Effects of Burning and Folivory on Growth of Oak Saplings for Oak Advance Regeneration and Commercial Use in Oak Forests and Savannahs

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Abstract

The interactive effects of fire and herbivory were examined to assess oak advanced regeneration potential and commercial selective harvesting. This study quantified loss of oak sapling leaf area to insect herbivores in recently burned or unburned oak forest and oak savanna in Missouri. Foliar area and damage were measured on 180 oak saplings (< 1.5 m height) across the four habitat types; water status and foliar nitrogen (N) concentration were measured on 75 oak saplings. Foliar area of saplings was significantly greater in savannas than forests. Foliar damage was significantly greater in forests, with the greatest amount of foliar damage occurring in burned forest. Oak saplings in forest were less water stressed and had greater foliar N concentration than oak saplings in savanna. These data suggest that oak saplings in forests are potentially more susceptible to herbivore damage than oaks managed in savannas, especially following a prescribed burn.

Keywords: Advanced Regeneration Potential, Commercial Value, Hardwoods, Herbivory, Oaks, Prescribed Fire

1. Introduction

Oak forest, whether open or closed, or classified as forest or open savannah, is the dominant habitat type of the Ozark Highlands in the United States; this region includes northeastern Oklahoma, northern Arkansas, southwestern Illinois, and southwestern Missouri (Johnson et al. 2002). In Missouri, oak forests cover 5,665,800 hectares of land (14 million acres) (see Wait and Aubrey 2014). Since oak forests are one of the most dominant habitats in Missouri, and the potential commercial value of selectively harvested oaks for the hardwood industry is great, it is important to understand the impact that prescribed fire and herbivorous insects have on the growth of oak saplings (Hutchinson et al., 2012; Schowalter 2012; Dey 2014). Only a few studies have examined the extent of loss of primary production of oak saplings to insect herbivores, but none as a function of forest or savannah, or the effects after a spring burn. However, general surveys suggest that 18 ± 1% of the primary production of *Quercus alba* and *Q. velutina* in the understory can be consumed in a growing season (Marquis and Forkner 2004).

Although there is little known about the extent of foliar damage in oak forests and savannahs of Missouri, the insect herbivore community has been examined extensively. Lepidopteran larvae are the dominant group of insect herbivores in Missouri oak forests (Marquis and Whelan 1994; Hochwender et al. 2003; Marquis and Forkner 2004). There are over 200 species of Lepidopteran herbivores associated with *Q. alba* alone (Covell 1984). The herbivore community in Missouri forests tend to be generalists: 75 to 90% of insect species are shared among oak species (Marquis and Whelan 1994). For example, of the 138 species of leaf chewing insects associated with *Q. alba* and *Q. velutina*, only 25 specialize on *Q. alba* and 13 are *Q. velutina* specialists (LeCroff and Marquis 1999). Generally, the understory of Missouri oak forests is thought to have greater herbivore species richness and abundance than the canopy (LeCroff and Marquis 1999; Marquis and Forkner 2004). Forests that have a closed canopy versus those that have an open canopy (woodland or savannah) have differences in abiotic variables (e.g., light, soil water, and nitrogen) that have been shown to be associated with foliar damage-both directly and indirectly via change in foliar quality and quantity (Martinant 1987; Larsson 1989; Fleming and Candau 1998; Balager et al. 2001; Baraza et al. 2004).

Light environment has been shown to play a role in determining foliar quality and quantity. For example, saplings grown in shaded environments can have higher foliar N concentration and lower levels of chemical defenses than those grown in high light environments (Balager et al. 2001; Baraza et al. 2004). However, saplings grown in high light environments often have higher leaf weight per unit area and more leaves than saplings grown in shaded environments (Baraza et al. 2004).

