

Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities

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Abstract. We compared the effects of late dormant-season and late growing-season prescribed fires on herbaceous species in restored shortleaf pine- (*Pinus echinata*) grassland communities in the Ouachita Highlands of western Arkansas. Herbaceous species richness, diversity, and total forb and legume abundance increased following fire. Late growing-season burns reduced distribution and abundance of panicums (primarily *Panicum boscoii*, *P. dichotomum*, and *P. linearifolium*) while late dormant-season burns increased *Panicum* distribution and abundance. Density of legumes (such as *Stylosanthes biflora*) increased following frequent or annual dormant-season fires. However, season of fire influenced the distribution and abundance of fewer than 10 % of the species. Fire plays an essential role in pine-grassland communities by creating and maintaining open canopy conditions that perpetuate understory herbaceous plant communities.

Keywords: Arkansas; Fire ecology; Fire frequency; Fire season; Ouachita Mountains; Restoration ecology.

Nomenclature: Smith (1988).

Introduction

Fire played an important role in shaping formerly abundant pine- (*Pinus* spp.) grassland communities in the southeastern United States (Buckner 1989; Platt et al. 1988; Waldrop et al. 1992; Masters et al. 1995). Historical accounts before settlement describe these pine-grassland communities as open 'park-like' pine stands with a distinct grass-dominated herbaceous layer and recurrent woody layer, depending on fire frequency (James 1823; Featherstonhaugh 1844; Komarek 1965; Nuttall 1980; Waldrop et al. 1992; Masters et al. 1995). The accumulation of herbaceous material provided adequate fuels for frequent fires of aboriginal and lightning origin which maintained the open structure of these pine-grassland communities (Komarek 1965; Buckner 1989; Foti & Glenn 1991; Waldrop et al. 1992; Masters et al. 1995).

Similar to other forest communities of the World, settlement in the southeastern United States (18th to mid-19th century) altered these landscapes by removing or changing much of the natural vegetation, resulting in fragmented and dissected landscapes (Cottam 1949; Stearns 1949; Curtis 1956; Forman & Godron 1986; Kreiter 1995). The frequency and scale of fires in the region declined after settlement because of aboriginal displacement, fragmentation of habitats causing artificial fire breaks, and fire suppression by settlers (Pyne 1982). This decline in fire frequency caused once open pine-grassland communities to become much more densely forested. Dense forests minimize light reaching the forest floor, thus reducing the herbaceous plant community, understory forage, and habitat quality for many species of wildlife (Lewis & Harshbarger 1976; Masters 1991a; Wilson et al. 1995). The endangered red-cockaded woodpecker (*Picoides borealis*), an endemic of southeastern pine forests, is one example of a species that has declined, in part, as a result of increased forest density in the southeastern United States.

The U.S. Forest Service has begun to reconstruct or restore shortleaf pine- (*Pinus echinata*) grassland communities to benefit both plant and wildlife species dependent on these systems. In the Ouachita National Forest of western Arkansas, the Forest Service uses a program known as Wildlife Stand Improvement (WSI) that consists of thinning midstory and codominant pine and hardwood trees to near pre-settlement basal areas. Currently, WSI treated stands are burned during the dormant season on 3-yr intervals to maintain open structure. However, recent studies in the Ouachitas suggest that the historical fire regime was one of predominantly late growing-season fires and to a lesser extent dormant-season burns (Foti & Glenn 1991; Masters et al. 1995). To effectively restore this system, knowledge of the effects of both growing-season and dormant-season prescribed burns is necessary (Masters et al. 1995, 1996).

Numerous studies have compared the effects of growing-season and dormant-season fires on vegetation



Fig. 1. Restored pine-grassland in the Ouachita Mountains with *Pinus echinata*.

in Coastal Plain regions of Florida, Louisiana, and South Carolina (Grelen 1975; Hughes 1975; Lewis & Harshbarger 1976; Platt et al. 1988; Waldrop et al. 1992; Glitzenstein et al. 1995). Masters (1991a, b) and Masters et al. (1993) described the effects of dormant-season burns of varying frequency on vegetation under a variety of overstory conditions in interior highlands. Masters et al. (1996) described the effects of WSI and dormant-season burns on restored pine-bluestem communities. However, no information is available on the effects of growing-season burns in the Ouachita Mountains. Our main objective was to compare the effects of growing-season and dormant-season burns on herbaceous vegetation richness, diversity, and abundance in WSI-treated stands.

