season, we visited each site ten times during the season and recorded

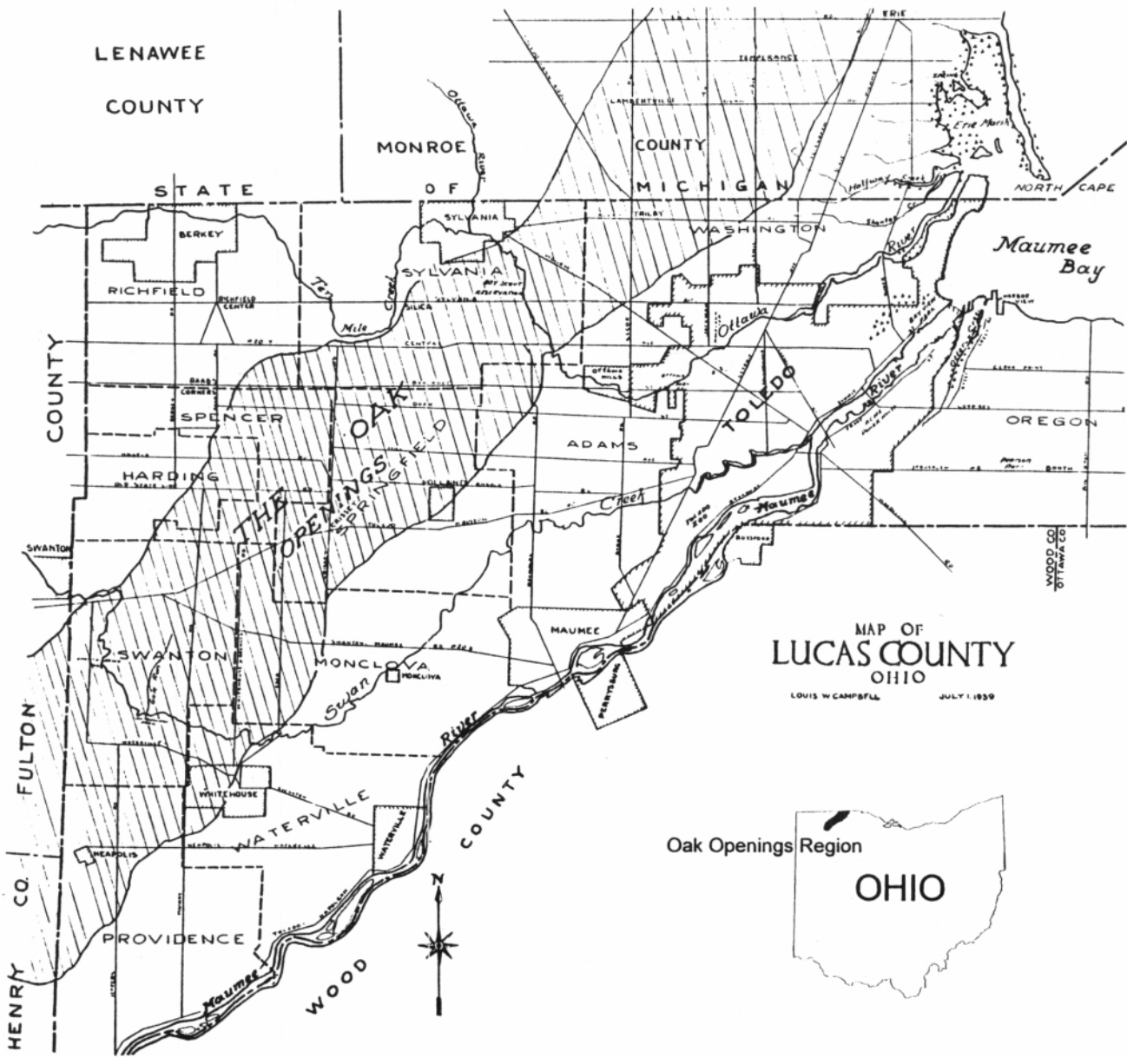


Figure 1. The Oak Openings geologic region in Northwest Ohio (adapted from Campbell 1940).