Saplings growing under conditions of moisture stress have been shown to be more prone to herbivore attack due to reduced defensive chemicals and increased nutritional quality resulting from increased N concentrations (White 1984; Mattson and Haack 1987; Atkinson and Nuss 1989; Willis et al. 1993). Increased temperatures can lead to increased plant water stress (Teskey and Hinckley 1986) and result in changes in foliar nutritional quality such as chemical defense concentration and digestibility (Martinant 1987; Larsson 1989; Fleming and Candau 1998), which can make saplings more susceptible to herbivore damage. However, the opposite relationship has been observed; for example, *Corythucha arauata* preferred *Q. alba* leaves that were from unstressed and mildly water stressed saplings over more highly water stressed saplings (Conner 1988).

Foliar N concentration is also known to influence foliar quality and quantity, and hence, amounts of foliar damage by insect herbivores (Jones and Coleman 1991; Kyto et al. 1996; Wait et al. 1998, 2002; De Bruyn et al. 2002). Plant tissue typically contains 0.03 to 7.0% N, with higher concentrations occurring in saplings (Mattson 1980; Wait et al. 1998). High N concentration in plant tissue is thought to be beneficial to insects due to the increased nutritional value of the leaves or by decreasing levels of carbon-based defensive compounds and other secondary metabolites (Kyto et al. 1996). High N concentrations can also increase the amount of foliar tissue available for herbivore damage (Wait et al. 1998, 2002; De Bruyn et al. 2002).

Periodic fires are often used to maintain oak dominated communities. Oak communities in Missouri have undergone periodic burning since the time Native Americans inhabited the area. Fire scar analyses suggests that prior to European settlement in southern Missouri, burn intervals spanned from 2.8 to 3.2 years (Guyette and McGinnes 1982; Cutter and Guyette 1994). Following European settlement, fire intervals increased to 24 years (Cutter and Guyette 1994). Since the 1980s, burning has been prescribed as a management strategy in Missouri (Peterson and Reich 2001). Prescribed burning has been shown to decrease competition, increase light penetration, and increase quantity and quality of plant foliage (Adams and Rieske 2003). For example, Rieske (2002) found that chestnut oak seedlings grown in burned plots had higher leaf N concentration, relative to control plots. However, fire's impact on foliar damage caused by insects is relatively unknown.

This study was conducted to estimate amounts of foliar leaf area consumed by insect herbivores in an Ozark oak community comprised of recently burned and unburned savanna and forest habitats. This study was conducted in the Drury Conservation Area (DCA) in southwest Missouri, where the predominant community types are upland oak forest (60%) and oak savanna (35%) (Wait and Aubrey 2014). Oak saplings less than 1.5 m in height (hereafter, oak saplings) were the focus of this study since these saplings represent prospective canopy recruitment that could serve for commercial value. Leaf chewing insects (herbivores) were the primary focus of this study since they are one of the most prevalent herbivore groups in Missouri oak communities (Marquis and Forkner 2004). Leaf area, plant moisture status and foliar N concentration were measured to qualitatively associate biotic variables (i.e., measures of foliar quantity and quality) with damage levels by herbivores. The objectives for this study were to examine the following as a function of forest habitat and spring burn: (1) determine amounts of leaf area available for consumption; (2) estimate amounts of folivory; (3) determine if patterns in folivory and oak nutritional quality were related; and (4) examine if folivory could be attributed to plant water status and leaf N concentration.

2. Methods

2.1 Study Habitat

This study was conducted at Bull Shoals Field Station 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. The average annual temperature ranges from 32° C to -4° C and the average annual rainfall is 1092.2 mm. DCA has a karst topography, with elevation ranging from 180 to 340 meters (600 to 1100 ft). At DCA, two primary forest habitat types exist: oak-hickory forest and post-oak savanna. The forest is thought to be the result of 50 years of fire suppression, causing an increase in stocking density of savanna habitat. The current savanna habitat at DCA is the product of the re-introduction of fire to the area.

Near the end of the 19th century, periodic fires were suppressed in portions of this area, allowing the encroachment of non-oak species and the degradation of the savanna landscape.

