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Herbaceous response to canopy removal in southwestern oak woodlands

GUY R. MCPHERSON AND JAKE F. WELTZIN

Authors are associate professor and graduate research associate, School of Renewable Natural Resources, University of Arizona, Tucson, Ariz. 85721

Abstract

An understanding of overstory-understory relationships in southwestern oak woodlands is important for predicting response of these systems to disturbance or manipulation. The objective of this study was to evaluate the response of herbaceous plants to removal of the overstory in evergreen oak woodlands. Overstory plants were removed from 30 × 30 m plots in January 1993 and January 1994, and the response of herbaceous plants in these plots was compared to untreated controls for 5 and 4 years, respectively. The C_4 graminoid and total biomass increased after overstory removal to as much as 10 times greater than controls, remained at elevated levels the second year, declined in subsequent years to 3–7 times the production of controls, and increased slightly during the final year of the study (1997). Overstory removal was necessary but not sufficient to affect herbaceous dicot biomass, which increased relative to controls during years with above-average winter precipitation. The C_3 graminoids did not respond to overstory removal.

Key Words: encinal, forage, overstory-understory relations.

Resumen

Una comprensión de las relaciónes de los estratos superior y inferior en los bosques de encino del suroeste es importante para estimar las respuestas de estas sistemas a perturbación o úmanipulación. El objeto de este estudio fue evaluar la respuesta de plantas herbaceas a remoción del estrato superior en los bosques de encino siempre verde. Plantas del estrato superior fueron removida de parcelas experimentales, del tamano 30 x 30 m, en Enero 1993 y Enero 1994. La respuesta de las plantas herbaceas en estas parcelas fueron comparados a parcelas control sin tratamiento para 5 años (estrato superior removida 1993) y 4 años (estrata superior removida 1994). En total, grama de C_4 y biomasa incrementaron despuesõ de remoción del estrato superior como 10 veces mayor que parcelas sin tratamiento. Biomasa de los grupos quedo elevado el segundo año despues de remoción de cobertura de follaje, y bajo en año subsecuente a 3–7 veces el producción de parcelas control sin tratamiento. En fin, biomasa incremento solamente un poquito durante el último año del estudio (1997). Remoción del estrato superior fue necessario, pero insuficiente a afectar biomasa de dicotiledoneas herbaceas, los que incrementaron relativo a parcelas control durante años con precipitacón de invierno arriba medio. Gramas de C_3 no respondieron a remoción de estrato superior.

Oak woodlands occupy several million hectares of arid and semi-arid lands in the southwestern United States and northern Mexico (McPherson 1992). These evergreen oak woodlands are subject to a variety of uses, including livestock grazing, recreation, and fuelwood harvest. Despite the areal extent and ecological and economic importance of this vegetation type, it has been characterized by little research (Ffolliott et al. 1992). The paucity of ecological information about southwestern oak woodlands represents an important gap in understanding and managing these systems (McPherson 1992, McClaran and McPherson in press).

Data on overstory-understory relationships in southwestern oak woodlands are particularly scarce, despite the importance of these data for predicting response to disturbance or manipulation. Furthermore, research on overstory removal in other woodlands provides a poor basis for comparison because of differences between systems and because previous studies have not been replicated in space and time. Most previous research in oak woodlands has been conducted in regions dominated by winter rainfall (e.g., Heady and Pitt 1979, Jansen 1987, Kay 1987, Bartolome et al. 1994). In contrast, southwestern oak woodlands are characterized by substantial summer precipitation (McPherson 1997). In addition, most previous studies confound site and canopy effects, as discussed by Bartolome et al. (1994).

Overstory-understory relationships have potentially important implications for management goals focused on wildlife habitat, watershed values, biological diversity, livestock production, and recreation. However, the paucity of research on overstory-understory interactions in southwestern oak woodlands severely constrains the ability to address any of these important issues. For example, the rudimentary issue of herbaceous response to canopy removal remains unknown. If grasslands are constrained by edaphic or climatic factors, then the presence of an overstory canopy may not interfere with herb production and removal of the canopy may not facilitate herb production (*sensu* Bartolome et al. 1994). Conversely, if overstory plants occupy sites that could be occupied by grasses, then removal of the canopy could enhance herb production. The virtual absence of understory herbs beneath the canopy of oaks implies that the response of understory herbs to canopy removal may be negligible.