Study area

Our study focused on stands under active management for the endangered red-cockaded woodpecker within the 40 000-ha Pine-bluestem Ecosystem Renewal Area, on the Poteau Ranger District of the Ouachita National Forest (ONF) in Scott County Arkansas. The

ONF lies in the 2 280 000 ha Ouachita Mixed Forest Meadow Province and comprises 648 000 ha throughout the Ouachita Mountains in Arkansas and Oklahoma (Neal & Montague 1991; Bailey 1995). The Ouachita mountains are east-west trending, strongly dissected and range in elevation from 150 - 790 m (Fenneman 1938: 669). South-facing slopes tend to be dominated by shortleaf pine and more mesic north-facing slopes tend to be dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.) and other hardwoods (Johnson 1986; Foti & Glenn 1991). Ouachita Mountain soils developed from sandstone and shales and are thin and drought prone. A semi-humid to humid climate prevails with hot summers and mild winters (Smith 1989).

Pinus echinata was the dominant overstory species in all stands (Fig. 1). Codominant and intermediate overstory species included *Quercus stellata*, *Q. marilandica*, *Q. alba*, *Q. rubra*, *Q. velutina*, *Carya texana* and *C. tomentosa*. Tree heights in our study stands ranged from 15 - 23 m (\bar{x} = 18.3 m; S.D. = 3.1). Canopy cover ranged from 68 - 93 % (\bar{x} = 84.1% ; S.D. = 7.5). Woody sprouts (≤ 3 m tall) dominated the understory of these stands. The dominant understory woody species and vines included *Toxicodendron radicans*, *Vaccinium pallidum*, *Quercus stellata*, *Carya tomentosa*, *Rubus* spp., *Parthenocissus quinquefolia*, *Ceanothus americanus*, *Vitis rotundifolia*, *Quercus alba* and *Pinus echinata* (Sparks 1996).

Methods

Experimental design

Our experimental design encompassed two studies (Study 1 and Study 2) and was completely randomized. In these studies we used 12 stands (13.8 to 26.7 ha) that had been previously subjected to WSI and prescribed fire at 3-yr intervals (≥ 3 prescribed fire cycles). Overstory pine density and basal area was similar across all stands (Sparks 1996). Study 1 consisted of three treatments with four replications of each treatment ($n = 12$). Study 2 used the control and dormant-season fire stands from Study 1 ($n = 8$). Treatments are as follows:

Study 1

- (1) No-burn control (CON1; $n = 4$);
- (2) Late growing-season burn, September 1994 (GS1; $n = 4$);
- (3) Late dormant-season burn March-April 1995 (DS1; $n = 4$);

Study 2

- (4) Late growing-season burn, October 1995 (GS2; $n = 2$);
- (5) Late dormant-season burn, March 1996 (DS2; $n = 2$);
- (6) Frequent dormant-season fire, March-April 1995 and March 1996 (FDS; $n = 2$);
- (7) Infrequent dormant-season fire, burned March-April 1995, no-burn 1996 (IFDS; $n = 2$).

Study 1 and Study 2 dormant-season and growing-season fire treatments differed in that prescribed burns were applied after three vs. four growing seasons, respectively, following previous dormant-season fire. Study 2 used the dormant-season fire treatments from Study 1 to determine the effects of fire frequency on the herbaceous community. In both studies, late growing-season fires were performed because of poor burning conditions (primarily fuel moisture, presence of live vegetation and high relative humidities) earlier in the season.

Vegetation sampling

We sampled herbaceous vegetation during a two week period in late July 1994 (Study 1 pre-treatment), July 1995 (Study 1 post-treatment; Study 2 pre-treatment), and July 1996 (Study 2 post-treatment). In each stand, we established 30, 1 m × 1 m permanent plots (after Oosting 1956) at 30-m intervals on two to four randomly spaced lines perpendicular to the contour (after Masters 1991a, b). To avoid bias from surrounding stands, we did not sample within 50 m of any edge (Mueller-Dombois & Ellenberg 1974: 123). For each herbaceous species, we recorded percent frequency of occurrence and stem density within plots. Percent cover for vascular plant groups and objects such as rocks, tree boles, and logs was also estimated. Voucher specimens were collected, verified and deposited in the Oklahoma State University Herbarium.

Data analysis

We calculated species richness and diversity (Shannon-Weaver H') after Ludwig & Reynolds (1988) at the sample (m^2) and stand scales. In both studies, we summarized herbaceous species by mean density and percent frequency of occurrence for each year and treatment. All plant species were classified according to plant growth form (e.g., forb, legume, grass, etc.) and season of growth (cool vs. warm). Season of growth was determined by flowering dates described by the Great Plains Flora Association (1986) with cool-season species flowering from November to mid May, and warm-season species flowering from mid May through October. To account for pre-treatment differences, we determined the percent change [(post-treatment – pre-treatment / pre-treatment) × 100] in density and frequency of occurrence caused by treatments. All variables were tested for homogeneity of variance using Levene's test (Snedecor & Cochran 1980). These tests indicated homogeneity of variances, so we tested for treatment differences in percent change using a one-way GLM in which treatment was the factor of interest (Anon. 1985).