2.2 Experimental Design

Foliar damage was assessed across four habitats: control (unburned) savanna, burned savanna, control (unburned) forest, and burned forest. The savanna habitat has been maintained with periodic fire since the mid-1980s. The control forest had not been burned in over 50 years, while the burned forest was burned for the second time in the spring prior to the study. Within each study habitat, three 50 m by 5 m (250 m^2) belt transects were established. Within each transect, 15 oak saplings < 1.5 m in height were tagged for a total of 45 oaks per habitat. Oak species used in this study included *Q. stellata*, *Q. alba*, *Q. muhlenbergi*, *Q. falcata*, *Q. velutina*, *Q. rubra*, and *Q. shumardi*.

2.3 Leaf Area Determination

To calculate leaf area from length and width measurements, a total of 70 randomly selected oak leaves were collected from the control forest. The leaves ranged in area from 18.95 to 203.63 cm^2, and were taken from a range of plant sizes that were representative of oak saplings from all habitats. The length and width (to the nearest 0.1 cm) of these leaves were measured using a clear plastic ruler. The area of each leaf was determined using a CI-420 leaf area meter (CID, Inc., Camas Washington, USA). The product of the length and width was used in a linear regression model to predict leaf area. The linear model (R = 93.3 %, Appendix C) yielded a best fit regression of: Area (cm) = 5.45913 + 0.54909 (Length*Width).

Each leaf on each of the 45 oak saplings per study habitat that was initially tagged had length and width measurements taken to the nearest millimeter in the field using a clear plastic ruler at the end of August. The product of the length and width of each leaf was calculated and then entered into the regression equation for leaf area (cm^2). The leaf areas of each oak from each habitat were then summed to obtain an estimate of the total leaf area available for herbivore consumption.

2.4 Visual Scoring of Leaves

Each leaf on each tagged oak plant was visually scored to estimate the area removed due to insect herbivores. A modified ranking system based on the methods of Futuyma and Wasserman (1980) was used to visually score leaves. Numbers were assigned to each leaf corresponding to a range of percentages of leaf area removed: 0 = 0%, 1 = 1-5%, 2 = 5-20%, 3 = 20-40%, 4 = 40-60%, 5 = 60-80%, and 6 = 80-100% leaf area removed, respectively. Once each leaf of each plant had been visually scored, the individual leaf scores were 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 study habitat. Visual scores from August were used to estimate the amount of foliar damage on oak saplings because the length and width measurements used to calculate total leaf area were also taken at that time.

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. For example, a rank of 1 indicated that 1 to 5% of the leaf area was damaged and had a mean of 3%, while a rank of 2 corresponded to 5 to 20% foliar damage and had a mean of 12.5%. The visual scores for each oak plant were replaced with the mean percentage of leaf area damaged (i.e., a rank from 1 to 1.9 was replaced with 3% and a rank from 2 to 2.9 was replaced with 12.5%). The mean percent of damage per plant (obtained from the visual score data) were then multiplied by the total leaf area of each plant in each habitat to estimate the leaf area removed. The leaf area removed per habitat was estimated by summing the leaf area removed from each plant.

2.5 Water Potential Measurements

Mid-day water potential measurements were taken during May, June, July, and August. Due to the destructive nature of water potential measurements (i.e., removing an entire leaf at the petiole) five oak saplings were randomly selected adjacent to each transect (15 oak saplings used per habitat) each month for water potential measurements. The same oak saplings were used when obtaining pre-dawn and mid-day measurements each month. A pressure chamber (PMS Instrument Co., Corvallis Oregon, USA) was used to obtain all water potential measurements. Stems < 3.0 millimeters in diameter were cut using a clean razor blade. The pressure applied to the stem (in Mega Pascals) to force water out was equivalent to the amount of moisture stress that an oak was experiencing.