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The objective of this study was to determine the response of herbaceous plants to removal of the overstory in closed-canopy oak woodlands, and to determine if this response changed with time since overstory removal.

Study Site

Research was conducted on a 6-ha study site in southeastern Arizona, USA. The site is located at the mouth of Blacktail Canyon (31° 35' N, 111° 35' W) on Fort Huachuca Military Reservation (FHMR). Livestock have been excluded from FHMR since about 1950 (Haworth and McPherson 1994). The site is 1,570 m elevation on a 10% slope with a northern aspect. Soil is mapped as a complex of Terrarossa (fine, mixed, thermic Aridic Paleustalfs), Blacktail (fine, mixed, thermic Aridic Argiustolls), and Pyeatt soils (coarse-loamy, mixed, thermic Aridic Calciustolls) (U.S. Department of Agriculture Soil Conservation Service 1994).

The climate is semi-arid, with an average annual temperature of 14.2°C. Annual precipitation is bi-modal, with about 60% of the 452-mm average annual precipitation occurring in summer and 20% in winter (long-term data based on Canelo Hills, Arizona station, National Oceanic and Atmospheric Administration 1995). The region is characterized by an absence of precipitation between late March and early July during nearly all years.

Vegetation is southwestern encinal, or evergreen oak woodland, and is near the lower-elevation boundary of evergreen oak woodland. Vegetation was typical with respect to other southwestern oak woodlands in the United States (McPherson 1997, McClaran and McPherson in press). For example, overstory tree cover was visually estimated at 75% before application of treatments. Overstory cover consisted almost entirely of the evergreen Emory oak (*Quercus emoryi* Torr.), the typical dominant species in southwestern oak woodlands (Mehlert and McPherson 1996). Understory herbaceous cover was sparse. Taxa present included the C_4 perennial bunchgrasses sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], Texas bluestem (*Andropogon cirratus* Hack.), green sprangletop [(*Leptochloa dubia* (H.B.K.) Nees.], plains lovegrass (*Eragrostis intermedia* Hitchc.), and three-awns (*Aristida* L. spp.) and very few C_3 perennial graminoids {pinyon ricegrass [*Piptochaetium fimbriatum* (H.B.K.) Hitchc.], bottlebrush squirreltail (*Sitanion hystrix* J.G. Smith), sedges [*Cyperus* (Tourn.) L. spp.]} and herbaceous dicots [star-glory (*Ipomoea coccinea* L.), cudweed (*Gnaphalium chilense* Spreng.)].

Methods

Nine homogeneous, 30 × 30 m plots were located and permanently marked in autumn 1992. One of 3 treatments was assigned at random to each plot: overstory removal in 1993, overstory removal in 1994, or control (overstory intact). This completely randomized design was employed because of the perceived overall homogeneity of the study site and because a block design would have required canopy removal over a larger area, which was not feasible. Similarly, logistical constraints precluded use of more replicates. Overstory removal treatments were initiated in January of each year and were maintained by cutting recently established woody plants and oak sprouts several times each year with axes.

We clipped herbaceous biomass from 15, 0.5-m^2 quadrats randomly located within the center 20 × 20 m of each plot to minimize edge effects in late October from 1993 to 1997. Quadrats were re-located if they coincided with woody plant stumps or previously clipped quadrats. Plants were clipped to a 2-cm stubble height, removed immediately, and separated into the following categories: C_4 graminoids, C_3 graminoids, and herbaceous dicots. Biomass was dried at 50°C for 4 days and weighed to the nearest 0.1 g. The size and number of quadrats was based on the variability of herbaceous biomass at a nearby savanna (Haworth and McPherson 1994).