In Study 1, we used orthogonal contrasts (burn vs no-burn and growing-season fire vs. dormant-season fire) and separated treatment means ($P \leq 0.05$) with the protected least significant difference test (Steel & Torrie 1980; Conover & Iman 1981).

We performed Detrended Correspondence Analysis (DCA) using CANOCO (ter Braak 1988), to analyze the species composition data. We checked the results for instability caused by a bug in the program (Oksanen & Minchin 1997). DCA is a multivariate indirect gradient analysis that uses variation in species abundance data to display species and stand locations in a two-dimensional ordination space (ter Braak 1986). DCA axes are in units of constant beta-diversity, where one unit is equal to one standard deviation of species turnover (Hill & Gauch 1980). In DCA, changes in location of a stand over time indicate corresponding changes in real or relative species composition of the stand (Wyant et al. 1991). DCA was used to analyze importance values (relative density + relative frequency) to determine changes in stand composition from pre-treatment to post-treatment (after Mueller-Dombois & Ellenberg 1974; Smith 1990). We square-root transformed species abundances before analysis.

Results

Response to fire and fire season

We observed more than 150 herbaceous species during these two studies. Fewer than 10% of these species were influenced ($P \leq 0.05$) by season of fire. Late dormant-season fires produced a greater frequency of occurrence of *Panicum dichotomum* (Study 1: $F = 26.9$; $P = 0.0006$, Study 2: $F = 29.7$, $P = 0.0320$) and *Scleria triglomerata* (Study 1: $F = 15.3$; $P = 0.0035$, Study 2: $F = 19.9$, $P = 0.0467$) than late growing-season fires. Density of *Panicum dichotomum* ($F = 54.5$; $P = 0.0001$) and *Scleria triglomerata* ($F = 5.6$; $P = 0.0416$) was less after late growing-season fires than after late dormant-season fires in Study 1.

Although few species were influenced by season of fire, differences ($P \leq 0.05$) in density and frequency of major plant categories were apparent (Tables 1 and 2). Late dormant-season fires increased panicum density (primarily *Panicum boscii*, *P. dichotomum*, and *P. linearifolium*) while late growing-season fires greatly reduced total panicum density (Tables 1 and 2). *Panicum* frequency also declined after late growing-season fires in Study 1 (Table 1). Grasses showed a tendency to decrease in percent cover following fire (Table 3), and a tendency for further decline in density following late growing-season fires (Table 2).

Table 1. Study 1, herbaceous stem density (stems/m²) and percent frequency of occurrence response to season of fire in restored pine-grassland communities on the Ouachita National Forest, Arkansas, summer 1994 and 1995.¹

Parameter, Group	Treatment ²						Treatment	<i>P</i> > <i>F</i> Contrasts ³	
	No-burn control		Dormant season		Growing season				
	1995 Mean (SE) (<i>n</i> = 4)	Percent ² change (<i>n</i> = 4)	1995 Mean (SE) (<i>n</i> = 4)	Percent ² change (<i>n</i> = 4)	1995 Mean (SE) (<i>n</i> = 4)	Percent ² change (<i>n</i> = 4)			
Density (stems/m²)									
Grasses	42.7 (1.1)	16	37.4 (6.3)	0	24.8 (5.1)	-35	0.3477	0.2806	0.3292
Panicums	17.2 (5.7)	6 a	27.5 (6.2)	34 a	8.4 (2.2)	-77 b	0.0194	0.3519	0.0077
Sedges	8.0 (0.9)	-27	22.3 (2.4)	29	13.8 (1.8)	-19	0.1085	0.1850	0.0872
Legumes	20.8 (7.6)	2 b	24.8 (4.1)	98 a	23.5 (6.7)	65 ab	0.0259	0.0115	0.2864
Forbs	21.0 (1.8)	5 a	48.4 (1.2)	126 a	29.5 (4.8)	42 ab	0.0353	0.0451	0.0625
Cool-season species	26.8 (3.5)	16	54.0 (5.2)	87	31.6 (4.0)	-12	0.1599	0.6160	0.0692
Warm-season species	82.7 (7.2)	2	106.3 (8.0)	31	68.4 (11.8)	-24	0.2005	0.9604	0.0811
Percent frequency of occurrence									
Grasses	77 (3)	-3	77 (4)	2	69 (6)	-12	0.3026	0.8060	0.1364
Panicums	82 (6)	-4 a	93 (3)	9 a	63 (2)	-33 b	0.0005	0.1874	0.0002
Sedges	58 (3)	-5	79 (6)	6	70 (7)	-10	0.5019	0.7559	0.2691
Legumes	80 (11)	-6	85 (7)	3	88 (10)	15	0.2330	0.1732	0.2922
Forbs	95 (2)	-1	99 (1)	5	95 (5)	-3	0.1181	0.5692	0.0500
Cool-season species	93 (2)	-1	98 (2)	2	95 (5)	-4	0.4027	0.9852	0.1894
Warm-season species	99 (1)	-1	100 (0)	1	98 (3)	1	0.6252	0.3511	0.8828