2.6 Leaf Nitrogen Analysis

Leaf tissue nitrogen (N) was assessed using microkjeldahl analysis following the methods of Anderson and Polis (1999). Due to the destructive nature of Kjeldahl analysis (removing an entire leaf at the petiole) the leaf material removed from the five oak saplings adjacent to each transect for water potential measurements were also used for N analysis (15 oak saplings per habitat). Leaves were dried at 60° C and ground, 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, Maryland, USA).

2.7 Statistical Analysis

The effects of habitat on total leaf area, leaf area removed, herbivore damage, plant water status and foliar N concentration were assessed using a multi-factorial ANOVA. Habitat and month were treated as fixed factors. transect, which was nested under habitat was treated as a random factor. In the herbivore damage ANOVA model, individual was nested under habitat and transect, and was treated as a random factor. In addition, Tukey's pairwise comparisons were done to assess differences between habitats in total leaf area, leaf area removed, herbivore damage, plant water status, and foliar N concentration. All statistical tests were performed with the GLM procedure on Minitab 14 (Minitab, Inc., 2003). All ANOVA conclusions were based on a type-I error rate of 0.05.

3. Results

3.1 Total Leaf Area and Herbivore Damage

Total leaf area was significantly greater in the two savanna habitats than in the two forested habitats ($P = 0.004$) (Table 1, Figure 1). The control savanna had 115.02% more leaf area than the control forest. There was no significant difference in total leaf area between the control and burned savanna (Tukey's $P = 0.9949$) and between the control and burned forest (Tukeys $P = 0.6910$).

Foliar damage was significantly greater in the forested habitats than in the savanna habitats ($P < 0.001$) (Table 1, Figure 2). The control savanna had 26.19% less foliar damage than the control forest did. Foliar damage did not significantly differ between the control and burned savanna habitats (Tukeys $P = 0.8249$). Foliar damage was 28.05% higher in the burned forest than in the control forest. Month had a significant effect on herbivore damage ($P < 0.001$) because it increased over time at each habitat. The month-by-habitat interaction was also significant ($P < 0.001$) because of the sharp increase in foliar damage in the two forested habitats between June and July.

3.2 Leaf Area Removed and Herbivore Impact

The burned forest had the greatest amount of leaf area removed which resulted in a significant habitat effect ($P = 0.004$) (Table 1, Figure 3). Leaf area removed did not differ significantly between the control savanna and control forest or between the control and burned savanna (Tukeys $P = 0.9927$ and 0.8303). The burned forest had 76.29% more leaf area removed than the control forest.

To estimate the proportion of leaf area removed (i.e., herbivore impact) from each habitat, the percentage of total leaf area removed in each habitat was calculated by dividing the leaf area removed by the total leaf area. Herbivores had the greatest impact in the burned forest, removing 19.67% of the total leaf area, followed by the control forest (13.08%), the burned savanna (4.93%) and the control savanna (4.58%), respectively.

3.3 Plant Water Stress

Oak plant water stress was significantly higher in oak saplings grown in the two savanna habitats than in the oak saplings grown in the two forested habitats ($P = 0.002$) (Table 1, Figure 4). The oak saplings in the control savanna were 16.41% more water stressed than those in the control forest and 21.55% less water stressed than oak saplings in the burned savanna. There was no significant difference (Tukeys $P = 0.4654$) in water stress in oak saplings in the control and burned forest. Month had a significant effect on oak plant water stress ($P < 0.001$) because oak saplings became more water stressed with time. The month-by-habitat interaction was also significant ($P < 0.001$) because of the sharp increase in oak plant water stress in the burned savanna between June and July. In addition, measurements of pre-dawn water potential were taken as an estimate of soil moisture; however, since the pattern was the same as that of oak plant water stress, those data are not presented.

