PRESCRIBED FIRE AND OAK SAPLING PHYSIOLOGY, DEMOGRAPHY, AND FOLIVORE DAMAGE IN AN OZARK WOODLAND

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Abstract.—Prescribed fire is a tool in wildlife management for restoring and maintaining midwestern oak woodlands. The success of some of the wildlife management objectives depends upon opening the canopy, new oak (*Quercus* spp.) saplings entering the canopy, and removal of cedar (*Juniperus virginiana* L.). We examined population characteristics of oak saplings based on changes in canopy light penetration, gas exchange, abiotic environment, and folivory. After 60 years of fire suppression, one portion of the study area was initially burned in 1980 (continuously burned), another portion was initially burned in 1999 (recently burned), and a third portion is still unburned (unburned). Fire opened the canopy from 6 percent in the unburned area to 8 percent and 40 percent in the recently burned and continuously burned areas. Saplings from the white oak group and red oak group responded to increased light availability with higher net photosynthetic rates. The resprouting ability of all oaks resulted in low mortality. Cedar mortality and recruitment were higher in burned than unburned areas. Sapling foliar area and total folivory was greater in burned than in unburned areas. Our data suggest reasons why, under the current biennial fire regime, potential oak canopy recruits will likely remain as large multistemmed sprouts and fail to enter the canopy.

INTRODUCTION

Historically, oak (*Quercus* sp.) woodlands were common throughout much of the midwestern United States (Nuzzo 1986). Oak woodland communities are characterized by widely spaced canopy trees and high light penetration to the ground layer (Anderson, 1998, Cottam 1949, Curtis 1959). Frequent fires historically played an integral role in the development and maintenance of midwestern oak woodland communities (Abrams 1992, 1996; Anderson and Fralish 1975; Gleason 1913). In the extended absence of fire, oak woodlands have become closed canopy woodlands (Anderson and Brown 1986, Cole and Taylor 1995, Nuzzo 1986). Oak sapling growth may then be limited by low light conditions caused by a closed canopy (Burns and Honkala 1990, Crow 1988, Lorimer 1994).

Leaf nitrogen (N) concentrations, plant water stress levels, and light are probably three of the most important variables affecting leaf quantity, quality, and feeding by folivores (Baraza et al. 2004, De Bruyn et al. 2002, Warring and Cobb 1992). Prescribed burning has been hypothesized to increase quantity and quality of plant foliage (Adams and Rieske 2003), and therefore, insect folivory (Rieske 2002). However, there have been very few studies of oak sapling leaf quantity, quality, and folivory as a function of prescribed fire.

In this paper we examine the efficacy of prescribed fire for increasing canopy light penetration, the physiological and demographic response of oak saplings to canopy light penetration, and insect folivory on oak saplings in a woodland area in the Ozark Mountains region of southwestern Missouri

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managed for deer and turkey with varied prescribed fire regimes. Physiological responses (e.g., gas exchange) of saplings were measured to better understand mechanisms influencing population-level responses to management efforts, while folivory was measured to assess potential impacts of leaf area loss on plant responses to light. We tested the following predictions: (1) prescribed burning increases canopy light penetration; (2) oak saplings are light limited in unburned woodlands and will respond positively to increased light with increased net photosynthetic rates; (3) total sapling density and dominance will increase in response to increased light availability; and (4) foliar loss to insect herbivores will be higher in burned woodlands and will be associated with leaf quality and abiotic conditions that result from increasing canopy light penetration.

METHODS

Study Site

This study was conducted at Bull Shoals Field Station (BSFS) within the 809.4 ha (2000 acre) Drury Conservation Area (DCA) in Taney County, Missouri (36° N latitude, 93° W longitude). The climate at DCA is continental. Growing season (April through September) mean daily maximum temperature was 28 °C, and mean annual precipitation was 1097 mm during this study. DCA has karst topography with elevations ranging from 180 to 340 m (600 to 1100 feet). Soils at DCA are predominantly Gasconade-Opequon-Clarksville association (Nigh and Schroeder 2002).

At DCA, two primary woodland habitat types existed in 1999. The habitat types included closed canopy oak woodland (60 percent of area with 80-95 percent overstory cover) and open oak woodland (35 percent of area with 40-60 percent overstory cover), with 5 percent of the habitat considered glade (<30 percent overstory cover). The oak woodland with high overstory cover is thought to be the result of 50 years of fire suppression. The current open woodland habitat at DCA is thought to be a result of the reintroduction of fire to the area in 1980. Periodic (generally every 2 years) prescribed burning since 1980 by the Missouri Department of Conservation (MDC) over 35 percent of the area was used to manage for deer and turkey and increase understory species diversity, resulting in open woodland habitat. In the spring of 1999, the MDC implemented prescribed burns over an additional 50 percent of the woodlands with biennial frequency to begin managing for wildlife. Ten percent of the area has not burned in over 60 years.