diameter, height, and number of flowering stems for each clump. The six sites were visited on the same days to reduce variation due to weather. At five of the sites, 10 tagged plants were randomly chosen for biomass and nutrient analysis in mid-June of 1991. Because lupine is rare in Ohio, 10 was chosen as the maximum number of plants that could be removed without adversely affecting the smallest populations. Even so, at one burn site located on a state nature preserve, permission to remove 10 plants was withheld.

Lupine plants were excavated by hand to a maximum depth of 1.25 m during the first week of July and separated into below-ground, leaf and stem, and reproductive structures. Pods, seeds, any remaining flowers, and the peduncle down to its attachment with the vegetative stem were included in reproductive biomass. Below-ground structures were separated from the stem where chlorophyll was no longer visible. Rhizomes and taproots as well as nodules were included in root biomass. The root system was washed to remove soil. Plants were dried at 60 °C for at least 96 hours and weighed immediately on a balance. Total mean biomass allocated to root, reproductive, and vegetative tissue was compared for lupines from burned and unburned sites. A paired (independent) t-test was employed, using the sites at the experimental units to avoid pseudoreplication (Hurlbert 1984).

These same plants were homogenized in a grinder and then sent to the Ohio State University Research Extension Analytical Laboratory, Wooster, Ohio, for standard nutrient analysis of plant tissues (Table 1). These data were used to determine the effect of fire on nutrient content of lupines, again using a paired t-test to test the differences between the means of burned and unburned sites.

Lupine Growth, Flowering, and Seed Set—1992 Transect Studies

In spring 1992, study sites at Campbell Prairie (CAMP), Lou Campbell State Nature Preserve (LCSNP), and the Monclova Road Sand Pits (MRdSP) were divided into burned and unburned halves, and detailed

comparisons of vegetation, flowering, and seed set of adult lupine plants were made. Burning half of the same population enabled us to use the paired comparisons as blocks; the three sites were considered as representative lupine populations. Ten permanent 1-m by 1-m plots were established along a transect through the burned and unburned halves of each lupine population. Plots were visited four times during the growing season to determine the maximum percent cover, maximum height of vegetative and flowering stems, number of leaves, number of flowering stems, percentage of flowering stems that set seed, and total reproductive effort based on numbers of developed seed pods from each plot.

Lane (1992) noted a strong correlation between lupine stem number and percent cover estimates. However, shaded lupine plants tend to grow tall, have few leaves, and frequently fall over, making height and percent cover difficult to measure accurately. Conversely, densely growing lupine plants have overlapping leaves, preventing accurate estimation of vegetative production from percent cover estimates. Therefore, total number of lupine leaves was used, in conjunction with the other population measurements, to give a more accurate estimate of aboveground biomass in the lupine populations.

As previously mentioned, data from the three lupine sites were treated as blocks and a paired t-test was conducted using the means for each treatment within a block. The burning treatment was replicated in that it was conducted at three sites; the sites were treated as being representative of existing lupine populations.

Fire Effect on Lupine Seedlings

Twenty randomly chosen lupine seedlings were tagged in burned and unburned halves of each population, and seedling mortality was observed from April 15 through August 20, 1992. Seedlings were identified by persistent hypocotyls. At two of the burned sites, the seedlings were tagged immediately before or just after a prescribed burn.

The cause of seedling damage was recorded. Desiccation (wilting of stems and leaves)

and insect herbivory (holes in vegetation, feeding galleries in stems and leaves) appeared to be the main causes of mortality; in those seedlings tagged before the burn, fire damage was also recorded. Mortality in burned and unburned portions of each lupine population was compared using a G-test to assess fire effect.