3.4 Foliar Nitrogen Concentration

Habitat had a significant effect on oak plant foliar nitrogen (N) concentration ($P < 0.001$) (Table 1, Figure 5). The oak saplings in the control savanna had 10.06% less foliar N than the oak saplings in the control forest, but they had 10.53% more foliar N than those in the burned savanna. There was no significant difference in oak plant foliar N between the control and burned forest habitats (Tukeys $P = 0.2151$). Month had a significant effect on foliar N ($P < 0.001$) because foliar N generally declined in oak saplings in all four habitats. The month-by-habitat interaction was significant ($P < 0.001$) due to the sharp declines in oak foliar N between May and June and July and August in the burned forest habitat.

4. Discussion

This study estimated foliar damage to oak saplings in forest and savannah habitat to gain a better understanding of how fire may alter the quality and quantity of oak species for advanced regeneration and potential commercial value. Control and burned savanna lost 4.58% and 4.93% of their total leaf area, while the control and burned forest lost 13.08% and 19.67% of their total leaf area, respectively. The percentage of leaf area removed in the control and burned forest habitats fell within the range found by Hochwender et al. (2003). However, the damage amounts in the savanna habitats were much lower than those found by Hochwender et al. (2003) and Marquis and Forkner (2004). Herbivores had the greatest impact in the burned and control forest habitats, both of which had less leaf area than the two savanna habitats (Table 1, Figure 1). The greater amount of foliar area in the savanna habitats than that of the forest habitats could be attributed to the differences in the light environment. It has previously been shown that saplings grown in a high light environment can have more leaves, higher leaf dry mass, and greater leaf weight per unit area than shade grown saplings (Dudt and Shure 1994; Crone and Jones 1999; Baraza et al. 2004). The savannas have more light penetrating their canopies than the forest habitats, resulting in more leaves and greater leaf area in the savanna.

The spring burn played a role in the differences in total leaf area in both the forest and savannah. It has been shown that following a burn event in oak forests, oaks re-sprout and produce more stems (e.g., Wait and Aubrey 2014). Since fire has been used at the savanna habitats for a longer period of time than in the forest habitat, the oaks have re-sprouted many times and produced more stems; and ultimately, have more leaves and greater leaf area than the forested habitats. This is an important consideration when predicting the future commercial value of oak in a habitat.

Since the control forest habitat had 26.19% more foliar damage than the control savanna habitat, it would be expected that there would be differences in plant water stress and foliar N concentrations. We found that the oak saplings in the control forest habitat were 16.41 % less water stressed than the oak saplings in the control savanna. Oak saplings in the control forest had 10.06% more foliar N than oak saplings in the control savanna. The lower light level in the forest was possibly a contributing factor to the higher foliar N concentration of the oak saplings. In addition, foliar N concentration was probably higher in the control forest than the control savanna because there is more leaf litter in the control forest, ultimately resulting in more nutrient cycling.

The amounts of foliar damage were virtually the same between the burned and control savanna habitats, so it would be predicted that there would not be any differences between plant water stress and foliar N concentration as a function of a spring burn. However, oak saplings in the recently burned savanna were 21.55% more water stressed and had 10.53% less foliar N than the oak saplings in the control savanna. The lower foliar N concentration in the burned savanna could have resulted from a delay in post-burn nutrient influx. For example, Adams and Rieske (2003) showed that concentrations of many foliar nutrients, including nitrogen were higher one year following a burn event.

There was 28.05% more foliar damage in the burned forest habitat than in the control forest habitat; therefore, it would be expected that differences in plant water stress and foliar N exist between habitats. Oak saplings in the control forest were 6.14% more water stressed and had 4.35% more foliar N than the oak saplings in the burned forest. Swift et al. (1993) and Rieske (2002) showed that prescribed fire can increase the soil moisture and reduce plant water-stress, which may be related to decreased evapotranspiration in the burned area. The foliar N concentration in the control forest could have been higher because of the presence of the litter layer, resulting in more nutrient cycling than in the burned forest. In addition, Adams and Rieske (2003) showed that the post-fire influx of nutrients can be delayed up to one year.