We established three experimental habitat areas (100 m x 100 m) representing the following:

- Unburned (n = 2): last known fire in 1950.
- Recently burned (n = 2): fire resumed in 1999 and repeated every 2 years.
- Continuously burned (n = 2): fire resumed in 1980 and repeated every 2 years.

An overview of understory species richness, midstory structure, and overstory basal area in the three habitat areas in 2008 is provided in Tables 1, 2, and 3. The data in this paper were collected between 2001 and 2003.

Table 1.—Descriptive statistics for understory species richness in twelve 1-m^2 plots in three habitat areas with different burn histories located in southwest Missouri

		Habitat area		
		Unburned woodland	Recently burned woodland	Continuously burned woodland
Species richness	Mean	21.67	31.80	60.38
	Standard deviation	6.22	4.22	13.87
	Minimum	16	27	30
	Maximum	30	39	76

Table 2.—Descriptive statistics for midstory tree structure in six 0.01-ha plots in three habitat areas with different burn histories located in southwest Missouri

		Habitat area		
		Unburned woodland	Recently burned woodland	Continuously burned woodland
Density (stems/0.01ha)	Mean	13.33	2.67	0.75
	Standard deviation	9.99	1.51	0.89
	Minimum	29	4	2
	Maximum	3	0	0
Height (m)	Mean	3.48	5.87	3.42
	Standard deviation	1.38	3.27	4.25
	Minimum	11.20	1.09	9.50
	Maximum	1.46	0	0
Dominant species		*Rhamnus caroliniana*	*Cornus florida*	*Quercus alba*

Canopy Light Penetration

We used leaf area index (LAI) as a measure of canopy light penetration (CLP) to determine if prescribed burns resulted in a more open canopy. Based on the complementary relationship of LAI and CLP, we defined CLP as:

$$CLP = 12 - LAI$$

where 12 is the theoretical maximum value for LAI (Boyles and Aubrey 2006). Values were converted in this way for a more intuitive illustration of canopy light penetration as opposed to interception. We obtained LAI indirectly using an AccuPAR PAR-80 light interception device (Decagon Devices, Inc., Pullman, WA). Measurements were collected 1.2 m above ground level at five randomly spaced points along a 100 m transect within each habitat area. These five measurements were averaged to calculate one LAI value, and therefore, one CLP value for each transect per sample period. Measurements were collected throughout two growing seasons (2002 and 2003).

Table 3.—Descriptive statistics for overstory basal area (m^2/ha) in six 0.1-ha plots in three habitat areas with different burn histories located in southwest Missouri

		Habitat area		
Species		Unburned woodland	Recently burned woodland	Continuously burned woodland
Total	Mean	23.75	26.04	17.27
	Standard deviation	7.69	6.86	8.79
	Minimum	15.16	18.71	4.87
	Maximum	36.41	37.32	29.78
Red oak species	Mean	12.58	13.69	5.95
	Standard deviation	7.95	7.46	6.93
	Minimum	3.00	4.25	0.00
	Maximum	23.67	26.29	19.00
White oak species	Mean	5.57	7.53	9.61
	Standard deviation	3.83	4.18	7.74
	Minimum	0.76	4.52	1.45
	Maximum	9.43	14.61	23.20
Hickory species	Mean	3.38	2.10	1.22
	Standard deviation	1.78	1.39	0.88
	Minimum	1.58	0.26	0.00
	Maximum	6.49	4.11	2.30
Cedar	Mean	1.43	1.62	0.15
	Standard deviation	2.10	1.66	0.30
	Minimum	0.00	0.00	0.00
	Maximum	4.96	4.49	0.81
Other species	Mean	0.60	1.08	0.29
	Standard deviation	0.77	0.95	0.39
	Minimum	0.00	0.00	0.00
	Maximum	2.06	2.46	1.12