Biomass data were tested for normality with the Shapiro-Wilk W-statistic (Shapiro and Wilk 1965) and for homogeneous variances with Hartley's (1950) test. Data were not normally-distributed ($P < 0.05$), so were log-transformed. Log-transformed data were distributed normally and had homogeneous variances, so we used profile analysis to analyze these repeated-measures data with multivariate analysis of variance (MANOVA) ($\alpha = 0.05$) (von Ende 1993). Because not all treatments were present during each year (i.e., the 1994 overstory-removal treatment had not been applied when herbaceous biomass was sampled in 1993), we used 2 models, one with MANOVA on the 2 treatments present between 1993 and 1997 (overstory removal in 1993, overstory intact), and a second MANOVA with all 3 treatments present in 1994 through 1997. Because MANOVA does not enable detailed comparisons within treatments or years, we used analysis of variance (ANOVA) to compare treatments within years, and paired *t*-tests to compare years (i.e., time since overstory removal) within treatments. Fisher's LSD (Fisher 1960) *a posteriori* mean separation tests were conducted when MANOVA and ANOVA revealed differences ($P < 0.05$). Quadrats were treated as subsamples in all analyses.

Results

Biomass of C_3 graminoids was not affected by main or interactive effects of overstory treatment and time-since-treatment ($P > 0.14$) for either MANOVA model (canopy removed in 1993, or 1994). C_3 graminoids, which were represented by an approximately equal mix of grasses (predominantly pinyon ricegrass and bottlebrush squirreltail) and sedges, accounted for little biomass (mean ± SE = 1.3 ± 0.5 g·m^{-2}).

An interaction between treatment and time-since-treatment was evident for C_4 graminoid, herbaceous dicot, and total herbaceous biomass for both MANOVA models. Beneath intact canopies, C_4 graminoid, herbaceous dicot, and total herbaceous biomass did not vary through time (Table 1); C_4 graminoids dominated these sparse communities (20.0 ± 3.2 g.m^{-2}), and contributed nearly 90% to total herbaceous biomass (23.3 ± 3.4 g.m^{-2}).

Overstory removal increased C_4 graminoids relative to controls in all years (Table 1). The magnitude of the response to overstory removal depended on time since canopy removal for the first 3 years (Fig. 1), regardless of which year the canopy was removed: C_4 graminoids increased in the first year after clearing, remained elevated for the second year after overstory removal, and then decreased in the third year ($P < 0.05$). Thereafter, the response of C_4 graminoids in the cleared treatments was year-dependent: biomass decreased in 1996, then increased in 1997 ($P < 0.05$). After removal of the canopy, C_4 graminoids that were dominant included taxa present before treatments were applied (see Study Site).

Table 1. Mean (± SE) herbaceous biomass ($g \cdot m^{-2}$) during 5 years in southeastern Arizona, USA. Experimental plots were left intact or were subjected to removal of the tree canopy in 1993 or 1994 (n = 3).

Year	Treatment[1]	C_4 graminoid		C_3 graminoid		Dicots		Total	
		(g/m^2 ISE)							
1993	Control	27.0	(9.3)	0.3	(0.2)	2.2	(1.2)	29.4	(10.6)
	CR 1993	145.0	(7.0)	1.4	(0.8)	14.0	(3.8)	160.5	(8.2)
1994	Control	18.9	(5.5)	0.9	(0.5)	0.6	(0.4)	20.4	(6.2)
	CR 1993	207.8	(27.1)	4.4	(1.2)	5.7	(1.6)	218.0	(25.8)
	CR 1994	121.3	(13.6)	2.5	(2.2)	8.6	(3.7)	132.4	(13.7)
1995	Control	19.0	(4.2)	0.4	(0.2)	1.7	(1.1)	21.1	(4.8)
	CR 1993	87.7	(9.0)	5.2	(5.1)	107.2	(34.9)	200.1	(48.9)
	CR 1994	158.7	(26.4)	1.4	(0.8)	80.8	(21.2)	240.9	(26.8)
1996	Control	16.7	(1.5)	0.0	(0.0)	4.5	(2.0)	21.2	(1.8)
	CR 1993	55.5	(6.5)	0.2	(0.1)	54.9	(3.5)	110.6	(8.2)
	CR 1994	112.3	(19.1)	0.5	(0.4)	36.8	(14.6)	149.6	(5.8)
1997	Control	18.3	(13.5)	0.1	(0.1)	5.8	(2.0)	24.2	(13.8)
	CR 1993	102.2	(34.3)	0.4	(0.3)	23.1	(4.7)	125.6	(39.9)
	CR 1994	151.6	(27.6)	0.0	(0.0)	32.6	(13.6)	184.2	(17.1)

[1]Control = canopy not manipulated; CR 1993 = canopy removed in January 1993; CR 1994 = canopy removed in January 1994.