This study indicates that insect herbivores remove the largest proportion of leaf area from oak saplings in forested habitat, and thus have a greater impact than in oak savanna. Generally, it is thought that habitats that have larger amounts of leaf area have more herbivore damage because they can support a larger herbivore population. However, the opposite result is found in these oak forests, there was more herbivore damage in the forested habitats which had less leaf area than the savanna habitats. In addition, herbivore damage was not related to foliar quality. Many studies suggest that water stressed saplings are more susceptible to herbivore damage (White 1984; Mattson and Haack 1987; Atkinson and Nuss 1989; Warring and Cobb 1992; Willis et al. 1993). However, there was more herbivore damage to oak saplings in the two forested habitats, which were less water stressed than those in the two savanna habitats. Insect herbivores have also been shown to do more damage to saplings that are high in foliar N (Kyto et al. 1996). However, insect herbivores removed more leaf area from the burned savanna and forest habitats, both of which were lower in foliar N than the unburned habitats. Finally, prescribed fire was not associated with greater amounts of herbivore damage in the savanna habitats, but foliar damage did seem to be associated with a prescribed spring burn in the forest. The results of this study, along with other recent analyses (e.g., Bettinger et al., 2013; Dey 2014), should be beneficial to understanding the effects of management of oak forests because it aids in understanding where insect outbreaks could occur and where insects will have the greatest negative effects on the future commercial value of oak trees.

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Table 1: **Grand mean (± standard deviation) total leaf area, leaf area removed, visual score, pre-dawn water potential, mid-day water potential, and foliar nitrogen concentration of oak saplings (< 1.5 m height) as a function of habitat. Significant differences (Tukeys P = 0.05) between habitats are indicated with different letters.**

Habitat	Total Leaf Area (cm^2)	Leaf Area Removed (cm^2)	Rank Damage Score	Mid-Day Water Potential (MPa)	% Foliar Nitrogen
Control Savanna	88,155 (1,404) A	4,036 (118.3) A,B	1.46 (0.43) A	-1.78 (0.96) A	1.70 (0.23) A
Control Forest	23,780.3 (507.2) B	3,110.9 (79.3) A	1.90 (0.73) B	-1.51 (0.82) C	1.88 (0.31) C
Burned Savanna	90,705 (1,470) A	4,472.2 (105.8) B	1.49 (0.46) A	-2.21 (1.18) B	1.53 (0.27) B
Burned Forest	35,314 (714) B	6,947.4 (159.6) C	2.52 (0.88) C	-1.42 (0.76) C	1.80 (0.53) C

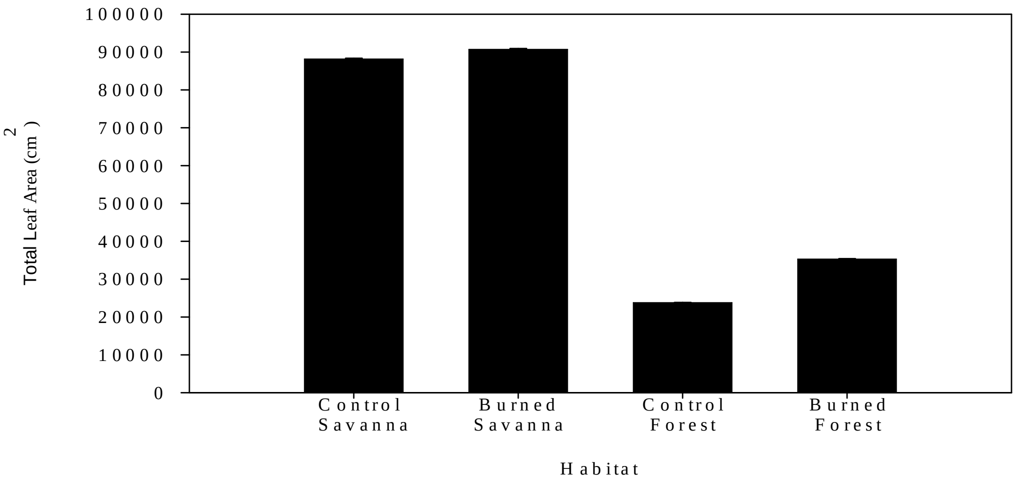

Figure 1: Mean (± standard error) total estimated oak plant (<1.5 m height) leaf area in oak forest and savanna habitat in Southwest Missouri. N = 45 oak saplings per study site.