Because most tagged lupine seedlings subjected to fire died, 20 new seedlings (post-fire emergent) were marked in mid-May so that equal numbers of living individuals were present in burned and unburned halves for the study.

RESULTS

Germination Studies

During the burn, the ground-level temperature in little bluestem clumps reached almost 500 °C. All lupine seeds subjected to this temperature failed to germinate; many were black and cracked and some succumbed to fungus in the petri dish after a month of observations. Burns in sweet-fern and dewberry reached 171 °C.

The mean germination time for seeds in sweet-fern and dewberry litter (moderate fuel type) was 15.29 days. Seeds buried 1 cm below the surface in oak litter required a mean of 34.72 days, and the control seeds germinated in an average of 36.44 days. Burned lupine seeds took significantly less time to germinate than buried or control seeds (two-way ANOVA: Fs treatments 18.83, $p < 0.01$). This agrees with the findings of Quinlivan (1968, 1970, 1971) on *Lupinus* spp. in Australia. There also were significant differences between envelopes of seed within treatments (Fs envelopes = 11.15, $0.005 > p > 0.001$), with no seeds germinating in one envelope subjected to moderate heat treatment.

Significantly fewer burned lupine seeds germinated (mean = 3.5, Fs treatments = 84.17, $p < 0.001$) when compared to stratified (mean = 18.75) and control seeds (mean = 17.25, Figure 2). There was no significant difference between envelopes in number of seeds germinated within treatments (Fs envelopes = 0.52). None of the lupine seeds subjected to hot burns and

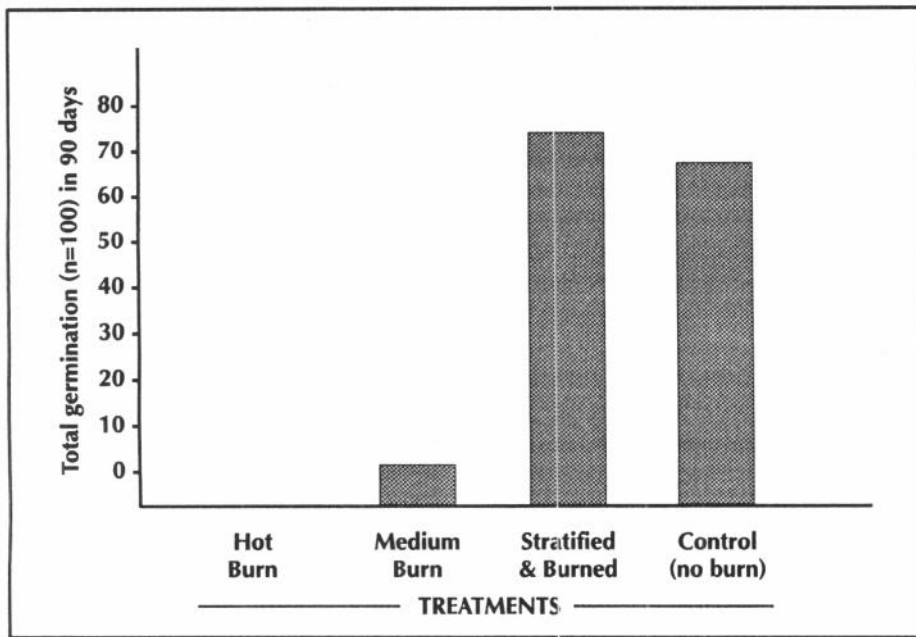


Figure 2. Number of lupine seeds germinating after different heat treatments ($p = 0.001$).

only 7 out of 100 seeds subjected to moderate temperatures germinated, compared to 69 and 75 seeds for control and buried groups, respectively.

Growth, Flowering, and Seed Set—1991 Biomass Studies

When we excavated lupine plants for biomass and nutrient studies, we discovered

that some tagged plants were actually parts of two separate individuals that, from above ground, appeared to be one. Other plants had sent ramets out farther than 1 m, so that the whole plant was not counted when diameter, height, and flowering stem measurements were made. Excavation of lupine plants was therefore necessary to identify individuals for biomass-based comparisons.