Abiotic Environment

Air temperature, relative humidity, soil temperature, soil moisture, solar radiation, and wind speed were monitored using two portable weather stations (Campbell Scientific, Logan, UT). These abiotic parameters were logged every 30 seconds with averages calculated every 30 minutes. The weather stations were rotated through six combinations of the three woodland habitat areas during the summer of 2003. During any one of the six rotations, data were collected for a minimum of 10 days at a time. Data were collected from May 19 (Julian Day 139) to August 25 (Julian Day 237). Raw data were revised to remove the first and last day of each 10-day period. In addition, at least one day was randomly selected to be removed to equal 7 days of data per rotation. For each variable, the mean for the 7 days in each habitat area was calculated. The means of these data sets were then compared to a reference mean obtained over the same time periods from a permanently placed weather station (Campbell Scientific, Logan, UT). The permanent weather station was selected as a reference because it is located in a large open prairie-like field at BSFS within 1 km of each woodland area.

Physiological Characteristics

We measured leaf level net photosynthesis of oak saplings (stems < 1.0 m) at ambient (A_{AMB}) and saturating (A_{MAX}) light levels using a portable gas exchange system (LI-6400, Li-Cor, Lincoln, NE). A single leaf of five randomly selected saplings located along a transect within each habitat area was measured. Ambient light levels were measured at each sample leaf using the quantum sensor on the gas exchange system, and light levels were held constant in the measurement chamber to obtain A_{AMB}. A_{MAX} was then obtained at saturating light levels (1500 µmol/m/s). Temperature (25 °C), CO_2 concentration (360 ppm), and flow rate (500 µmol/s) were also maintained at constant levels within the measurement chamber. The same permanently tagged individuals were measured once per month throughout one growing season.

Population Characteristics

Three permanent variable area belt transects (Dobrowski and Murphy 2006), hereafter referred to as transects, with an average area of 102 m^2 (4 m wide with various lengths) were established within each habitat area. During plot establishment we identified, tagged, and mapped all oak (*Quercus* spp.) and cedar (*Juniperus virginiana* L.) individuals less than 2.0 m in height. We categorized oaks into two groups due to small sample sizes of individual species. Hereafter, all members of the red oak group (*Quercus falcata* Michx., *Q. marilandica* Muenchh., *Q. rubra* L., *Q. shumardii* Buckl., and *Q. velutina* Lam.) are collectively referred to as red oak, and all members of the white oak group (*Quercus alba* L., *Q. macrocarpa* Michx., *Q. muhlenbergii* Engelm., and *Q. stellata* Wangenh.) are collectively referred to as white oak.

We assessed oak and cedar sapling characteristics by measuring stem number of all individuals within each transect during June or July of 2001, 2002, and 2003. We determined stem density, mortality (absence of an individual previously present), and recruitment (introduction of a new individual) in 2001-2002 and 2002-2003 at each plot.

Leaf Quantity, Quality, and Folivory

Total sapling leaf area was determined across the three habitat areas throughout the growing season. Within each habitat area, three 50 m by 5 m (250 m^2) belt transects were established. Within each transect, 15 red oak and 15 white oak saplings less than 2 m in height were randomly chosen and tagged for a total of 45 oaks per habitat type. The area of each leaf was determined using a CI-420 leaf area meter (CID Bio-Science, Inc., Camas, WA).

To assess leaf quality, leaf tissue nitrogen (N) was determined using micro-Kjeldahl analysis following the methods of Anderson and Polis (1999). Due to the destructive nature of leaf N analysis (i.e., removing an entire leaf at the petiole), five oak plants were randomly selected adjacent to each tagged plant, and 15 oak plants were used per habitat area each month. Leaves were dried at 60 °C and ground, and then approximately 0.1 g samples were weighed with 0.0001 precision. Following digestion of leaf samples and the N concentration assay, samples were analyzed using a Shimadzu UV 1601 spectrophotometer (Colombia, MD). Predawn and midday water potential measurements were obtained on the same plants using a pressure chamber (PMS Instrument Co., Corvallis OR) to assess water stress. Predawn measurements indicate levels of soil water availability and midday measurements, along with photosynthetic rates, indicate limitations to carbon gain by stomatal

Table 4.—Mean (±standard deviation) monthly canopy light penetration (CLP = 12 – Leaf Area Index) in three habitat areas with different burn histories located in southwest Missouri

	Habitat area		
Month	Unburned woodland	Recently burned woodland	Continuously burned woodland
April	10.9 ± 0.1	11.2 ± 0.1	12.0 ± 0.1
May	9.1 ± 1.0	10.1 ± 0.5	11.5 ± 0.3
June	7.8 ± 2.3	10.1 ± 1.1	11.6 ± 0.3
July	7.6 ± 1.9	10.2 ± 0.4	11.5 ± 1.2
August	7.9 ± 0.5	10.3 ± 0.3	11.6 ± 0.9
September	7.8 ± 0.4	9.9 ± 0.2	11.7 ± 1.1

regulation. Stems less than 3.0 mm in diameter were cut using a clean razor blade. The pressure applied to the leaf blade (in megapascals) to force water out was equivalent to the amount of soil moisture (predawn) and water stress (midday) that an oak was experiencing.