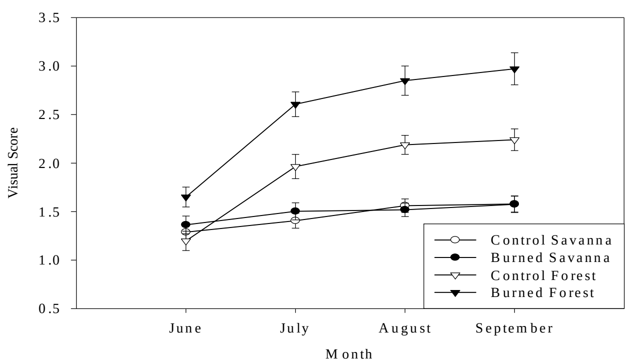

Figure 2: Mean (± standard error) leaf area removed from oak plants (< 1.5 m height) by insect herbivores each month in oak savanna and forest habitat in Southwest Missouri. N = 45 saplings per habitat and date. See Methods for visual scoring procedure.

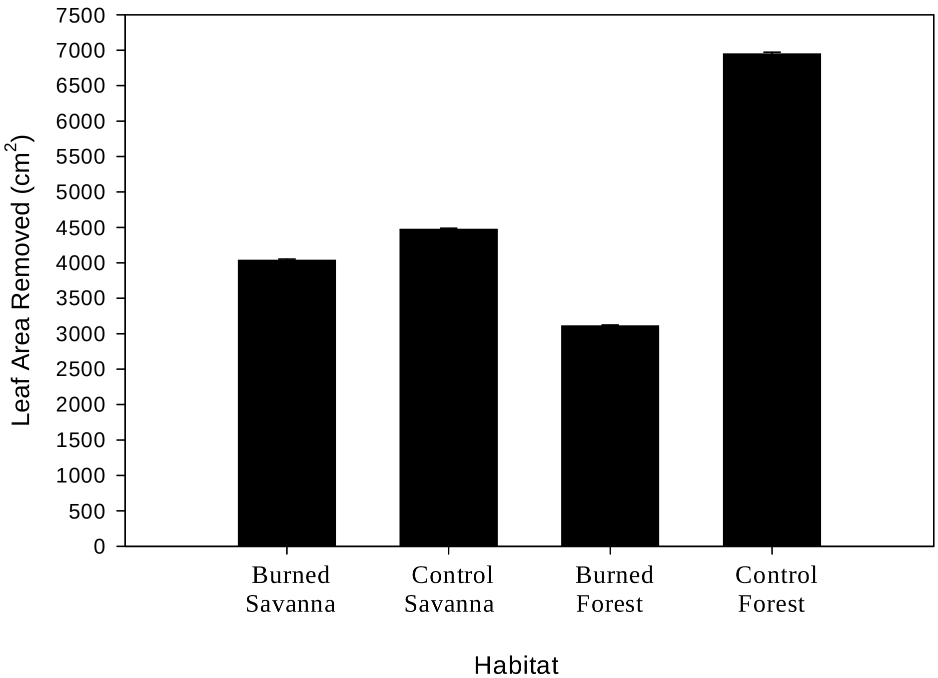

Figure 3: Estimated amount of leaf area (± standard error) damaged by insect herbivores in oak savanna and forest habitat in Southwest Missouri. Estimates are given in cm^2. See Methods for calculation of estimated leaf area.