¹Row means followed by different letters are different ($P < 0.05$, Least Significant Difference); ²Percent change = [(post treatment (1995) - pre-treatment (1994)) / pre-treatment (1994)] × 100, presented $P > F$ values are for this category; ³Contrasts: C = Control; B = Burned stands regardless of season; D = Dormant-season fires; G = Growing-season fires.

Table 2. Study 2, herbaceous stem density (stems/m²) and percent frequency of occurrence response to season of fire in restored pine-grassland communities on the Ouachita National Forest, summer 1995 and 1996.¹

Parameter, Group	Treatment ²				<i>P</i> > <i>F</i> Treatment
	Dormant season		Growing season		
	1996 Mean (SE) (<i>n</i> = 2)	Percent ² change (<i>n</i> = 2)	1996 Mean (SE) (<i>n</i> = 2)	Percent ² change (<i>n</i> = 2)	
Density (stems/m²)					
Grasses	47.9 (6.9)	15	16.7 (6.1)	-62	0.0724
Panicums	20.4 (12.3)	17 a	9.1 (5.4)	-49 b	0.0100
Sedges	12.2 (3.7)	42	8.0 (1.7)	4	0.1758
Legumes	29.6 (14.6)	84 a	23.8 (11.8)	4 b	0.0451
Forbs	28.7 (1.9)	43	21.6 (0.4)	2	0.1918
Cool-season species	37.6 (4.4)	24	20.1 (5.6)	-12	0.3087
Warm-season species	101.1 (10.0)	40 a	58.6 (16.3)	-37 b	0.0451
Percent frequency of occurrence					
Grasses	77 (17)	5	67 (3)	-16	0.5680
Panicums	80 (7)	1	68 (2)	-18	0.0949
Sedges	67 (3)	23	60 (3)	0	0.3688
Legumes	85 (15)	20	93 (0)	10	0.7496
Forbs	98 (2)	2	100 (0)	7	0.2660
Cool-season species	100 (0)	6	98 (2)	7	0.7863
Warm-season species	100 (0)	2	100 (0)	0	0.4226

¹Row means followed by different letters are different ($P < 0.05$, Least Significant Difference); ²Percent change = [(post treatment (1996) - pre-treatment (1995)) / pre-treatment (1995)] × 100 presented $P > F$ values are for this category.

Table 3. Post-treatment percent cover in restored red-cockaded woodpecker clusters on the Ouachita National Forest in 1995.¹

Group	Treatment						Contrasts ²		
	Control (n = 4)		Dormant season (n = 4)		Growing season (n = 4)		Treatment	C vs B	D vs G
	Mean	SE	Mean	SE	Mean	SE			
Bare Ground	0.1 b	0.1	6.4 a	0.6	1.4 b	0.6	0.0001	0.0001	0.0001
Litter	74.5	2.4	51.3	14.2	73.8	6.3	0.1787	0.3114	0.1149
Rock	0.5 b	0.2	3.9 a	0.8	1.3 b	0.2	0.0019	0.0057	0.0045
Logs	2.9	0.8	2.7	0.5	3.6	0.7	0.6449	0.7773	0.3842
Tree Bole	0.3 b	0.1	0.8 a	0.2	0.1 b	0.1	0.0111	0.3599	0.0042
Cryptogams	1.0	0.5	1.8	1.2	0.1	0.0	0.3233	0.9020	0.1447
Woody species	24.7	4.1	16.6	3.0	18.0	3.1	0.2609	0.1141	0.7979
Forbs	7.8	1.9	10.4	0.9	9.2	3.0	0.7161	0.4756	0.7180
Grasses	10.9	3.5	5.3	0.8	4.8	1.2	0.1474	0.0582	0.7991

¹Row means followed by different letters are different ($P < 0.05$, Least Significant Difference); ²Contrasts: C = Control; B = Burned stands regardless of season; D = Dormant-season fires; G = Growing-season fires.