Burned lupine sites exhibited more total plant biomass than unburned sites ($t = 3.67$, $p = 0.035$, Figure 3). There was also a significant difference in the biomass of stems and leaves ($t = 4.31$, $p = 0.023$), with plants from burned sites allocating more biomass to stems and leaves than unburned-site plants. Means of total flower and fruit biomass ($t = 0.836$, $p = 0.46$) and root biomass ($t = 1.155$, $p = 0.33$) were not significantly different between burned and unburned sites.

With the exception of nitrogen and potassium, no significant differences in nutrient content were detected between plants from burned and unburned sites for 10 of 12 nutrients using the paired t-test (Table 1). Lupine from burned sites did contain significantly more nitrogen ($t = 3.38$, $p = 0.04$) and less potassium ($t = 6.44$, $p = 0.008$).

Growth, Flowering, and Seed Set—1992 Transect Studies

Trends were observed in all parameters tested from burned and unburned halves of the same population; significance levels are shown in Table 2. Some of the differences fell just outside of the arbitrary 0.05 threshold for statistical significance but are suggestive of a trend. Burned portions of all three populations produced significantly more seed pods ($t = 18.24$,

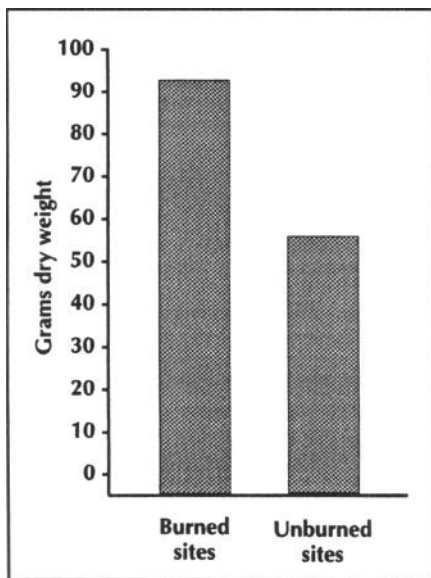


Figure 3. Total biomass of lupine plants from burned and unburned sites ($p = 0.035$).

Table 1. Nutrient content of lupine plants from burned and unburned sites (site means)^a and results of a paired t-test.

Nutrient	Burned (mcg/g)	Unburned (mcg/g)	p Value
Aluminum	784.23	622.38	.094
Boron	21.98	21.21	.820
Calcium	8,418.70	6,858.30	.424
Copper	6.13	5.51	.600
Iron	363.27	286.73	.258
Magnesium	3,107.05	3,534.57	.584
Manganese	53.92	76.98	.642
Nitrogen	2.31	2.25	.043
Phosphorus	1,628	1,657	.871
Potassium	6,581.35	11,611.57	.008
Sodium	529.94	369.64	.293
Zinc	33.08	26.83	.411

^a Each value is a mean of $n = 30$ plants for burned sites and $n = 20$ for unburned sites.

Table 2. Lupine growth, flowering, and seed set in burned (B) and unburned (U) halves of sites (see Methods for site abbreviations).^a

Lupine Characteristic	Sites						p Value ^b
	LCSNP		CAMP		MRdSP		
	B	U	B	U	B	U	
% lupine cover	44.6	47.2	37.5	30.0	24.5	26.3	0.16
# lupine leaves	880	632.7	588.5	262.5	366.5	245.5	0.06
# flowering stems	38.4	32.9	18.7	13.9	20.4	6.5	0.1 .1
leaf height (cm;)	25.2	27.2	24.4	25.2	25.2	28.4	0.10
flower stem height (cm)	43.4	39.4	42.3	37.6	39.1	31.0	0.047
# seed pods	73.7	20.1	73.8	20.3	55.9	10.7	0.003
% flower stems set seed	56.9	22.1	64.4	32.4	64.3	28.8	0.001

^a All values are means per m².