Response of total herbaceous biomass mirrored response of C_4 graminoid biomass for all treatments and years ($P < 0.05$). The magnitude of the difference between intact and overstory-removed plots varied from about 3-fold (C_4 graminoids, 1996) to over 10-fold (total herbaceous biomass, 1995) (Table 1).

Herbaceous dicots were poorly represented in both canopy-removal treatments in 1993 and 1994 (Table 1). However, dicots increased markedly during 1995 and 1996 in both treatments, then declined slightly in 1997 ($P < 0.05$). Camphorweed [*Heterotheca subaxillari* (Lam.) Britton & Rusby], sunflower (*Helianthus petiolaris* Nutt.), and cudweed were locally abundant in disturbed plots, but remained absent from intact woodlands.

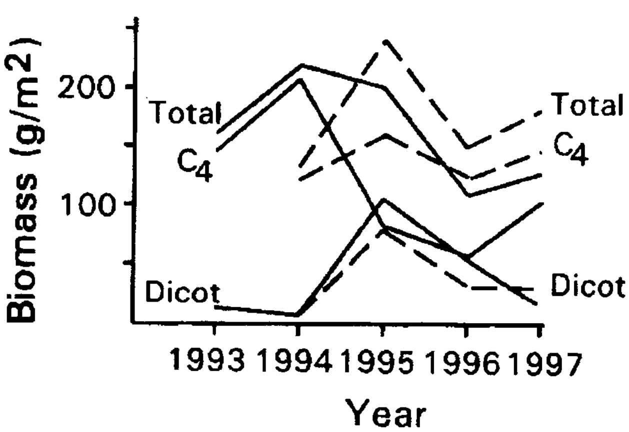

Fig. 1. Mean biomass of C_4 graminoids, herbaceous dicots, and all herbaceous plants (total = sum of C_4 graminoids, C_3 graminoids, and herbaceous dicots) after removal of evergreen oak woodland overstory in southeastern Arizona. Solid lines and broken lines indicate overstory removal in January 1993 and January 1994, respectively. Herbaceous biomass in uncleared (control) treatments and biomass of C_3 graminoids was uniformly sparse in all treatments (Table 1), and therefore is not shown.

Discussion

Emory oak trees in the current study occupied sites capable of considerable herbaceous biomass production. The presence of mature Emory oak trees clearly interferes with production of both C_3 dicots and C_4 graminoids. This finding is consistent with studies of interactions between these life-forms at earlier life-history stages, when Emory oak seedlings compete with seedlings for soil resources (McPherson 1993, Weltzin and McPherson 1997, McClaran and McPherson in press). In addition, the response of herbaceous biomass after canopy removal of Emory oak is similar to that observed after removal of blue oak (*Quercus douglasii* H. & A.) on mesic sites in northern California (400–500 mm average annual precipitation) (Heady and Pitt 1979, Jansen 1987, Kay 1987).

The sharp increase in herbaceous biomass after removal of the overstory parallels comparative research in a nearby savanna, where herbaceous standing crop was about 40% lower beneath isolated Emory oak trees than in interstitial zones during 2 successive years (Haworth and McPherson 1994). Because trees in the savanna were isolated, solar radiation incident to the understory zones depended on solar zenith angle and time of day, and belowground interference may have been restricted to the immediate subcanopy area. Differences in solar radiation and/or belowground interference thus likely contributed to differences in herbaceous production between the savanna study (40% reduction beneath trees) and the current study (80–90% reduction). However, comparative studies of subcanopy understories with adjacent canopy gaps confound microsite and canopy effects (Bartolome et al. 1994). For example, soils beneath woody plants often exhibit greater concentrations of nutrients than do adjacent grassland zones (Garcia-Moya and McKell 1970, Schlesinger et al. 1990, McPherson 1997). Thus, comparative studies represent poor analogs for determination of the effects of overstory removal on herbaceous response.