Regardless of season, fire increased density of legumes, however legume frequency did not increase with burning (Tables 1 and 2). Legume species such as *Stylosanthes biflora* increased in density ($F = 16.9$; $P = 0.0026$) after fire, while other legumes such as *Desmodium ciliare* ($F = 6.58$; $P = 0.0334$) and *Lespedeza procumbens* ($F = 8.37$; $P = 0.0179$) increased in frequency of occurrence after fire. Fire also increased density and frequency of occurrence of numerous forbs such as *Coreopsis tinctoria*, *Polygala alba*, and *Erechtites hieraciifolia*, resulting in an increase in total forb density in Study 1 (Table 1). We found that forbs after late dormant-season fires occurred more frequently than after late growing-season fires and generally increased

with fire, although it was not biologically significant (Table 1). Cover of herbaceous vegetation was similar for all treatments, but stands burned during the late dormant season had more bare ground and exposed rock (Table 3). Warm season species had lower densities in response to late growing-season burns than late dormant-season burns (Tables 1 and 2).

Response to frequent fire

Panicum frequency increased with frequent late dormant-season burns (Table 4). However, density of *Chasmanthium sessiliflorum* declined ($F = 35.6$; $P = 0.0270$) after frequent late dormant-season fire. Legume density

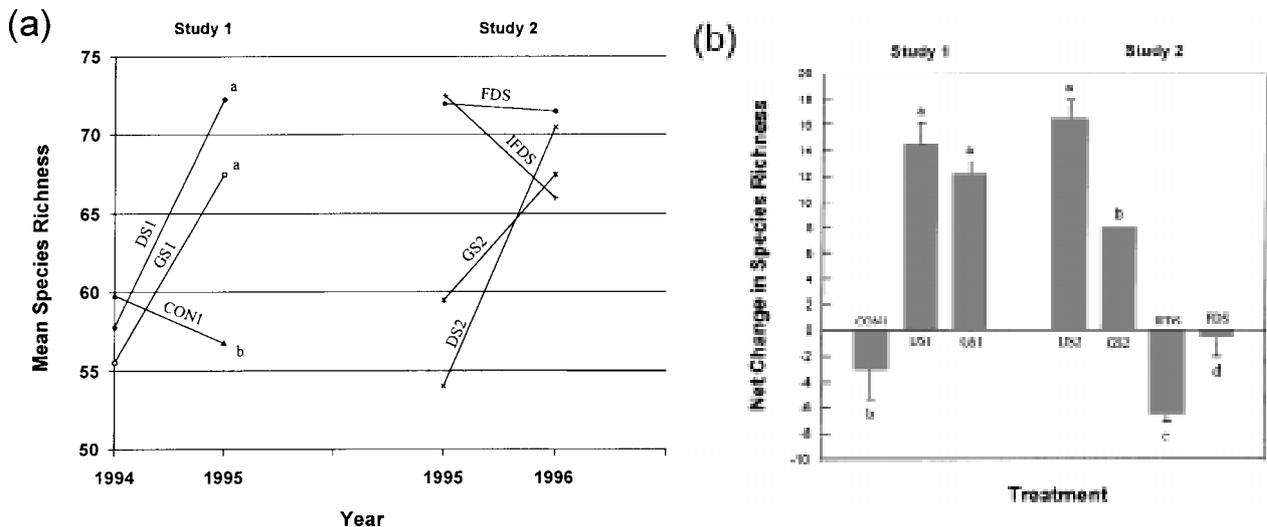


Fig. 2. a. Stand species richness by study and treatment; **b.** Net-change and standard errors in stand species richness by study and treatment. Means followed by different letters are different ($P \leq 0.05$, Least Significant Difference). CON1 = Study 1, no-burn control; GS1 = Study 1, growing-season burn; DS1 = Study 1, dormant-season burn; GS2 = Study 2, growing-season burn; DS2 = Study 2, dormant-season burn; FDS = Study 2, frequent dormant-season burn; and IFDS = Study 2, infrequent dormant-season burn.