^b p values are from paired t-tests using the means for each treatment within a block.

$p = 0.003$) and set more seed than unburned halves ($t = 31.89$, $p = 0.001$). Flowering stems were also taller ($t = 4.42$, $p = 0.047$) and more numerous in lupine plants subjected to fire ($t = 2.76$, $p = 0.11$) and exhibited more leaves ($t = 3.88$, $p = 0.06$) and higher percent cover ($t = 2.23$, $p = 0.16$) than unburned plants. Shorter stem length was found in the burned portions of the lupine populations ($t = 2.87$, $p = 0.1$) when compared to unburned portions.

Fire Effect on Lupine Seedlings

Of the 20 tagged lupine seedlings at CAMP subjected to a prescribed burn on April 6, 1992, 80% were dead on April 12, and 95% mortality had occurred by May 15. Many of these seedlings were green immediately after the burn but then browned and wilted. At LCSNP, the 20 seedlings were tagged six days after the spring burn. Nine of these seedlings already exhibited browning when tagged on April 12, and

all of them died by April 27. None of the seedlings in the unburned plots died during this period. Newly emerged seedlings were tagged in May at the burn sites so that equal numbers of seedlings were available in burned and unburned halves for a study of seedling mortality in postfire-emergent lupine.

There was no significant difference in the percent mortality of postfire-emergent seedlings in burned and unburned halves of LCSNP (chi-square goodness of fit test: $Ci\ adj = 0.94$, $p > 0.1$) and CAMP populations ($G\ adj = 0.99$, $p > 0.1$). We observed a significant difference at MRdSP ($G\ adj = 8.739$, $p < 0.01$), where 60% of the 20 tagged seedlings died in the burned half but only 15% died in the unburned half (Table 3).

DISCUSSION

Fire appears to reduce recruitment in a lupine population by killing seeds on the soil surface. Unlike Australian lupines,

Lupinus perennis apparently does not require fire treatments for germination, although in this study, heat treatments decreased the germination time in seeds that survived. Under favorable temperature and moisture conditions, lupine continues to germinate throughout the year.

Fire also killed newly germinated lupine seedlings. Ninety-five percent of the pre-fire seedlings did not survive the prescribed burn; seedlings in the unburned halves of the plot did not suffer any mortality during this time. For seedlings that did survive burns, desiccation and extensive insect herbivory were noted in those that died before the end of summer. Boyonoski (1992) found that grazing by insects and slugs caused mortality in Ontario lupine seedlings. In New York, Zaremba et al. (1991) attributed grazing pressure to deer, rabbits, and chipmunks; insect damage was rarely observed there. In Ohio, insects appeared to be the main grazers of lupine seedlings.

Table 3. Percent mortality in lupine seedlings from May 15 to August 20, 1992, in burned (B) and unburned (U) halves of three lupine populations (n = 20). (See Methods for site abbreviations.)

	Sites					
	LCSNP		CAMP		MRdS	
	B	U	B	U	B	P U
% Mortality	0	5	40	25	85	40
G adj ^a	0.94		0.99		8.74	
p value	>0.1		>0.1		<0.01	

^a Results of a chi-square goodness of fit test.

Boyonoski (1992) also concluded that treatments that removed litter cover and eliminated competing herbaceous vegetation, such as fire, promoted seedling establishment. In our study of seedling mortality, two of the three lupine sites showed no difference in seedling mortality between burned and unburned halves. However, we note that these two sites had been subjected to prescribed burning for the 2 years prior to this study. It is possible that some residual benefit of burning, such as litter reduction, still influenced the unburned halves of the population. This could have reduced seedling mortality differences in these sites to insignificant levels in 1992. One site that did show significantly increased seedling mortality in the burned plot had not been burned for at least 10 years prior to this study. More research is needed on previously unburned sites to determine if fire significantly reduces the mortality of lupine seedlings that germinate after the burn.