To estimate folivore damage, each leaf on each tagged oak plant was visually scored using a ranking system based on the methods of Futuyma and Wasserman (1980) to estimate the area removed due to insect herbivores. Individual leaf scores were then averaged into one overall score for each oak plant. Visual scoring took place in mid June, July, August, and September. The visual scores for the month of August were applied to the total available leaf area to estimate the amount of leaf area that was removed by herbivores from each habitat area. Leaf area loss due to herbivory was obtained by calculating the mean of the range of percent leaf area removed that corresponded with each rank. The mean percent of damage per plant (obtained from the visual score data) was then multiplied by the total leaf area of each plant in each habitat area to estimate the leaf area removed. The leaf area removed per habitat area was estimated by summing the leaf area removed from each plant.

RESULTS AND DISCUSSION

Canopy Light Penetration

The reintroduction of fire positively influenced CLP (Table 4). Canopy light penetration was higher in continuously and recently burned than unburned habitat areas, and CLP declined through June in unburned areas but remained constant in burned areas.

The higher CLP in habitat areas treated with prescribed fire is an important result as the long-term goal of burning is to open the canopy and restore woodland communities back to their presettlement characteristics, of which CLP is a key driving force and a defining characteristic (Curtis 1959, Leach and Ross 1995, Nuzzo1986, Taft 1997). Other studies have also demonstrated that prescribed fire is an effective tool in opening closed woodland canopies in the Midwest (Anderson and Brown 1986, McCarty 1998). If canopy opening results in photosynthetically active radiation being greater than saturation levels for oaks, then oak growth should not be light limited.

Earlier maximum leaf expansion in habitat areas treated with prescribed fire suggested burning may have altered leaf phenology. This potential effect of fire on overstory leaf phenology has not been studied, but it is possible that altered phenology is an important component of understanding fire effects on sapling physiology and growth. For example, fire may alter leaf phenology by temporarily increasing plant-water status (Borchert 1994, Eamus 1999) which may result in earlier bud break and leaf expansion (Saha 2001). However, it could be that seasonal patterns are an artifact of canopy and subcanopy tree composition.

Abiotic Environment

Forest microclimate below the canopy is expected to vary with canopy light penetration and influence growth and survival of tree seedlings and saplings (von Arx et al. 2013). There may be threshold canopy densities that support the regeneration of tree saplings through both light penetration and associated microclimate. We measured air temperature, relative humidity, soil temperature, soil moisture, solar radiation, and wind speed at each woodland habitat type to provide a baseline for interpreting how canopy light penetration might affect the microclimate below the canopy (Table 5). The continuously burned areas generally had higher air and soil temperatures and solar radiation but had lower relative humidity and soil moisture than the more closed, recently burned or unburned habitat areas. In the recently burned habitat areas there were higher air and soil temperatures, higher soil moisture, and greater solar radiation than in unburned habitat areas. These data suggested that in the recently burned habitat areas, microclimate was still more similar to unburned habitat areas than continuously burned habitat areas. Therefore, the amount of water stress to oaks is expected to be the greatest in continuously burned habitat areas, and oak sapling gas exchange is potentially going to be limited by water stress in open canopies (e.g., closing stomata) even though light is not limiting. Soil moisture may also explain extended overstory leaf expansion.

Physiological Characteristics

There was a positive relationship between CLP and A_{AMB} suggesting that red and, especially, white oak saplings are capable of responding to increased light availability (Table 6). Higher light saturated photosynthetic rates (A_{MAX}) among saplings in burned habitat areas indicate that oak saplings are light limited in closed canopy woodlands. Elevated A_{AMB} in burned habitat areas suggest a positive response to increased light availability, especially in white oaks. These physiological patterns may be due to both increased light and nitrogen availability, as both light and nitrogen are common limiting resources for plant photosynthesis and growth (Fahey et al. 1998, Reich et al. 1997, Sipe and Bazzaz 1995, Walters and Reich 1997). Burning has been shown to increase nitrogen availability in forests (Boerner 1988, Raison 1979, Reich et al. 1990), but our estimates of foliar nitrogen concentrations did not support this, nor did water stress limitations as measured by predawn and midday water potential (Table 7). Therefore, light availability was likely the major limiting resource within closed woodland habitat areas in our study, a result found in forests in the northeastern United States (Finzi and Canham 2000).