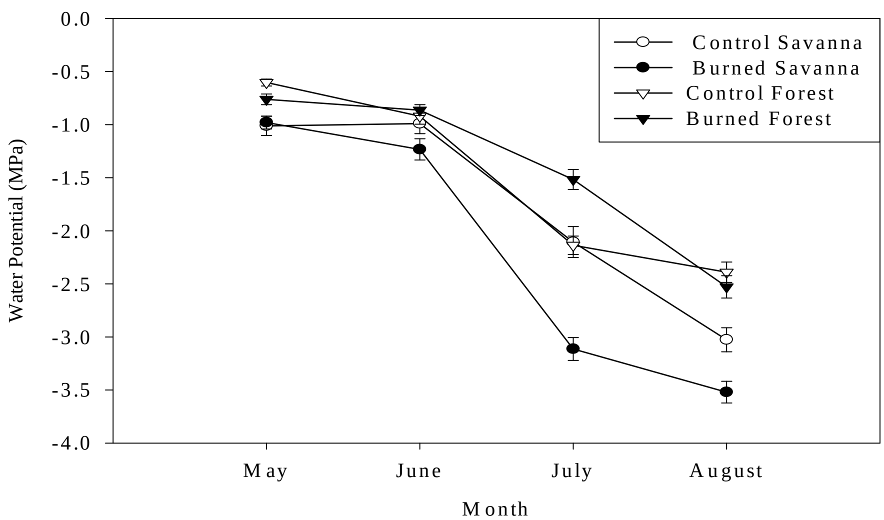

Figure 4: Mean (± standard error) mid-day water potential of oak plants (< 1.5 m height) in oak savanna and forest habitat in Southwest Missouri. N= 15 oak saplings per habitat and date.

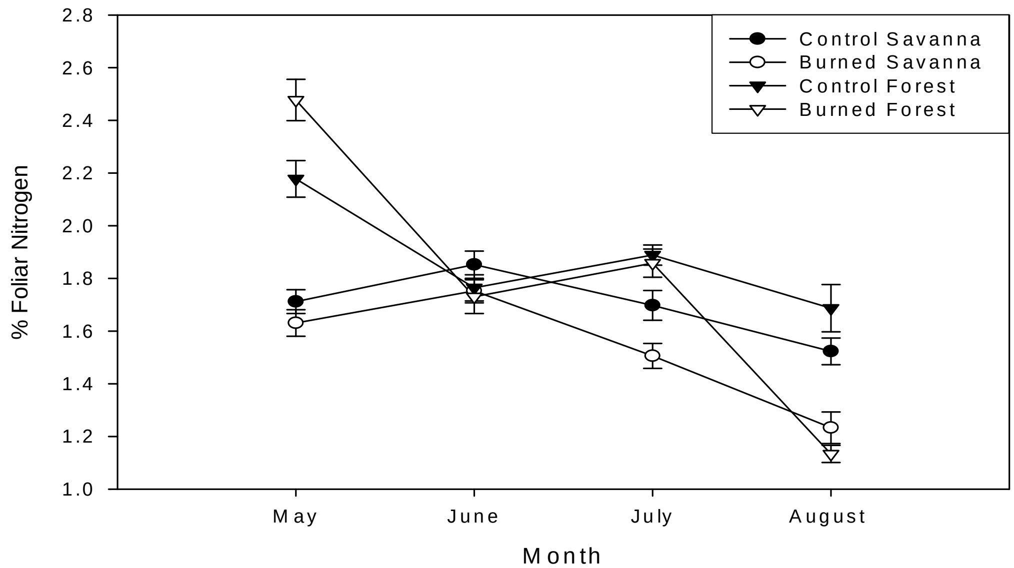

Figure 5: Mean foliar N concentration (± standard error) for leaves of oak saplings (< 1.5 m height) as a function of forest habitat in Southwest Missouri. N = 15 oak saplings per habitat and month.