Lupine seedling survival is generally poor. In New York, only 25% of seedlings survived the first growing season (Zaremba et al. 1991). Boyonoski (1992) found that mortality in Ontario ranged from 27 to 85%, depending on the site, and that only 20% of the seedlings that emerged in 1990 re-emerged in the spring of 1991. Most of these seedlings were still alive on August 22. We observed seedling mortality ranging from 15 to 100%, depending on the

site (Table 3). Seedlings that disappeared before August 18 in our study may have died, because adequate rainfall and moderate temperatures were present during this period and they were not observed in the following spring when the other tagged plants appeared.

Owing to the nature of lupine growth, individual plants could not be positively identified without excavation; some ramets extend further than 1 m from the genet and mix their vegetation with other lupine plants above ground. Excavation of plants yielded a satisfactory way to identify ramets and genets and to measure biomass allocation to vegetative, root, and reproductive tissue.

Lupine plants from burned sites exhibited more total biomass and more stems and leaves than plants from unburned sites, possibly owing to the same factors that benefit other prairie plants following a burn (i.e., nutrient release, blackening of the soil, reduction in competition and litter, and increased light availability). Lupine plants from burned sites did contain higher nitrogen content (a nutrient needed for vegetative growth) than those from unburned sites. Potassium content, however, was higher in unburned lupine plants, though this was not reflected in increased flowering or seed set. Indeed, no significant difference in reproductive biomass was noted between burned and unburned

sites during the 1991 season. This was also true for root biomass, which is probably a reflection of the age of the plant (Zaremba, The Nature Conservancy, Albany, New York, pers. com.) and not subject to immediate changes from fire.

Pitelka (1977) found that a perennial lupine (*L. variicolor*) invested an average of 18% total energy to reproductive tissue, 35% to roots, and the remaining 47% to stems and leaves. In our study, *L. perennis* plants from burned sites allocated 56% of their biomass to stems and leaves versus 46% for plants from unburned sites. Thus, fire stimulates *L. perennis* to produce more shoot biomass, increasing the total size of the plants.

The 1992 transect studies showed that fire stimulated a higher percentage of lupine flowering stems to set seed and resulted in a higher mean number of seed pods per meter, or greater reproduction, in burned halves of the population. If conditions are right for germination and seedling establishment, this could lead to higher lupine recruitment in burned populations in the year following a fire. Flowering stems in burned areas were also taller than their unburned counterparts and there were more of them. Unburned areas of lupine populations exhibited taller stems bearing vegetation and fewer number of leaves—a characteristic found in lupine growing in lower light conditions. Burned halves of the lupine populations had higher percent cover of lupine and greater numbers of leaves than unburned halves, reinforcing the conclusions of the 1991 biomass study.

MANAGEMENT RECOMMENDATIONS

This study suggests that *Lupinus perennis* sites can be burned to increase vegetative growth and seed set. However, fire may have a negative effect on recruitment by killing lupine seeds and seedlings that are on or above the ground, respectively, during the burn. Burning in spring, before seedlings emerge, and burning at intervals of at least 2 years, instead of annually, may minimize fire damage to seeds and seedlings yet provide the benefit of competitive release.

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Michelle Trudeau Grigore is Assistant Programs Manager for the Metropolitan Park District of the Toledo Area, where she facilitates research and land management projects on the oak savannas and prairies of Northwest Ohio. As a restoration ecologist and burn boss for the Metroparks, Michelle has a keen interest in how fire shapes the Oak Openings region in Northwest Ohio.

Elliot J Tramer is Professor of Biology and Director of the Stranahan Arboretum at the University of Toledo. He has published 45 papers on the dynamics of ecological succession, avian ecology, and related topics.

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