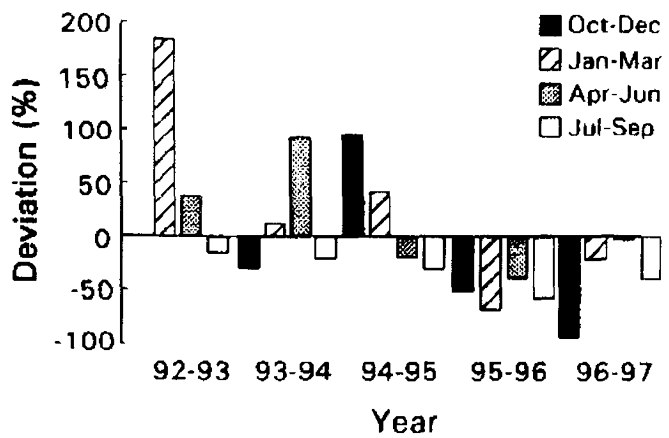

Fig. 2. Departures from long-term average seasonal precipitation at the southeastern Arizona study site.

Response of C_4 graminoids and total herbaceous biomass appeared to be unrelated to seasonal or total precipitation during the first 3 years of the current study. The C_4 biomass and total herbaceous biomass increased sharply in response to overstory removal, then remained elevated during the second year after the overstory was removed. Elevated levels of biomass during the second year after overstory removal occurred despite below-average summer precipitation in 1994 and 1995 (Fig. 2). Biomass of C_4 graminoids declined substantially during 1996 in both overstory-removal treatments, presumably because growing-season and annual precipitation were markedly below the long-term average. The C_4 biomass and total herbaceous biomass recovered slightly in the final year of the study, coincident with a slight increase in precipitation relative to 1996. Overstory removal apparently is necessary and sufficient to stimulate a response of C_4 graminoids (hence, total herbaceous biomass) if summer precipitation does not drop below about 60% of the long-term average.

We propose 2 hypotheses for the 1-year delay between overstory removal and maximum response of C_4 graminoids. First, at least 1 year may be required for complete colonization of the understory by bunchgrasses. Second, there may be a lag between overstory removal and increased nutrient availability: nutrients likely increase in cleared plots as a result of increased soil temperatures and/or decomposition of oak leaves and fine roots. The hypothesized nutrient "pulse" is short-lived, or dependent on precipitation during the growing season, as indicated by declines in herbaceous biomass 3 years after removal of the overstory. These hypotheses, or their potentially likely interaction, have not been tested in southwestern woodlands.

Unlike the response of C_4 graminoids, overstory removal was necessary but not sufficient to produce significant increases in biomass of herbaceous dicots. In addition to removal of the overstory, response of herbaceous dicots probably depended on cool-season precipitation, as suggested by the increase in dicots in 1995 when precipitation during the previous autumn and winter substantially exceeded the long-term average. Increased production of herbaceous dicots in 1995 was partially sustained through 1996 and 1997, despite the relative lack of precipitation in the autumn and winter of 1995–96 and 1996–97. Increased winter precipitation stimulated production of herbaceous dicots only when the overstory was removed, as evidenced by the lack of response in uncleared plots. Thus, increased light associated with overstory removal, in association with increased availability of precipitation during the cool season (possibly in association with increased nutrient availability), apparently provided conditions both necessary and sufficient for abundant growth of herbaceous dicots. Similar to C_4 graminoids, the drought that preceded the 1996 sample date likely contributed to the observed decline in dicot production.

Neither overstory removal nor increased winter precipitation experienced in the current study were sufficient to elicit a response from C_3 graminoids. These plants were uncommon in all treatments and years.

Implications for management of southwestern oak woodlands are relatively clear. Removal of the Emory oak overstory produces a substantial increase in biomass of C_4 graminoids, but no increase in C_3 graminoids. Given sufficient growing-season precipitation, C_4 biomass can remain elevated for several years after overstory removal. A positive response of herbaceous dicots is dependent on overstory removal and above-average winter precipitation.

Objective and comprehensive evaluation of overstory removal depends on site-specific management objectives and several factors not evaluated by this research (e.g., species composition, species diversity, infiltration, runoff, erosion, wildlife habitat). However, the substantial increase in production of perennial grasses associated with overstory removal suggests that management goals that depend on herbaceous production may be facilitated by overstory removal in these woodlands.

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