Population Characteristics

Increased CLP (Table 4) and subsequent enhanced photosynthetic capacity (Table 6) did apparently lead to increased dominance for red and white oak in recently burned woodland areas (Table 8). Red oak rootstock density was greater than white oak in all but the continuously burned woodland areas (Table 8). White oak had higher basal area in recently burned woodland areas than would be expected based on its proportional contribution to density. White oak density was three times higher in recently burned than unburned woodland areas, but dominance was 21 times greater. This suggests

Table 5.—Differences between mean values of environmental conditions in three habitat areas with different burn histories located in southwest Missouri relative to an open prairie field

Environmental parameter	Habitat area		
	Unburned woodland	Recently burned woodland	Continuously burned woodland
Air temperature (°C)	-1.66	-0.75	+1.79
Relative humidity (%)	+4.16	+1.77	-4.14
Soil temperature (°C)	-4.73	-2.47	+3.21
Soil moisture (%)	+3.76	+3.92	-8.10
Solar radiation (W/m^2)	-375.82	-359.50	-170.16
Wind speed (m/s)	-0.59	-0.39	-0.34

Note: Comparisons between habitat areas and open field are based on 7 days of comparisons collected from May 19 (Julian Day 139) to August 25 (Julian Day 237).

Table 6.—Mean (± standard deviation) maximum (A_{MAX}) and ambient (A_{AMB}) photosynthetic rates of red and white oaks in three habitat areas with different burn histories located in southwest Missouri

	Habitat area		
	Unburned woodland	Recently burned woodland	Continuously burned woodland
Red oak A_{MAX} (μmol $CO_2/m^2/s$)	5.05 ± 0.21a†	5.40 ± 0.22a	8.54 ± 0.63b
Red oak A_{AMB} (μmol $CO_2/m^2/s$)	1.48 ± 0.21a	3.82 ± 0.42b	5.80 ± 0.74c
White oak A_{MAX} (μmol $CO_2/m^2/s$)	5.65 ± 0.19a	8.14 ± 0.28b	9.47 ± 0.37b
White oak A_{AMB} (μmol $CO_2/m^2/s$)	1.58 ± 0.21a	4.44 ± 0.43b	6.77 ± 0.69b

†Significant differences (Tukeys; P = 0.05) between habitat areas within a row are indicated with different letters.

Table 7.—Mean (± standard deviation) values for leaf parameters of oak plants (< 2.0 m height) as a function of habitat areas with different burn histories located in southwest Missouri

	Habitat area		
	Unburned woodland	Recently burned woodland	Continuously burned woodland
Total leaf area (cm^2)	23,780 ± 507a†	35,314 ± 714a	90,705 ± 1,4700b
Leaf area removed (cm^2)	3,110 ± 79a	6,947 ± 159c	4,472 ± 105b
Foliar nitrogen content (%)	1.88 ± 0.31b	1.80 ± 0.53b	1.53 ± 0.27a
Pre-dawn water potential (MPa)	-0.57 ± 0.49a	-0.55 ± 0.44a	-1.42 ±1.27b
Mid-day water potential (MPa)	-1.51 ± 0.82a	-1.42 ± 0.76a	-2.21 ± 1.18b

†Significant differences (Tukey's; P = 0.05) between habitat areas are indicated with different letters.

Table 8.—Mean (± standard deviation) population characteristics of cedar, red oak, and white oak saplings (< 2.0 m in height) in three habitat areas with different burn histories located in southwest Missouri

Population characteristic†	Unburned woodland			Recently burned woodland			Continuously burned woodland		
	Cedar	Red oak	White oak	Cedar	Red oak	White oak	Cedar	Red oak	White oak
Density (#/m^2)	0.018 ± 0.007	0.200 ± 0.038	0.022 ± 0.006	0.009 ± 0.004	0.270 ± 0.088	0.070 ± 0.008	0.15 ± 0.041	0.09 ± 0.010	0.21 ± 0.033
Dominance (cm^2/m)	0.067 ± 0.056	0.811 ± 0.413	0.030 ± 0.009	0.0007 ± 0.000	1.180 ± 0.110	0.461 ± 0.250	0.004 ± 0.002	0.210 ± 0.046	1.650 ± 0.440
Mortality (%)	10.00 ± 10.00	7.10 ± 4.00	8.35 ± 8.35	88.10 ± 1.00	8.90 ± 3.20	7.65 ± 2.85	53.40 ± 21.90	2.68 ± 1.96	2.90 ± 1.96
Recruitment (#/m^2)	0.023 ± 0.010	0.051 ± 0.029	0.013 ± 0.013	0.033 ± 0.033	0.034 ± 0.015	0.050 ± 0.009	0.500 ± 0.200	0.073 ± 0.030	0.160 ± 0.083