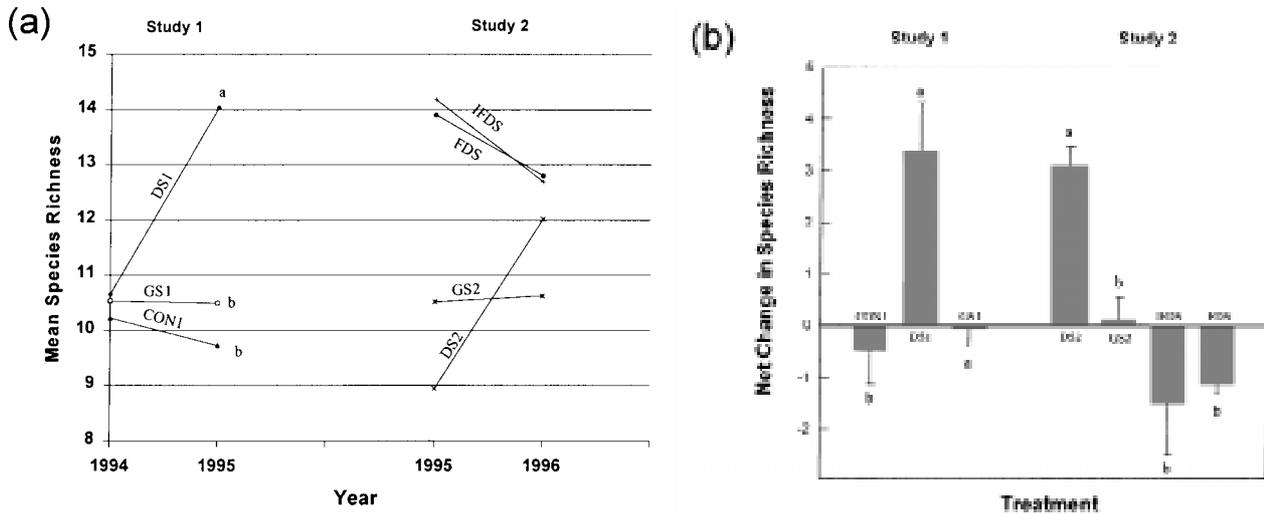


Fig. 3. a. Sample (m²) species richness by study and treatment; **b.** Net-change and standard errors in sample species richness by study and treatment. Means followed by different letters are different ($P \leq 0.05$, Least Significant Difference). CON1 = Study 1, no-burn control; GS1 = Study 1, growing-season burn; DS1 = Study 1, dormant-season burn; GS2 = Study 2, growing-season burn; DS2 = Study 2, dormant-season burn; FDS = Study 2, frequent dormant-season burn; and IFDS = Study 2, infrequent dormant-season burn.

was greater after frequent late dormant-season fires (Table 4). Density of *Lespedeza procumbens* ($F = 124.0$, $P = 0.0080$) and *Stylosanthes biflora* ($F = 124.9$; $P = 0.0079$) was greater after frequent late dormant-season fires. *Helianthus hirsutus* ($F = 33.7$; $P = 0.0284$) frequency of occurrence was also greater after frequent fire. Stand species richness in frequently burned stands remained stable, but declined in control stands (Fig. 2).

Table 4. Study 2, herbaceous stem density (stems/m²) and percent frequency of occurrence response to frequent fire in restored pine-grassland communities on the Ouachita National Forest, summer 1995 and 1996.¹

Parameter, Group	Treatment				$P > F$ Treatment
	Control		Frequent Fire		
	1996 Mean (SE) (n = 2)	Percent ² change (n = 2)	1996 Mean (SE) (n = 2)	Percent ² change (n = 2)	
Density (stems/m²)					
Grasses	57.7 (4.4)	30	32.5 (8.7)	9	0.3744
Panicums	20.0 (9.4)	-19	22.1 (2.5)	-22	0.8797
Sedges	25.3 (3.0)	-4	15.5 (1.1)	-14	0.4414
Legumes	17.0 (5.8)	-21 b	32.6 (2.8)	18 a	0.0234
Forbs	30.9 (5.5)	-35	30.2 (1.9)	-38	0.8458
Percent frequency of occurrence					
Grasses	78 (5)	-6	75 (2)	8	0.2951
Panicums	88 (2)	-9	91 (2)	4	0.0940
Sedges	82 (2)	6	72 (5)	-10	0.3854
Legumes	85 (15)	3	95 (2)	10	0.3906
Forbs	98 (2)	0	98 (2)	-2	0.4226

¹ Row means followed by different letters are different ($P < 0.05$, Least Significant Difference); ² Percent change = [(post treatment (1995) - pre-treatment (1994)) / pre-treatment (1994)] × 100, presented $P > F$ values are for this category.

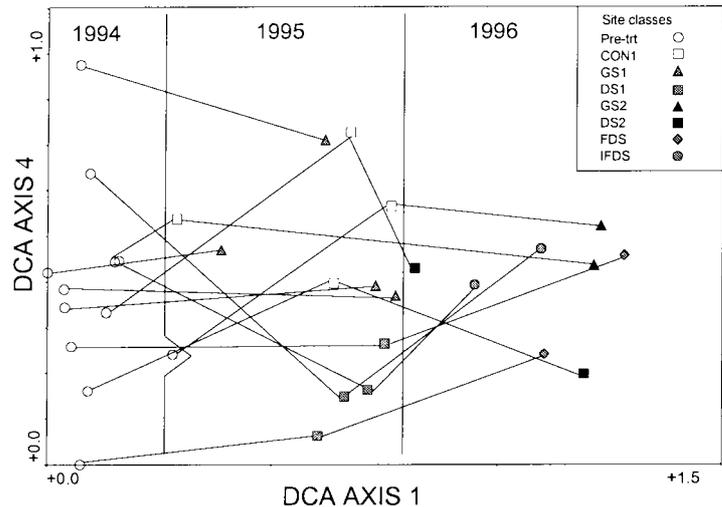
Community response to fire

Fire dramatically influenced community composition in restored pine-grassland stands. Species diversity when compared to unburned stands was greater ($P \leq 0.05$) after both late growing-season and late dormant-season prescribed fires. Stand species richness increased after both late growing-season and late dormant-season fires, while declining in unburned stands (Fig. 2b). Furthermore, post-treatment stand species richness after late dormant-season and late growing-season fires was greater than the unburned controls in Study 1 (Fig. 2a). Sample (m²) species richness increased dramatically after late dormant-season fires with net change in stand species richness being greatest after late dormant-season fires (Fig. 3b).

Detrended Correspondence Analysis illustrated the nature of change in these stands over time and in response to fire (Fig. 4). Axis 1 indicated that year-to-year variation may be the most important factor in determining species composition of these stands (Fig. 4). Axis 2 indicated that geographical location of stands also determines species composition. Axis 3 was tentatively interpreted as an indicator of stand openness with species assemblages more characteristic of prairies being grouped together versus those more characteristic of closed forest being grouped together. Axis 4 may be interpreted as a treatment axis (Fig. 4). We included Axis 4 because treatment effect was our primary interest.

Control stands shifted to the right on Axis 1 and upward on Axis 4 indicating a year and treatment effect, while late dormant-season fire stands shifted right on

Fig. 4. Detrended Correspondence Analysis of stand importance values by treatment, Ouachita National Forest. Stands are connected by vectors to indicate change from pre-treatment sampling to post-treatment sampling. CON1 = Study 1, no-burn control; GS1 = Study 1, growing-season burn; DS1 = Study 1, dormant-season burn; GS2 = Study 2, growing-season burn; DS2 = Study 2, dormant-season burn; FDS = Study 2, frequent dormant-season burn; and IFDS = Study 2, infrequent dormant-season burn.



Axis 1 and down on Axis 4 also indicating a year and treatment effect (Fig. 4). Late growing-season fire stands shifted directly to the right on Axis 1 indicating that year effects had an overriding influence on treatment (Fig. 4). The shift in stands after treatment indicates a similar change in species composition among the treatments. Axes 1 through 4 had eigenvalues of 0.161, 0.081, 0.060, and 0.040 respectively. Together all axes account for 26.7% of the total variation in species data. With an eigenvalue of only 0.042, and the fact that the apparent 'treatment axis' is the 4th axis, it is obvious that the effects of treatment, while highly significant, is minor compared with year-to-year effects and site location effects.

Discussion

Treatment response

Burned stands had higher stand species richness and diversity than no-burn controls (Fig. 2). These results are similar to many studies that indicate an initial increase in species diversity and richness following fire (Trabaud & Lepart 1980; Armour et al. 1984; Thanos et al. 1996). In Study 2, stands in the 2nd growing season since late dormant-season fire (DSC), declined in species richness, indicating that the initial increase in stand richness after fire is short lived (Figs. 2 and 3) and probably influenced by environmental conditions during a given year (Fig. 4). The majority of individual species in both studies did not respond favorably to any one treatment, but were common in all treatments. We believe this is because species present (e.g. *Andropogon* spp. and various legume species) in restored pine-grass-

land communities are well adapted to fire, and community changes are small and of short duration. Waldrop et al. (1992) noted that the pine-grassland ecosystem once common throughout the southeastern U.S. was fire derived and fire maintained. Herbaceous species in these restored pine-grassland communities were likely present in pre-settlement communities that developed under a periodically frequent fire regime during both the dormant and growing seasons (Masters et al. 1995).

Fire does not drastically alter species composition in stands with a recent history of fire. Pre-fire composition is a major factor in determining post-fire composition (Armour et al. 1984; Stickney 1986; Rego et al. 1991). Adjacent forests without WSI treatment have dense midstories minimizing light from reaching the forest floor, so species richness and abundance of herbaceous species is much less than in WSI-treated areas (Masters et al. 1996). We also suggest that post-fire species richness and composition is influenced by fire intensity, which is related to litter consumption and reduction in the stature of woody species (Masters et al. 1993; Sparks 1996).