†Density = number of individuals per meter squared. Dominance = sum of basal areas/cm^2 for each species per area sampled. Mortality = absence of an individual that was previously present. Recruitment = presence of a new individual. Values are means across 3 years (or 2 years for mortality and recruitment).

that the increase in CLP in recently burned areas has already resulted in increased carbon gain for white oak, but not red oak.

Increased recruitment in white oaks in recently burned woodlands (Table 8) may be attributed to increased stump sprouting, seed production, increased germination rates, or a combination of these factors. The similarity in mortality of red and white oaks between woodland types (Table 8) suggests tolerance to fire. Red and white oak experienced topkilling by fire but resprouted immediately, generally with more stems of smaller diameter (data not shown). The resprouting capabilities of oak in response to fire have been well documented (Abrams 1992, Stearns 1991) and are likely the reason mortality did not differ between woodland areas (Reich et al. 1990). Under continued prescription of the biennial fire regime, we suggest that red and white oak will persist, but only as multistemmed shrubs unlikely to be recruited into the canopy. We have no evidence of canopy recruitment (data now shown).

The maintenance of oak woodlands depends upon the right frequency of new individuals entering the canopy (Ladd 1991, Leach and Ross 1995, McCarty 1998). Studies have shown oak resprouts develop rapidly once burning is withheld (Anderson 1998, Bowles and McBride 1998, Crow 1988) and may grow up to 6 m in less than a decade (Cain 1995). Therefore, if burning were excluded from this area for a decade, sprouts should grow through the susceptible stage of topkilling and likely enter the canopy. After a cohort group reaches this height, a biennial burn cycle should help keep competition in check. However, in order to determine an ideal burn frequency, it is imperative to understand how long it will take for red cedar saplings to reach fire-tolerant size. We found that the current biennial fire regime appears to be effective at removing (high mortality), although not eradicating (high recruitment), red cedar saplings (Table 8).

Leaf Quantity, Quality, and Folivory

Increased light along with increased photosynthetic rates probably played a role in the difference in foliar area between the habitat areas (Table 7). Our results were similar to those reported by Dudt and Shure (1994) and Baraza et al. (2004) that indicate that plants grown in a high light environment have greater leaf area than shade grown plants. We found that oak saplings in continuously burned habitat areas lost 5 percent of their total leaf area, while in the unburned and recently burned habitat areas oak saplings lost 13 percent and 20 percent of their total leaf area to folivory, respectively (Table 7). The percentage of leaf area removed in the more closed areas was within the range (10 to 20 percent) found by Hochwender et al. (2003). However, the damage amounts in the continuously burned habitat areas were much lower than the 18±1 percent found by Hochwender et al. (2003) and Marquis and Forkner (2004). Oak saplings in the closed canopy habitat, independent of recent burning, had 13 percent more foliar N and were 30 percent less water stressed than oak saplings in the continuously burned habitat areas. We found that less water stressed saplings had more foliar damage, which supports the notion that insects do not always have a positive response to water stressed foliage (Warring and Price 1990). Ultimately, we found that insect folivores had the greatest potential impact in recently burned habitat areas.

CONCLUSIONS

We found that prescribed burning increased canopy light penetration. Oak saplings were light limited in unburned woodlands and responded to increased light with increased net photosynthetic rates and leaf area even though abiotic conditions were more stressful (higher temperature and lower soil moisture). Total sapling density and dominance increased in response to increased light availability only after continuous burning for 20 years, yet there was no recruitment into the overstory. Foliar loss to insect herbivores was greatest in recently burned habitats, but clear associations with leaf quality and abiotic conditions that result from increasing canopy light penetration were not found. We suggest that prescribed fires should occur at longer intervals along with physical gap formation to promote oak regeneration into the canopy, and that changes in folivory or abiotic conditions associated with an open canopy are not currently limiting oak canopy recruitment.

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