Stand structure

Prescribed fire plays a major role in determining the vegetation structure and composition in restored pine-grassland communities (Wilson et al. 1995). Understories of stands treated with WSI are characteristically dominated by woody sprouts (> 50 000 stems/ha) that restrict light from reaching the forest floor. Late dormant-season fires in these stands on average produce greater fireline intensity than growing-season fires (1300 Kw/m versus < 300 Kw/m), and are more effective at maintaining an open forest structure by reducing the stature of woody sprouts (Sparks 1996).

The effect of a disturbance such as fire on any community or ecosystem depends on the intensity, scale, and frequency (Sousa 1984; Perry 1994; Sparks 1996). Late dormant-season fires in these stands act as more intense disturbances than late growing-season fires, by more effectively reducing stature of the woody community and reducing the litter layer. Increased light penetration due to the reduced stature of the woody understory and reduction of litter after fire provides an opportunity for new herbaceous species to become established, thereby significantly increasing species richness and diversity (Sousa 1984; Masters 1991a, b; Masters et al. 1993). But, fire in either season increases light and allows species already present to prosper, thus the increase in density and percent frequency of occurrence of forbs after fire.

Species composition

Herbaceous species actively growing at the time of a fire in grassland systems are more susceptible to injury than species that are dormant or in early stages of development (Towne & Owensby 1984). Fires during the dormant season reduce cool-season species while favoring many warm-season species (Owensby & Anderson 1967; Hover & Bragg 1981; Towne & Owensby 1984; Hulbert 1988; Howe 1994a). In contrast, growing-season fires reduce warm-season species while favoring cool-season species (Hover & Bragg 1981; Ewing & Engle 1988; Biondini et al. 1989; Howe 1994a). Our results in Study 2 showed an increase in density of warm-season species after burning, Study 1 also showed an increase, but not significantly. Neither study showed an increase for cool-season species when late dormant- and late growing-season burns were compared. Growing-season burns may have increased cool-season species had our growing-season fires been conducted earlier in the growing season and before cool-season species initiated new growth. It is important to note that in both studies we attempted to burn earlier in the growing season, but burning conditions (primarily fuel moisture, presence of live vegetation and high relative humidities) were not conducive to fire until later in the growing season.

Several studies have noted that growing-season fires when compared to dormant-season fires and unburned areas increase diversity and richness by increasing the number of annuals and promoting cool-season grasses and forbs (Biondini et al. 1989; Howe 1994b). Platt et al. (1988) noted that growing-season fires produced more flowering stems than fires in other seasons. Many warm-season grasses such as wiregrass (*Aristida stricta*) and little bluestem (*Schizachrium scoparium*) flower profusely after growing-season fires (Lewis 1964; Robbins

& Myers 1992). Hodgkins (1958) noted that composites and legumes increase in response to growing-season fires. Our results indicate an aggressive response from legumes and forbs (Tables 1 and 2), and a larger increase in species richness after dormant-season fires (Fig. 2 and 3). Other studies have found similar results (Grelen & Lewis 1981; Landers 1981; White et al. 1991). Legumes in particular are adapted to fire and benefited because of a hard seed coat and subsequent persistence in the soil seed bank (White et al. 1991; Arianoutsou & Thanos 1996; Thanos et al. 1996).

In Study 2, legume density (primarily *Amphicarpa bracteata*, *Clitoria mariana*, *Lespedeza repens*, and *Stylosanthes biflora*) was $2 \times$ greater after two frequent late dormant-season fires, similar to Masters et al. (1993), who found legume biomass $> 4 \times$ greater after 5 years of annual burning compared to unburned controls. White et al. (1991) found that 43 years of annual winter fires increased legumes by $> 25 \times$ over periodic summer and winter burns or annual summer burns. The lack of an increase in legume frequency in our study may be due to relatively high frequency for legumes (80 - 88 %), especially since we observed that most of these species had a tendency towards aggregation. Stem densities within aggregations or sample plots can increase without increasing frequency (Mueller-Dombois & Ellenberg 1974). Further, initial high legume frequency may have been related to the previous fire history within these stands.

Conclusions

Because pine-grassland communities developed under a fire regime that included both dormant and growing season fire, both seasons of fire should be used as management tools in a restoration context. Fire in either season increased species richness, diversity, and total abundance of forbs and legumes, while herbaceous species abundance and richness declined in no-burn controls. Fire reduces woody structure, which influences herbaceous plant composition in restored pine-grassland ecosystems. Increased light and presence of bare ground after fire provide the opportunity for many herbaceous species to become established. Change in species composition and abundance is linked to change in stand structure. Late dormant-season fires are more effective than late growing-season fires at reducing woody sprouts in the understory and at providing bare ground for colonization. As a result, herbaceous species abundance and richness was greater after late dormant-season fires.

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